Interhemispheric Processing: Evidence from Behavioral and Electrophysiological Studies

Dissertation

zur Erlangung des akademischen Grades
eines Doktors der Naturwissenschaften

Eingereicht an der Universität Konstanz,
Naturwissenschaftlich-Mathematischen Sektion,
Fachbereich Psychologie
von

Tanja Endraß

2004

Tag der mündlichen Prüfung: 08.10.2004
1. Referent: Prof. Dr. Brigitte Rockstroh
2. Referent: PD Dr. Bettina Mohr-Pulvermüller

Dank

An dieser Stelle möchte ich mich ganz herzlich bei allen bedanken, die mich bei der Erstellung dieser Arbeit unterstützt haben.

Allen Voran gilt mein Dank Bettina Mohr-Pulvermüller. Ich bedanke mich für die Unterstützung und für die freundschaftliche Arbeitsatmosphäre bei der Entstehung dieser Arbeit. Selbst nach ihrem Umzug nach Cambridge hatte sie stets ein offenes Ohr für meine Fragen.

Brigitte Rockstroh möchte ich ebenfalls für ihre Diskussionsbereitschaft und Unterstützung in allen Phasen der Arbeit danken. Bedanken möchte ich mich auch bei Friedemann Pulvermüller, Olaf Hauck und Yuri Shtyrow, die mit ihrer Expertise zur erfolgreichen Durchführung des *„Konstanzer Mismatch-Experiments*" beigetragen haben.

Ein besonderer Dank gilt auch Patrick Berg, der mich beim Einstieg in die Psychophysiologie unterstützt und angeleitet hat (und BESA Bugs ausgemerzt hat).

Ich möchte mich auch bei den wissenschaftlichen Hilfskräften und Diplomandinnen für ihre tatkräftige Unterstützung bei der Erhebung und Auswertung der Daten bedanken: Gabi Geiger, Katja Hannemann, Nadine Maier-Weiser.

Natürlich bedanke ich mich auch bei allen anderen Mitarbeitern der klinischen Arbeitsgruppe in Konstanz, die mich bei der Erstellung dieser Arbeit unterstützt und begleitet haben.

Nicht zuletzt bedanke ich mich bei meiner Familie und meinen Freunden, die mich die Arbeit auch manchmal vergessen lassen haben... vor allem Marco Radtke kann ich gar nicht genug danken.

Table of Content

I. Summary

A. Abstract

The present thesis deals with behavioral and neurophysiological aspects of interhemispheric processing. Studies and models on interhemispheric processing suggest various sometimes controversial mechanisms how the two hemispheres might process information. One aspect of interhemispheric processing is examined within tasks with bilateral redundant stimulus presentation. Previous behavioral studies revealed superior performance after bilateral redundant stimulation compared to unilateral stimulation. This effect has been called bilateral advantage and was obtained for meaningful stimuli (e.g. words, familiar faces) but not for meaningless stimuli (e.g. pseudowords, unfamiliar faces). Within this thesis the bilateral advantage was examined with different experimental designs.

The first experiment replicated early findings regarding the bilateral advantage, which was present for words and absent for pseudowords. Further, this experiment was also designed to find a neurophysiological correlate of the bilateral advantage. Evoked potential and minimum norm data revealed that bilaterally presented words were accompanied by more negative amplitudes and more source activation than bilaterally presented pseudowords and than unilaterally presented words. These findings are interpreted in terms of the cell assembly theory. Bilateral stimulation of the transcortical cell assemblies might cause the summation of activation which might be reflected in higher cortical activation.

The second experiment was conducted to examine bilateral processing of objects, non-objects and simple patterns. This experiment employed two tasks: a object decision task and a simple reaction task. While the decision task required subjects to decide whether an object or an non-object was seen, the simple reaction task merely required stimulus detection. As expected a bilateral advantage was reveled for objects, but not for non-objects. However, a smaller but nevertheless significant bilateral advantage was also obtained in the simple reaction task. These findings provided further support for the assumption that only meaningful stimuli which have neural representations might elicit a bilateral advantage when full stimulus identification was required. Conversely, the bilateral

advantage in the simple reaction task might not agree with this explanation, because in this task no meaningful stimuli are processed. This finding suggests that not only stimulus properties but also task properties might determine the occurrence of a bilateral advantage. Interhemispheric summation might also take place when only stimulus detection and no further processing is required.

The third experiment was carried out to determine whether a processing advantage in bilateral condition depended on bi-hemispheric stimulation or on redundant stimulus presentation. This question was approached with a lexical decision task employing unilateral and bilateral redundant stimulation. Consistent with earlier findings words but not pseudowords elicited a bilateral advantage and a unilateral redundancy advantage, as well. The comparison of the two effects indicated a larger bilateral than unilateral redundancy advantage. Bi-hemispheric stimulation caused a wider distributed activation and interhemispheric summation might therefore outrange intrahemispheric summation regarding behavioral performance.

The fourth experiment in this thesis considered a different aspect of bilateral processing. Previous experiments demonstrated a bilateral advantage for meaningful stimuli in tasks with visual stimulation and in tasks that required subjects focused attention on task accomplishment. This experiment was conducted to examine bilateral processing in the auditory modality and in a task independent of subjects attention. Therefore a passive oddball paradigm was used to investigate brain response elicited by spoken words and pseudowords played monaurally or simultaneously to both ears, while subjects were instructed to watch a silent movie. Analysis of mismatch negativity (MMN) confirmed larger MMN to words than pseudowords. But more interestingly, MMN also differentiated between monaural and binaural conditions. Binaurally presented words were found to elicit a larger MMN than monaurally presented words and than binaurally presented pseudowords. This neurophysiological manifestation of a word-specific bilateral redundancy gain is interpreted as evidence for interhemispheric cooperation in the automatic access to memory traces for spoken words. Accordingly, word-related cortical networks distributed over both hemispheres may allow summation of neural activity between and within hemispheres, thereby potentiating the word-related MMN.

Together, the neurophysiological results demonstrate that a behavioral bilateral processing advantage might be explained with summation of neuronal activation. Moreover, a neurophysiological correlate of the bilateral advantage was revealed during visual as well as auditory stimulus presentation and independently of subjects focused attention. These findings indicate that cooperation between the two cerebral hemispheres might be influenced by certain aspects of processing. Interhemispheric cooperation in terms of superior behavioral performance or higher cortical activation was observed for different kinds stimuli (verbal and non-verbal) and for different perceptual channels (visual and auditory). However, interhemispheric cooperation might depend on task requirements. Tasks requiring full stimulus processing generate only a bilateral advantage when previously learned meaningful stimuli are processed as opposed to meaningless stimuli. In contrast, tasks requiring only stimulus detection, generate a bilateral advantage independently of stimulus type, due to a summation of perceptual activation.

B. Zusammenfassung

Die vorliegende Arbeit beschäftigt sich mit behaviouralen und neurophysiologischen Aspekten der interhemisphärischen Verarbeitung. Studien und Modelle der interhemisphärischen Verarbeitung schlagen vielfältige und teilweise kontroverse Mechanismen vor, wie die beiden Hemisphären Information verarbeiten könnten. Ein Aspekt der interhemisphärischen Verarbeitung wird mit Aufgaben untersucht, die eine bilateral redundante Stimuluspräsentation verwenden. Frühere behaviourale Studien zeigen überlegene Leistungen nach bilateraler verglichen mit unilateraler Stimulation. Dieser Effekt wurde als Bilateralvorteil bezeichnet und konnte nur für bedeutsame Stimuli (z.B. Wörter, bekannte Gesichter) gezeigt werden, nicht aber für bedeutungslose Stimuli (z.B. Pseudowörter, unbekannte Gesichter). In dieser Arbeit wurde der Bilateralvorteil mit verschiedenen experimentellen Paradigmen und Methoden untersucht.

Das erste Experiment replizierte frühere Befunde bezüglich des Bilateralvorteils, welcher für Wörter und nicht für Pseudowörter vorhanden ist. Darüber hinaus sollte ein psychophysiologisches Korrelat des Bilateralvorteils identifiziert werden. Evozierte Potentiale und Minimum Norm Daten zeigten, dass bilateral präsentierte Wörter von einer stärkeren Negativierung bzw. stärkeren Aktivierungen begleitet werden als bilateral präsentierte Pseudowörter und unilateral präsentierte Wörter. Diese Ergebnisse wurden im Rahmen der Cell Assembly Theorie interpretiert. Bilaterale Stimulation der transkortikalen Zellverbände könnte eine Summation von Aktivierung verursachen, die eine größere kortikale Aktivierung bewirkt.

Das zweite Experiment wurde durchgeführt, um die bilaterale Verarbeitung von Objekten, Non-Objekten und einfachen Mustern zu untersuchen. Dazu wurden zwei experimentelle Aufgaben verwendet: eine Objektentscheidungsaufgabe und eine einfache Reaktionszeitaufgabe. Während in der Entscheidungsaufgabe die Versuchspersonen unterscheiden sollen, ob sie ein Objekt oder ein Non-Objekt gesehen hatten, sollte in der Reaktionszeitaufgabe lediglich auf das Vorhandensein eines Reizes reagiert werden. Wie erwartet zeigte sich ein Bilateralvorteil für Objekte und nicht für Non-Objekte. Allerdings zeigte sich in der Reaktionszeitaufgabe ebenfalls ein kleinerer aber dennoch signifikanter Vorteil für bilaterale Stimuluspräsentation. Diese Ergebnis unterstützen die Annahme, dass

nur bedeutungsvolle Stimuli, welche über eine neuronale Repräsentation verfügen, einen Bilateralvorteil hervorrufen, wenn eine Verarbeitung des Stimulus erforderlich ist. Die Ergebnisse der einfachen Reaktionszeitaufgabe zeigen allerdings auch, dass nicht nur Stimuluseigenschaften, sondern auch Aufgabeneigenschaften einen Einfluss auf die Ausprägung einen Bilateralvorteils haben. Interhemisphärische Summation könnte bei einer einfachen Stimulusdetektion unabhängig von Stimuluscharakteristiken erfolgen.

Mit dem dritten Experiment sollte herausgefunden werden, inwiefern der Verarbeitungsvorteil nach bilateraler Stimulation auf der bi-hemisphärischen Stimulation bzw. auf redundanter Stimulusdarbietung beruht. Dazu wurde eine lexikalische Entscheidungsaufgabe durchgeführt, bei der eine unilateral und bilateral redundante Stimulation erfolgte. Für Wörter und nicht für Pseudowörter ergab sich ein Bilateralvorteil und ein unilateraler Redundanzvorteil. Der Vergleich der beiden Effekte weißt darauf hin, dass der Bilateralvorteil größer ist als der unilaterale Redundanzvorteil. Eine mögliche Erklärung für diesen unterschiedlichen Verarbeitungsvorteil könnte darin liegen, dass bi-hemisphärische Stimulation eine weiter verteile Aktivierung verursacht. Dadurch könnte die interhemisphärische Summation stärker ausfallen als intrahemisphärische Summation.

Im vierten Experiment wurde auf einen anderen Aspekt der bilateralen Verarbeitung eingegangen. In bisherigen Experimenten wurde der Bilateralvorteil bei visueller Stimulation und bei Aufgaben mit aufmerksamer Verarbeitung untersucht. In diesem Experiment sollte der Bilateralvorteil in der auditorischen Modalität untersuchen, und zwar bei einer Aufgabe, die unabhängig von Aufmerksamkeit ist. Dafür wurde ein passives Oddball-Paradigma herangezogen, bei dem die Gehirnaktivität aufgezeichnet wurde während gesprochene Worte und Pseudoworte monaural bzw. binaural präsentiert wurden. Die Analyse der Mismatch Negativity (MMN) ergab eine größere MMN für Wörter als für Pseudowörter. Weiterhin differenzierte die MMN auch zwischen der binauralen und monauralen Bedingung. Binaral präsentierte Wörter lösten eine größere MMN Amplitude aus als binaural präsentierte Pseudowörter und monaural präsentierte Wörter. Diese neurophysiologische Manifestation des wort-spezifischen Bilateralvorteils wird als Bestätigung für das Vorhandensein interhemisphärischer Kooperation beim automatischen Zugriff auf Gedächtnisrepräsentationen gesprochener Worte betrachtet.

Die neurophysiologischen Ergebnisse unterstützen die Annahme dass der behaviorale Verarbeitungsvorteil nach bilateraler Stimulation auf die Summation von neuronaler Aktivierung erklärt werden kann. Darüber hinaus, konnte ein neurophysiologisches Korrelat des Bilateralvorteils sowohl bei visueller als auch bei akustischer Verarbeitung gezeigt werden, wobei dies unabhängig von aufmerksamer Verarbeitung zu sein scheint. Diese Ergebnisse weisen jedoch auch darauf hin, dass die Zusammenarbeit zwischen den beiden Hemisphären von bestimmten Aspekten der Verarbeitung beeinflusst werden. Interhemisphärische Zusammenarbeit, im Sinne einer besseren Verhaltensleistung oder größerer kortikaler Aktivierung, konnte für verschiedene Stimulusarten (verbale und nonverbale) und für verschiede Sinneskanäle (visuell und auditiv) gezeigt werden. Interhemisphärische Zusammenarbeit scheint jedoch auch von den Anforderungen der jeweiligen Aufgabe abzuhängen. Aufgaben, bei denen eine Stimulusverarbeitung erfolgt, um eine Reaktion bestimmen zu können, erzeugen nur für gelernte, bedeutungsvolle Stimuli einen Bilateralvorteil. Bedeutungslose Stimuli dagegen erzeugen keinen Bilateralvorteil. Andererseits, können Aufgaben bei denen lediglich eine Stimuluserkennung erforderlich ist, einen Bilateralvorteil unabhängig von Stimuluseigenschaften auslösen. Dies könnte mit Summationsprozessen auf perzeptueller Ebene erklärt werden.

II. General Introduction

A. Models of Interhemispheric Processing

Interhemispheric processing has been described with cognitive models since different experimental designs suggested different mechanisms, how the two hemispheres might process and divide information. Models of interhemispheric processing might be classified into unilateral specialization, parallel processing and cooperation models. Cooperation models can be further subdivided into positive cooperation and negative cooperation models.

In the following section of introduction models of interhemispheric processing with their different explanatory approaches will be presented. These models predict different outcomes when both hemispheres are involved in task accomplishment compared to processing within one hemisphere. Unilateral specialization models assume that each hemisphere is competent for certain tasks, whereas the other hemisphere is not. Therefore, the performance of both hemispheres should resemble the performance of the hemisphere specialized for the task. Parallel processing models assume better bilateral performance due to independent, simultaneous processing in both hemispheres. Interhemispheric inhibition models state a performance loss when both hemispheres are involved in processing of different stimuli. In contrast, positive cooperation models predict a performance gain when both hemispheres participate in processing.

Finally, a neurobiological model of interhemispheric processing is presented which is capable of explaining differential performance patterns during interhemispheric processing. This model assumes that interhemispheric processing relies on the existence of transcortical cell assemblies (Pulvermüller and Mohr, 1996).

1. Unilateral Specialization Models

Unilateral specialization models are based on hemispheric capacity. Each hemisphere has been associated with certain psychological functions (Hellige, 1993). For example in visual processing, the right hemisphere is superior in processing global aspects, whereas the left hemisphere is superior in processing local stimulus characteristics (Hellige, 1996). Hemispheric dominance is most pronounced for language processing which is associated with better processing in the left than the right hemisphere (Hellige, 1993).

Unilateral specialization model mainly account for processing advantages found after unilateral stimulation. In case of language processing a right visual field advantage (RVFA) has repeatedly been found. This RVFA is indicating left hemispheric superiority.

Zaidel and colleagues stated two models of interhemispheric processing: the “direct access model” and the “transcallosal relay model” (Zaidel, 1983; Zaidel et al., 1990). The two models mainly differ in respect of the place where information is processed. The trancallosal relay model suggests that each hemisphere has its own processing capabilities. After unilateral stimulus presentation to the hemisphere, which is less capable to process the applied task, a transfer of stimulus information through the corpus callosum into the dominant hemisphere takes place. In case of stimulus presentation to the right hemisphere with linguistic stimuli, information will instantly be transferred into the left hemisphere before processing starts. Therefore, a RVFA would reflect slowing down and degradation of information processing due to callosal relay. Following the trancallosal relay model, processing of a certain task will always be accomplished by the same hemisphere regardless of initial stimulus location. Performance in unilateral conditions would vary only with stimulus location but not with stimulus characteristics.

Transcallosal Relay Model: (Zaidel, 1983)

➔ VF performance = dominant hemispheric performance

In contrast, in terms of the direct access model it is assumed that both hemispheres have processing capabilities for all kind of tasks but differ regarding their performance levels (Zaidel, 1983; Zaidel et al., 1990). According to this model, unilateral stimulus presentation would initiate processing only in the stimulated hemisphere. Stimulus presentation to only one hemisphere can be accomplished with tachistoscopic stimulation. Due to the complete crossing of the visual pathways, this tachistoscopic stimulus presentation ensures that information presented to the left or right visual hemifield (LVF or RVF) is restricted to one hemisphere in the first place. Therefore, performance after stimulus presentation to the RVF reflects left hemispheric processing, whereas stimulus presentation to the LVF reflects right hemispheric performance. According to the direct access model, a difference between left and right visual field performance might arise from different processing strategies of the two hemispheres. Independent processing strategies of the two hemispheres would be confirmed when different visual field advantages would be obtained for different stimuli (processing dissociation, Zaidel, 1983). In fact, the visual field advantage was found to differ between content and function words (Chiarello and Nuding, 1987; Mohr et al., 1994b). Whereas content words had only a slight RVFA, function words revealed higher performance in the RVF (left hemisphere) than in the LVF (right hemisphere). Following the assumptions of the direct access hypothesis, the differential visual field advantage might suggest that both hemispheres are equally capable to process content words, whereas the right hemisphere is less effective in function word processing.

Direct Access Model: (Zaidel, 1983)

➔ LVF performance = right hemispheric performance
➔ RVF performance = left hemispheric performance

The metacontrol model is based on the assumption that both hemispheres have the actual capacity to process all tasks, but use different strategies or differ in their competence. According to this model, the one hemisphere that is specialized for a certain task dominates processing on bilateral trials, when both hemispheres receive the same stimuli. The metacontrol concept was introduced by Levy and Trevarthen (1976). They tested commissurotomy patients with tachistoscopical simultaneous stimulus presentation to both hemispheres. One hemisphere always gained control over processing depending on

the required task (left hemisphere: function matching; right hemisphere: appearance matching).

Metacontrol Model: (Levy and Trevarthen, 1976)
➔ bilateral performance = the best unilateral (LVF or RVF) performance

Hellige (1993) further developed the metacontrol concept and applied it to healthy controls. Alike direct access models, testing the metacontrol concept requires tasks producing qualitative hemispheric differences in unilateral conditions. Information about hemispheric control is deduced from the comparison of performance in unilateral conditions (LVF or RVF) with performance in bilateral condition, when both hemispheres received the same information. Further, qualitative similarity between bilateral and one unilateral condition should be interpreted as domination of one hemisphere on bilateral trials. The metacontrol concept was supported with several experiments of Hellige and colleagues (1988, 1989, 1989). Left hemispheric metacontrol was obtained since bilateral performance resembled right visual field (left hemisphere) performance, during face matching (Hellige et al., 1988) and letter comparison (Hellige and Michimata, 1989). In contrast, right hemispheric metacontrol was revealed for error patterns during a consonant-vowel-consonant (CVC) identification task with fast stimulus presentation (Hellige et al., 1989). The processing mode applied in bilateral conditions is not always controlled by the hemisphere, which is advantageous for the respective task (Hellige and Michimata, 1989; Hellige et al. 1989).

Metacontrol Model: (Hellige and Michimata, 1989; Hellige et al. 1989)
➔ bilateral performance = unilateral (LVF or RVF) performance

Bilateral processing has been explained in terms of unilateral processing models. In summary, these approaches suggest that in case of bilateral stimulation, performance always resembles performance in one unilateral condition. Bilateral processing would always rely on single hemisphere processing even though both hemispheres are stimulated with same stimuli. Therefore, according to unilateral specialization models, bilateral performance would never exceed unilateral performance.

2. Parallel Processing Models

Parallel processing models suggest the involvement of both hemispheres in interhemispheric processing. It is assumed that the two hemispheres operate simultaneously and independently of each other. Similar to cooperation models, parallel models are characterized as bilateral, because both hemispheres are suggested to be involved in processing, but unlike cooperation models, parallel processing models are described as noninteractive, because the two hemispheres do not interact during task accomplishment (Allen, 1982).

Independent but simultaneous hemispheric processing is proposed by a probabilistic model of interhemispheric processing (originally: Raab, 1962). These models are called “race models”. Redundant stimuli presented to different channels, for example the two hemispheres or different perceptual modalities, are processed independently (Raab, 1962; Miller, 1982). In case of redundant stimulation of two channels, either of the two channels would control the response. The system never combines activation from different channels in order to meet its criterion for responding (Miller, 1982). Responses to redundant signals are faster, because they are produced by the faster of the two processes with randomly varying durations. According to the race model, facilitation after redundant stimulation is a result of statistical probability. On average, the time of the winner will be less than the time for either racer, assuming that completion times vary from trial to trial and that the two completion time distributions overlap (Miller, 1982; Raab, 1962).

Independent Race Model: (Raab, 1962)

➔ Bilateral performance > unilateral (LVF or RVF) performance
➔ reason: parallel race of independent hemispheric processing

3. Inhibition Models

In contrast to unilateral processing models, inhibition models consider the involvement of both hemispheres during interhemispheric processing. In terms of inhibition models the two hemispheres would inhibit or suppress each other's activity after bilateral stimulation, when both hemispheres are equally capable for executing a certain task (Allen, 1983). Models of interhemispheric inhibition are mainly based on the finding that bilateral presentation of two different stimuli caused larger and more reliable visual field differences than unilateral stimulus presentation when subjects are cued to respond to only one stimulus on each trial located in either the left or right visual field (Boles, 1987; Boles, 1990; refer also to section: B.2).

Boles stated the mutual inhibition hypothesis (Boles, 1979; Mackavey et al., 1975) assuming that stimulus presentation directed to one hemisphere activates that hemisphere proportional to the hemisphere's ability to process the stimulus. This activation is also proposed to inhibit the opposite hemisphere. Thus, bilateral presentation will always produce activation in both hemispheres and therefore, will always produce a partial inhibition in the other hemisphere, which will further reduce hemispheric performance on bilateral trials compared to unilateral trials. Since activation is higher in the hemisphere with higher ability to accomplish the task, inhibition of the other (non-dominant) hemisphere is also higher. This will further reduce the performance of the hemisphere with lower processing capacity. For example, stimulation of both hemispheres with linguistic stimuli elicits greater activation of the left language dominant hemisphere. Therefore the right hemisphere will be more affected by mutual inhibition. On bilateral trials (with different stimuli presented in each visual field), the resulting performance pattern shows reduced overall performance (compared bilateral with unilateral conditions) of both hemispheres due to mutual inhibition of each other. But, the performance of the right hemisphere will be more affected from mutual inhibition because of lower processing capability and greater inhibition from the left hemisphere.

Mutual Inhibition Model: (Boles, 1979; Mackavey et al., 1975)

➔ bilateral performance < unilateral performance
➔ reason: mutual inhibition due to interhemispheric transfer

The homologous activation hypothesis (Boles 1987, 1990, 1995) provides a more detailed description of the mechanism which might produce greater visual field asymmetries during bilateral trials with different stimuli appearing in each visual field. According to this hypothesis, bilateral stimulation of both hemispheres with similar but different stimuli would activate homologous areas of the two hemispheres. Boles suggested that the homologous activation would disrupt communication between hemispheres. Greater similarity of the two stimuli is accompanied by greater homologous activation and greater visual field differences (Boles, 1995). Following the homologous activation model, bilateral stimulation would force the hemispheres to process the stimuli more independently than in unilateral conditions, because homologous activation disrupted interhemispheric communication. Whereas in unilateral conditions normal interhemispheric communication would allow both hemispheres to contribute to task accomplishment.

Homologous Activation Hypothesis: (Boles 1987, 1990, 1995)

➔ bilateral performance < unilateral performance
➔ reason: reduced interhemispheric communication in bilateral condition

The hypothesis of increased intrahemispheric competition (McKeever and Hulling, 1971; Moscovitch and Klein, 1980; Eglin, 1987) gives an alternative explanation for increased visual field asymmetries during bilateral stimulation with different stimuli. It is suggested that interhemispheric transmission of stimulus information to the other hemisphere takes place during bilateral stimulation. Information received by one hemisphere is immediately transferred via the corpus callosum to the other hemisphere. Consequently, both hemispheres receive and process both stimuli. Therefore, an intrahemispheric competition of both processes takes place and performance would be diminished compared to single stimulus processing. This interference is affecting the non-dominant hemisphere more than the dominant hemisphere and overall processing will be less effective than in unilateral conditions.

Intrahemispheric Competition Hypothesis: (McKeever and Hulling, 1971; Moscovitch and Klein, 1980; Eglin, 1987)

➔ bilateral performance < unilateral performance
➔ reason: intrahemispheric interference of processes due to interhemispheric cooperation

The homotopic inhibition theory (Cook, 1984, 1986) also suggests inhibitory mechanisms of interhemispheric cooperation. Cook (1984, 1986) proposes, that similar information is represented in homologous areas of each hemisphere. These areas are assumed to be connected through the corpus callosum. Activation of a cortical area of one hemisphere would cause inhibition of surrounding areas within that hemisphere. In the contralateral hemisphere, the homologous area is inhibited via the corpus callosum and surrounding areas are activated. Stimulation of both hemispheres would therefore cause inhibition in the respective contralateral hemisphere and diminish overall performance.

Homotopic Inhibition Theory: (Cook, 1984, 1986)

➔ bilateral performance < unilateral performance
➔ reason: ipsilateral activation causes contralateral inhibition

4. Positive Cooperation Models

Positive cooperation models are also based on the assumption that both hemispheres contribute in bilateral processing. Unlike earlier models, these models suggest enhanced performance when both hemispheres are involved in processing. The major difference between inhibition models and positive cooperation models concerns the processing outcome. Positive cooperation models propose better performance during bilateral stimulation compared to unilateral stimulation, whereas inhibition models suggest a performance loss in the bilateral condition.

According to positive cooperation models, both hemispheres perform the function in question simultaneously and they interact positively. Thus, overall performance is some integrated, conjoint function of the two hemispheres (Allen, 1982). Allen (1982) gives two possibilities how performance is enhanced by positive interaction. One possibility is that both hemispheres perform approximately the same processes and the overall performance in a given task is simply their interactive vector. The other possibility is that the two hemispheres are distinctively performing different and necessary subprocesses of the given task, with overall performance dependent on dynamic coordination of the subprocesses.

The race model (Raab, 1962) also suggests the contribution of both hemispheres in processing, however interhemispheric interaction was not included of this model. Miller (1982) modified this model and used it to establish a coactivation model. Separate hemispheric processing according to the race model was replaced in the coactivation model by bihemsipheric processing. In case of bilateral stimulation, processing in the left and the right hemisphere does not race against each other, but is pooled across both hemispheres into a common value (Mordkoff and Yantis, 1991). Two targets produce faster total activation than single targets, resulting in faster reactions. All information concerning the presence of at least one target is “pooled” prior to the decision. The redundant-signals effect results from the fact, that a certain criterion is reached more rapidly when redundant targets are processed and contribute to activation.

Coactivation Model: (Miller, 1982)

➔ Bilateral performance > unilateral (LVF or RVF) performance
➔ Reason: activation from both hemispheres contribute to common activation prior decision

Mordkoff and Yantis (1991) suggested an interactive race model. This model is an independent race model which also includes a certain proportion interaction during identification and decision making. As in the independent race model, separate decisions and a race of parallel processes are assumed. But the interactive race model also includes information exchange between the perceptual channels. This differs from the assumption of the independent race model that the channels are independent. Only specific forms of information (and not general activation) may be exchanged, and each channel makes a separate decision. This is the distinction from the coactivation model, which assumes that the activation from redundant signals is pooled prior to a decision (Mordkoff and Yantis, 1991). The interactive race model includes mechanisms that allow the exchange of information between separate processing channels.

Interactive Race Model: (Mordkoff and Yantis, 1991)

➔ Bilateral performance > unilateral (LVF or RVF) performance
➔ Reason: parallel race of interactive hemispheric processing

The direct connections model developed by Collins and Coney (1998) explains interhemispheric communication during linguistic processing. It is assumed that both hemispheres are capable of processing, without the necessity for callosal relay of information. Information is encoded in the hemisphere to which it was initially projected. The direct connections model proposes the existence of direct callosal connections between concepts in one hemisphere and particular related concepts in the opposite hemisphere. According to this model, interhemispheric communication occurs at a semantic level via activation spreading through these direct connections. Moreover, it is assumed that concepts directed to a particular hemisphere may activate related concepts in the contralateral hemisphere without activating those concepts within the directly stimulated hemisphere. Although, this model does not state predictions for bilateral

processing, it seems bihemispheric processing should be facilitated due to activation spreading through the corpus callosum.

Direct Connection Model: (Collins and Coney, 1998)

➔ bilateral performance > unilateral performance (at semantic level)
➔ reason: excitatory activation spreading due to direct connections via the corpus callosum

In the previous section different cognitive models of interhemispheric processing have been presented. These models state different processing outcomes in bilateral conditions depending on the extent of assumed hemispheric independence. Highest hemispheric independence is supposed with unilateral specification models. In the context of these models performance during bihemsipheric processing would never exceed performance during unilateral processing. Bilateral performance would resemble either randomly left or right hemispheric performance or the performance of the best unilateral condition or the performance of the hemisphere which is dominant for a certain task. So, in terms of these models, it would not be possible to explain higher bilateral than unilateral performance levels. This is also true for inhibition models, which would predict inferior performance in case of bilateral stimulation. In contrast to unilateral processing models, inhibition models do not take the two hemispheres as separate processor, but take them as somehow integrated units. However, inhibition models mainly suggest inhibitory interhemispheric connections. Therefore, stimulation of both hemispheres would not improve performance, due to mutual inhibition (Boles, 1979; Mackavey et al., 1975), homologous activation (Boles, 1987, 1990, 1995), interhemispheric competition (Eglin, 1987), or homotropic inhibition (Cook, 1984, 1986).

Parallel processing models and positive cooperation models predict an enhancement of performance during bilateral conditions compared to unilateral conditions. These models state advantageous performance when both hemispheres are involved in the accomplishment of a certain task. However, the two types of models employ different explanations for the enhanced performance in bilateral conditions. Parallel processing models assume a simple hemispheric competition of independent processing, and therefore would predict higher (or faster) performance after bilateral stimulation. Positive cooperation models rely on interhemispheric exchange and state more complex

mechanisms of facilitation. These mechanisms were called coactivation (Miller, 1982), interactive hemispheric processing (Mordkoff and Yantis, 1991), or excitatory activation via direct connections (Collins and Coney, 1998). In contrast to parallel processing models, positive cooperation models are based on actual hemispheric exchange or coordination of processing between hemispheres.

Apart from different predictions about processing outcomes, cognitive models have a common weakness. These models are all developed based upon certain experimental results and no particular model is capable to explain the huge variety of findings on interhemispheric processing. Further, they provide little or no information on underlying neurobiological mechanisms causing the predicted outcome.

5. The concept of transcortical cell assemblies

A neurobiological approach on interhemispheric processing was established employing the concept of transcortical cell assemblies (Pulvermüller and Mohr, 1996). This model is capable to explain different aspects of hemispheric processing.

Hebb (1949) originally introduced the concept of cell assemblies. A cell assembly is a set of neurons that are strongly and reciprocally connected to each other. Activation of certain neurons which are part of a cell assembly will consequently activate the whole assembly because of the strong intra-assembly connections. This activation process is called ignition (Braitenberg, 1978). After ignition, activity is retained in the cell assembly network.

It is assumed, that cell assemblies are formed, due to frequent co-activation of neurons located in different cortical regions. For example, during neurophysiological learning mechanisms acoustic, visual, and motor associations of a certain word are learned. When complex stimuli are learned, neurons located in diverse brain regions are frequently activated simultaneously; leading to strongly coupled interhemispheric transcortical cell assemblies (Mohr et al. 2002). Therefore, neurons of one cell assembly are not restricted to a small cortical region. It is rather assumed that cell assemblies are composed of local clusters of neurons that are distributed over both hemispheres and are strongly connected via excitatory connections through the corpus callosum (**Figure II.A.1**).

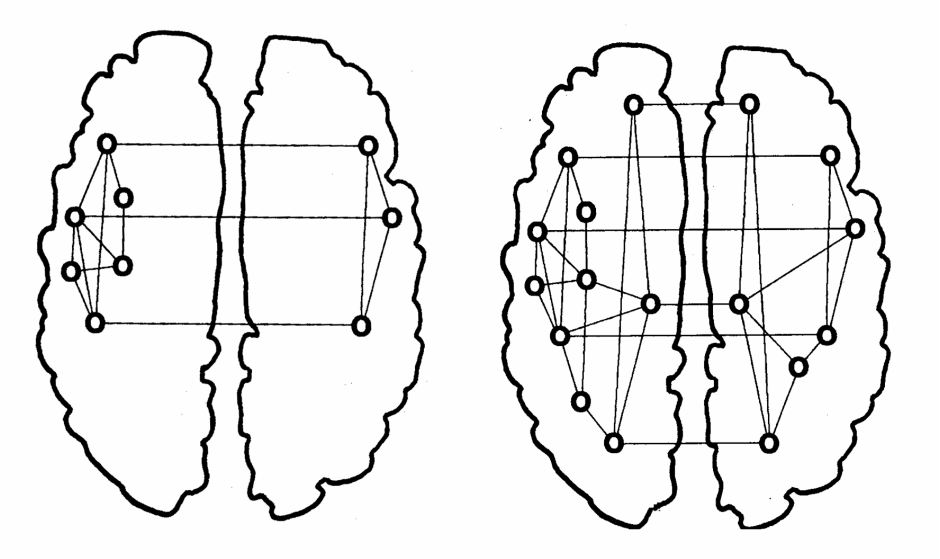

Figure II.A.1. Transcortical cell assemblies: cell assemblies are distributed over both hemispheres with different degrees of lateralization. Whereas grammatical function words (left) are represented in highly lateralized assemblies, cell assemblies representing content words (right) are probably less lateralized (from Pulvermüller and Mohr, 1996).

In their framework on transcortical cell assemblies, Pulvermüller and Mohr (1996) provide evidence that the "transcortical cell assembly model" may account for functional laterality as well as interhemispheric processing. The cell assembly model is capable to explain differences in cortical laterality which are obtained for different word forms (e.g. function and content words, Chiarello and Nuding, 1987; Mohr et al., 1994b). Whereas cell assemblies for function words are strongly localized to perisylvian regions of the left hemisphere, cell assemblies for content words do also have visual associations and may be distributed over perisylvian and visual cortices of both hemispheres (**Figure II.A.1**). Laterality differences of different word forms might therefore be explained with different topographies of cell assemblies.

The present model also contains predictions for bi-hemispheric processing. Since cell assemblies are distributed over both hemispheres, bi-hemispheric activation should occur during the processing of a certain stimulus. Activity of both hemispheres should therefore contribute to stimulus processing and performance: When both hemispheres are stimulated, the amount of activity reaching the transcortical assembly is assumed to be larger compared to a condition in which only one hemisphere is stimulated. More activity

in the assembly should then lead to faster cell assembly ignition and superior performance (Pulvermüller and Mohr, 1996).

It has been assumed that transcortical cell assemblies are formed during associative learning processes. Therefore, cell assemblies do not only underlie the processing of language units, but also the processing of concepts, perception of gestalt, imagination of visual scenes, and execution of motor programs. It has also been assumed that only entities with a certain degree of complexity are represented in transcortical cell assemblies (Pulvermüller and Mohr, 1996). For example, a simple movement is presumably controlled by the activation of a small cortical area, while more complex sequential movements are controlled by a more widely distributed assembly including neurons of both hemispheres (Roland et al, 1980; Seitz and Roland, 1992).

Transcortical Cell Assemblies: (Pulvermüller and Mohr, 1996)

- ➔ Bilateral performance > unilateral (LVF or RVF) performance, for stimuli with transcortical cell assemblies
- ➔ Bilateral performance = unilateral (LVF or RVF) performance, for stimuli with only local cell assemblies or no cell assemblies at all

B. Studies on Interhemispheric Processing

The question how the two cerebral hemispheres process information, has been addressed in many studies using various experimental settings. In this section findings on interhemispheric processing from different experimental settings are reviewed.

Interhemispheric interaction was first examined with a paradigm introduced by Dimond and Beaumont (1971). Stimuli were tachistocopically presented unilaterally to the left visual field (LVF) or to the right visual field (RVF) or bilaterally to both visual hemifields (bilateral condition, BVF). Due to the complete crossing of the visual pathways, this stimulation technique ensures that information in unilateral conditions (LVF and RVF stimulation) is restricted to one hemisphere in the first place. In the bilateral condition, both hemispheres receive information at the same time. Interhemispheric interaction is obtained from comparison of bilateral with unilateral performance. This presentation technique has been applied to various experimental paradigms with different experimental questions. Differences among experimental paradigms lie in stimulus properties (same or different stimuli) and in experimental task (matching or identification).

Interhemispheric interaction has been examined with designs comparing performance when both hemispheres are involved with performance when only one hemisphere is involved in task accomplishment. This was done with matching designs using unilateral and bilateral presentation of different stimuli to compare, for example, with respect of physical identity or semantic affiliation. Apart from matching tasks there have also been employed simple reaction, familiarity and identification tasks in which either one stimulus appeared unilaterally or tow redundant stimuli appeared bilaterally. The different tasks were also used in designs with serial stimulus presentation, instead of simultaneous stimulus presentation.

Interhemispheric interaction was also examined with unilateral displays. The extent of unilateral processing was varied by either presenting only one stimulus to one hemisphere or presenting one target stimulus to one hemisphere and a distractor stimulus to the other hemisphere. In case of presenting only one stimulus both hemispheres might be involved in task accomplishment, whereas in case of presenting two different stimuli, the hemisphere which received the distractor might be occupied and would not be involved

in task accomplishment. The presentation of a distractor to one hemisphere would force the other hemisphere to process more independently. Hemispheric interaction during unilateral presentation is estimated by the comparison of performance from unilateral and bilateral stimulation.

Crossed vs. uncrossed designs also provide the possibility to analyze interhemispheric interaction. These designs are based on the crossing of sensory and motor pathways in the brain: the left hemisphere receives visual input from the right visual field and controls right hand movement; the right hemisphere receives visual input from the left visual field and controls left hand movement. In uncrossed condition, the locations of visual stimulus presentation and response hand are congruent, whereas these locations are incongruent in crossed conditions. Interhemispheric interaction is expected in crossed conditions, because stimuli are presented to one hemisphere and motor response is controlled by the other hemisphere.

1. Bilateral Processing in Matching Designs with different Stimuli

Interhemispheric interaction has been assessed with tasks requiring integration of information provided to each hemisphere independently. One possibility is to present simultaneously two stimuli either both to the same visual field (unilateral condition) or one to each visual field (bilateral condition). For the matching task, pairs of same or different stimuli are presented. In the bilateral condition stimulus information is divided between the two hemifields (partially to the LVF and partially to the RVF) and has to be integrated across hemispheres (Dimond and Beaumont, 1971). The task requires matching or semantic categorization of stimuli presented in bilateral condition or in unilateral conditions. It is determined whether it is advantageous (in terms of better behavioral performance) to divide cognitive processing between the hemispheres or whether it is more effective to restrict processing to one hemisphere only.

Dimond and Beaumont (1971) examined how performance is affected by the involvement of both hemispheres in contrast to only one hemisphere. During a digit recall task, two digits were either presented to the LVF or to the RVF, or one digit appeared in each visual field (bilateral condition). Performance was better in the bilateral condition than in either unilateral condition. They concluded that performance is maximized, if stimuli are presented to both hemispheres. This result suggests, that performance on bilateral trials cannot be predicted on the basis of unilateral trials. Therefore, Banich and Belger (1990) concluded that interhemispheric processing couldn’t be predicted by the sum of the parts. Dimond and Beaumont (1972) applied the divided visual field presentation to a matching task, which required matching of nonverbal visual stimuli within one hemisphere (left or right hemisphere) or across hemispheres. Again, increased performance was revealed in the across hemisphere matching condition compared to within hemisphere matching.

Berger (1988) examined bilateral processing on a semantic relation judgment task with tachistoscopic presentation of words. Two words were simultaneously directed to one hemisphere (left or right) or one word was presented to either hemisphere. Higher performance was obtained in the bilateral condition than in the two unilateral conditions.

Liederman and colleagues (1985) obtained a different result. Bilateral vs. unilateral word pairs were tachistoscopically presented during a semantic matching task. They found that bilateral performance was only as fast as the better of the two unilateral conditions, but faster as their average. Further, unilateral performance improved with practice during the experiment, whereas bilateral performance did not.

Davis and Schmit (1973) found better bilateral than unilateral performance during letter matching tasks for both physical similarity (e.g. A A) and name identification (e.g. A a). In contrast, Coney (1985) revealed only superior bilateral performance for name matching, but not for physical similarity matching. Further, he applied a same/different task with letter name matching and obtained only for "same" decisions a bilateral distribution advantage, whereas "different" judgments were associated with more errors bilaterally than unilaterally. Liederman and Meechan (1986) also found a differential bilateral advantage during a letter naming task. A bilateral advantage was revealed only when the input of information was separated, so that one hemisphere received upright letters and the other the inverted letters. But no bilateral advantage was shown when the hemispheres received the same kind of letters.

Consequently, task difficulty was suggested to be an important moderator for bilateral performance. Norman and colleagues (1992) manipulated task difficulty in a same-different dot pattern-matching task with the number (two, four or six) of dots included in a pattern. The two dot patterns presented on a given trial always had the same number of dots. Performance diminished with increased number of dots and overall bilateral performance was better than unilateral. Furthermore, the bilateral advantage increased with task difficulty for same judgments and only in comparison with RVF latencies but not compared with LVF latencies.

Banich and Belger (1990) examined the influence of task difficulty with a series of experiments. However, the matching technique was modified in order to equate perceptual processing load on within- and across-field trials. On each trial three stimuli were displayed: two in the upper half of each visual hemifield and the third in the lower half of either the LVF or RVF (**Figure II.B.1**). Subjects were instructed to decide whether the stimulus in the lower visual field matched with one of the stimuli in the upper visual fields. The concordant stimulus was either located in the same visual field (within hemisphere or

unilateral matching condition) or in the opposite visual field (across hemisphere or bilateral condition). This technique ensured also that post-perceptual processing was performed, rather than simply to make a perceptual identification of the items. Banich and Belger (1990) argued that if a matching decision is requested, and each item of the matching pair is initially directed to different hemispheres, some post-perceptual aspects of processing must be divided.

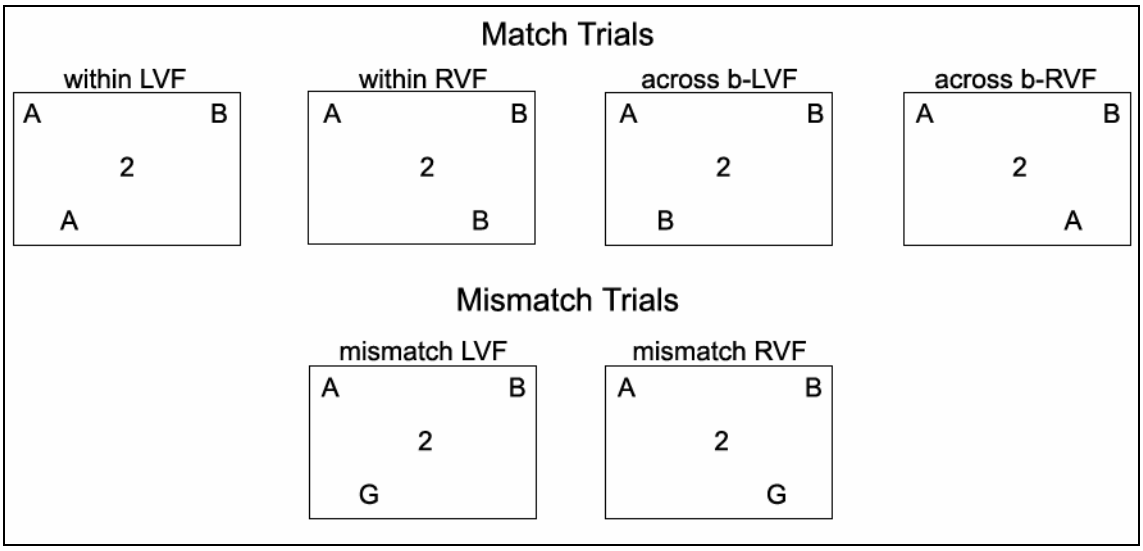

Figure II.B.1. Matching design applied by Banich and Belger (1990). On all trials stimuli appeared in both visual fields. On within visual field trials the two matching stimuli appeared in the same visual field, whereas on across visual field trials the two matching stimuli appeared in different visual fields.

First, during a letter-matching task processing difficulty was manipulated. Dividing processing between the hemispheres improved performance for the more difficult name-identity task (e.g. A-a) whereas it actually impaired performance for easier physical-identity task (e.g. A-A). A second experiment showed that interhemispheric performance was also reduced when a physical-identity task was applied to digit matching. The third experiment required more difficult decisions about digits. A summation task required judgment whether the sum of two digits was greater than or equal to ten and an ordinal task required the decision if the value of a digit less than two others. Both tasks produced an advantage for across hemisphere processing (Banich and Belger, 1990).

Marsoleck et al. (2002) found similar results for a letter-matching task. Pairs of letters were compared after presentation in different visual fields or in the same visual field. Bilateral performance was improved compared to unilateral performance, during an

abstract category comparison task when participants decided whether two letter exemplars belonged to the same abstract category (e.g. “k” and “K”) or not (e.g. “k” and P”). In contrast, the specific exemplar comparison task revealed higher unilateral than bilateral accuracy, when the decision was required whether the two letters within the same abstract category were the same specific exemplars (e.g. “k” and “k”) or not (e.g. “k” and “K”).

Belger and Banich (1998) examined whether task performance is aided by hemispheric interaction during demanding conditions and how this effect is moderated by computational complexity, the degree of lateralization for a task, and individual differences in asymmetric hemispheric activation. The advantage for distribution of stimuli between hemispheres increased as a function of task complexity. However, instead of a bilateral distribution advantage, left hemispheric superiority was found for a highly lateralized rhyme decision task. They concluded that interhemispheric division of processing was only advantageous when task complexity was high and when the required operations can be divided between the hemispheres.

Weissman and Banich (2000) adjusted their matching design by presenting the target stimulus in the lower RVF or LVF or on the midline. The matching stimulus appeared either in the same visual field (within hemisphere condition) or in the opposite visual field (across hemisphere condition) or not at all (non-matching condition). Midline presentation allowed either within or across hemisphere processing. It was revealed that in case of low task complexity (physical identity comparison) midline target condition resembled within hemisphere performance, whereas in case of high task complexity (name identity comparison) midline target condition resembled across hemisphere performance. Weissman and Banich (2000) interpreted this result as further evidence for the dependence of degree of hemispheric cooperation on task difficulty. The midline target conditions indicated that the two hemispheres dynamically couple or uncouple their processing as a function of task complexity. Low task difficulty is associated with independent hemispheric processing, whereas across hemispheric processing is more likely to occur in case of high task difficulty.

Hatta and Yoshizaki (1996) also examined the influence of task demand and task familiarity on interhemispheric processing with a mental calculation task. In their first experiment, subjects were asked to add two numbers (either two Arabic or Kanji

numerals), which were presented unilateral, bilateral or central. A tendency toward a bilateral advantage was found, but central condition was superior to bilateral condition. Task familiarity was examined with an increased number of trials, but no variation of the bilateral advantage was found. Task difficulty was modified in a third experiment, by presenting the two numbers on each trial either both in Arabic numerals or one in Arabic and one in Kanji numeral. The bilateral advantage was more pronounced during the higher demanding task. Hatta and colleagues (2002) further examined the relationship between cognitive task demand and bilateral processing advantage. In unilateral conditions one stimulus appeared either in the LVF or in the RVF and in bilateral condition two copies of a stimulus appeared in both visual fields simultaneously. During three experiments task demand was systematically increased by displaying one or two digit numbers and presenting one or three numbers successively. A bilateral advantage for number recollection was revealed only in the highly demanding conditions, when three two digit numbers were recollected.

Koivisto (2000) applied a semantic categorization task to examine interhemispheric processing. Two identical, semantically related or semantically unrelated objects were presented either unilaterally both to the same hemisphere or bilaterally to opposite hemispheres. A bilateral advantage was found for categorization of semantically related pictures but not for categorization of less demanding identical pictures. Koivisto and Revonsuo (2003) compared semantic categorization between objects and words. Semantically related or unrelated objects, words or object-word pairs were presented unilaterally or bilaterally. Bilateral categorization was faster when word pairs and object pairs were presented. In contrast word-object pairs were not categorized faster in bilateral than in unilateral displays.

Interhemispheric interaction has been repeatedly examined with interhemispheric vs. intrahemispheric matching designs. Although there is some inconsistency in applied experimental designs and in the resulting performance on bilateral trials the presented results allow a limited number of conclusions about interhemispheric interaction mechanisms. Task complexity seems to be the most reliant predictor for facilitated interhemispheric processing. Many studies found that interhemispheric cooperation facilitated performance for complex tasks more than performance of simple tasks (e.g. Banich and Belger, 1990; Hatta et al, 2002; Hatta and Yoshizaki, 1996; Marsoleck et al.,

2002; Koivisto, 2000; Weissman and Banich, 2000). These studies showed that as task complexity increases, it becomes more advantageous to divide information between the hemisphere than to direct the information to the same hemisphere. Relatively simple task like the decision whether two items are physically identical or different are performed better when the critical items are directed to the same hemisphere rather than to different hemispheres. More complex tasks like name identification (Weissman and Banich, 2000) or semantic categorization (Koivisto, 2000) are performed better when the two critical items are directed to different hemispheres than directing them to the same hemisphere.

Banich and colleagues (Banich, 1995; Banich and Belger, 1990; Weissman and Banich, 2000) explained the effect of task difficulty on interhemispheric cooperation by an interaction between "two opposing forces": On the one hand, interhemispheric cooperation was assumed to increase the computational power of task performance because each hemisphere would process information somewhat independently of its partner. On the other hand, interhemispheric cooperation was also suggested to entail time costs not associated with intrahemispheric processing because it required that information is integrated between the hemispheres by the corpus callosum. According to Banich and colleagues these two aspects should have different effects on high and low difficulty tasks. During simple tasks the benefits associated with greater computational power would not be great enough to outweigh the costs associated with integrating information across the hemispheres, leading to a within hemisphere advantage. In contrast, during complex tasks, the benefits associated with grater computational power would become more substantial than the costs incurred by integrating processing between the hemispheres, leading to an across hemisphere advantage.

Task difficulty seems an important variable for interhemispheric processing. However, there are also studies reporting an advantage for across hemisphere processing with relatively simple tasks (e.g. Brown & Jeeves, 1993; Ludwig et al. 1993). Furthermore, Koivisto and Revonsuo (2003) did not reveal an across hemisphere processing advantage for a difficult task which required semantic categorization of words presented along with objects. Belger and Banich (1998) demonstrated that an across hemisphere processing advantage also required that both hemispheres are capable of performing the required operations. Therefore, it is likely that the occurrence of an advantage for dividing processing across hemispheres is not only a simple ratio of benefits and costs.

Matching designs examine information processing when information is presented within one visual field (or hemisphere) or when information is divided across visual fields (or hemispheres). Within the matching paradigm, interhemispheric processing is assessed with the comparison of performance between unilateral and bilateral conditions. This approach seems quite appropriate in order to gain knowledge on interhemispheric processing. An advantage of interhemispheric processing would be obtained when performance is improved due to the division of information across hemispheres relative to unilateral presentation. However, the comparison between unilateral and bilateral conditions includes also a difference in processing load: in unilateral conditions, two stimuli are presented to one hemisphere, whereas in bilateral conditions each hemisphere receives only one stimulus. Therefore, the two stimulation conditions differ not only in respect of stimulus location but also in respect of hemispheric perceptual processing load. An advantage for the bilateral condition might not generally reflect that bilateral processing is superior to unilateral processing but that it is advantageous to divide information across hemispheres rather than provide it to one hemisphere only.

Banich and Belger (1990) tried to reduce the influence of different processing loads by a modification of the matching design. They always presented one stimulus in the upper part of each visual field and a third stimulus in the lower part of one visual field. With this design it is possible to apply within and across visual field matching, without changing the number of presented stimuli. This would reduce the influence of perceptual processing load per hemisphere, because there is always one hemisphere which handles two stimuli, in unilateral and bilateral condition. Therefore, a difference between unilateral and bilateral conditions should more reliably reflect an influence of bihemispheric processing. However, there is always an unattended or distractor stimulus included in the display. In unilateral or within visual field matching conditions, the distractor stimulus appears in visual field opposite to the one which is relevant for processing. In the bilateral condition, the distractor stimulus appears together with a target stimulus in one visual field. Studies regarding unilateral processing with bilateral stimulation of different stimuli it is known that a distractor stimulus on the unattended visual field does influence performance (Boles, 1983, 1987, 1990, 1994; for a detailed discussion, pleas refer to the upcoming section). Assuming that the influence of the distractor is similar in bilateral conditions, this sophisticated matching design, might actually examine interhemispheric interaction. Unfortunately, the distractor might have a different influence on the bilateral condition.

2. Unilateral Processing with Bilateral Stimulation of Different Stimuli

Boles tried to assess interhemispheric interaction by comparing hemispheric asymmetries in unilateral and bilateral conditions. In unilateral conditions only one stimulus appears in either visual filed. During the bilateral condition competing different, but similar stimuli are tachistocopically presented simultaneously in opposite visual fields. In the bilateral condition, an arrowhead was presented at the fixation point indicating to which stimulus the subject should respond.

With various tasks, Boles demonstrated increased hemispheric asymmetry due to larger visual field differences during bilateral relative to unilateral stimulation (Boles 1983, 1987, 1990, 1994). This enhancement of hemispheric asymmetry by bilateral displays has been called bilateral advantage (Boles, 1990). For example, Boles (1983) employed a word identification task with unilateral and bilateral stimulation. In unilateral conditions one word appeared either in the left or in the right visual field. In bilateral conditions two different words, one target and one distractor, appeared in opposite visual fields, whereof only processing of the target stimulus one visual field was required. Greater asymmetry between visual fields was revealed from bilateral than from unilateral trials (Boles, 1983). This effect was obtained in latency and accuracy data for words, letters, bargraphs, numbers or dot patterns (Boles, 1987, 1990, 1994).

Boles (1987) suggested that greater asymmetry in bilateral conditions would reflect increased hemispheric independence compared with unilateral conditions, because in bilateral conditions the two hemispheres receive different stimuli and both are occupied with the processing of its own stimulus. In contrast, in unilateral conditions the hemisphere which was not originally stimulated might contribute in stimulus processing. Therefore, Boles (1987) argued that in unilateral conditions, the two hemispheres act as one nearly integrated unit with only minimal delay or inaccuracy occurring when information is transferred from one to the other. In bilateral condition the hemispheres act as more independent units, each dealing with its own stimulus and with more substantial delays occurring when information is transferred. The homologous activation hypothesis (Boles 1987, 1990, 1995) was assumed to account for this effect. During bilateral stimulation homologous areas of both hemispheres are activated, which disrupts communication

between hemispheres and forces the hemispheres to process information more independently.

Boles (1990) analyzed the influence of the lexical status of the distractor on words and pseudowords during a lexical decision task. All presentation conditions were bilateral. Target stimuli were words and pseudowords presented in the LVF or RVF with simultaneous presentation of a distractor (word or pseudoword) of same or different lexical status (2 words, 2 pseudowords or one word and one pseudoword). The lexical status of the distractor selectively influenced word processing. Visual field asymmetry during word processing was larger for distractor words than for distractor pseudowords. Pseudoword processing did not significantly change with lexical status of the distractor. Boles took these findings as further support for his homologous activation hypothesis, since only stimulation with two words should result in homologous activation. Presumably this should disrupt the transfer of word stimuli between hemispheres and result in larger visual field asymmetry.

Iacoboni and Zaidel (1996) also used bilateral presentation of different stimuli to increase hemispheric independence during word recognition. In a lexical decision task one word or pseudoword was presented unilaterally in the LVF or RVF or two different words or pseudowords were presented in the bilateral condition. In the bilateral condition, an arrow indicated the target stimulus. They showed that bilateral presentation selectively impaired word decisions. Processing of pseudowords did not differ between unilateral and bilateral conditions, and therefore was not influenced by presentation of a second stimulus. Asymmetry between visual fields was increased during word processing, when a second stimulus was presented in the opposite visual field. These results were interpreted as evidence for interhemispheric interaction during word processing. It was suggested that word processing benefits from interhemispheric interaction, whereas pseudoword processing did not. These data also support the conclusion that each single hemisphere can control word recognition independently of the other, however with decreased performance compared with bihemispheric processing.

Olk and Hartje (2001) applied a lexical decision task with unilateral and bilateral presentation of word and pseudoword stimuli. In unilateral trials, only one letter string appeared either in the LVF or RVF. In bilateral trials, two different letter strings (both

words or both pseudowords) appeared in each visual field (one letter sting in each visual field). A centrally presented arrow indicated the target during bilateral trials. Reactions were only required when a word was presented, whereas pseudoword reactions were refrained. The RVF advantage for words was significantly enhanced under bilateral compared to unilateral stimulation. Reaction times were more prolonged after LVF than after RVF stimulation.

In summary, these findings suggest that hemispheric asymmetry is enhanced due to bilateral presentation of two different stimuli. Similarity between target and distractor stimulus plays an important role, as hemispheric asymmetry for words was less influenced by pseudoword distractors than by word distractors (Boles, 1990; Iacoboni and Zaidel, 1996). In addition, the presented findings allow conclusions about interhemispheric processing. Overall performance diminishes when the two hemispheres are engaged in processing of different but similar stimuli. Asymmetry is increased probably due to a greater performance reduction in the hemisphere, which is less specialized for the certain task (Olk and Hartje, 2001). Different models of interhemispheric processing would explain this with different mechanisms. In general it might be assumed that performance is declined when both hemispheres are engaged in processing of different stimuli. This effect is more pronounced for the performance of the hemispheres, which is less capable for task accomplishment. This allows the conclusion that the two hemispheres do not process independently even during unilateral conditions. It is rather assumed that the two hemispheres are interacting under normal circumstances. In particular, the performance of the less specialized hemisphere is enhanced by interhemispheric exchange.

Thus, bilateral stimulation with different stimuli has been applied during bilateral and unilateral processing. However, the reason for application of these paradigms differ: Bilateral processing designs examine how performance might be influenced by either presenting information across or within hemispheres. Unilateral processing designs examine to what extent processing is affected by presenting a second stimulus to the hemisphere which is not involved in task accomplishment. These are totally different aspects of interhemispheric processing. Bilateral processing of different stimuli examines the ability to process and integrate stimulus information even when it is distributed across hemispheres. In contrast, the unilateral processing condition determines how processing is disturbed by unintended interhemispheric processing. The two methods revealed that under

certain circumstances it is advantageous to divide information across hemispheres (bilateral processing) and that presentation of a different but irrelevant stimulus to one hemisphere affects the performance of the other hemisphere. These findings suggest that performance is always influenced by both hemispheres whether it is required and advantageous or not. However, designs with different stimuli give information about how the hemispheres might combine their processing possibilities. Designs with bilateral redundant stimulus presentation vs. unilateral stimulus presentation might help to answer this question because these tasks do not necessarily require interhemispheric interaction for a stimulus processing but provide the possibility for interhemispheric interaction.

3. Bilateral Processing in Redundancy Designs with Same Stimuli

Another attempt to examine interhemispheric processing was made with designs comparing unilateral stimulation of one hemisphere with bilateral redundant stimulation of both hemispheres. In contrast to the designs outlined in previous sections in which different stimuli are presented on bilateral trials, within bilateral redundancy designs identical copies of the same stimulus are always presented in both visual fields. With these designs it has been investigated whether it is advantageous when both hemispheres have access to the same stimuli in contrast to unilateral stimulus presentation to only a single hemisphere.

Simple reaction time tasks have been applied with simultaneous redundant stimulation. Different kinds of race models as well as cooperation models were to examine with simple reaction tasks. Miller (1982) implemented a letter search task with visual hemifield stimulation. A target letter ("A") appeared either unilaterally in the LVF or RVF or bilaterally in both visual fields (redundant signal trials). In unilateral conditions the target letter appeared either with a second noise letter in the other visual field (signal-noise trials) or without a second letter in the other visual field (signal alone trials). Statistical analysis revealed that the redundant signal trials were faster than both unilateral signals alone and signal-noise trials. Response latencies on signal alone trials with the signal letter in the RVF were intermediate. Signal alone trials with signal letter in the LVF and signal-noise trials had slowest responses. Miller (1982) also demonstrated that not only two visual signals accelerated response but also bimodal stimulation in which one visual and one auditory signal was presented. Van der Heijden et al. (1983) also applied a letter detection task with the letter "E" as target and two other letters as distractor ("F" and "O"). In four experiments, a clear redundancy gain was observed. Reactions times were reduced with increased number of simultaneously presented targets. Jones (1982) used a task, which required identification of letters. Stimuli were presented tachistocopically in the RVF, in the LVF, or in both visual fields simultaneously (two identical stimuli appeared in each visual field). Identification performance for bilaterally presented letters was superior to unilaterally presented letters.

More recently, Miniussi, Girelli and Marzi (1998) attempted to find an electophysiological correlate of the redundant targets effect (the speeding up of reaction

time for redundant vs. single targets). They presented checkerboards to the left or right of fixation or to a pair of identical checkerboards simultaneously to both hemifields during a simple signal detection task. Both single and double targets appeared either in the upper or lower visual hemifield. During this task event-related potentials (ERPs) elicited by the checkerboards were recorded. Reaction time data revealed faster responses for redundant compared to unilaterally presented stimuli. In ERPs they found that the P1 and N1 components of the visual ERP had a shorter latency for bilateral than for unilateral stimuli presented to the two hemifields. Miniussi et al. (1998) suggested these findings might indicate that the redundant target effect occurs at the level of early visual processing, rather than at late decisional or premotor stages.

Mullin and Egeth (1989) examined how word processing is affected by redundant stimulation. However, target stimuli were not presented unilaterally in the non-redundant condition but centrally below or above fixation. On redundant trials two copies of a target stimulus were presented on both positions. Note, that this design does not allow a comparison between intra- and interhemispheric cooperation, because of the central stimulus presentation, which allows both hemispheres to access stimuli. Instead the influence of redundant vs. non-redundant stimulation was determined. Semantic categorization of words did not reveal a redundancy gain. In a second experiment words and pronounceable pseudowords were presented on redundant and non-redundant positions. Subjects were asked to respond to words and to refrain from responding when they detected pseudowords. For this task a reliable redundancy gain was obtained. Reactions were faster and more accurate in response to redundant target trials compared to non-redundant trials. Further, with two other experiments redundant presentation of two different stimuli was examined during lexical decision and semantic categorization. The two stimuli on redundant trials were different but were both targets and led to the same decision. Processing interference, in the form of a redundancy loss, was evident in the lexical decision task, but not in the semantic categorization task. From these results it was concluded that lexical but not semantic processing was influenced by redundant stimulation.

Redundant bilateral displays also allow the analysis of processing strategies from unilateral and bilateral displays and to compare them. It might be possible to determine the relative contribution of each hemisphere to the processing of bihemsipherically available

stimuli by analyzing the processing strategy differences between LVF, RVF and bilateral condition. This analysis requires tasks for which the hemispheres process the stimuli differently and therefore one hemisphere is superior to the other. Since language related tasks repeatedly revealed differences in processing between the two hemispheres, they seem suitable for this kind of analysis. When bihemispheric processing strategies differ from both unilateral processing strategies, cooperation between hemispheres in the bilateral condition would be assumed. In contrast, if the pattern of performance on bilateral trials is qualitatively similar to the one of the unilateral conditions, one can infer that the mode of processing characteristic of one hemisphere dominated in bilateral trials (Hellige, 1993).

Hemispheric processing strategies are reflected in performance but also in types of errors made by a certain hemisphere. Levi et al. (1983) demonstrated an analysis of error patterns during nonsense syllable (consonant-vowel-consonant letter strings) identification. Incorrect responses were classified into three categories: first letter errors (FLE) in which the first letter is missed; last letter errors (LLE) in which the last letter is missed; and other errors (OE), which encompass all other possible types of incorrect responses. Levy et al. (1983) found significant differences in the patterns of errors made for LVF and RVF syllables. The number of LLEs was higher in the LVF than in the RVF and more FLEs occurred for syllables presented in the RVF than in the LVF. Further, the difference between LLEs and FLEs was greater in the LVF than in the RVF.

Hellige and colleagues have repeatedly compared bilateral redundant stimulation with unilateral conditions. Hellige, Jonsson and Michimata (1988) used a face comparison task. Subjects indicated whether two successively presented face drawings were the same or different. The first face always appeared at the fixation point and the second face was presented to the LVF, RVF, or both visual fields simultaneously (bilateral). Errors and reaction times were both higher on bilateral trials. On different trials, the reaction time of correct responses depended on which feature differed. This feature location effect differed on LVF and RVF trials, and on bilateral trials it was identical to that obtained on RVF trials. Hellige and Michimata (1989) applied a letter comparison task with letter pairs projected to the LVF, or RVF, or the same letter pairs were presented to both visual fields simultaneously. Whereas on RVF trials reactions were faster for same pairs than for different pairs, this effect was absent for LVF trials. This suggested different processing

modes for the two hemispheres. Error patterns on bilateral trials resembled to RVF trials, which was interpreted as evidence for a left hemispheric metacontrol on bilateral trials.

Hellige, Taylor and Eng (1989) investigated performance and error patterns for the identification of consonant-vowel-consonant (CVC) nonsense syllables presented unilaterally or bilaterally when two redundant syllables were given. Different qualitative error patterns were obtained for the two unilateral conditions, suggesting that each hemisphere has its own preferred mode of processing the CVC stimuli. The qualitative pattern of errors on bilateral trials was identical to that obtained on LVF trials, which suggested that the right hemisphere dominates processing on bilateral trials. However, they also found superior overall performance on bilateral trials, which is incompatible with a strict right hemisphere metacontrol interpretation. This bilateral advantage rather implies that both hemispheres are involved in processing bilateral stimuli and suggests hemispheric cooperation. In contrast to Hellige et al. (1989), Luh and Levy (1995) did not reveal a processing advantage for syllable identification after bilateral compared to unilateral presentation. Further, they did not obtain a processing advantage for central presentation compared to unilateral presentation. However, analysis of error patterns revealed that the error patterns in bilateral and central conditions were jointly predicted by LVF and RVF variances. Luh and Levy (1995) concluded that both hemispheres contribute to the processing of bihemispherically presented syllables.

Marks and Hellige (1999) pointed out that unilateral and bilateral redundant trials, which are compared to investigate interhemispheric interaction, differ from each other in both the number of locations stimulated and the number of redundant stimulus copies. They conducted two experiments on CVC syllable identification in which these factors were controlled. During the first experiment the number of locations was controlled. On bilateral trials, one of two identical stimulus copies appeared in each visual field. On unilateral trials one copy of a stimulus appeared in the respective visual field, whereas a nonsense string (“XXX”) appeared in the opposite visual field. Superior identification performance was revealed on bilateral trials and performance differed between the two unilateral conditions with better performance in RVF condition than in LVF condition. Noteworthy, the magnitude of the bilateral advantage was much greater than that in other experiments. Marks and Hellige (1999) indicated that the percentage of errors in the bilateral condition was virtually identical to the error rate predicted by the binomial

formula [P(BVF) = P(LVF) + P(RVF) – P(LVF) * P(RVF)]. This formula predicts bilateral error rates from unilateral performance. However, it is required that performance in unilateral conditions was measured independently from each other. Probably, Marks and Hellige (1999) increased independence between unilateral conditions by presenting distractor stimuli in the opposite visual fields, and therefore obtained a bilateral advantage, which was congruous with the prediction of the binominal formula. In their second experiment, Marks and Hellige (1999) controlled both the number of locations stimulated and the number of redundant stimulus copies. During unilateral trials two copies of the same stimulus appeared in the upper and lower half of one visual field, whereas in the opposite visual field two nonsense strings were presented in the respective positions. On bilateral trials also two target CVC stimuli appeared, one stimulus was placed in the upper half of one visual field and one stimulus was placed in the lower half of the other visual field. The remaining two positions were filled with nonsense letter strings. This stimulation method also revealed better performance in RVF condition than in LVF condition. However, no difference was found between bilateral and RVF performance. Upon these results, the authors suggested that performance differences between unilateral (one copy) and bilateral (two copies) trials might not have been caused by the stimulation of both hemispheres, but rather by the actual number of stimuli presented. Interestingly, the error rates in the second experiment were significantly higher than in the first experiment (44.1% vs. 26.8%). This worsening of bilateral performance in the second experiment might also be explained by interference effects caused by distractors presented to each hemisphere.

Banich and Karol (1992) used a modified matching design with serial presentation. In a rhyming task, subjects decided whether a word rhymed with a previously presented target. In several experiments, the influence of the degree of redundancy was carefully investigated. Presentation of two identical vs. two different stimuli within one visual field or between visual fields was compared. In the RVF condition highest differences in performance were obtained. Performance after bilateral presentation of two identical words did not differ from performance after presentation of one word in the RVF, when the presented words rhymed with the target. However, performance after bilateral presentation of two different, but also rhyming words was reduced compared to the presentation of two identical words were presented in bilateral condition and compared to unilateral condition when a single word was presented. In another experiment (experiment 4) they also

presented two identical or different stimuli to one visual field and compared this conditions with dividing the two stimuli across hemifields. Performance decreased (identical vs. different stimuli) more in the RVF condition than in bilateral condition.

Hellige, Jonsson and Michimata (1988) also examined interhemispheric interaction with a serial matching task. Two successively presented drawings of faces had to be identified as identical or different in a certain feature. The first face of each pair was presented at the fixation point and the second was presented to the LVF, RVF or to both visual fields simultaneously. On different trials performance patterns were obtained depending on which feature differed. Performance patterns differed between LVF and RVF trials. On bilateral trials performance pattern resembled RVF feature location pattern and was distinct from LVF pattern. Overall performance on bilateral trials was reduced compared to unilateral trials for this task. Since bihemsipheric performance resembled left hemispheric performance, it was assumed that the left hemisphere controlled performance on bilateral trials during this task. Hellige et al. (1988) considered these findings as evidence for the metacontrol concept.

Hasbrooke and Chiarello (1998) used word stimuli to examine interhemispheric cooperation on bilateral redundant trials. In a primed lexical decision task a related or unrelated word prime was followed by a word or pseudoword. Target stimuli were placed either unilaterally in the LVF or RVF, or bilaterally two copies of the target stimulus appeared in both visual fields. Subjects indicated whether they had seen a word or a pseudoword. Overall performance was significantly faster and more accurate for bilaterally presented stimuli than for both unilaterally presented ones. The difference between presentation conditions interacted also with word or pseudoword target. Separate analyses revealed that for words, both accuracy and responses were superior in bilateral condition compared to both unilateral conditions. For pseudowords only responses were superior in bilateral vs. both unilateral conditions. Accuracies did not differ between bilateral and RVF condition. Further, Hasbrooke and Chiarello (1998) analyzed the influence of dominant vs. subdominant related and unrelated priming. In the LVF condition performance was only improved after dominant related primes. In the RVF and bilateral condition performance was improved by both primes dominant and subdominant related primes. However, no bilateral gain was revealed for priming effect. Bilateral performance was improved for

both related and unrelated primes. This finding suggested that the advantage of bilateral presentation occurs before semantic activation.

Mohr and colleagues (1994b) applied a lexical decision task and compared performance in a bilateral redundant display with performance in unilateral displays. Words and pseudowords were presented unilaterally in the LVF or RVF, or two redundant stimuli were presented bilaterally in both visual fields simultaneously. Word stimuli comprised content and function words. Consistent with reaction time studies, superior performance was obtained after bilateral stimulation compared to unilateral stimulation. Faster reactions and higher accuracy was found for words presented in both visual fields. Mohr et al. (1994b) demonstrated that the bilateral advantage differed between content and function words. The bilateral advantage was largest for content words but also highly significant for function words. In contrast, bilateral presentation of pseudowords did not elicit this so-called bilateral advantage. Mohr et al. (1994b) suggested that the presence of a bilateral advantage for words indicates that both hemispheres can collaborate rather than inhibit each other or act independently when processing the same linguistic stimuli. This bilateral advantage was explained in terms of cortical cell assemblies based on Hebb's theory (1949). Simultaneous redundant activation within one cell assembly summates and improves performance compared to nonredundant stimulation. Since only previously learned stimuli are represented in cortical cell assemblies, pseudoword processing is not affected by redundant stimulation.

Zaidel and Rayman (1994) compared intrahemispheric with interhemispheric redundancy gain during a lexical decision task. One to four identical copies of words or pseudowords were presented within the LVF, within the RVF, or divided between them. For words they also found the bilateral condition with two copies (one in each visual field) was significantly more accurate than one copy in either the RVF or the LVF. Accuracy for pseudowords was reduced in the bilateral condition compared with either unilateral condition. Accuracy for words was also increased when two copies instead of only one copy were presented unilaterally. However, the bilateral condition was superior to LVF stimulation with two copies, it was not significantly inferior to RVF stimulation with two copies. Presentation of more than two copies of one word did not further increase performance. In contrast, pseudoword processing produced even a bilateral loss. Redundant intrahemispheric stimulation with pseudowords improved performance only in

the LVF. Presentation of three or four identical pseudowords reduced performance compared to presentation of only two copies. Zaidel and Rayman (1994) interpreted the processing differences between words and pseudowords as evidence that interhemispheric exchange is not early sensory but lexical. A different result was obtained by a second experiment with identical stimulation but different task and location cues. An alternating go/no-go lexical decision task was employed with arrow cues directing attention to a particular stimulus location. There was no effect for number of word copies in the RVF. In the LVF higher number of copies tended to improve performance. After bilateral stimulation, only the two-copy condition differed from the four-copy condition. Most interestingly, bilateral presentation with two words was only superior to LVF presentation of one word, but did not differ with RVF presentation of one word. Pseudowords had a more inconsistent performance pattern for redundant copies within one visual field. In this task pseudowords had a bilateral advantage. The bilateral stimulation with two copies was significantly more accurate than LVF stimulation and insignificantly more accurate than RVF stimulation. In summary, the two experiments differed in respect to bilateral performance and to word vs. pseudoword performance. These results indicate that depending on the task demands different processing strategies might be applied in the coordination of the resources of the left and right hemisphere.

Mohr et al. (1996) further investigated the bilateral advantage with several experiments. In their first experiment they replicated that the bilateral advantage was specific for words and did not occur for pseudowords. The second experiment indicated that the bilateral advantage was present for words of different frequencies of occurrence. The bilateral advantage was slightly stronger for high frequency words than for low frequency words. The third experiment examined the influence of number of redundant copies on performance. Words and pseudowords were presented during a lexical decision task. Two identical stimuli were presented either unilaterally to the LVF or RVF, or bilaterally (one copy in the LVF and one copy in the RVF) in the upper or lower visual field, or two identical stimuli were presented in each visual field. Higher number of stimuli led to an additional improvement of word processing, but not of pseudoword processing. Further, a difference between unilateral and bilateral stimulation was not obtained when the number of simultaneously presented copies was constant. These results were taken as evidence for the neurobiological model of word representation assuming that words were

represented in widely distributed interhemispheric cell assemblies. Summation of activity in such assemblies should occur within one hemisphere and between hemispheres.

Yoshizaki (2001) investigated the influence of visual familiarity of words on interhemispheric processing. During a lexical decision task words and pseudowords were presented unilaterally (one copy) in the LVF, in the RVF, or two identical stimuli appeared simultaneously in both visual fields. Two types of words were used as stimuli: words typically written in the Katakana script from of Japanese and words typically written in the Hiragana script form. Two word conditions were set up in terms of visual familiarity. In the visually familiar condition words were presented in the familiar script form and in the visually unfamiliar condition words were presented in less familiar script form. Words written in visually familiar script form of Japanese turned out to elicit a bilateral advantage, whereas words written in unfamiliar script form but phonetically correct and pseudowords did not. Yoshizaki (2001) suggested that not only phonetic information (in case of pseudowords) but also visual familiarity of words influenced interhemispheric processing.

Mohr and Pulvermüller (2002) examined temporal aspects of the bilateral advantage. First they replicated the bilateral processing advantage for words, but not for pseudowords, when two redundant copies are simultaneously presented in contrast to presentation of only one copy. In several experiments they carefully investigated the influence of varying stimulus onset asynchronies (SOA) on the processing of redundant information. On nonredundant trials one stimulus was presented in the center of a computer screen. On redundant trials one stimulus appeared in the upper visual field and the second stimulus in the lower visual field. The two stimuli on redundant trials appeared either simultaneously or with a delay ranging from 50 ms to 300 ms. It has been demonstrated that a redundancy gain for words was obtained only after simultaneous presentation or with a SOAs of 150 ms and 180 ms. They also observed a gradual performance decline with increasing SOAs for both words and pseudowords. Mohr and Pulvermüller (2002) suggested that both positive and negative priming might be explained by a time course of excitatory and inhibitory processes. They suggested that cell assembly ignition might occur around 150 ms after sensory activation. Therefore the redundancy gain obtained at an SOA of 150 ms was explained based on the simultaneity of sensory activation caused by the second stimulus and cell assembly ignition caused by the first

stimulus. Both processes cause neuronal excitation processes that lead to summation of neuronal activity in cortical cell assemblies and therefore to increased performance.

Interhemispheric processing was also examined during face recognition tasks (Mohr et al. 2002; Schweinberger et al., 2003). In these experiments it was investigated whether the bilateral advantage was restricted to lexical material or whether it is a more global phenomenon occurring for meaningful stimuli in general. During a familiarity decision task familiar and unfamiliar faces were presented tachistocopically to the RVF, to the LVF or to both visual fields simultaneously. Bilateral performance was superior to unilateral performance when familiar faces were presented. This bilateral advantage was absent when unfamiliar faces were presented (Mohr et al., 2002; Schweinberger et al., 2003). It was concluded that interhemispheric cooperation only occurs for meaningful stimuli, which are represented in cortical cell assemblies. A second experiment examined whether bilateral presentation influenced the perception of facial expressions (Schweinberger et al., 2003). This task required the classification of facial expressions (happy vs. neutral) of unfamiliar faces, which were presented in the three presentation conditions (LVF, RVF, and bilateral). No bilateral advantage was obtained for this task. Schweinberger et al. (2003) suggested that interhemispheric cooperation therefore clearly depended on the presence of acquired cortical representations rather than on the presence of a relatively informative “target” stimulus.

In summary, performance is enhanced after redundant stimulation with two identical stimuli in both hemispheres compared to stimulation of only one hemisphere with one stimulus. However, performance is also improved when two stimuli are simultaneously presented to one hemisphere. Several experiments demonstrated that two-choice discrimination or recognition tasks, like lexical decision or face recognition (opposed to simple stimulus detection) elicited a differential bilateral advantage. A bilateral advantage was only found for meaningful stimuli (e.g. words or familiar faces), which are recognizable because of earlier learning processes. In contrast, no bilateral advantage has been found for meaningless stimuli (e.g. pseudowords or unfamiliar faces). Zaidel and Rayman (1994) even found a bilateral loss for bilaterally presented pseudowords.

Mohr and colleagues explained the bilateral advantage in terms of a neurobiological model based on Hebbs cell assembly theory (1949). This model is capable of explaining the differential bilateral advantage. A certain stimulus necessarily requires the presence of cortical cell assemblies to elicit a bilateral advantage since summation is assumed to take place within these cell assemblies. Though cell assemblies are developed during learning mechanisms, they exist only for meaningful but not for meaningless stimuli. Therefore meaningless stimuli would never elicit a bilateral advantage when they are actually processed.

In contrast, the bilateral advantage in simple stimulus detection task might rather be established on an earlier perceptual processing level. This has been demonstrated with a bilateral advantage for pattern detection (Minussi et al., 1998) or for letter detection (Miller, 1982). Zaidel and Rayman (1994) even found a bilateral advantage for pseudowords during a go-/no-go task whereas during a lexical decision task no bilateral advantage was revealed. This indicated that the bilateral advantage might also be influenced by task requirements.

4. Unilateral Processing with Crossed or Uncrossed Stimulation

The question of how the cerebral hemispheres interact has also been addressed with studies, examining the speed of information transfer between the hemispheres, referred as interhemispheric transmission time (IHTT). Poffenberger (1912) originally introduced the concept in reaction times studies. IHTT was computed by subtracting the reaction time of the response made on the side ipsilateral to hemiretinal stimulation from the reaction time to contralateral stimulation. Unimanual reaction time is recorded from the hand located at the same side (ipsilateral) as the visual hemifield (uncrossed condition) and from the opposite to the visual hemifield (contralateral) sided hand (crossed condition). Because of the contralateral organization of the visual and motor projections in the brain, the crossed condition refers to the fact that the visual stimulus projects to one hemisphere but the manual response is emitted by the other hemisphere. Respectively, in the uncrossed condition, visual input and motor output are mediated by one hemisphere. Therefore the reaction time difference between crossed and uncrossed condition (CUD) was considered to be an estimate of IHTT.

Marzi et al. (1991) conducted a meta-analysis of 16 studies using a simple unimanual reaction time paradigm and lateralized visual stimuli to estimate the IHTT in normal right-handed persons. Reactions were faster after LVF than after RVF stimulation and were faster for right hand than for left hand responses. It has also been suggested that transmission from the right to the left hemisphere is faster than reverse. Marzi et al. (1991) proposed that the observed asymmetry in response was due an asymmetry in callosal connections with a grater number of neurons projection from the right hemisphere to the left, than vice versa. Therefore transmission would always be faster from the right to the left hemisphere.

In a meta-analysis, Braun (1992) obtained similar findings. He reports a directional asymmetry in CUDs. The CUD for the hand ipsilateral to the hemifield, which is associated with the fastest reactions, was always longer than the CUD for the contralateral hand. Braun (1992) stated that there are fast and slow interhemispheric channels from each hemisphere. When hemispheric specialization is present for a certain task the slow channels are selected by each hemisphere. In contrast, when one hemisphere is highly specialized transmission through the fast channels from the non-specialized hemisphere is

activated. According to Braun (1992) the pattern of transmission asymmetry was linked to the direction of the visual field advantage. A LVF advantage would be associated with faster transfer from the right hemisphere to the left one and a RVF advantage with faster transfer in the opposite direction.

However, reaction time estimates of interhemispheric transmission time have several limitations. Reaction time methods of computing IHTT necessarily involve only one hand responding to a stimulus presented to only one hemisphere at a time. There is no way to measure responses from both sides of the brain at once (Saron and Davidson, 1989). Therefore other variables rather than interhemispheric transfer may influence the difference between conditions. Consequently, electrophysiological methods have been introduced to estimate IHTT. This approach does not require manual responses and brain activity is simultaneously recorded form both hemispheres. After unilateral tachistoscopic stimulation in the left or right visual hemifield, initially a contralateral ERP activation can be observed, which is followed by a time delayed ipsilateral activation. IHTT is defined by the ipsilateral minus contralateral peak latency difference of the N1 ERP component and can be determined separately for RVF and LVF stimulation (Rugg et al., 1984; Rugg, 1982, for a review). In their meta-analysis on IHTT, Brown et al. (1994) showed, that in the majority of studies on visual evoked potentials, a directional asymmetry of IHTT was reported. IHTT was shorter after stimulation in the LVF, when transmission occurs from the right to the left hemisphere. But six out of 18 experiments did not find faster right-to-left than left-to-right transmission (Brown et al., 1994). Directional asymmetries were found for different experimental task (e.g. simple reaction time, go/no-go task) and different kinds of stimuli. A possible connection between directional asymmetry and visual field advantage could not be established, either because visual field advantage data were not available or because the two variables were not correlated.

Further evidence for IHTT asymmetries came from Brown and Jeeves (1993) who conduced an event-related potential study using a letter-matching task with unilateral and bilateral presentation of letter pairs. In unilateral conditions, they found shorter IHTT after LVF stimulation (transfer from RH to LH) than after RVF stimulation. Behavioral data revealed a bilateral advantage with faster reaction times for letter matching after bilateral compared to unilateral presentation. This bilateral advantage was compared to EP-IHTT after unilateral stimulation. They found that EP-IHTT was negatively correlated with the

bilateral field advantage in reaction time data. Faster EP-IHTT was associated with a larger advantage for bilateral processing. The correlation was particular strong for the transmission from the left hemisphere to the right hemisphere, while transmission in the opposite direction was not correlated with bilateral advantage.

Noviacka et al. (1996) measured evoked potential IHTT with two types of stimuli to determine whether there is an asymmetry in the transmission of information to and from the hemispheres specialized in its processing. A go-/no-go task was applied with random stimulus presentation in the LVF or RVF. Consonant vowel consonant (CVC) syllables were selected as left hemisphere stimuli and gratings of low spatial frequency were chosen as right hemisphere stimuli. For CVC syllables transmission was faster from RH to LH, whereas for gratings transmission was faster from LH to RH. Results indicated that IHTT was shorter when the information was transferred from the non-specialized hemisphere to the specialized one than in the opposite direction. Nowicka et al. (1996) suggested the existence of a physiological mechanism that ensures fast transmission of information to that hemisphere which is more efficient in it's processing.

Larson and Brown (1997) examined the relationship between the bilateral processing advantage, hemispheric specialization and IHTT. EP-IHTT was measured while subjects performed a matching task involving letters (left hemispheric superiority) or dot patterns (right hemispheric superiority). Pairs of letters or patterns were presented to the LVF, RVF or distributed across both visual fields. Results indicated a significant LVF advantage for pattern stimuli but no significant visual field advantage for letter stimuli. Both tasks produced a significant bilateral distribution advantage. In contrast to the findings of Nowicka et al. (1996), both tasks resulted in faster IHTTs form right to left hemisphere than reverse, regardless of visual field advantage for the task. Similarly, for both tasks, the faster bilateral reactions were negatively correlated with transmission from left to right hemisphere.

Hagelthorn et al. (2000) determined the influence of developmental progression of myelination of the corpus callosum on EP-IHTT and on the bilateral distribution advantage. Children aged 7 to 17 years were included in the study. During a letter matching task, letters were presented either unilaterally both in the same visual field or bilaterally one letter in each visual field. Hagelthorn et al. (2000) found age related

changes for EP-IHTT and the bilateral advantage. Whereas the bilateral advantage significantly increased, the EP-IHTT significantly decreased and therefore interhemispheric transmission got faster with increasing age. It has been suggested, that callosal maturation results in faster IHTT and increasing ability to integrate information of both hemispheres.

The findings on interhemispheric transmission time indicated that the corpus callosum plays an important role in interhemispheric processing. Since the bilateral distribution advantage is somehow connected with IHTT (Brown and Jeeves, 1993; Larson and Brown, 1997), it is likely that callosal transfer mediates bilateral processing. Performance during interhemispheric processing in terms of IHTT and bilateral distribution advantage is even influenced by developmental progression of myelination of the corpus callosum (Hagelthom, 2000).

5. Interhemispheric Processing in Patients

Interhemispheric processing has also been examined in individuals who do not have a normal commissural system since the corpus callosum is the major connection between the two cerebral hemispheres and therefore might play a major role in interhemispheric processing.

Interhemispheric transmission was examined with reaction time studies in subjects with agenesis of the corpus callosum and in subjects who underwent a section of the corpus callosum. Both patient groups were found to have clearly prolonged overall CUDs than normal subjects (e.g. Clarke and Zaidel, 1989; Sergent and Myers, 1985).

Rugg et al. (1985) demonstrated the importance of the corpus callosum in EP-IHTT when comparing the unilateral EPs of normal subjects with EPs recorded in two subjects with agenesis of the corpus callosum. Visual evoked potentials to lateralized light flashes were recorded during a reaction time task. Visual evoked potentials from electrode sites contralateral to the stimulated visual field resembled those of healthy controls. Whereas, EPs from ipsilateral electrode sites were found in normal subjects, the two acallosal subjects showed no such response. Rugg et al. (1985) concluded that the generation of ipsilateral EPs relied on trancallosal transfer of information processed initially by the contralateral hemisphere.

Brown et al. (1998) examined five acallosal subjects (two with commissurotomy, two with complete and one with partial callosal agenesis). Visual evoked potentials were recorded during a letter-matching task in which a pair of letters appeared either in the LVF or in the RVF. In healthy participants the initial EP response (P1 and N1) contralateral to the stimulated visual field was followed by a shortly delayed ipsilateral EP response. In acallosal subjects the ipsilateral EP response was clearly reduced. The signal to noise ratio differentiated between contralateral and ipsilateral EP responses in both groups. The signal to noise from the ipsilateral EP response was decreased in acallosal subjects compared to healthy controls. These results also support the importance of the corpus callosum for interhemispheric transfer to occur.

Brown et al. (1999) carefully investigated interhemispheric processing in individuals with different callosal deficits. They examined four individuals with complete agenesis of the corpus callosum, two individuals with partial agenesis, one total commissurotomy patient, and normal subjects. During two matching task pairs letters or patterns were presented both in the LVF or RVF or one in each visual field (bilateral distribution). EP-IHTT was recorded for the visual sensory response. They found, that neither the commissurotomy nor the acallosal patients had ipsilateral hemisphere visual EPs (P1 and N1). This result demonstrated that the posterior callosum was necessary for interhemispheric transmission of these components of visual evoked potential. Differences among patients were found for the bilateral condition, when bilaterally presented letters were compared. The commissurotomy patient (L.B.) was unable to perform above chance on bilateral letter matching. The acallosal individuals were clearly above chance on these trials, and some individuals even showed a bilateral advantage in either accuracy or reaction time. In contrast, complete agenesis patients showed significant deficits in bilateral pattern comparison. This finding indicated that the intact anterior commissure in all four acallosal individuals appeared to be sufficient for interhemispheric comparison of single letters, but not of more complex pattern information. Patients with partial callosal agenesis showed normal bilateral letter comparison and nearly normal pattern comparison.

In contrast to the findings on increased interhemispheric transmission time in split brain patients, these patients often show a redundancy gain in simple reaction time tasks, which sometimes exceeded the redundancy gain in normal subjects (Corballis, 1998; Iacoboni et al., 2000; Pollmann and Zaidel, 1999; Reuter-Lorenz et al., 1995). This redundancy gain was obtained when redundant stimuli are separately presented to both hemispheres which are disconnected to a certain extent.

For example, Pollmann and Zaidel (1999) examined the redundancy gain in two commissurotomy patients. Either one target was presented unilaterally or two redundant targets were presented unilaterally in within-hemifield conditions or bilaterally in both hemifields simultaneously. One patient (L.B.) with complete commissurotomy showed no evidence of visual interhemispheric transfer. But he exhibited a paradoxical enhancement of the redundancy gain in the bilateral compared with the within-hemifield redundant-targets conditions. The second patient also exhibited a bilateral redundancy gain, which was not enhanced compared to unilateral redundancy gain.

Corballis (1998) examined the redundancy gain in split-brain patients with different luminance and equiluminance between stimuli and background. He examined one patient with complete forebrain commissurotomy, two patients with callosotomy, one patient with callosal agenesis, and healthy controls during a simple reaction time task in which one copy of a visual stimulus was presented in either the LVF or the RVF, or in both visual fields simultaneously. All participants had faster bilateral than unilateral reactions. Corballis (1998) compared the obtained redundancy gain with the probability summation according to the horse-race model. He found that the redundancy gain in controls did not exceed the probability prediction, whereas the redundancy gain of all split brain patients exceeded this prediction, when stimuli were brighter than the background. The redundancy gain in the three surgical cases was greatly diminished when the stimuli where equiluminant. In contrast, the redundancy gain did not diminish in the acallosal subject.

Iacoboni et al. (2000) tested nine patients with callosal pathology in a reaction time task with and without redundant targets in the same or opposite visual hemifield. While four patients showed a redundancy gain exceeding the probability summation models, five patients showed a redundancy gain not exceeding the probability models. However, the violation of probability models was not associated with a specific type of callosal lesion. Functional MRI pointed out that activation was increased in the extrastriate cortex in a patient with callosal agenesis and large redundancy gain, whereas this was not found in a patient without large redundancy gain. The authors concluded that the activation in the extrastriate cortex might modulate the magnitude of the redundancy gain.

Mohr et al. (1994a) also examined a split-brain patient with complete commissurotomy (L.B.) with a bilateral redundant stimulation design. During a lexical decision task, words and pseudowords were presented either unilaterally in the LVF or RVF, or two redundant stimuli appeared simultaneously in both visual fields. When stimulated with words, healthy controls exhibited superior performance on bilateral trials compared to unilateral trials (bilateral advantage). Stimulation with pseudowords did not elicit this bilateral advantage (Mohr et al., 1994b). The split-brain patient did not improve performance after bilateral stimulus presentation compared to RVF presentation (which was the better unilateral condition). This result clearly suggested that transcallosal connections are required for the bilateral advantage in lexical processing. A similar result was obtained when schizophrenia patients were examined (Mohr et al. 2000). These

patients did not show a bilateral advantage for words and are also supposed to have deviations in interhemispheric processing (2000).

In summary, the findings from split-brain patients showed that the corpus callosum is an important connection between the two cerebral hemispheres when information has to be transferred between them or has to be processed across hemispheres. As obtained from behavioral experiments, split-brain patients exhibit prolonged interhemispheric transmission time (Clarke and Zaidel, 1989; Sergent and Myers, 1985). While conralateral visual evoked potentials show normal characteristics, ipsilateral components are almost absent (Rugg et al., 1985; Brown et al., 1999). It has also been demonstrated that split-brain patients exhibit a paradoxical interhemispheric summation reflected in a bilateral redundancy gain in simple reaction time tasks (Corballis, 1998; Iacoboni et al., 2000; Pollmann and Zaidel, 1999). In contrast, bilateral comparison of more complex stimuli is impaired (Brown et al., 1999) and bilateral redundant simulation did not facilitate performance for word stimuli during lexical decision (Mohr et al. 2000). These findings indicate that different processing strategies are present in simple reaction time tasks and more complex comparison or decision tasks. Therefore the redundancy gain in simple reaction time tasks apparently does not require interhemispheric interaction via the corpus callosum. Stimulus comparison between hemispheres needs interhemispheric exchange especially when stimulus complexity was high. This might also be required for the bilateral advantage after redundant word stimulation.

C. Interhemispheric Processing: The Aims of the Present Thesis

Hemispheric interaction has been characterized by various models suggesting hemispheric independence with parallel processing, unihemispheric metacontrol, cooperation, or even inhibitory mechanisms. Studies on interhemispheric processing have demonstrated that performance is mostly facilitated when both hemispheres are involved in task accomplishment. For example, when stimulus comparison or category affiliation decisions of two stimuli are required it is advantageous to divide the processing load between both hemispheres. This is especially true for highly complex tasks rather than low complex tasks (e.g. Banich and Belger, 1990; Hatta et al, 2002; Hatta and Yoshizaki, 1996; Marsoleck et al., 2002; Koivisto, 2000; Weissman and Banich, 2000). Since processing is facilitated when the processing load is divided across hemispheres, these findings provide support for an interhemispheric cooperation model, while inhibitory interaction mechanisms seem unlikely.

In contrast, when unilateral processing is required but both hemispheres are stimulated with different stimuli performance is diminished and more asymmetric than in unilateral stimulation conditions (e.g. Boles, 1990; Iacoboni and Zaidel, 1996). This constellation would support inhibitory mechanisms of interhemispheric processing.

Further, interhemispheric processing has also been examined with simultaneous presentation of two redundant stimuli to both hemispheres compared to unilateral stimulus presentation. This design revealed various performance outcomes. Simple reaction time tasks suggested that redundant stimulation of both hemispheres improves performance (Miller, 1982; Van der Heijden et al., 1983; Miniussi et al., 1998). However, there is also evidence for unihemispheric metacontrol during bilateral redundant stimulation supported by similar performance in one of the unilateral and bilateral conditions (e.g. Hellige et al., 1988; Hellige and Michimata, 1989). Mohr and colleagues (Mohr et al., 1994b; Mohr et al. 1996; Mohr and Pulvermüller, 2002; Mohr et al., 2002; Schweinberger et al., 2003) found evidence for a differential facilitation of bilateral processing in familiarity and lexical decision tasks. Meaningful stimuli were found to elicit a bilateral advantage whereas meaningless stimuli did not. The authors explained their findings on the basis of a neurobiological model rooted in Hebb's cell assembly theory (1949). The bilateral

advantage was explained with neuronal summation within cell assemblies, which are formed during learning mechanisms and therefore exist for meaningful stimuli only.

The aim of the present thesis was to further investigate interhemispheric processing after simultaneous bilateral redundant stimulation in terms of behavioral and neurophysiological measures. The intention was to replicate the bilateral advantage for different kinds of meaningful stimuli and in different perceptual modalities. Four experiments were carried out to examine different aspects of the bilateral advantage.

The first experiment examined interhemispheric processing during a lexical decision task. As in earlier experiments, a bilateral advantage should emerge for words but not for meaningless pseudowords. The main objective of this study was to determine an electrophysiological correlate of this differential bilateral advantage. Therefore evoked potentials (EP) were recorded with a 64-channel electroencephalogram (EEG). Differences between words and pseudowords in bilateral and unilateral conditions should be revealed from analysis of EPs and minimum norm source distribution. Additionally, the interhemispheric transmission time was examined from visual evoked potentials in unilateral conditions separately for words and pseudowords. Differences between bilateral processing of words and pseudowords might be reflected in differences in interhemispheric transmission.

In earlier studies, a bilateral advantage was repeatedly obtained for meaningful stimuli, like words and faces, but not for meaningless stimuli, like pseudowords or unfamiliar faces (Mohr et al., 1994b; Mohr et al. 1996; Mohr and Pulvermüller, 2002; Mohr et al., 2002; Schweinberger et al., 2003). The second experiment of the present thesis was designed to examine whether other meaningful stimuli, like line drawings of familiar objects, would also elicit a bilateral advantage. Therefore, line drawings of familiar objects and meaningless non-objects were presented in unilateral and bilateral conditions. According to the cell assembly explanation of interhemispheric processing, a bilateral advantage should be observed for objects but not for meaningless non-objects. In this experiment it was also intended to compare the magnitude of the bilateral advantage in object processing with the redundancy gain in a simple reaction time task. Since the redundancy gain in simple reaction time tasks does not depend on the presence of meaningful stimuli but is rather elicited by all kinds of stimuli, it might not rely on the

same processing mechanisms like the bilateral advantage for meaningful stimuli. A magnitude difference between bilateral advantage and redundancy gain would support this view. In particular, a smaller redundancy gain during the simple reaction time task and a larger bilateral advantage for meaningful stimuli, would support the assumption, that different processing mechanisms might account for the two effects.

The question whether unilateral redundant or bilateral redundant simulation is more advantageous when the number of presented stimuli is constant was examined with the third experiment. For this purpose words and pseudowords were presented unilaterally and bilaterally. In the unilateral presentation condition either one or two copies of a stimulus appeared in the respective visual field. In the bilateral presentation condition either one copy of a stimulus appeared in each visual field (two stimuli) or two copies of a stimulus were provided in each visual field (four stimuli). The comparison between unilateral presentation of two stimuli and bilateral presentation of one stimulus in each visual field should reveal whether the bilateral advantage is simply due to stimulus redundancy or if it is due to the involvement of both hemispheres in task accomplishment.

The bilateral advantage has been repeatedly reported for visually presented stimuli during tasks requiring attentional processing. The last experiment was designed to determine whether a bilateral advantage would also occur during a task requiring auditory processing without attention. Therefore, a mismatch negativity design was employed with monaural and binaural presentation of a word and pseudoword. Evoked potentials were recorded using a 64-channel EEG. Mohr et al. (2001) already examined the bilateral advantage with auditory presentation of words and pseudowords during a lexical decision task, which required subject’s attention to the task. However, contrary to the findings during visual processing, words did not significantly gain from binaural presentation compared to monaural presentation. The authors explained the absence of a bilateral advantage with a ceiling effect, because overall accuracy was already high in monaural conditions and could not be improved during binaural stimulation. The present mismatch negativity experiment did not require the interpretation of behavioral data, but provided evoked potential measures during monaural and binaural conditions. A bilateral advantage would be reflected in larger mismatch negativity for words in the binaural condition compared to monaural conditions. In contrast, pseudowords should not elicit larger binaural mismatch negativity.

III. General Method

A. Overview

Four experiments were conducted in order to examine different aspects of interhemispheric processing. For an overview of applied experimental designs (**see Table III.A.1**).

Experiment A: Evoked potential measures of the bilateral advantage and interhemispheric cooperation

Experiment B: Interhemispheric cooperation while processing familiar and unfamiliar objects

Experiment C: Effects of unilateral and bilateral redundancy on lexical processing

Experiment D: Enhanced MMN after binaural word stimulation

Table III.A.1. Schematic overview of the experiments that were conducted for the present thesis.

	Modality	Stimuli	Task
Experiment A (EEG)	visual	words and pseudowords	lexical decision
Experiment B Object decision task	visual	objects and non-objects	object decision
Simple reaction task	visual	patterns	simple reaction
Experiment C	visual	words and pseudowords	lexical decision
Experiment D (EEG)	auditory	words and pseudowords	passive listening

B. Stimuli

Experiment A - C used visual stimulus presentation whereas auditory stimuli were presented in experiment D.

1. Visual Stimulation

In *experiment A and C* words and pseudowords were presented in black upper-case letters on a gray background to reduce visual afterimage. All stimuli were bisyllabic and were four to eight letters long. Words were German content words with a high frequency of occurrence (100 – 1000 per million, according to Ortmann, 1975). Pseudowords were obtained either by permutation of letters within words or by exchanging letters between word stimuli. Pseudowords were pronounceable and orthographically regular but not homophonous to real words.

In *experiment B* two tasks were given: an object decision task and a simple reaction task. For the object decision task objects and non-objects were shown. Drawings of real objects were selected from the picture set of Snodgrass and Vanderwart (1980). Only pictures of inanimate objects like furniture or tools with familiarity values higher than 3.5 (on a scale ranging from 1 to 5, 5 representing high familiarity) were selected. Non-objects were taken from Kroll and Potter (1984). Objects and non-objects were matched for size, complexity, and brightness. During the simple reaction task, checkerboard-patterns were displayed.

2. Auditory Stimulation

In *experiment D* auditory stimuli were presented, while subjects watched a silent movie. The stimuli were a German word [ap] (written as “ab”, meaning: down) and a pseudoword [ak]. A female speaker recorded multiple repetitions of the two stimuli. Stimuli were carefully selected in order to optimize acoustical similarity between the two stimuli. They were normalized to have equivalent peak sound energy in both stimuli, fundamental frequency (211 Hz) and duration (235 ms). In addition, the syllable bodies, voice onset times and durations of the final click were exactly matched.

C. Procedure

Visual stimuli were presented tachistoscopically either unilaterally to the RVF or to the LVF or simultaneously to both visual fields (BVF) (see **Figure III.C.1**). In *experiment A and B* one copy of a stimulus appeared in unilateral conditions and two identical copies of a stimulus appeared simultaneously in the bilateral condition (one copy in each visual field). In *experiment C* the number of presented copies was varied: either one copy or two copies of a stimulus were presented in unilateral condition and two or four copies in bilateral condition (one or two copies in each visual field).

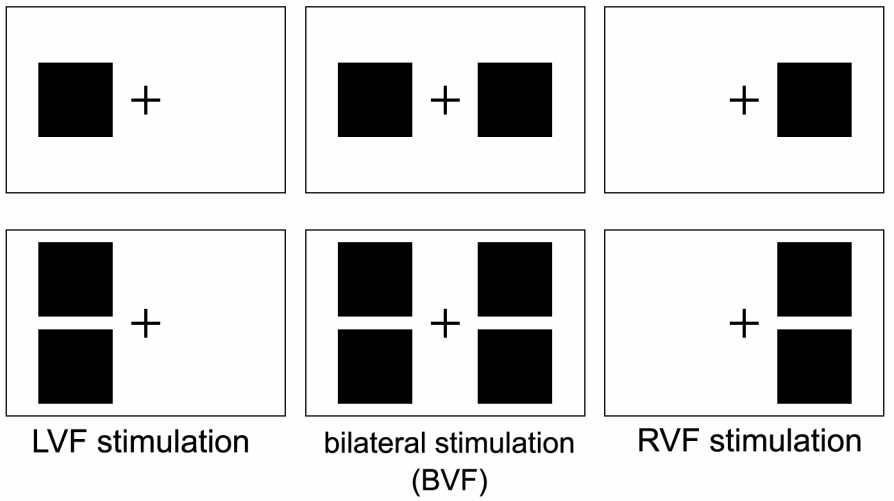

Figure III.C.1. Schematic presentation of visual stimulation. In *experiment A* and *B* (upper row) either one stimulus appeared unilaterally, or one stimulus appeared in both visual fields (bilateral stimulation). In *experiment C* either one copy (upper row) or two copies (lower row) of a stimulus appeared within a visual field.

Duration of visual stimulus presentation also varied between the experiments. In *experiment A* stimuli were presented for 150 ms, *in experiment B* duration was 40 ms, and in *experiment C* stimuli were seen for 100 ms. The rather long stimulus duration in *experiment A* was selected because high error rates were observed in a pretest for this task. In contrast, very low error rates showed up in a pretest for *experiment B.* Therefore, a short stimulus presentation was selected.

In *experiment A and C* subjects were instructed to perform a lexical decision task, which required the identification of words and pseudowords. Two different tasks were

given in *experiment B*. During the object decision task subjects were asked to distinguish between real objects and non-objects. The simple reaction task required only a fast button press after stimulus appearance. In all experiments, participants were instructed to respond as fast and accurate as possible.

In *experiment D* a mismatch negativity design was applied during participants watched a silent movie. Two stimulation conditions were applied: a word as standard stimulus and a pseudoword as deviant and the reversed combination with a pseudoword as standard and a word as deviant. All standard and deviant stimuli were presented either to the left or to the right ear or to both ears simultaneously. All stimuli were presented for 235 ms. Each of the two conditions contained 2250 standard stimuli presented with a probability of 83.3 % and 450 deviant stimuli presented with 16.7 % probability.

Stimuli were presented with the Experimental Runtime System software (ERTS; Experimental Runtime System software (BeriSoft Cooperation, Frankfurt, Germany).

D. EEG-Recordings and Data Analysis

In *experiment A and D* evoked potentials were recorded during stimulus presentation. The electroencephalogram (EEG) was recorded with two 32-channel DC-amplifiers (SYNAMPS, Neuroscan, El Paso, USA) from 64 head positions referenced to Cz using an extended 10-20 system electrode cap (EasyCap, Falk Minow Services, Herrsching-Breitbrunn, Germany). **Figure III.D.1** gives a schematic representation of the electrode configuration. Data were recorded with a sampling rate of 200 Hz and a bandpass of DC to 30 Hz. Impedances were kept below 5 kOhm. Data were recorded continuously and stored for off-line analysis. After the experimental session, electrode positions were digitized using a 3D digitizer (Polhemus Inc., Colchester, USA).

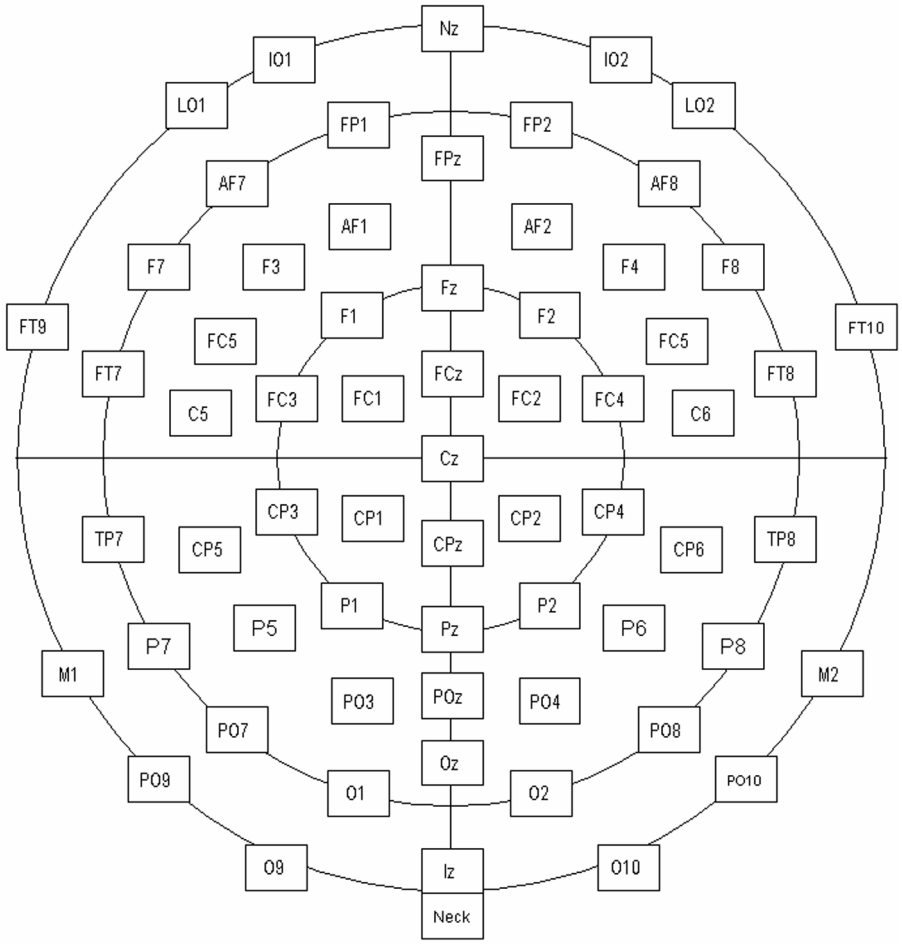

Figure III.D.1. Layout of the 65 electrode positions which were used for EEG recording

Vertical, horizontal and blink electrooculograms (EOG) were recorded for later artifact correction following the MSEC (multiple source of eye correction) method (Berg

and Scherg, 1994). After correction of eye movements, trials were averaged separately for each subject and condition across trials. Trials still containing artifacts with voltage variation exceeding 75 μV were omitted.

A baseline correction was performed for each individual and each condition by subtracting the average scalp distribution during a 100 ms epoch prior to stimulus onset. After average referencing event-related potentials (ERP), electrode positions were corrected by spline-interpolation of the data sets from individually digitized electrode positions on a standardized electrode montage. If significant interactions of the factor with a topographical variable were found, the analysis was repeated after amplitude normalization according to McCarthy and Wood (1985). Only significant effects that survived this normalization are reported.

E. Statistical Analysis

The statistical analyses of all experiments were carried out with multivariate ANOVA tests. Analyses of behavioral data (accuracy or response latency) from Experiment A – C included as within-subject factors: stimulus type (like Wordness or Category), presentation condition, or task. A summary of the analyzed factors in each experiment is given in **Table III.E.1** If degree of freedom (df) was greater than two, Greenhouse-Geisser correction was applied.

Evoked potential data were collected in Experiment A and D and were analyzed with ANOVAs. Apart from stimulation properties (Wordness and Presentation Mode), the factors Hemisphere and Gradient were also submitted to ANOVAs as within-subject factors.

Table III.E.1. Overview of within-subject factors submitted to statistical analysis in the different experiments.

Experiment A:	Wordness (words vs. pseudowords) Presentation Mode (LVF, RVF vs. BVF) Topography (Hemisphere and Gradient)
Experiment B:	
Object decision task:	Category (object vs. non-object) Presentation Mode (LVF, RVF vs. BVF)
Simple reaction task:	Presentation Mode (LVF, RVF vs. BVF)
Comparison between the two tasks:	Task (objects vs. patterns) Presentation Mode (LVF, RVF vs. BVF)
Experiment C:	Wordness (words vs. pseudowords) Presentation Mode (LVF, RVF vs. BVF) Redundancy (one copy vs. two copies)
Experiment D:	Wordness (words vs. pseudowords) Presentation Mode (LVF, RVF vs. BVF) Topography (Hemisphere and Gradient)

IV. Experiments

A. Evoked Potential Measures of the Bilateral Advantage and Interhemispheric Cooperation

1. Summary

Simultaneous bilateral stimulation with meaningful stimuli leads to better performance in a lexical decision task than unilateral stimulations. Bilateral presentation of meaningless stimuli does not lead to improved performance. This bilateral advantage has been interpreted in terms of a neurocognitive model based on Hebb's cell assembly theory (Hebb, 1949). According to this model, bilateral presentation of meaningful stimuli would initiate the ignition of cell assemblies originating from both hemispheres. The bilateral advantage would result from the summation of activation of interhemispheric cell assembly connected via the corpus callosum.

The present experiment was designed to examine the bilateral advantage with electrophysiological measures. A lexical decision task was applied with word and pseudoword stimulation in unilateral and bilateral conditions. Evoked potentials were recorded during this task and further analyzed. Interhemispheric interaction was determined by analyzing behavioral but also electrophysiological measures of interhemispheric processing, like mean amplitudes, source analysis and interhemispheric transmission time (IHTT).

Behavioral results confirmed previous findings. A bilateral advantage was revealed for words, but not for pseudowords. Electrophysiological data indicated enhanced overall interhemispheric cooperation for words than for pseudowords. Bilaterally presented words elicited more negative amplitudes than bilaterally presented pseudowords and than unilaterally presented words. Source analysis indicated higher cortical activity over temporal regions of both hemispheres after bilateral word presentation compared with both unilateral word conditions. Additionally, analysis of IHTT revealed for words faster transmission from the right to the left hemisphere compared with reverse transmission and compared with pseudowords in either direction.

The present findings provide additional support for the explanation of the bilateral advantage in terms of the cell assembly theory. The faster ignition of cell assemblies and summation of activation within interhemispheric cell assemblies for words was reflected in higher cortical activation and in faster transmission from the right into the left hemisphere.

2. Introduction

The bilateral advantage has been repeatedly reported from behavioral experiments. A bilateral advantage is reflected in superior performance after simultaneous bilateral stimulation. Several experiments with familiarity tasks demonstrated that bilateral performance is only facilitated after presentation of meaningful stimuli, like words (Mohr et al., 1994b; Mohr et al., 1996; Yoshizaki, 2001), familiar faces (Mohr et al., 2002; Schweinberger et al., 2003) or objects (see Experiment two). Meaningless stimuli (like pseudowords, unfamiliar faces or objects) did not reveal a bilateral advantage.

A neurobiological model based on Hebb's cell assembly theory (Hebb, 1949) was used to explain the bilateral advantage (Mohr et al., 1994b; Mohr et al., 1996). According to this explanation, the main reason, why a bilateral advantage would occur only to meaningful stimuli, is an earlier learning process. It was assumed, that during learning, interhemispheric cell assemblies are formed out of neurons, that are frequently and simultaneously active. Bilateral stimulation with meaningful and therefore earlier learned stimuli would activate neurons in both hemispheres. In case of bilateral stimulation with meaningful stimuli, the relevant cell assembly is stimulated twice, leading to a summation of neuronal activity and therefore, to faster ignition. This explanation is supported by the absence of a bilateral advantage for pseudowords, which is not represented in cell assemblies and by the absence of a bilateral advantage after commissurotomy (Mohr et al. 1994a), when interhemispheric cell assemblies are no longer available.

However, behavioral experiments give only indirect evidence for underlying neuronal activity. Experiments using neurophysiological methods would provide more details about the nature of the bilateral advantage and why bilateral presentation facilitates

performance. Especially, details about temporal and topographical differences between bilateral and unilateral conditions would be obtained.

Miniussi et al. (1998) investigated the neurophysiological mechanisms of the bilateral redundancy gain, or redundant target effect (RTE) obtained in behavioral studies. In a simple stimulus detection task, shorter latencies of early visual event-related potentials (C1, P1 and N1) in the bilateral condition were found. These data suggest that neuronal co-activation mechanisms might already start at an early perceptual processing level. This early bilateral effect was explained by the rather simple task, which only required stimulus detection not requiring a complete identification of the entire stimulus. The authors argue that the timing of the RTE is likely to depend on the paradigms applied and on the cognitive processing stage required by the task (Miniussi et al., 1998).

Interhemispheric interaction is not only investigated with bilateral stimulation, but also with unilateral stimulation. Interhemispheric transmission is measured by the crossed-uncrossed difference (CUD) after unilateral tachistoscopic stimulation of either the right or left visual field (Marzi, 1999). Unimanual reaction time is recorded from the hand located on the same side (ipsilateral) as the visual hemifield (uncrossed condition) and from the opposite of visual hemifield (contralateral) sided hand (crossed condition). A modification of this method is to look at evoked potential interhemispheric transmission time (EP-IHTT, e.g. Brown et al., 1994). After unilateral tachistoscopic stimulation in the left or right visual hemifield, initially a contralateral ERP activation can be observed, which is followed by a time delayed ipsilateral activation. Interhemispheric transmission time (IHTT) can be defined by the ipsilateral minus contralateral peak latency difference of the N1 ERP component and can be determined separately for RVF and LVF stimulation.

In their meta-analysis on IHTT, Brown et al. (1994) showed, that in the majority of studies on visual evoked potentials, a directional asymmetry of IHTT was reported. IHTT was shorter after stimulation in the LVF, when transmission occurs from the right to the left hemisphere. But six out of 18 experiments did not find faster right-to-left than left-to-right transmission. Directional asymmetries were found for different experimental tasks (e.g. simple reaction time, go/no-go task) and different kinds of stimuli. A possible connection between directional asymmetry and visual field advantage could not be established, either because visual field advantage data were not available or because the

two variables were not correlated. Directional asymmetry was also found in studies on CUD, reporting shorter CUD after LVF stimulation (Braun, 1992; Marzi et al., 1991).

Further evidence for IHTT asymmetries came from Brown and Jeeves (1993) who conduced an event-related potential study using a letter-matching task with unilateral and bilateral presentation of letters. In unilateral conditions, they found shorter IHTT after LVF stimulation (transfer from RH to LH) than after RVF stimulation. Behavioral data revealed a bilateral advantage with faster reaction times for letter matching after bilateral compared to unilateral presentation. This bilateral advantage was compared to EP-IHTT after unilateral stimulation. A positive correlation was found; suggesting a larger bilateral advantage in reaction time data is associated with faster EP-IHTT. The correlation was particular strong for RVF stimulation suggesting that in this task the transfer time from the left to the right hemisphere is of behavioral relevance in healthy volunteers (Brown and Jeeves, 1993). Larson and Brown (1997) used a letter matching task and a pattern-matching task with lateralized half-field presentation. For both tasks, they found faster transfer times from the LH to the RH. The same pattern of directional asymmetry in IHTT seems to be present independently from the visual field advantage elicited in the task. In contrast, Nowicka et al. (1996) found directional asymmetry to be congruent with a visual field advantage occurring in a certain task. They presented either consonant-vowel-consonant syllables or square wave gratings of different spatial frequencies unilaterally to the LVF or the RVF. Healthy participants had to decide whether the presented stimulus was shown on the response card or not. For syllables, faster transmission from the RH to the LH was found, whereas for gratings, faster LH to RH transmission occurred. They concluded that interhemispheric transmission is faster when information is transferred from the non-specialized hemisphere to the specialized one. For verbal material, a consistent RVFA and a faster transmission via the corpus callosum from the RH to the LH was found (Brown et al., 1994; Larson and Brown, 1997; Nowicka, 1996).

The present study was designed to investigate the neurophysiological mechanisms underlying interhemispheric transfer and interhemispheric cooperation. In a lexical decision task, words and pseudowords were presented either to the LVF or to the RVF or two copies of an identical stimulus were presented simultaneously to both visual fields (BVF). In order to obtain brain activity during this task, the EEG was recorded through 65 electrodes.

Behavioral data should replicate earlier findings (Mohr et al, 1994b; Mohr et al., 1996). A bilateral advantage was expected, reflected in higher accuracies and lower reaction times in bilateral condition than in both unilateral conditions. This bilateral advantage should occur only after word stimulation, and should not occur after pseudoword stimulation. A right visual field advantage (RVFA) is expected from unilateral conditions, indicating a left hemispheric superiority for this task.

A neurophysiological manifestation of the bilateral advantage was expected from analysis of ***evoked potential data***. Overall activation should be higher in bilateral word condition than in unilateral word conditions and than in all pseudoword conditions. Since cortical activation obtained from ERP data is difficult to interpret, minimum norm estimates of source activation were calculated. Differences in activation among conditions can be located more precisely by following this method. From studies concerning differences between words and pseudowords as well as between different word categories (e.g. Pulvermüller, 1999), we expect this bilateral advantage between 150 and 250 ms after stimulus onset.

Further, ***interhemispheric transmission times*** were analyzed after unilateral stimulation with words and pseudowords. Though IHTT was determined from latency differences of N1 peaks, it was not possible to analyze IHTT after bilateral stimulation. As faster transmission from the RH to the LH after LVF stimulation was revealed in previous studies (Brown and Jeeves, 1993; Larson and Brown, 1997), we also expected shorter IHTT after RVF than after LVF stimulation. Moreover, differences in IHTT between words and pseudowords were also possible. Since a bilateral advantage in behavioural experiments was only revealed for words, faster IHTT after RVF stimulation might also occur only to word stimuli.

3. Methods

Subjects

Fifteen healthy participants (7 females; mean age: 23.9; education 12.6 years) were paid for their study participation. All subjects were native speakers of German and right-handed as verified by a modified version of the Edinburgh handedness questionnaire (Oldfield, 1971) (handedness quotient: 96.0). None of the participants had a history of neurological or psychopathological disorders. Subjects had normal or corrected to normal vision.

Procedure

In a lexical decision task, participants were instructed to decide whether a visually presented letter string was a meaningful German word or a meaningless pseudoword by bimanually pressing two out of four response buttons. In case of word presentation a response with both index fingers was required and in case of pseudoword presentation, a button press with both middle fingers should be executed. Subjects were instructed to respond as fast and as accurately as possible. During the whole experimental block subjects were requested to fixate their eyes on a fixation cross in the middle of a computer screen. A schematic presentation of the experimental design is given in **Figure IV.A.1**.

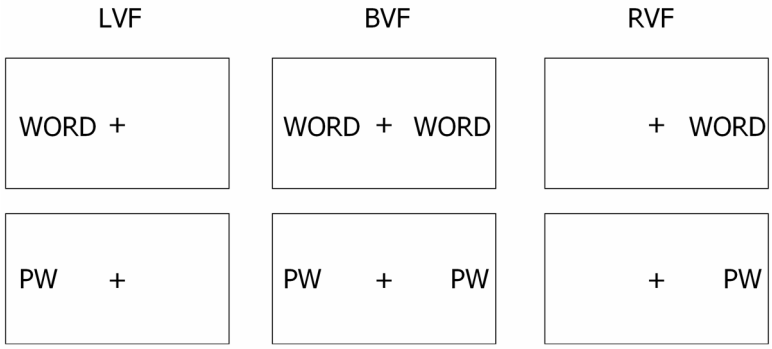

Figure IV.A.1. Experimental design: words and pseudowords (PW) were either presented unilaterally in the LVF or RVF condition or bilaterally in both visual fields (BVF).

Stimuli were presented tachistoscopically for 150 ms either unilaterally to the RVF or to the LVF or simultaneously to both visual fields (BVF). The inter-stimulus-interval (ISI) varied between 2.5 and 3.5 s. A 60 trials practice block preceded the experiment. The

experiment comprised 240 stimuli (120 words and 120 pseudowords), which were presented in pseudo-randomized order. Each item occurred only once during the experiment. The duration of the experimental session was approximately 30 min.

Stimuli

Words and pseudowords were presented in black upper-case letters on a gray background to reduce visual afterimages. All stimuli were bisyllabic and were four to eight letters long. Words were German content words with a high frequency of occurrence (100 – 1000 occurrences per 1 million words, according to Ortmann; 1975). Pseudowords were obtained either by permutation of letters within words or by exchanging letters between word stimuli. Pseudowords were pronounceable and orthographically regular but not homophonous to real words.

Apparatus

Stimuli were presented on a 17-inch monitor of an IBM compatible Pentium PC placed at a distance of one meter in front of the participants. Stimuli appeared between 1.5° and 4.5° of horizontal and 0.6° of vertical visual angle. During the experiment, all participants had their chins in a chin rest with a forehead restraint bar centered relative to the viewing screen. Two keypads each comprising two easily manageable micro switches served for response collection and were positioned on a table in front of the subject.

Data acquisition

The EEG (electroencephalogram) was recorded with two 32-channel DC-amplifiers (SYNAMPS, Neuroscan) from 64 electrodes mounted on a cap referenced to CZ (Electrocap Inc.). Data were recorded with a bandpass of DC to 30 Hz and a sampling rate of 200 Hz. Impedances were kept below 5 kOhm. Data were recorded continuously and stored for off-line analysis. After the experimental session, electrode positions were digitized using a 3D digitizer (Polhemus Inc.). Vertical, horizontal and blink electrooculograms (EOG) were recorded for later artifact correction following the MSEC (multiple source of eye correction) method (Berg and Scherg, 1994). Additionally, trials were visually inspected. Only artifact free trials with correct responses performed within two seconds after stimulus onset were analyzed (72.9% SD=11.3 of all trials were included in data analysis).

ERP data were averaged separately for each of the six conditions (words, pseudowords presented to the LVF, RVF and BVF) and filtered with a 20 Hz low pass filter. A baseline correction was performed for each individual and each condition by subtracting the average scalp distribution during a 200 ms epoch prior stimulus onset. After average referencing the ERPs, variability of the electrode positions were reduced by spline-interpolation of the data from individually digitized electrode positions on a standardized electrode montage. Finally, data were normalized by calculating z-values (McCarthy and Wood, 1995).

Analysis of Behavioral Data

Behavioral data (accuracy and latency) were analyzed by ANOVAs with the factors Wordness (words vs. pseudowords) and Presentation Mode (LVF, RVF vs. BVF).

Statistical Analysis of Evoked Potential Data

The bilateral advantage was analyzed by comparing the bilateral condition (BVF) with both unilateral conditions (RVF and LVF). In order to localize the bilateral advantage in a temporal and topographical way, we performed statistical analysis on evoked potential data and on the minimum norm solution.

For analyzing the evoked potential data, head positions of the electrodes were combined into four electrode arrays (each comprising mean amplitude of three electrodes) within each hemisphere: frontal, fronto-central, centro-parietal and parieto-occipital (see also **Figure IV.A.2**).

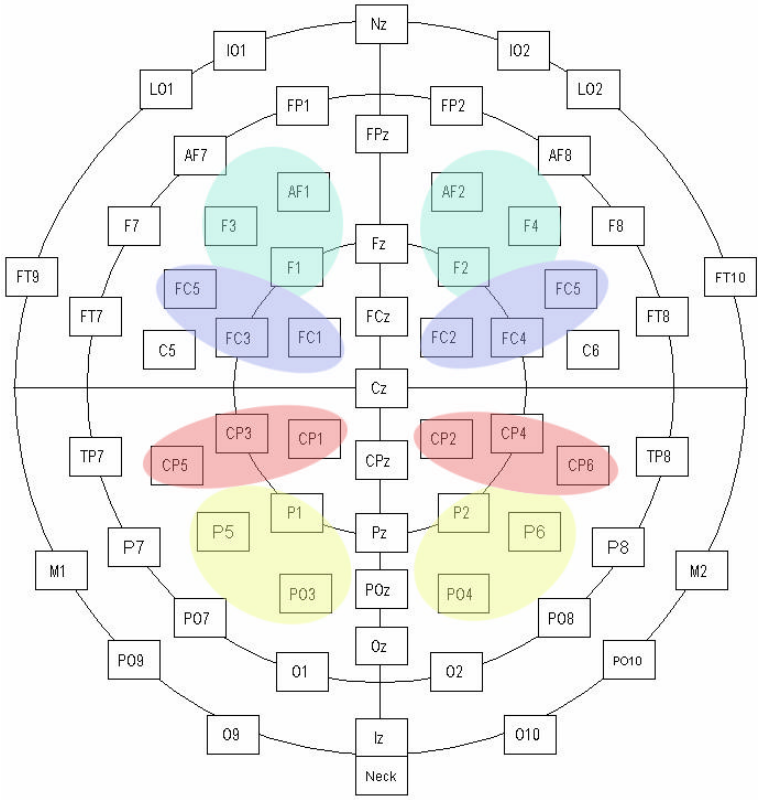

Figure IV.A.2. Mean amplitudes of four electrode arrays over each hemisphere were determined by combining three electrodes: frontal (green), fronto-central (blue), centro-parietal (red) and parieto-occipital (yellow).

Mean amplitudes for each electrode array were determined for words and pseudowords in the three presentation conditions (LVF, RVF and BVF). Global field power analysis revealed that ERPs peaked around 180 ms in all six conditions and both groups. A time window from 160 to 200 ms after stimulus onset was selected for statistical analysis of the bilateral advantage because earlier data indicated effects of lexical processing in this time range (e.g., Pulvermüller, 1999). Means were compared by analysis of variance (ANOVA) with the factors Wordness (Words vs. Pseudowords), Presentation Mode (LVF, BVF vs. RVF), Hemisphere (LH vs. RH) and Gradient (frontal, fronto-central, centro-parietal and parieto-occipital).

Source Analysis (Minimum Norm Analysis)

ERP data are difficult to interpret in terms of neuronal generators. Sources that are tangentially oriented to the scalp produce their peaks of activity at considerable distances from the true source location. If multiple sources are active, their potential distributions are likely to interfere with each other, such that the contributions from particular sources cannot be discerned. Source analysis in general attempts to deal with this problem. Various algorithms, incorporating different kinds of modeling assumptions, have been suggested (Baillet et al., 2001). If the source distribution can be expected to be complex (as for cognitive ERP components) and if the signal-to-noise ratio is low (as for single subject data), a method relying on minimal modeling assumptions is recommended.

Such a method is the classical minimum L2-norm (MN) method (Hamalainen and Ilmoniemi, 1994; Grave de Peralta et al., 1997). It is capable of producing a two-dimensional blurred version of the real source distribution, even if the signal-to-noise ratio is low (Hauk et al., 2002). The method can therefore be applied to individual subject data, which in turn can be submitted to statistical analysis.

The implementation of the MN method used in this experiment follows the suggestions of Hauk et al. (2002). Because current sources can be distributed in the whole brain volume, initially a three-dimensional source space was chosen. It consisted of 1655 dipolar current sources distributed over four concentric shells with radii 0.8, 0.6, 0.4 and 0.2, respectively (electrodes at radius 1). The MN method produces maximal amplitudes always on the outermost shell. However, the deeper the shell, the lower the spatial resolution, but the higher the relative sensitivity to deeper current sources (Hauk et al., 1999). As a compromise between these two aspects and for data reduction we chose the shell with radius 0.6 for further analysis.

The influence of noise on MN estimates can be controlled by imposing a certain degree of smoothness. This was accomplished by Tikhonov regularization, which is optimal for suppressing spatially uncorrelated noise, such that the mean residual variance of our estimates over all data sets was 5% (Bertero et al., 1988).

The minimum norm (MN, L2 – Norm) estimates were computed separately for conditions and subjects according to Hauk et al. (2002). Six sensor arrays were selected,

each containing a number of sensors over anterior, medial and posterior areas of the right and left hemisphere. The same time window from 160 – 200 ms as for ERP-analysis was chosen. Statistical analysis was computed using ANOVAs with the factors Wordness (words vs. pseudowords), Presentation Mode (LVF, BVF vs. RVF), Gradient (frontal, temporal vs. parietal) and Hemisphere (left vs. right).

Analysis of Interhemispheric Transmission Time

In order to determine interhemispheric transmission time as an indicator of interhemispheric efficiency of information transfer, the latency of the N1 was analyzed over parietal electrode sites. Parietal electrode sites were selected as in previous studies (Brown et al., 1994; Larson and Brown, 1997) because the visual N1 amplitude was most pronounced over these cortical areas.

Over each hemisphere, three parietal electrodes were selected to calculate the N1-latencies. The electrode arrays comprised P5, P7 and PO7 located over the LH and P6, P8 and PO8 located over the RH (see **Figure IV.A.2**). The N1-latency was determined by the most negative peak during the time window from 100 to 300 ms. Interhemispheric transmission time (IHTT) was computed by the N1 latency difference of ipsilateral minus contralateral N1 peaks. In the LVF condition, IHTT was determined by subtracting the latency of the right hemispheric N1 peak from the latency of the left hemispheric N1 peak. Analogous, in the RVF condition, IHTT was determined by subtracting the left hemispheric N1 peak latency from the right hemispheric N1 peak latency. IHTT was not analyzed in the bilateral condition, though stimulation of both hemispheres simultaneously caused N1 peaks over both hemispheres to emerge at the same time and no latency difference could be obtained.

Statistical analysis was computed for the IHTT with an ANOVA including the factors Wordness (words vs. pseudowords) and Presentation Mode (LVF vs. RVF).

For all analyses, p-values were corrected with Greenhouse-Geisser procedure, when appropriate (if df > 1). Significant interactions were further analyzed by planned comparisons using one-way ANOVAs.

4. Results

Behavioral Data: Accuracy and Latency

Figure IV.A.3 illustrates the mean percentage of correct responses for the lexical decision task. Overall accuracy was higher for pseudowords than for words (Wordness $F(1,14)=10.42$, $p<0.01$). Performance in the three presentation condition was highest in the bilateral condition and lowest in the LVF condition (Presentation Mode: $F(1,14)=33.02$, $e=0.59$, $p<0.001$). A significant Wordness (words vs. pseudowords) x Presentation Mode (LVF, BVF vs. RVF) interaction was obtained ($F(2,28)=24.28$, $e=0.89$, $P<0.001$).

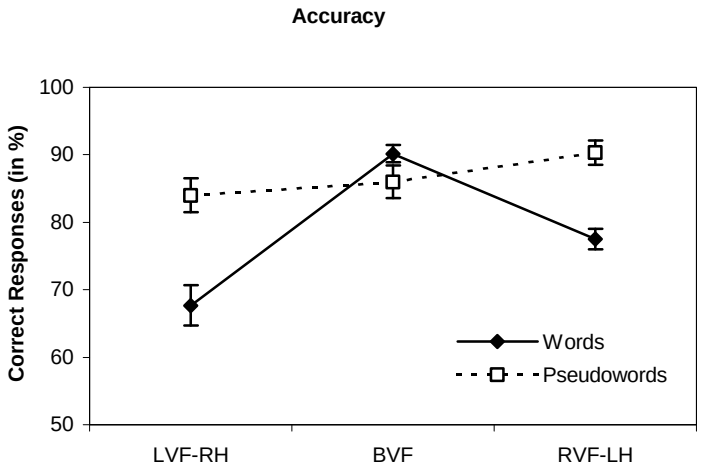

Figure IV.A.3. The Wordness x Presentation Mode interaction is displayed for mean percentages of correct responses. Participants obtained a bilateral advantage when words were simultaneously presented to the LVF and the RVF (bilateral condition). Error bars indicate standard errors of the means.

Planned comparisons revealed a ***right visual field advantage*** (RVFA, left hemispheric superiority) for words ($F(1,14)=12.74$, $P<0.01$). A ***bilateral advantage*** is reflected in a superior performance in the bilateral condition in comparison to the best unilateral condition. The crucial comparison is between BVF and RVF condition in which stimuli are delivered to the language-dominant hemisphere alone. Controls showed a bilateral advantage for words (BVF vs. LVF: $F(1,14)=45.97$, $P<0.001$; BVF vs. RVF ($F(1,27)=76.00$, $P<0.001$). No bilateral advantage for pseudoword was found.

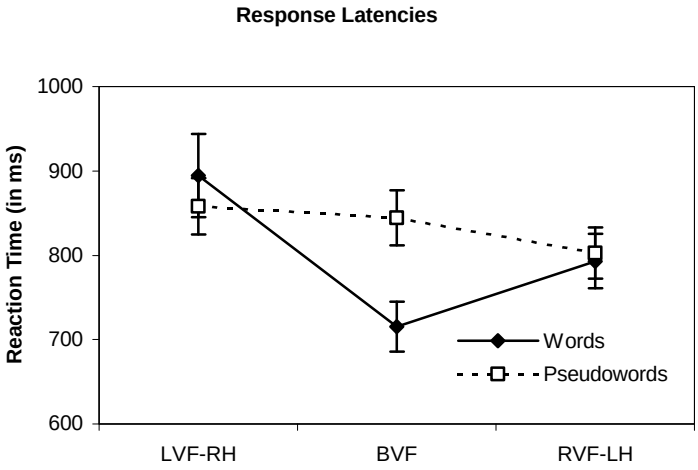

Figure IV.A.4. The Wordness x Presentation Mode interaction is displayed for latencies. A bilateral advantage with faster reactions in the bilateral condition was revealed for controls. Error bars indicate standard errors of the mean.

Latencies of correct responses are displayed in **Figure IV.A.4**. A significant main effect for Presentation Mode ($F(1,14)=19.92$, $e=0.63$, $p<0.001$) indicated slowest reaction times after stimulus presentation in the LVF and fastest responses after bilateral presentation. The marginal significant main effect for Wordness ($F(1,14)=3.23$, $p<0.1$) was explained by overall faster reactions for words than for pseudowords.

A significant Wordness x Presentation Mode interaction was revealed ($F(1,14)=20.76$, $e=0.77$, $p<0.001$). Planned comparisons revealed a ***right visual field advantage*** for words and pseudowords (words: $F(1,14)=12.15$, $P<0.01$; pseudowords: $F(1,14)=8.91$, $P<0.01$). In contrast, a **bilateral advantage** with faster reactions in the bilateral compared with both unilateral conditions was obtained for words (BVF vs. RVF: $F(1,14)=50.77$, $P<0.001$; BVF vs. LVF: $F(1,14)=39.43$, $P<0.001$). For pseudowords no bilateral advantage emerged. Faster bilateral reactions were obtained for words than for pseudowords ($F(1,14)=25.42$, $p<0.001$).

Evoked Potential Data

A time window from 160 to 200 ms was selected because earlier data indicated lexical processing in this time window (e.g., Pulvermüller, 1999). ERP topographies for words and pseudowords show pronounced differences between the three Presentation Modes in participants (**Figure IV.A.5**).

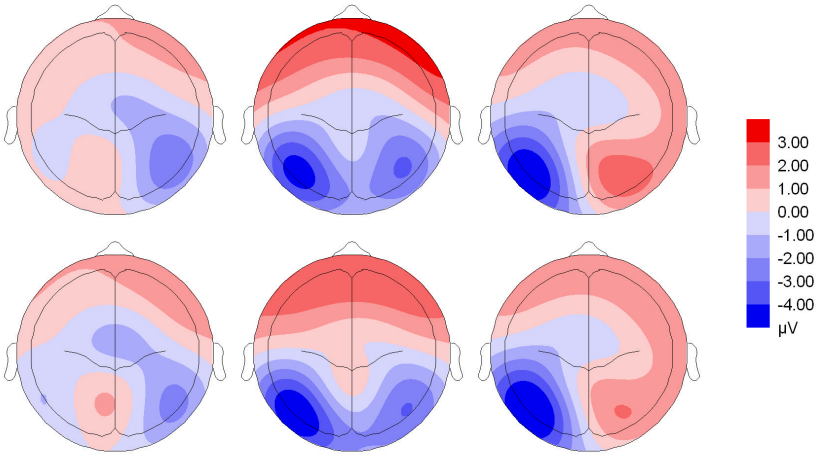

Figure IV.A.5. Grand average topographies (average reference) of words and pseudowords in the three presentation conditions (LVF, BVF and RVF) in the time window 160-200 ms after stimulus onset for healthy controls.

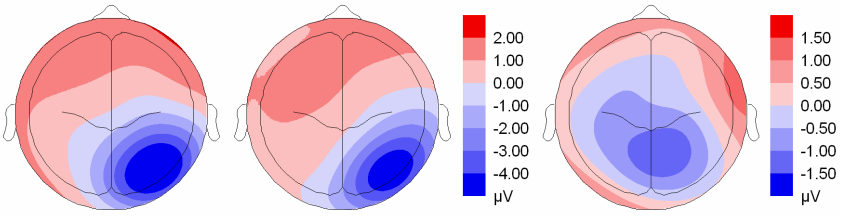

Figure IV.A.6. Topographies (average reference) of the difference BVF minus RVF are displayed for words and pseudowords in the time window 160-200 ms after stimulus onset for healthy controls. On the right side word minus pseudoword differences are displayed. This contrast is bi-hemispherically distributed in controls.

The differences topography BVF minus RVF condition (see **Figure IV.A.6.**) is indicating an increased negativity over the right hemisphere after bilateral stimulation compared with RVF stimulation. This increased negativity was more pronounced for words in contrast to pseudowords.

A four-way ANOVA on mean amplitudes of ERP data revealed a main effect for the factor Wordness ($F(1,14)=10.77$, $p<0.01$) with more pronounced negativity for words than for pseudowords. Overall highest negativity was located over parieto-occipital electrodes (Gradient: $F(3,42)=3.81$, $p<0.02$). Amplitudes in the three presentation conditions vary also with topography (Presentation Mode x Gradient: $F(6,84)=23.60$, $p<0.001$; Presentation Mode x Gradient x Hemisphere: $F(6,84)=25.82$, $p<0.001$). Over frontal electrode sites amplitudes were more positive and over parietal electrode sites amplitudes were more negative in the bilateral condition compared with unilateral conditions. Laterality was most pronounced over parieto-occipital electrode sites. Right laterality was found in the LVF condition and left laterality in the RVF condition, whereas no significant laterality was observed in the bilateral condition.

Differences in amplitudes among words and pseudowords were obtained from a significant Wordness x Presentation Mode interaction ($F(2,54)=3.55$, e=0.87 $P<0.05$) (see **Figure IV.A.7**). However Wordness and Presentation Mode did not interact with topography. Planned comparisons showed that the mean amplitude for words after bilateral stimulation is more negative than for pseudowords ($F(1,14)=15.00$, $P<0.001$). Comparing bilateral with unilateral amplitudes after word stimulation, a significant difference emerged only in comparison with RVF stimulation ($F(1,14)=14.87$, $p<0.05$).

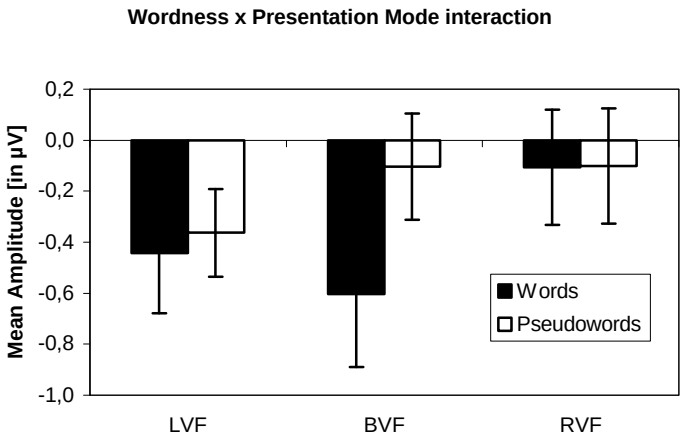

Figure IV.A.7. ERP data: Wordness x Presentation Mode interaction. Overall negativity was more pronounced for words bilaterally presented than presented in the RVF. Bilateral negativity for words was also increased compared with bilaterally presented pseudowords. Error bars indicate standard error of the mean.

Bilateral Advantage:

In a separate analysis, bilateral condition was compared with RVF condition in order to look at topographical differences and to obtain a neurophysiological correlate of the redundancy gain (the LVF condition was excluded from analysis).

The ANOVA revealed overall amplitudes to be more negative for words (Wordness: $F(1,14)=10.62$, $p<0.01$), over the left hemisphere (Hemisphere: $F(1,14)=9.33$, $p<0.01$) and over parietal electrodes sites (Gradient: $F(3,42)=5.76$, $p<0.03$). Differences between RVF and bilateral condition vary with topography (Presentation Mode x Gradient: $F(3,42)=3.42$, $p<0.001$; Presentation Mode x Hemisphere: $F(1,14)=21.81$, $p<0.001$; Presentation Mode x Gradient x Hemisphere: $F(3,42)=25.47$, $p<0.001$). A significant laterality of parietal negativity was obtained from the RVF condition, whereas amplitudes were not lateralized in the bilateral condition.

The significant Wordness x Visual Field interaction ($F(1,14)=5.35$, $p<0.04$) indicated an overall increased negativity after bilateral word presentation compared to pseudowords ($p<0.001$) and compared to RVF word ($p<0.05$) and pseudowords ($p<0.02$) stimulation (see also **Figure IV.A.7**). Differences among presentation condition between words and pseudowords were also found to vary with topography (Wordness x Presentation Mode x Gradient x Hemisphere: $F(3,42)=3.14$, $p<0.05$). **Figure IV.A.8** depicts this four-way interaction, which was further analyzed with planned comparisons.

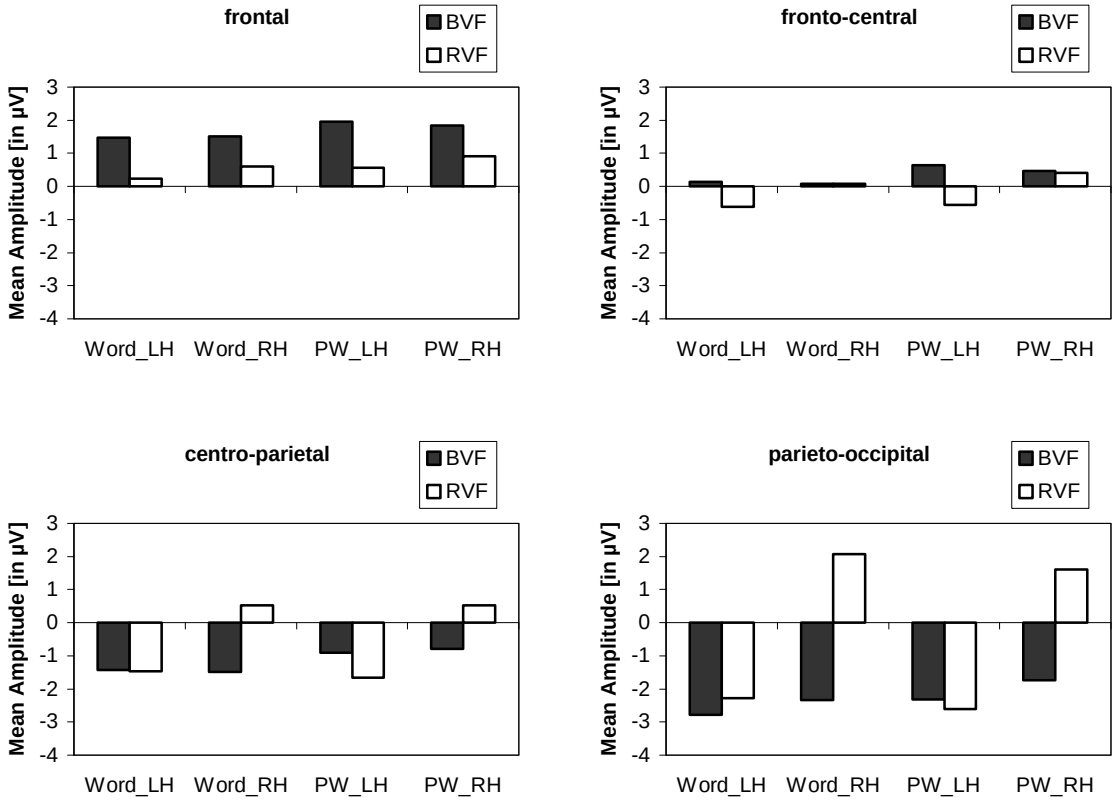

Figure IV.A.8. ERP data: Wordness x Presentation Mode x Gradient x Hemisphere interaction. Increased negativity was observed for the bilateral condition (BVF) in comparison to the right visual field condition (RVF) over centro-parietal and parieto-occipital electrodes of the right hemisphere (RH), but also over the left hemisphere (LH) in the word condition. Negativity for pseudowords (PW) was reduced over parietal electrodes of the LH.

Different topographies were obtained for bilateral and right visual field stimulation and for word and pseudowords in the two conditions. Amplitudes in the bilateral condition differ from RVF condition over the right hemisphere for words and pseudowords at frontal, centro-parietal and parieto-occipital electrode sites (all p-values <0.05). Hence, this is not surprising though the right hemisphere receives additional input in the bilateral condition. Over frontal and fronto-central electrode sites of the left hemisphere amplitudes in the bilateral condition were more positive for words and pseudowords (p-values <0.05). At parietal electrode sites of the left hemisphere a difference between words and pseudowords was revealed. Whereas for words negativity was more pronounced in the bilateral condition compared with RVF condition over parieto-occipital electrode sites ($p<0.04$), negativity for bilaterally presented pseudowords as even reduced at centro-parietal electrode sites ($p<0.05$).

Source Analysis: Minimum Norm Analysis

The minimum norm source distributions from 160 to 200 ms for words and pseudowords in the three presentation conditions (**Figure IV.A.9**) and difference source topographies between BVF and RVF condition (**Figure IV.A.10**) are displayed. In unilateral conditions, activation peaks at posterior regions of the respective contralateral hemisphere. A left lateralized, but bilateral distribution of activity was obtained after stimulus presentation in both visual fields. Whereas, activation was increased over right parieto-occipital areas in the bilateral condition compared with RVF condition for both, words and pseudowords, higher bilateral activation over left temporal regions was found only for word stimuli.

A four-way ANOVA on minimum norm topographies in the time window from 160 to 200 ms was calculated. Overall, cortical activation was highest at parietal electrode sites (Gradient $F(2,28)=16.57$, $p<0.01$) and in the bilateral condition (Presentation Mode $F(2,28)=5.21$, $p<0.03$). In unilateral conditions, higher activation was observed over the contralateral than over the ipsilateral hemisphere, whereas no hemispheric difference was revealed in the bilateral condition (Presentation Mode x Hemisphere $F(2,28)=6.90$, $p<0.02$). Laterality varied with electrode site (Gradient x Hemisphere $F(2,28)=4.89$, $p<0.02$): at frontal regions activity was lateralized to the right; activity at parietal sites was lateralized to the left. The laterality effect was more pronounced for words than for pseudowords (Wordness x Gradient x Hemisphere $F(2,28)=4.00$, $p<0.06$).

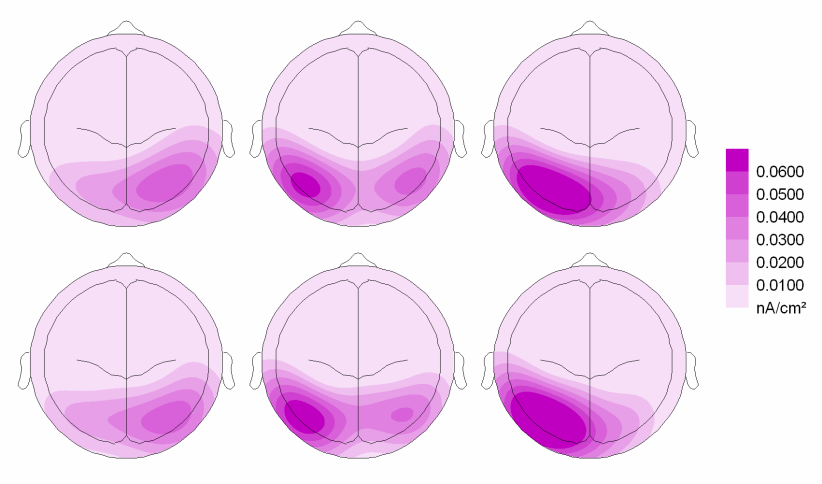

Figure IV.A.9. Grand mean topographies of source distribution estimated by the minimum norm solution are displayed. Topographies for words (upper row) and pseudowords (lower row) in the three conditions (LVF on the left side, BVF in the middle and RVF on the right side) in the time window 160-200 ms are presented. Pink colored areas represent regions of higher electro-cortical activity.

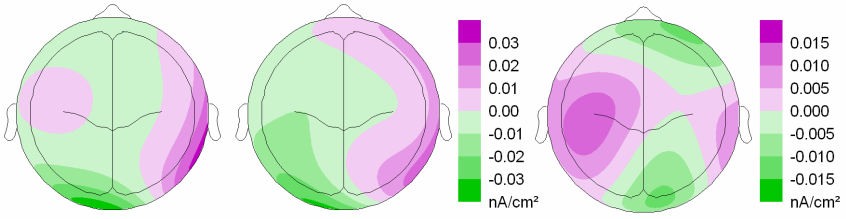

Figure IV.A.10. Topographies of source distribution BVF minus RVF for words (left position) and pseudowords (middle position) and the difference words minus pseudowords (right position). Pink areas represent regions of higher electrocortical activity after BVF stimulation and green areas represent higher electrocortical activity after RVF stimulation. Activity was increased over the right hemisphere for both stimulus categories. Further, only in the word condition activity was also increased over left temporal regions.

The significant Wordness x Presentation Mode x Gradient x Hemisphere interaction ($F(4,56)=4.99$, $p<0.01$) is summarized in **Figure IV.A.11** and was further analyzed with planned comparisons.

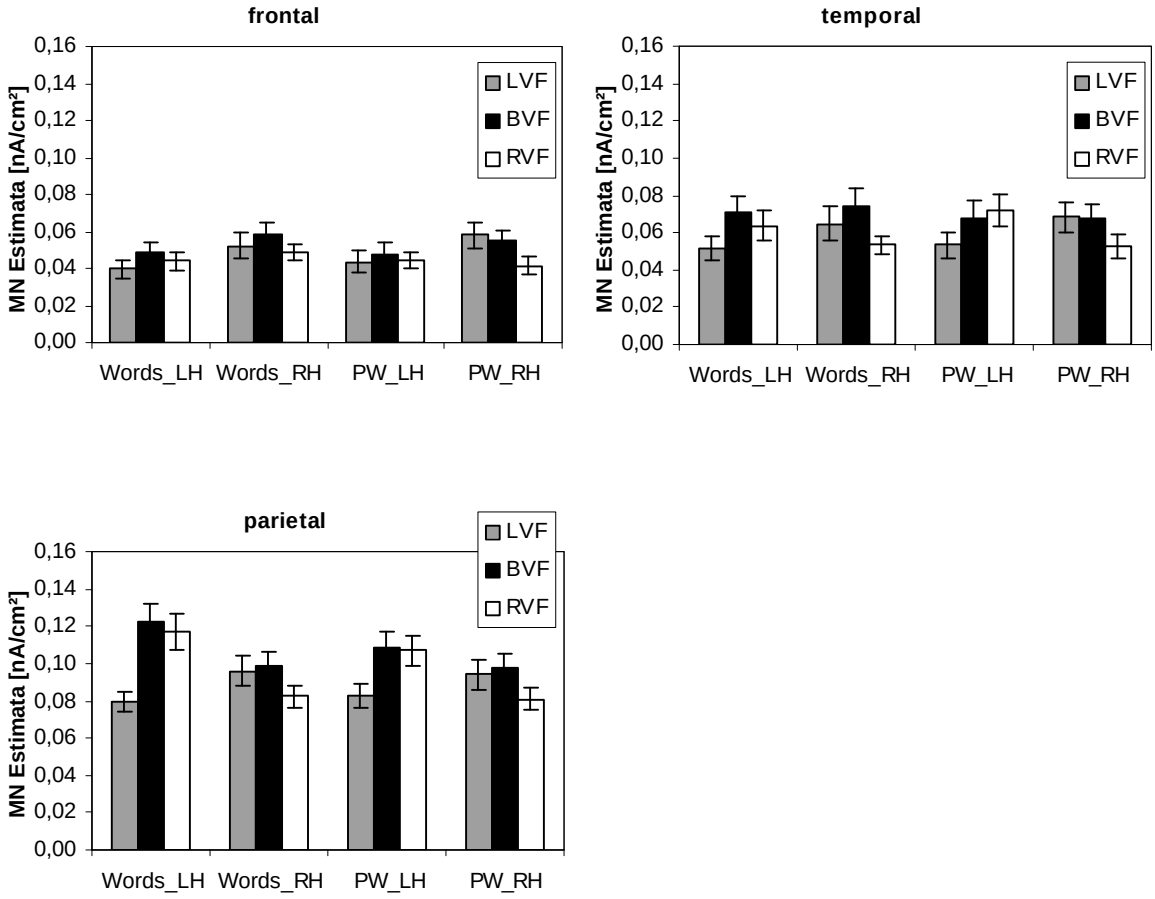

Figure IV.A.11. The Wordness x Presentation Mode x Gradient x Hemisphere interaction is displayed for the minimum norm source estimate (MN Estimate). Significant higher bilateral activation (compared with both unilateral conditions) was revealed for words over temporal regions of both hemispheres. Whereas, activation for pseudowords after bilateral stimulation was only increased compared to unilateral stimulation over the respective ipsilateral hemisphere. Error bars indicate standard error of the mean.

Planned comparisons were calculated for the comparison between bilateral and unilateral conditions (BVF vs. RVF and BVF vs. LVF) at all electrode sites. Overall differences were most pronounced over the contralateral hemisphere of the respective compared visual field. The difference in activation between bilateral and RVF condition was most pronounced over the right hemisphere at frontal and temporal sites for words and

pseudowords (p-values <0.05) and the BVF vs. LVF difference over the left hemisphere for words at all three sites (p-values <0.05) and for pseudowords at temporal and parietal sites (p-values <0.05). Only for words there are also differences over the ipsilateral hemisphere. Activation in the bilateral condition was higher compared to the RVF condition over left temporal regions (p<0.04) and compared to the LVF condition over right temporal regions (p<0.04). Additionally, bilateral activation over temporal regions was higher for words than for pseudowords over both hemispheres (p<0.05).

Topographies of the minimum norm source distribution are displayed in **Figure IV.A.12**. At temporal regions of both hemispheres, activity after bilateral stimulation was significantly higher than in *both* unilateral conditions. This difference was found only for words. Pseudowords had only higher activation in bilateral condition compared with unilateral conditions over the respective contralateral hemisphere. Enhanced activation at temporal sites in bilateral condition for word therefore might be responsible for the **bilateral advantage**.

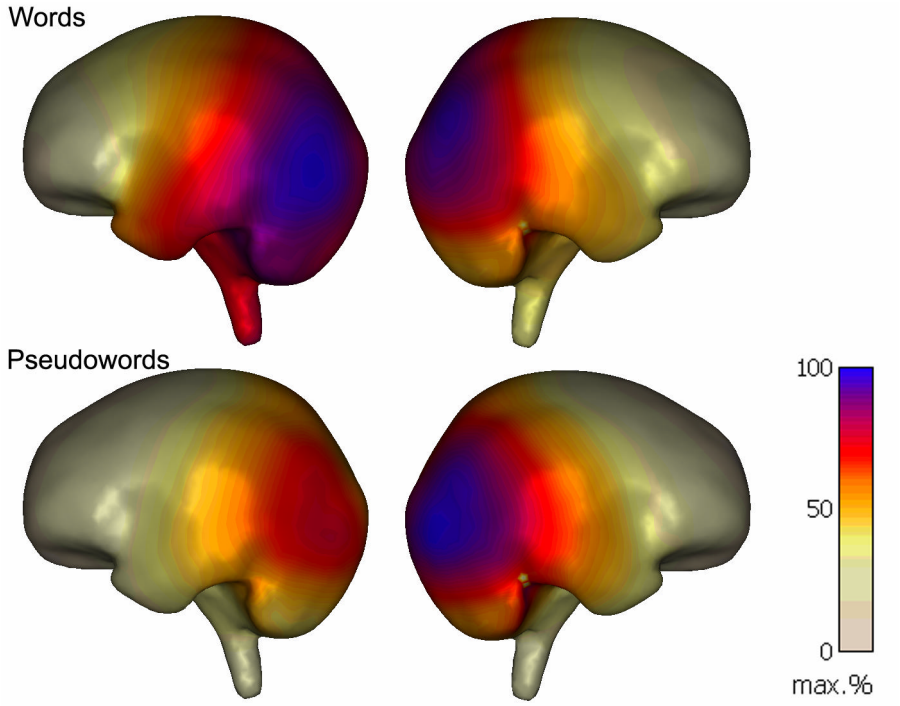

Figure IV.A.12. Topographies of the minimum norm source distribution (180 ms after stimulus onset) of the difference bilateral condition minus average of unilateral conditions separately for words (top row) and pseudowords (bottom row) over the left and right hemisphere. Words elicited stronger activation compared to pseudowords especially over the LH in bilateral condition compared with average unilateral simulation.

Analysis of Interhemispheric Transmission Time[1]

Figure IV.A.13 shows the time course of the event-related potentials (ERPs) at parietal electrode sites after LVF and RVF stimulation, for words and pseudowords, respectively. In all conditions, an initial contralateral (to the stimulated visual field) N1 peak was followed by an ipislateral peak. The latency difference of ipsilateral minus contralateral peak was interpreted as interhemispheric transmission time (a detailed description of IHTT is provided in the methods section of this experiment).

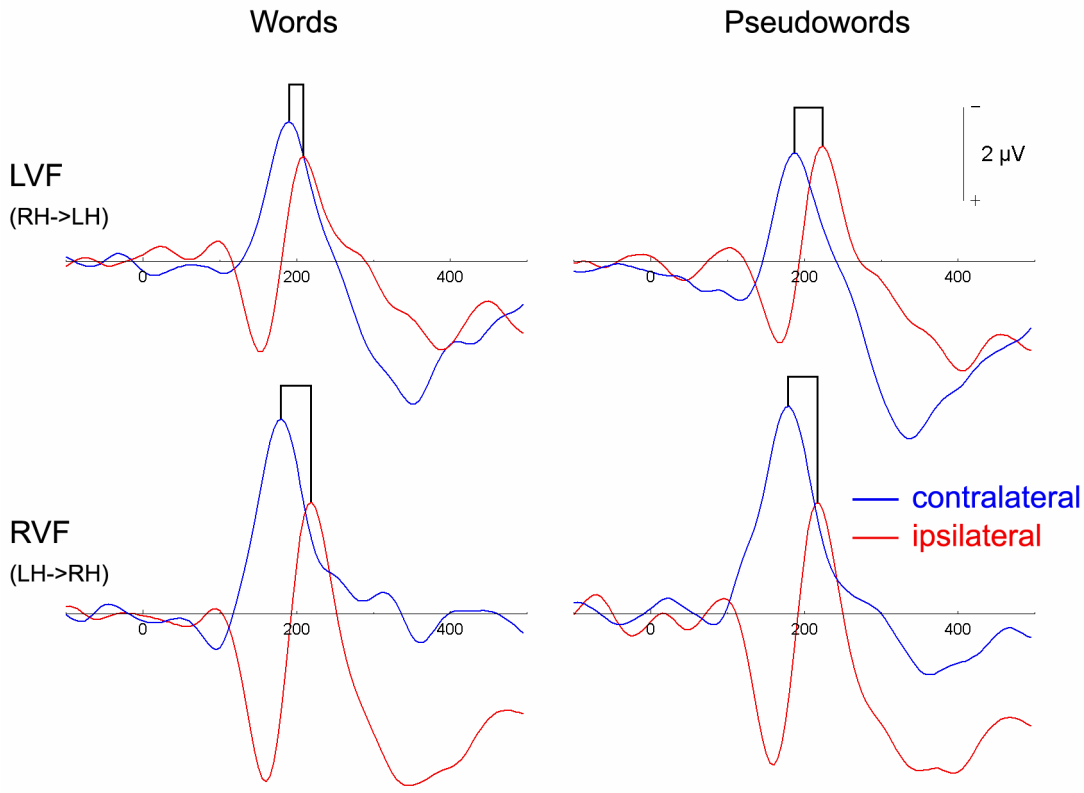

Figure IV.A.13. Errors are shown at parietal electrodes of the left hemisphere (LH, P5) and right hemisphere (RH, P6) after LVF (upper row) and RVF (lower row) stimulation with words (left side) and pseudowords (right side). Initially, a N1 peak is observed over the hemisphere, which is contralateral (blue) to the simulated visual field (RH in LVF and LH in RVF condition). Afterwards an ipsilateral (red) peak follows (LH in LVF and RH in RVF condition). Time distance between contralateral and ipsilateral peaks is interpreted as interhemispheric transmission time and was found to be significantly shorter after LVF stimulation with words than with pseudowords and than after RVF stimulation with either words or pseudowords.

[1] The report of interhemispheric transmission times in this experiment largely corresponds to the paper Endrass et al. (2002).

The two-way ANOVA for interhemispheric transmission time (IHTT) revealed an overall shorter IHTT after LVF stimulation (Presentation Mode: $F(1,14)=5.84$, $p<0.03$). Furthermore, IHTT tends to be shorter for words than for pseudowords (Wordness: $F(1,14)=3.20$, $p<0.10$). The two-way interaction is presented in **Figure IV.A.14** and indicates that IHTT varies with presentation condition and stimulus type (Wordness x Presentation Mode: $F(1,14)=4.83$, $p<0.05$).

Planned comparisons revealed shorter transmission time for words presented to the LVF than for words presented to the RVF ($p<0.01$). For pseudowords no IHTT difference between presentation conditions was found. In the LVF condition, when transmission occurs from the right hemisphere to the left hemisphere, transmission for words was faster than for pseudowords ($p<0.05$). In contrast, transmission from the left hemisphere to the right hemisphere (RVF condition) did not differ between words and pseudowords.

A directional asymmetry of IHTT with faster transmission from the RH to the LH than reverse was obtained for words but not for pseudowords.

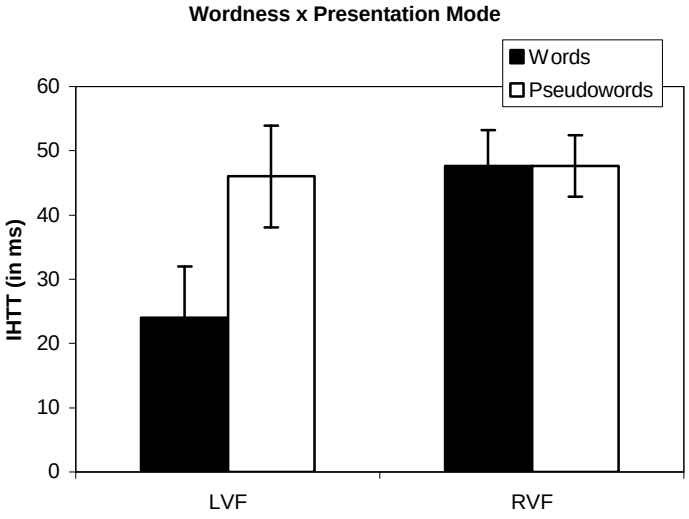

Figure IV.A.14. Mean IHTT (in ms) is displayed separately for words and pseudowords in the LVF and RVF. IHTT was significantly shorter for words presented in the LVF condition, than in any other condition. Error bars indicate standard error of the mean.

5. Discussion

The current study revealed differences between unilateral and bilateral stimulus presentation in behavioral and neurophysiological data. ***Behavioral data*** replicated previous findings (Mohr et al., 1994b; Mohr et al. 1996; Yoshizaki, 2001; Zaidel and Rayman, 1994). A bilateral advantage (higher accuracy and shorter reaction times) was obtained after bilateral word presentation compared with unilateral word presentation. Bilateral pseudoword presentation did not improve performance compared to unilateral presentation (Wordness x Presentation Mode interaction). Additionally, left hemispheric superiority was also found during this task, reflected in better overall performance after word presentation in the RVF (right visual field advantage). The right visual field advantage shows that language processing is improved after direct stimulation of the language dominant left hemisphere compared to stimulation of the right hemisphere. In the bilateral condition, additional stimulation of the right hemisphere, presumably improved performance. This shows that the right hemisphere was also involved in language processing (Pulvermüller et al., 1995; Pulvermüller, 1999; Pulvermüller et al., 1999).

From ***event-related potential data*** a significant Wordness x Presentation Mode interaction was obtained (**Figure IV.A.7**). Bilaterally presented words had a higher overall negativity than pseudowords in the bilateral condition in the time window from 160 – 200 ms. However, negativity for words differed only between the bilateral and RVF condition. The comparison with the LVF condition was not significant. Additional analysis for the comparison between bilateral and RVF condition indicated that the Wordness x Presentation Mode interaction varied with topography (**Figure IV.A.8**). The most interesting difference between the bilateral and unilateral condition is over parieto-occipital electrodes. Over both hemispheres, bilaterally presented words were more negative than words presented to the RVF. In contrast, pseudowords differed only over the RH. ***Source analysis*** revealed a more distinctive correlate for the bilateral advantage. The significant Wordness x Presentation Mode x Gradient x Hemisphere interaction pointed out that bilateral activity was more pronounced in temporal regions. Words bilaterally presented elicited more activity than both unilateral word condition over both hemispheres. Pseudowords had higher bilateral activation compared to RVF condition only over the RH and compared to LVF condition only over the LH. Bilateral activation over temporal regions was also higher for words than for pseudowords. In summary, analysis of

neurophysiological activation indicated that with bilateral word stimulation, activity over temporal brain regions should be increased.

Analysis of ***interhemispheric transmission time*** showed faster transmission after LVF stimulation for words, when transmission occurs from the RH towards the LH, than after RVF stimulation. This directional asymmetry is consistent with earlier findings (Brown et al., 1994; Larson and Brown, 1997; Nowicka, 1996). Pseudowords did not reveal this directional asymmetry, but had equal transmission times in both directions. After LVF stimulation words are faster transmitted from the RH into the LH than pseudowords. IHTT might reflect interhemispheric cooperation, which was facilitated after word stimulation in contrast to pseudowords stimulation.

In summary, the present findings indicate that interhemispheric cooperation is reduced or weakened in case of pseudoword presentation. Pseudowords revealed no bilateral advantage, no increased activation compared with unilateral stimulation over corresponding contralateral hemispheres, and no IHTT facilitation after LVF stimulation. In contrast, evidence was obtained for interhemispheric cooperation during word presentation, because of superior bilateral performance, activation was increased after bilateral compared with unilateral presentation and IHTT was faster after stimulus presentation in the LVF.

It has been proposed that words are represented in cell assemblies (Hebb, 1949; Braitenberg and Pulvermüller, 1992; Pulvermüller, 1999). During learning mechanisms these cell assemblies are formed, due to frequent co-activation of neurons located in different cortical regions (auditory, visual etc). Activation of neurons of a cell assembly will activate the whole assembly, what is called ignition. The neurons of one cell assembly are not restricted to a small cortical region. It is rather assumed that cell assemblies are composed of local clusters of neurons that are distributed over both hemispheres and are strongly connected via excitatory connections through the corpus callosum. Within the cell assembly framework, differences in cortical laterality of different word forms (e.g. function and content words) are explained with different topographies of cell assemblies. Whereas function words are suggested to be strongly localized to perisylvian regions of the left hemisphere, content words might also have visual associations and should therefore be distributed over perisylvian and visual cortices of both hemispheres. In contrast, it is

assumed that meaningless pseudowords are not represented in cell assemblies, since they have never occurred before.

The bilateral advantage in behavioral data has been explained in terms of simultaneous activation of cell assemblies in both hemispheres connected with pathways via the corpus callosum, when meaningful stimuli were presented (Mohr et al., 1994b; Mohr et al., 1996; Mohr et al., 2002; Schweinberger et al. 2003). Full activation of a cell assembly would lead to recognition of a meaningful word or familiar face. Activation of more neurons should cause faster ignition of the whole cell assembly. Simultaneous bilateral stimulation of a cell assembly would reach more neurons than unilateral stimulation with only one copy of a stimulus and than initiate a faster ignition and superior performance. Unfamiliar or meaningless stimuli, which have never been encountered or learned before, are not represented in cell assemblies. Therefore, redundant stimulation with these stimuli should not cause neuronal summation. Hence, meaningless stimuli like pseudowords do not benefit from bilateral stimulation.

Different explanations for the bilateral advantage have been discussed earlier (see general introduction). The present neurophysiological findings clearly support the explanation based on Hebb's (1949) cell assembly theory. Analysis of IHTT revealed a faster transmission for words from the right hemisphere to the left hemisphere, which is more capable for language processing. This is possibly due to faster dispersion of activation from the right hemisphere towards the left hemisphere, ensuring a fast ignition of also left hemispheric cell assemblies. In contrast, transmission from left to right is probably not accelerated because the right hemisphere is less capable for language processing. However, most studies on IHTT, revealed faster transmission from right to left hemisphere for different kinds of stimuli (Brown et al., 1994; Larson and Brown, 1997). Therefore, faster neuronal pathways from the RH to the LH might be assumed. But why was transmission then slowed down for pseudowords? Alternatively, it might be possible that in the case of pseudoword processing the lack of cell assemblies slowed down transmission speed.

A substantial argument for the explanation of the bilateral advantage based on the cell assembly theory was obtained from source analysis data. Bilateral stimulation with words produced higher activation over temporal regions of both hemispheres than

unilateral stimulation. Unlike words, pseudowords had only higher activation in bilateral condition compared with unilateral condition over respective ipsilateral hemisphere, which was not initially stimulated by unilateral stimulation. The higher activation obtained from bilateral word stimulation might reflect the neurophysiological representation of the bilateral advantage. Higher bilateral activation might originate from the summation of activation in interhemispheric cell assemblies. Pseudowords had no increased bilateral activation because of the lack of cell assemblies no summation process took place.

In contrast word, pseudoword activate randomly cell assemblies of similar words. But this activation is probably shorter in duration and faster terminated, because there is no corresponding cell assembly for a pseudoword.

B. Interhemispheric Cooperation while Processing Familiar and Unfamiliar Objects

1. Summary

The present study examined interhemispheric cooperation with two different tasks: a stimulus detection task and an object decision task. During the object decision task, line drawings of real and scrambled objects (non-objects) where presented either *unilaterally* to the left visual field (LVF) or right visual field (RVF) or *bilaterally* simultaneously to both visual fields (BVF). Subjects were instructed to make a familiarity decision, in which they decided, whether a line drawing of a real existing object or a meaningless non-object was presented. A significant Category x Presentation Mode interaction was revealed for both behavioral measures accuracy and reaction time data. When real objects were presented, a bilateral advantage was found. Performance in the bilateral condition exceeded unilateral conditions being significantly more accurate and faster. In contrast, non-objects did not gain from bilateral stimulation. Performance during bilateral trials resembled performance during unilateral trials.

In the second experiment, a stimulus detection task was used which did not require decision-making. Checkerboards were presented in unilateral and bilateral conditions. In this simple reaction task, subjects were instructed to press a button as soon as they detected a stimulus. Again, a bilateral advantage was found: Reactions to bilateral trials were faster than reactions to unilateral trials.

Comparing the two tasks it was found that the magnitude of bilateral advantage was higher for the familiarity task than for the simple reaction task.

The current results provide further evidence that the bilateral advantage is only achieved for meaningful, familiar stimuli like words, faces and objects. A bilateral advantage has never been reported for meaningless stimuli like pseudowords, unfamiliar faces or non-objects. An attempt to explain the bilateral advantage was made using a neurocognitive model. It states that during learning mechanisms cell assemblies are formed that spread across both hemispheres. Simultaneous stimulation of both hemispheres therefore activates interhemispheric cell assemblies in both hemispheres and ignites a

summation process that results in superior bilateral processing. Since only learned stimuli are represented in cell assemblies, no bilateral advantage is obtained after bilateral stimulation with meaningless, new stimuli.

In this study, bilateral advantage was found in a familiarity task that required decision-making, as well as in a simple reaction task that did not. It appears likely that the two tasks elicited bilateral advantages at different processing stages. Whereas only stimulus detection is required in the simple reaction task, the object decision task requires full stimulus identification. This suggests that the bilateral advantage in the simple reaction task is formed on a perceptual level. This means that better performance is obtained, when more visual information is presented. Therefore, a bilateral advantage during simple stimulus detection can be seen independently from stimulus properties.

2. Introduction

There is broad evidence for the existence of a bilateral advantage. Processing of meaningful stimuli presented bilaterally is superior to stimuli presented unilaterally. In contrast, the processing of meaningless stimuli does not gain from bilateral presentation. In a lexical decision task, the bilateral advantage was demonstrated for words but not for meaningless pseudowords (Mohr et al. 1994b, Mohr et al. 1996, Mohr et al. 2000). It was shown for words written in familiar script form of Japanese but not for words written in unfamiliar script form (Yoshizaki, 2001). Further, a bilateral advantage was found during a familiarity decision task for familiar faces but not for unfamiliar faces (Mohr et al. 2002, Schweinberger et al. 2003). In contrast, no bilateral advantage was reported during a facial expression classification task, when positive and neutral unfamiliar faces were presented (Schweinberger et al.2003).

A neurocognitive model, based on Hebb's (1949) cell assembly theory, was used for interpreting the bilateral advantage occurring only for meaningful stimuli but not for meaningless stimuli. Simultaneous activation of cell assemblies in both hemispheres is supposed to ignite a summation process that leads to improved processing. Cell assemblies are a consequence of learning mechanisms and are widely distributed over both

hemispheres. Therefore, only meaningful, familiar stimuli are represented in cell assemblies, whereas no cell assemblies exist for unfamiliar, meaningless stimuli that we have never encountered before.

However, the bilateral advantage after redundant bilateral stimulation of both hemispheres has not only been reported for tasks that required decision-making, but also during simple reaction tasks. Faster reactions were found in a pattern detection task when stimulation was presented bilaterally compared to unilateral stimulation (Miller, 1982). In a similar experiment, Minussi et al. (1998) found faster reactions after bilateral stimulation, as well as shorter latencies of early visual evoked potentials in the bilateral condition compared to unilateral conditions.

These findings are somewhat conflicting with the assumption that the bilateral advantage results from the summation of activation of cortical cell assemblies. An explanation might be that different processing strategies are predominant during simple reaction and decision-making. Simple reaction tasks require fast visual detection that probably benefits from redundant stimulation due to higher overall cortical activation in a bilateral condition. Decision tasks, however, require full stimulus identification. In this case only stimuli that are represented in neuronal networks (due to learning mechanisms) elicit higher cortical activation because they ignite the summation of activation in cortical cell assemblies.

The present experiment was designed to examine the bilateral advantage in an object decision task. Objects and non-objects were presented *unilaterally* in the LVF or RVF, or *bilaterally* in both visual fields. Earlier findings predict the occurrence of a bilateral advantage only for familiar objects. For non-objects performance in bilateral condition should resemble performance in unilateral conditions.

Additionally, the effect of bilateral stimulation was examined in a simple stimulus detection task. A bilateral advantage was also expected to occur in this task (Miller, 1982; Minussi et al. 1998). Both tasks were given to each participant, in order to compare bilateral performance in the object decision task with bilateral performance in the simple reaction task. More specifically, the magnitude of the bilateral advantage was expected to

differ between the two tasks, because cortical summation processes are assumed to occur at different processing stages (stimulus detection vs. stimulus identification).

3. Methods

Subjects

Twenty-four volunteer students (11 female and 13 male) were recruited from the University of Konstanz and were paid for study participation. Their mean age was 22.8 years (SD=2.5), and all of them had finished 13 years at a German secondary school. Handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Only right-handed participants with a minimum handedness score of 70 were included in the study. The mean handedness score was 92.1 (SD=10.2). All participants had normal eyesight, or their eyesight was corrected to normal. Subjects with a history of drug abuse, neurological or psychiatric impairment were not included in the study.

Procedure and Materials

Participants accomplished two behavioral tasks: an object decision task and a simple reaction time task. The order of task presentation was counterbalanced across participants. Lateralized visual hemifield stimulation was used in both tasks. In the object decision task line drawings of real objects and of non-objects were presented. Stimulus presentation was tachistoscopic. All stimuli appeared either *unilaterally* in the right visual field (RVF) or in the left visual field (LVF) or simultaneously in *both* visual fields (BVF). Drawings of real objects were selected from the picture set of Snodgrass and Vanderwart (1980). Only pictures of inanimate objects like furniture or tools with familiarity values higher than 3.5 (on a scale ranging from 1 to 5, 5 representing high familiarity) were selected. Non-objects were taken from Kroll and Potter (1984). 40 object and 40 non-objects were selected. They were matched for size, complexity and brightness. All stimuli were presented in each of the three presentation conditions: left visual field, right visual field and both visual fields (also see **Figure IV.B.1**).

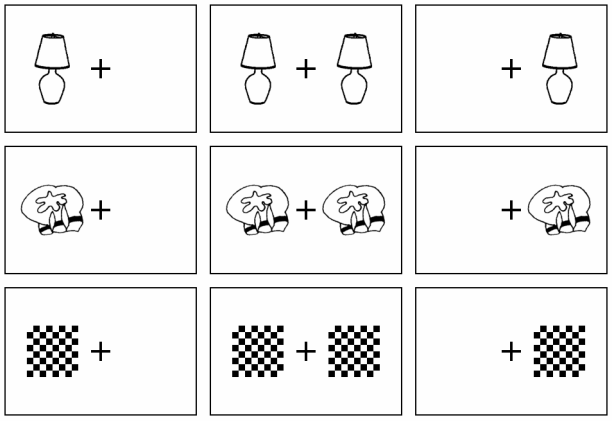

Figure IV.B.1. Experimental design of the object decision task: Line drawings of existing objects and of scrambled objects (non-objects) were presented either unilaterally to the LVF, RVF or simultaneously to both visual hemi-fields.

During the simple reaction task, stimuli were also presented tachistoscopically in unilateral and bilateral conditions. Stimuli were square black and white checkerboards. All stimuli subtended a maximum horizontal and vertical visual angel of 1.3°. Horizontal distance from the fixation cross to the inner stimulus edge was 2.3°, and 3.6° to the outer edge. Stimuli were on the screen for 40 ms in both tasks. The line drawings of objects and non-objects were white against a black background.

Participants were seated 1 meter in front of a 19-inch computer screen with their heads placed on a chin rest with a forehead restraint bar. Response buttons were four keys of a reversed computer keypad (F1, F2, F11, F12). Responses were given bimanually: both index fingers were used when a familiar object appeared; both middle fingers were used when an unfamiliar object appeared. In the simple reaction task, responses were given with both index fingers. An 18 trial practice block preceded each of the two experimental blocks. Experimental sessions always started with the object decision task. The duration of the whole experimental session was approximately forty minutes.

Participants were instructed to carefully fixate their eyes on the fixation cross in the middle of the computer screen and to be attentive to the stimuli presented in the three presentation conditions. In the object decision task, subjects were instructed to decide, whether a familiar/meaningful object or an unfamiliar/meaningless non-object was presented. They were asked to respond as quickly and accurately as possible. During the

simple reaction task, participants were told to respond as quickly as possible after the onset of a visual stimulus.

Each trial started with a warning tone of 100 ms duration that indicated the upcoming stimulus presentation. The tone was followed by a fixation cross that lasted 800 ms in the object decision task, and varied in length between 800 – 1800 ms in the simple reaction task. After that, stimuli (an object/non-object, or a checkerboard) were presented for 40 ms. Onset to onset interval was 3500 ms. In the object decision task a total of 120 objects and 120 non-objects were presented. Each stimulus appeared once in each presentation condition (LVF, RVF, or BVF). In the simple reaction task 150 checkerboards were shown; 50 trials in each presentation condition. Experimental stimulation was generated with ERTS (Experimental Run Time System, Berisoft Cooperation, Beringer, 1996).

Statistical Analysis

Accuracy (percentage of correct responses) and mean latency of correct responses were determined for all subjects. This was done separately for objects and non-objects in the three presentation conditions. In the simple reaction task only response latencies were collected in the three presentation conditions. A two-way ANOVA was calculated for accuracy and latency data with the factors Category (objects vs. non-objects) and Presentation Mode (LVF, BVF vs. RVF) in order to analyze the bilateral advantage in the object decision task. Response latencies of the simple reaction task were analyzed by means of an one-way ANOVA with the factor Presentation Mode (LVF, BVF vs. RVF).

Further, it was intended to compare the bilateral advantage for objects and non-objects during the object decision task with the bilateral advantage in the simple reaction task. For this purpose, the bilateral advantage was determined separately for objects, non-objects and the checkerboards of the simple reaction task by subtracting latencies in the bilateral condition from the mean latencies in both unilateral conditions [(LVF+RVF)/2 – BVF)]. Differences in bilateral advantage between the three conditions were analyzed by computing a one-way ANOVA with the factor Category (objects, non-objects vs. checkerboards).

When appropriate, p-values were corrected according to Greenhouse-Geiser; significant interactions were further analyzed with planned comparisons.

4. Results

Object Decision Task: Accuracy Data

Analysis of the mean percentage of correct responses revealed a significant main effect for **Presentation Mode** ($F(2,46)=5.70$, $p<0.01$) with overall better performance in the bilateral condition compared with both unilateral conditions. Performance after LVF and RVF did not differ. Differences in overall performance approaches significance: accuracy was higher for non-objects than for objects (Category ($F(1,23)=3.00$, $p<0.10$). This result might be explained with a response tendency towards non-object in case of uncertainty.

Analysis of the mean percentage of correct responses revealed a significant **Category x Presentation Mode** interaction ($F(2,46)=10.29$, $P<0.001$). As shown in **Figure IV.B.2**, a bilateral advantage was obtained, when real objects were presented. Performance was better in the bilateral conditions compared to both unilateral conditions (BVF vs. LVF: $F(1,23)=18.21$, $P<0.001$; BVF vs. RVF: $F(1,23)=18.21$, $P<0.001$). For non-objects performance did not differ significantly between bilateral and unilateral stimulus presentation. Differences in performance between LVF and RVF stimulation were obtained, neither for objects nor for non-objects. However, better performance was found for objects than for non-objects in LVF ($F(1,23)=11.55$, $p<0.01$) and RVF ($F(1,23)=4.75$, $p<0.04$) conditions, whereas no difference was found in bilateral condition.

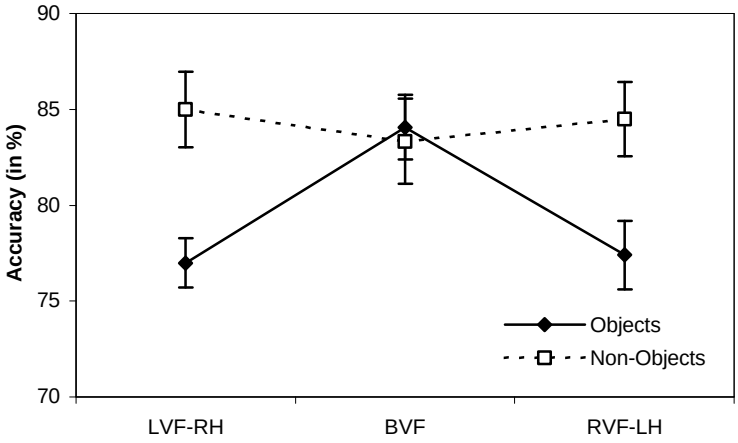

Figure IV.B.2. Category x Presentation Mode interaction for accuracy data: Percentage of correct responses are presented for objects and non-objects in the left visual field (LVF), right visual field (RVF) and the bilateral condition (BVF). Responses were more accurate when objects were presented bilaterally than unilaterally. Accuracy for non-objects did not benefit form bilateral presentation. However, overall accuracy was higher for non-objects than for objects. This is possibly due to the subjects´ tendency to respond towards non-objects in case of uncertainty. Error bars indicate standard error of the mean.

Object Decision Task: Latency Data

A two-way ANOVA calculated on the latency data revealed overall faster reactions for real objects than for non-objects (Category: $F(1,23)=33.17$, $p<0.001$). Comparing the three presentation conditions, fastest reactions were made in bilateral trials, whereas unilateral conditions did not differ (Presentation Mode: $F(2,46)=4.28$, $p<0.03$).

The Category x Presentation Mode interaction is shown in **Figure IV.B.3** Differences between objects and non-objects in the three presentation conditions were analyzed further with planned comparisons. Reactions to objects were faster than reactions to non-objects in all three presentation conditions (all p-values <0.01). Comparing the presentation conditions, objects had shorter response latencies in the bilateral condition than in the RVF ($F(1,23)=8.20$, $p<0.01$) and LVF ($F(1,23)=14.71$, $p<0.001$) condition. Object related reaction time did not differ between unilateral conditions. For non-objects no difference was found between the three presentation conditions (F-values <1).

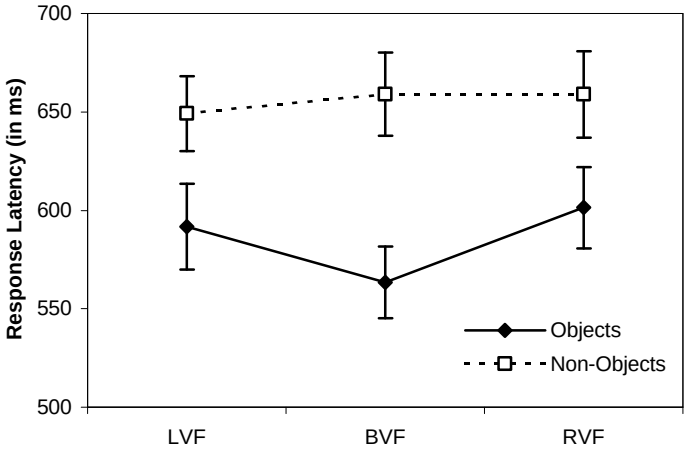

Figure IV.B.3. Category x Presentation Mode interaction for latency data: Response latencies are shown separately for objects and non-objects in the three presentation conditions. Overall response latencies were shorter for objects than for non-objects. Differences among presentation conditions were found only for objects. Reaction time for objects was significantly shorter after bilateral stimulus presentation than after stimulus presentation in either unilateral condition. Error bars indicate standard error of the mean.

Simple Reaction Task

Reaction times in the simple reaction task are presented in **Figure IV.B.4**. A one-way ANOVA calculated on response latencies revealed differences among the three presentation conditions (Presentation Mode: $F(2,46)=15.98$, $P<0.001$). Planned comparisons showed that reactions in the bilateral condition were significantly faster than reactions in both unilateral conditions (both p-values <0.001). No difference among the unilateral conditions was found.

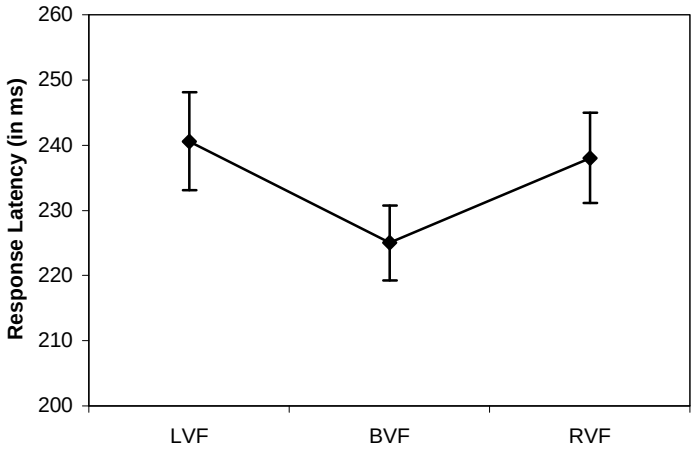

Figure IV.B.4. Simple reaction task: Response latencies are displayed in the three presentation conditions (LVF, RVF and BVF). Reactions were significantly faster when stimuli were presented bilaterally. Error bars indicate standard error of the mean.

Comparison of the Bilateral Advantage

At first a two-way ANOVA with the factors Presentation Mode and Category was computed. The factor Category included response latencies for objects, non-objects and the response latencies in the simple reaction task. Overall reactions where faster during the simple reaction task (Category: $F(2,46)=327.90$, $p<0.001$) and in the bilateral condition (Presentation Mode: $F(2,46)=7.48$, $p<0.01$). A Category x Presentation Mode interaction ($F(4,92)=3.54$, $p<0.04$) revealed differences in the bilateral advantage between objects, non-objects and the simple reaction task. Planned comparisons showed a bilateral advantage (shorter latencies in the bilateral condition than in both unilateral conditions) for objects and for the simple reaction task.

Earlier analyses had already revealed a bilateral advantage for objects and during the simple reaction task. In the present analysis it was intended to compare the magnitude of the bilateral advantage between the two tasks.

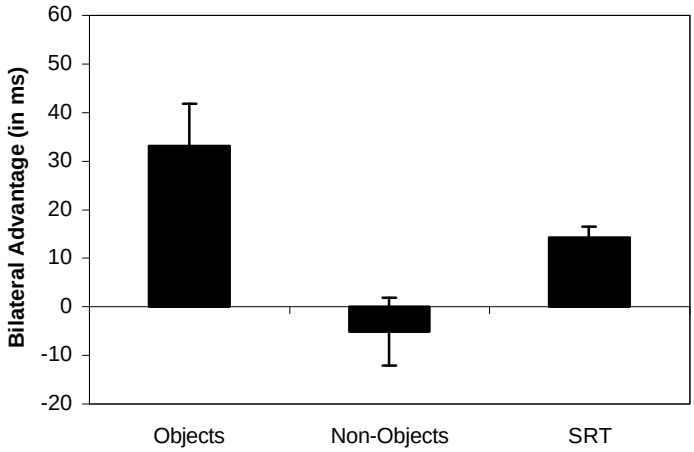

Figure IV.B.5. Bilateral advantage for objects, non-objects and during the simple reaction task (SRT) is displayed. The magnitude of the bilateral advantage was significantly higher for objects than during the simple reaction task. Error bars indicate standard error of the mean.

The bilateral advantage in the latency data was determined separately for objects, non-objects and the simple reaction condition (**Figure IV.B.5**). It was obtained by subtracting bilateral latencies from the average unilateral latencies. A one-way ANOVA revealed a significant difference between the three stimulus types (Category: $F(2,46)=7.76$, $p<0.01$). Magnitude of bilateral advantage was greater for objects than for non-objects ($p<0.02$) and it was also greater for objects than for patterns during the simple reaction task ($p<0.05$). Bilateral advantage was larger for the simple reaction task than for non-objects ($p<0.02$).

5. Discussion

The present study examined three hypotheses: 1) A bilateral advantage was expected for objects, but not for non-objects in an object decision task. 2) A bilateral advantage was also expected in a simple reaction task. 3) The magnitude of the bilateral advantage should differ between the two tasks, when they are performed on different levels of processing (simple detection in the simple reaction task vs. full stimulus processing in the object decision task).

Experimental results confirmed the assumptions. During the **object decision task**, superior bilateral performance with higher accuracy and shorter response latencies was found for objects, but not for non-objects. However, reactions to non-objects were found to be more accurate than reactions to objects. This might be explained with a response bias towards non-objects in case of uncertainty. It was found that the accuracy of bilateral responses was comparable for objects and non-objects, whereas accuracy was reduced in unilateral conditions for objects compared to non-objects. Therefore, bilateral accuracy was superior to unilateral performance only for objects. In contrast, response latencies were clearly superior for objects bilaterally presented compared to objects unilaterally presented and compared to non-objects. A bilateral advantage was also found for stimulus detection in the **simple reaction task**. Moreover, **differences in the magnitude of the bilateral advantage** were revealed. The latency difference between bilateral and unilateral conditions for objects was twice as high as in the stimulus detection task.

The current results provide further evidence for interhemispheric cooperation during the processing of meaningful stimuli. In other experiments, a bilateral advantage was found for words or familiar faces, but not for pseudowords or unfamiliar faces (Mohr et al., 1994b; Mohr et al., 1996; Mohr et al. 2000; Mohr et al. 2002; Schweinberger et al., 2003). The present results revealed a bilateral advantage (as an indicator of interhemispheric cooperation) only for objects, but not for non-objects.

Further, a bilateral advantage was found in a simple reaction time task in the current study. The magnitude of the bilateral advantage was found to be significantly higher during the familiarity task than during the simple reaction task, however. This result suggests that the bilateral advantage does not necessarily depend on familiarity of the

presented stimuli. The magnitude of bilateral advantage seems to depend on different aspects: A simple reaction task does not require full stimulus identification; therefore stimulus familiarity might be irrelevant. During a simple reaction task a bilateral advantage is already gained on a perceptual level. Presentation of two stimuli rather than one stimulus alone increases the amount of detectable information and therefore enhances performance. Overall cortical activation is higher for two stimuli than for one stimulus.

In a familiarity decision task, full stimulus identification is required in order to successfully perform the recognition task. In this case, stimulus familiarity is a crucial aspect for the bilateral advantage to emerge; and bilateral presentation does not per se elicit a bilateral advantage. This finding also supports the view that different bilateral advantages are measured in the different tasks.

The bilateral advantage found in the simple reaction task might be explained with an independent horse race model (Hellige, 1993; Miller, 1982; Mordkoff and Yantis, 1991; Raab, 1962; Zaidel et al. 1990). This model predicts that both hemispheres act as independent processors and the hemisphere that operates more efficiently, initiates the reactions. Since no lateralization effects were found in the simple reaction task, both hemispheres were equally capable to perform the task. Therefore, the faster hemisphere triggered the reaction on each bilateral trial, which produced faster overall reactions. Since the horse race model predicts faster and more accurate responses on bilateral trials of all kinds of stimuli, it is capable to explain the bilateral advantage in the simple reaction time task. In contrast, this model is not capable to explain the differential bilateral advantage found in the familiarity decision task in the present study.

In case of the familiarity task, double stimulation alone does not improve performance in general, because stimuli have to be fully processed and not only detected. We found a bilateral advantage for objects and no bilateral advantage for non-objects. According to the neurocognitve model, simultaneous activation of cell assemblies distributed over both hemispheres is responsible for the occurrence of the bilateral advantage. Cell assemblies are formed by learning mechanisms and are distributed across both hemispheres (Pulvermüller and Mohr, 1996; Pulvermüller, 1999). In case of bilateral stimulation of a cell assembly with familiar stimuli, the relevant cell assembly is stimulated twice, leading to a summation of neuronal activity and therefore to faster ignition. In case

of an unfamiliar stimulus that is not represented in cell assemblies, no interhemispheric summation occurs. This differential bilateral advantage therefore seems to be inevitably connected to stimulus recognition. Only familiar stimuli are represented in cortical cell assemblies and are therefore able to elicit a bilateral advantage.

The bilateral advantage found in the simple reaction task does not violate the assumptions of the neurocognitve model. It is also possible to explain the finding with this model. Simultaneous bilateral stimulation in this case does not ignite summation of activation in cell assemblies, but it also triggers higher overall cortical activation than unilateral stimulation and therefore leads to faster processing. No more stimulus processing is needed after stimulus recognition in the simple reaction task, processing is terminated after stimulus detection.

In summary, the present data provide further support for the assumption that the bilateral advantage in familiarity decision tasks occurs only for meaningful, familiar stimuli. A bilateral advantage was found for objects, but not for non-objects. Additionally, a bilateral advantage was found in a simple stimulus detection task that does not require stimulus recognition. This suggests that a *differential bilateral advantage* found for meaningful stimuli but not for meaningless stimuli, might only be observed in tasks requiring full stimulus processing.

C. Effects of Unilateral and Bilateral Redundancy on Lexical Processing

1. Summary

This study compared bilateral redundant stimulation with unilateral redundant stimulation in order to investigate inter-hemispheric cooperation. It has been argued that redundant stimulation with meaningful stimuli causes the summation of cortical activation. The present study was designed to compare the bilateral advantage with the unilateral redundancy gain. Words and pseudowords were presented unilaterally to the left and right visual field and bilaterally to both visual fields. Either one copy or two copies of a stimulus were presented simultaneously in each condition. A unilateral redundancy gain would be obtained when performance was better in the two copies condition compared with the one copy condition and a bilateral advantage would be obtained when performance in the bilateral condition exceeded performance in unilateral conditions. Consequently, the comparison between bilateral condition with one copy in each visual field and unilateral condition with two copies in one visual field would allow an estimation whether it is stimulating both hemispheres or whether it is stimulus redundancy that facilitated processing.

A bilateral advantage and a unilateral redundancy gain were obtained only for meaningful words. Performance in the pseudoword condition was not enhanced when stimuli were presented unilaterally or bilaterally redundant compared with presentation of only one copy of the stimulus. In contrast to an earlier study (Mohr et al., 1996), we found bilateral redundant stimulation to be superior to unilateral redundant stimulation for the word condition.

Unilateral and bilateral redundancy gain is usually explained by the Hebbian cell assembly model (Hebb, 1949). Redundant stimulation with meaningful material, regardless of stimulus location, produces a summation of simultaneously active cell assemblies and improves efficiency of processing. Interestingly, the present data suggest that stimulus location relevant. It seems that inter-hemispheric summation exceeds intra-hemispheric summation.

2. Introduction

The question, how the two cerebral hemispheres process information, has been addressed in many studies using various experimental designs. Independent processing, interhemispheric inhibition or cooperation have been suggested as mechanisms of interhemispheric interaction. A bilateral advantage after redundant bilateral stimulation was demonstrated for phonetically and orthographically correct words and for familiar faces, but not for meaningless pseudowords and unfamiliar faces (Mohr et al., 1994b; Mohr et al., 1996; Mohr et al. 2000; Mohr et al. 2002; Schweinberger et al., 2003; Yoshizaki, 2001).

Initially, the horse race model (Mordkoff and Yantis, 1991; Hellige, 1993; Miller, 1982; Zaidel et al., 1990) has been taken into account to explain the bilateral advantage. According to this model, both hemispheres work independently. The faster hemisphere (i.e. the one being more specialized for the task) controls the response in the bilateral condition. This model predicts superior bilateral performance for all kinds of stimuli.

However, no bilateral advantage has been observed for pseudowords, for words written in an unfamiliar script form of Japanese, and for unfamiliar faces. Since the bilateral advantage occurs only for familiar stimuli, one could argue that it is a recognition effect in response to target stimuli such as words or familiar faces. In contradiction to this hypothesis, Schweinberger et al. (2003) did not find a bilateral advantage in a facial expression recognition task. They used pictures of unfamiliar faces with positive and neutral facial expression. Pictures with positive facial expression might be considered as target stimuli. But no bilateral advantage was revealed, when discrimination between happy and neutral unfamiliar faces was required. Another finding that violated the assumptions of the horse race model was obtained from a split-brain patient whose callosal connections were surgically removed and therefore the two hemispheres processed more independently (Mohr et al., 1994a). No bilateral advantage was revealed after bilateral stimulation with words in this patient.

A neurocognitive model stating a more differential bilateral advantage was developed (Mohr et al. 1994b, Pulvermüller & Mohr, 1996) as an alternative explanation based on Hebb's cell assembly theory (Hebb, 1949). According to this model, meaningful

stimuli are previously learned and are cortically represented in cell assemblies with strong internal connections. These cell assemblies are formed as a result of frequent co-activation of neurons located in different cortical regions (auditory, visual etc) during a learning process. Activation of neurons of a cell assembly initiates the activation of the whole assembly. This is called ignition. The neurons of one cell assembly are not restricted to small cortical regions. Rather, it is assumed that cell assemblies consist of local clusters of neurons that are distributed over both hemispheres and are strongly connected by the corpus callosum via excitatory connections. Differences in cortical laterality for different word forms (e.g. function and content words) can be explained with different topographies of cell assemblies. Whereas function words are more represented in perisylvian regions of the left hemisphere, content words do also have visual associations, and may be distributed beyond perisylvian and visual cortices of both hemispheres. The cell assembly model is also able to explain the bilateral advantage found after bilateral redundant stimulation with two identical copies of a learned stimulus, and the absence of a bilateral advantage when meaningless stimuli are presented. In case of bilateral stimulation of a cell assembly with words, the relevant cell assembly is stimulated twice, leading to a summation of neuronal activity and therefore to faster ignition. This explanation is supported by the absence of a bilateral advantage for pseudowords that are not represented in cell assemblies, as well as by the absence of a bilateral advantage after commissurotomy (Mohr et al. 1994a) when interhemispheric cell assemblies are no longer available.

It has also been suggested that summation for meaningful learned stimuli occurs not only after bilateral but also after unilateral redundant stimulation (Mohr et al. 1996). Mohr et al. (1996) compared unilateral redundant stimulation (presentation of two stimuli either in the LVF or RVF), bilateral redundant stimulation (presentation of one stimulus in each visual field), and bilateral redundant stimulation (presentation of two stimuli in each visual field) (see **Figure IV.C.1**). When two-word stimuli were presented, no difference between RVF and bilateral conditions was revealed. In contrast, performance was increased compared to all other conditions when four stimuli were presented. Given these results, it was argued that the neurobiological model might explain why unilateral and bilateral redundant stimulation did not differ. Summation in interhemispheric networks might occur within or between hemispheres when several copies of a stimulus are presented at the same time, regardless of stimulus location (Mohr et al. 1996). However, it

was not possible to determine the influence of redundancy on unilateral stimulation using this design.

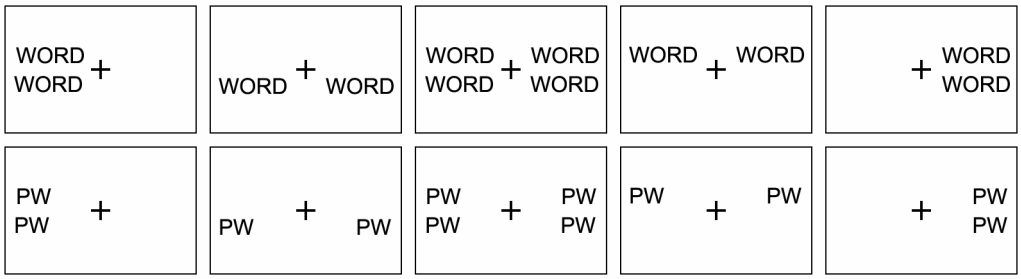

Figure IV.C.1. Experimental design used by Mohr et al. (1996). Two stimuli were presented either unilaterally in the LVF or RVF, or two stimuli were presented bilaterally in both upper or lower visual fields, or four stimuli were presented.

The present experiment was designed to distinguish the influence of stimulus redundancy and bilateral stimulation. Therefore, either one or two copies of the same stimulus were presented in each visual field in unilateral and bilateral conditions (**Figure IV.C.2.**).

Three different result patterns are possible:

1) If it was only *redundant stimulation* that facilitates processing, then equal performance would be expected for bilateral stimulation with one copy in each visual field and redundant unilateral simulation in the RVF. This hypothesis is in line with the findings of Mohr et al. (1996). A main effect for redundancy would be expected if it was valid. Simultaneous ignition of cortical cell assemblies should result in better performance, regardless of redundant stimulation within or across hemispheres.

2) Only bi-hemispheric stimulation improves performance. If this was the case, only a visual field effect would be expected. The prediction is that after bi-hemispheric stimulation ignition of cell assemblies in both hemispheres results in summation and a bilateral advantage. Whereas ignition of cell assemblies within one hemisphere would not be expected to be enhanced by redundant stimulation, possibly due to a ceiling effect. This means that presentation of only one stimulus is sufficient to ignite the intrahemispheric cell assembly.

3) A third possible outcome predicts both: a bilateral *and* a redundancy gain. After bilateral stimulation with two copies in each visual field, both effects would be expected to sum up. A difference in the size of the two effects might show up when the bilateral condition with one copy in each visual field (BVF1) and the right visual field condition with two copies in each visual field (RVF2) are compared. Better performance in the BVF1 condition would indicate that interhemispheric summation improves performance more than intrahemispheric summation. This might also be explained with the cell assembly theory. Bi-hemispheric stimulation might elicit the ignition of more widespread cell assemblies than stimulation within one hemisphere.

3. Method

Participants

Twenty-three volunteer students (14 female and 9 male) were recruited at the University of Konstanz. They were paid for study participation. Their mean age was 23.83 years (SD = 3.83; range = 19-34 years). Handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Only right-handed participants with a minimum handedness score of 70 were included in the study. The mean handedness score was 96.96 (SD = 8.22; Range: 70-100). All participants were monolingual native speakers of German and had normal vision (or corrected to normal vision). Participants with a history of neurological or psychiatric disease or drug abuse were not included in the study.

Procedure and Materials

Words and pseudowords were presented visually in a lexical decision task. Participants were instructed to decide whether a presented letter sting was a meaningful German word or a meaningless pseudoword by pressing two out of four response buttons bimanually. A tachistoscopic stimulus presentation was chosen, in order to present stimuli either unilaterally to the right visual field (RVF) or to the left visual field (LVF), or bilaterally simultaneously to both visual hemi-fields (BVF). In each presentation condition either one or two copies of a stimulus were presented in one visual field. Each word and pseudoword appeared twice during the experiment: once in the one-stimulus-condition and once in the two-stimulus-condition (see also **Figure IV.C.2**).

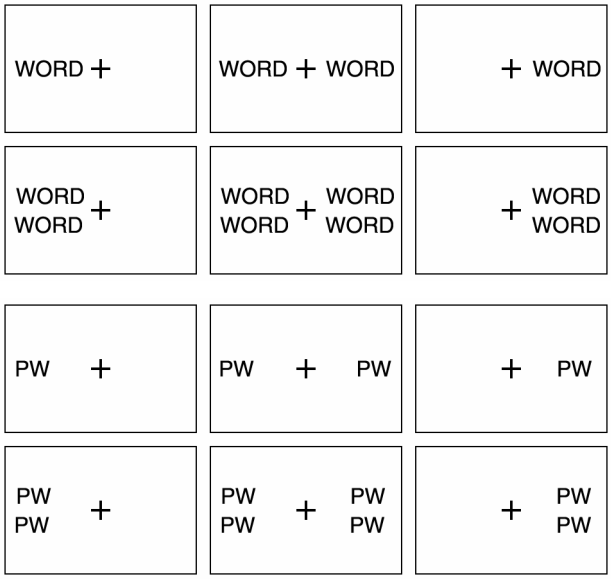

Figure IV.C.2. Applied presentation conditions are displayed. Words or pseudowords were presented as one stimulus or two stimuli in either the left visual field, the right visual field or both visual fields simultaneously.

Participants were seated 1 m in front of a computer screen (19-inch diagonal) with their heads placed on a chin rest and their foreheads leaned against a restraint bar. Four keys of a computer keyboard were used as response buttons. The duration of one experimental session was approximately 45 minutes. A verbal instruction and a practice block with 48 items preceded the actual experiment. Subjects were instructed to carefully focus on the fixation cross in the middle of the computer screen and to attend to the letter strings presented in the different conditions. Lexical decisions were made by pressing two out of four response buttons bimanually: with both index fingers after word presentation and with both middle fingers after pseudoword presentation. Participants were told to respond as quickly and as accurately as possible.

Each trial started with a fixation cross that was on the screen for 800 ms. It was followed by a warning tone (100 ms duration) that indicated the immediate stimulus presentation. Hereafter a word or a pseudoword was presented for 100 ms in one out of six conditions. Onset to onset interval was 4 seconds. Stimuli were presented in black upper-case letters on a gray background. Stimuli deviated between 1.5° and 4° from the fixation cross horizontally and 0.6° vertically. A total of 120 words and 120 pseudowords were presented. All stimuli were bi-syllabic and were four to eight letters long. Words were German content words with a high frequency of occurrence (100-1000 per million,

according to Ortmann, 1975). Pseudowords were created by shuffling letters of a real word or by exchanging letters between word stimuli. Pseudowords were pronounceable and orthographically regular but not homophonous to real words.

Statistical analysis

Accuracy (percentage of errors) and mean response times for correct responses were determined for each stimulus category, presentation mode and subject. A multivariate ANOVA was calculated for accuracy and reaction time data with the factors Wordness (words vs. pseudowords), Presentation Mode (LVF, RVF vs. BVF) and Redundancy (one copy vs. two copies in each visual field). Additional analyses for the word condition were computed in order to compare bilateral with unilateral redundant conditions. All p-values were corrected according to Greenhouse-Geisser when necessary. Significant interactions were further analyzed by planned comparisons.

4. Results

Accuracy Data

No significant interaction of Wordness x Presentation Mode x Redundancy ($F<1$) was revealed when analyzing the mean percentage of errors. In **Figure IV.C.3** accuracies are displayed.

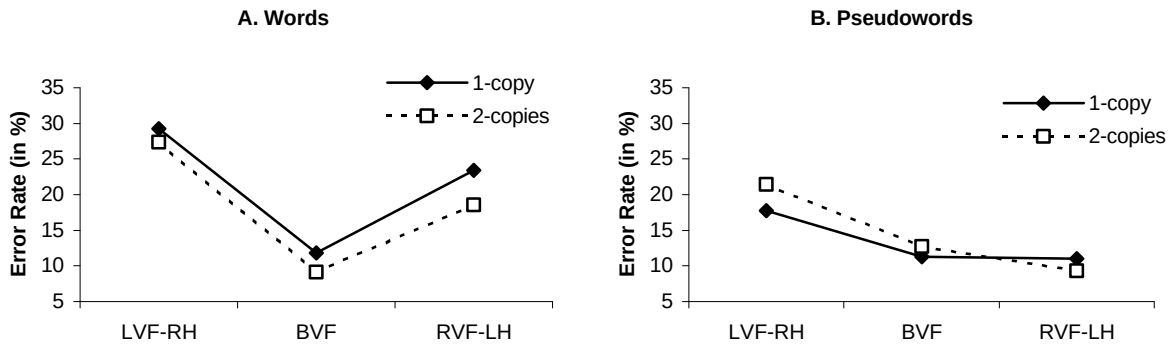

Figure IV.C.3. Accuracy data: Wordness x Presentation Mode x Redundancy.

A significant Wordness x Presentation Mode interaction ($F(2,44)=9.48$, $p<0.01$, $e=0.95$) was found. Planned comparisons showed that performance was significantly better for words after bilateral stimulation compared with unilateral stimulation (BVF vs. LVF: $F(1,22)=93.68$, $p<0.001$; BVF vs. RVF: $F(1,22)=22.96$, $p<0.001$). In the pseudoword condition only the LVF condition differed from the BVF condition (BVF vs. LVF: $F(1,22)=33.06$, $p<0.001$; BVF vs. RVF: $F<2.5$). For both wordness conditions an increased accuracy was observed after RVF compared to LVF stimulation (words: $F(1,22)=5.01$, $p<0.04$; pseudowords: $F(1,22)=24.67$, $p<0.001$). A significant Wordness x Redundancy interaction ($F(1,22)=8.03$, $p<0.01$) was found. Post hoc testing revealed that more accurate responses after redundant stimulation within one visual field (compared with only one copy in one visual field) were obtained only for words, but not for pseudowords (words: $F(1,22)=10.71$, $p<0.01$; pseudowords: $F<2$). A Presentation Mode x Redundancy interaction ($F(2,44)=4.17$, $p<0.05$, $e=0.95$) was obtained. Planned comparisons indicated a significant accuracy improvement after redundant stimulation compared with single stimulus presentation only in the RVF condition ($F(1,22)=8.63$, $p<0.01$). Significant main effects were found for Wordness ($F(1,22)=4.33$, $p<0.05$), with higher overall error rates in the word condition than in the pseudoword condition, and Presentation Mode ($F(2,44)=41.95$, $p<0.01$, $e=0.70$).

Only after stimulation with words 1superior processing after bilateral presentation was observed. Although, Wordness and Presentation Mode did not interact with the factor Redundancy, a separate analysis for words was calculated. The comparison between bilateral stimulation with one copy in each visual field (BVF1) and right visual field stimulation with two copies (RVF2) was considered the most interesting.

Analyzing the word condition revealed only main effects for Presentation Mode ($F(2,44)=25.44$, $p<0.001$, $e=0.72$) and Redundancy ($F(1,22)=10.71$, $p<0.01$). Planned comparisons found significant differences between both bilateral conditions and all four unilateral conditions (see **Table IV.C.1**). Most interestingly, the difference between BVF1 and RVF2 was significant ($F(1,22)=8.08$, $p<0.001$).

Table IV.C.1. One-way ANOVAs for the comparison between presentation conditions for word stimulation.

	Accuracy		Latency	
Presentation Mode	F(1,22)	P	F(1,22)	P
LVF1 vs. BVF1	61,38	<	23,37	<
LVF1 vs. RVF1	2,27	n.s.	1,05	n.s.
LVF1 vs. LVF2	1,18	n.s.	0,04	n.s.
LVF1 vs. BVF2	61,89	<	12,94	<
LVF1 vs. RVF2	9,94	<	3,34	0.09
BVF1 vs. RVF1	17,13	<	7,46	<
BVF1 vs. LVF2	76,43	<	23,60	<
BVF1 vs. BVF2	3,52	0.08	0,02	n.s.
BVF1 vs. RVF2	**8,08**	**<**	**5,66**	**<**
RVF1 vs. LVF2	1,28	n.s.	1,30	n.s.
RVF1 vs. BVF2	32,01	<	11,96	<
RVF1 vs. RVF2	9,00	<	2,71	n.s.
LVF2 vs. BVF2	84,66	<	15,61	<
LVF2 vs. RVF2	8,42	<	3,77	<
BVF2 vs. RVF2	21,81	<	12,67	<

Latency Data

As for the analysis of accuracy, the interaction between all three factors did not reach significance for the latency data. Shorter latencies after redundant stimulation within visual fields could only be observed after RVF stimulation (**Figure IV.C.4**).

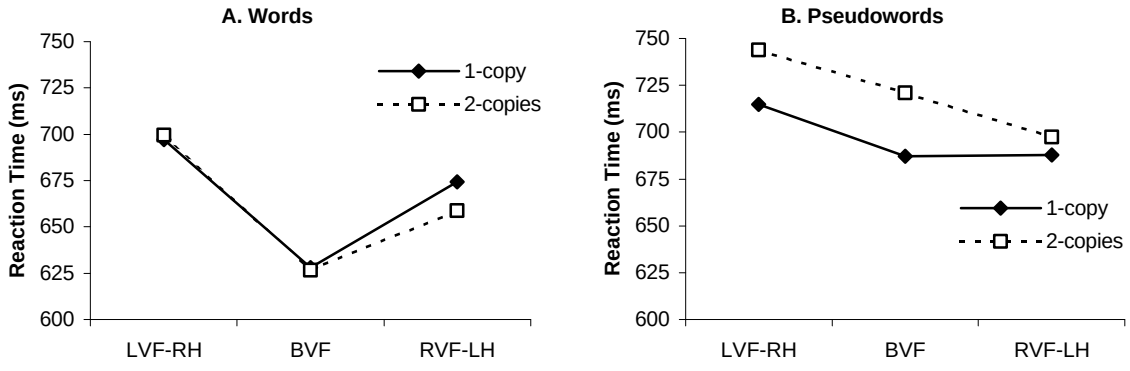

Figure IV.C.4. Latency data: Wordness x Presentation Mode x Redundancy.

The Wordness x Presentation Mode interaction ($F(2,44)=5.53$, $p<0.01$, $e=0.98$) was comparable to the respective interaction in the accuracy data: A bilateral advantage was

only observed after word presentation (BVF vs. RVF: $F(1,22)=11.02$, $p<0.01$; BVF vs. LVF: $F(1,22)=21.62$, $p<0.001$), but not after stimulation with pseudowords (both F-values < 2). Bilateral stimulation with words revealed shorter latencies than with bilateral stimulation with pseudowords ($F(1,22)=26.85$, $p<0.001$). Laterality is indicated by the difference between LVF and RVF stimulation; it approached significance only in the word condition ($F(1,22)=3.45$, $p=0.08$). The Wordness x Redundancy interaction ($F(1,22)=6.32$, $p<0.02$) showed increased reaction times after redundant stimulation with pseudowords compared to single stimulus presentation in each condition ($F(1,22)=6.70$, $p<0.02$). The main effect Wordness ($F(1,22)=10.67$, $p<0.01$) indicated faster reactions after word presentation than after pseudoword presentation. A main effect for Presentation Mode was also obtained ($F(2,44)=5.98$, $p<0.02$, $e=0.60$).

Effects of redundant stimulation within one visual field compared to across both visual fields were further investigated by a separate analysis including words only, as the bilateral advantage was limited to this condition. The main effect for Presentation Mode ($F(2,44)=9.65$, $p<0.01$, $e=0.72$) reached significance. Shorter response latencies were found after bilateral stimulation than after unilateral stimulation (BVF vs. RVF: $F(1,22)=11.02$, $p<0.01$; BVF vs. LVF: $F(1,22)=21.62$, $p<0.001$). Even though the interaction Redundancy x Presentation Mode ($F<1$) was not significant, planned comparisons were computed to determine differences between bilateral and redundant stimulation. As for accuracy data, all differences between both bilateral and the four unilateral conditions were significant (**Table IV.C.1.**). In particular, quicker responses were made after bilateral stimulation (one copy in each visual field) compared with redundant right visual field stimulation (two copies in the RVF) ($F(1,22)=5.66$, $p<0.03$).

5. Discussion

The present study revealed both a bilateral advantage and a redundancy gain for meaningful words. A bilateral advantage was manifested in the overall improved performance for words after bilateral stimulation compared to unilateral stimulation (Presentation Mode x Wordness interaction). Further, the redundancy gain for words was mirrored by higher performance after stimulation with two copies of a stimulus within one visual field, compared to stimulation with only one stimulus in one visual field (Redundancy x Wordness interaction). We did not find a bilateral advantage or a redundancy gain for pseudowords.

Further, with the present design, it was possible to compare bilateral and unilateral redundancy. We found bilateral redundant stimulation (BVF1) to differ from unilateral right visual field redundant stimulation (RVF2), although in both conditions two stimuli were presented.

The bilateral advantage obtained only for words, is in line with earlier findings. Improved performance was obtained after bilateral redundant stimulation compared with unilateral stimulation of meaningful stimuli such as words or familiar faces (Mohr et al., 1994b; Mohr et al., 2002; Schweinberger et al., 2003; Yoshizaki, 2001).

The redundancy gain with better performance after redundant stimulation bilaterally *or* unilaterally was also found for words only. It therefore confirms the findings of Mohr et al. (1996). Redundant unilateral stimulation, as well as redundant bilateral stimulation increased accuracy and reduced response latency.

The present experiment demonstrated improved performance in the bilateral condition compared to the RVF condition when the number of presented stimuli was constant. This result is inconsistent with the findings of Mohr et al. (1996) and Zaidel and Rayman (1994). Mohr et al. (1996) found bilateral conditions with two stimuli resembled unilateral conditions with two stimuli. Therefore they concluded that performance does not differ when the number of presented stimuli is kept constant. Zaidel and Rayman (1994) also compared the influence of redundant stimulation on unilateral and bilateral processing. In a lexical decision task one to four identical copies of a stimulus were presented

unilaterally (LVF or RVF); or two to four identical copies were presented bilaterally (LVF and RVF). For words, bilateral presentation of one copy in each visual field showed to have an advantage over presentation of a single copy in either visual field. A bilateral disadvantage was found for pseudowords. When the amount of presented copies was kept constant, however, bilateral performance exceeded only LVF performance, not RVF performance.

The experimental setting of the present experiment differed from the setting used by Mohr et al. (1996). Whereas we used only two-syllabic words, Mohr et al. (1996) also used short word stimuli with only one syllable. This discrepancy might account for the higher error rates and longer response latencies found in the current experiment. Unilateral performance was especially diminished relative to the performance reported by Mohr et al. (1996). Bilateral performance was similar in both experiments. Furthermore, there were variations in stimulus location. In the current experiment, positions in all conditions were fixed. In the bilateral condition with two copies, stimuli were vertically centered. Mohr and colleagues also used a fixed stimulus presentation. In the bilateral condition with two copies, however, they presented the two stimuli either in the lower or upper visual field. This assignment might have increased spatial uncertainty in the bilateral condition and possibly reduced differences between the bilateral condition (two copies) and unilateral conditions (two copies).

There are other findings suggesting that bilateral stimulus presentation facilitates processing compared to only unilateral presentation. The experiments by i.e. Brown & Jeeves (1993), Koivisto (2000), Larson & Brown (1997), Marsolek et al. (2002) and Norman et al. (1992) used a within or between hemisphere matching design with two stimuli that were presented either unilaterally or bilaterally. Performance after bilateral stimulation was found to be superior to performance after unilateral stimulation. However, the bilateral condition was not always found to be superior to unilateral conditions: Better performance after bilateral processing was observed for the categorization of two similar, but not for identical objects (Koivisto, 2000) or letters (Marsolek et al. 2002). Weissman and Banich (2000) suggested that the degree of hemispheric cooperation depends on task difficulty. Nevertheless, the overall findings indicate that processing is facilitated after bilateral stimulation compared to unilateral stimulation.

The bilateral advantage is a stable effect after bilateral redundant presentation of meaningful stimuli. But what happens in the bilateral condition and why is bilateral redundant stimulation more facilitating than unilateral redundant simulation? According to the horse race model, stimulation of both hemispheres initiates a “race” of independent processing in each hemisphere with the faster hemisphere controlling the response. Having two processing units will therefore lead to more efficient processing. However, the race model cannot explain different aspects of the bilateral advantage. At first, a bilateral advantage has not been shown for unfamiliar or meaningless stimuli (e.g. Mohr et al. 1994a, Mohr et al. 2002, Schweinberger et al. 2003, Yoshizaki, 2001). The horse race model explanation is also violated by the finding, that no bilateral advantage was revealed in a split-brain patient (Mohr et al. 1994a). One might argue that the bilateral advantage is modulated by attention, as it occurs only after some sort of target stimulus. However, Schweinberger et al. (2003) showed that bilateral processing is not always superior to unilateral processing. When facial expressions (positive vs. neutral) of unfamiliar faces were classified, a bilateral advantage did not emerge in any of the conditions. Due to these reasons, the horse race model seems inappropriate to explain the superior processing in bi-hemispheric conditions.

Hebb’s cell assembly theory (Hebb, 1949) offers a good explanation for the bilateral advantage. It has been proposed, that simultaneous stimulation initiates the summation of activation of cortical cell assemblies representing meaningful items. This process then leads to a facilitation of processing after redundant stimulation of meaningful stimuli (Mohr et al. 1994b; Pulvermüller and Mohr, 1996; Pulvermüller, 1999). Mohr et al. (1996) suggested that the cell assembly theory predicts the occurrence of summation after redundant stimulation regardless of stimulus location.

The current data are conflicting with this interpretation, since bilateral performance after redundant stimulation was found to be superior to unilateral redundant stimulation. Pulvermüller (1999) suggested that lexical cell assemblies are lateralized to the left hemisphere, but in case of highly imaginable words with high frequency of occurrence there are also a large number of cell assemblies in the right hemisphere. This could result in better performance after bi-hemispheric stimulation than after unilateral redundant stimulation, because bi-hemispheric stimulation activates a larger number of neurons of a cell assembly than double stimulation of only the left hemisphere. This hypothesis could be

tested by applying the current design to stimuli, which have more lateralized and fewer interhemispheric cell assemblies, for example low frequency words or function words (Pulvermüller et al. 1995).

The present data support the idea that both inter-hemispheric and intra-hemispheric summation occurs only after redundant stimulation with words. Moreover, we found inter-hemispheric summation being superior to intra-hemispheric summation, since performance in the bilateral redundant condition was superior to the unilateral redundant condition.

D. Enhanced MMN after Binaural Word Stimulation[2]

1. Summary

The present experiment was designed to investigate how bi-hemispheric processing was affected by attention and perceptual modality. A auditory mismatch negativity (MMN) design seemed appropriate for this purpose because it allowed to examine neurophysiological processing in the auditory modality without subjects attention focused on stimulus processing.

An oddball paradigm was applied to investigate brain processes elicited by spoken words and pseudowords played monaurally, to the left or right ear, or simultaneously to both ears of subjects instructed to ignore acoustic stimuli but watch a silent video film. Bilateral stimulation should result in superior processing only for meaningful stimuli for which a cortical memory trace can be assumed to have developed in the past, compared with unilateral stimulation (Mohr et al. 1994b, Mohr et al., 1996).

The MMN, a neurophysiological index of the automatic activation of cortical memory traces, was calculated as the difference between the event-related potential (ERP) elicited by an infrequent deviant stimulus and the ERP to the same item presented as frequent standard stimulus. Consistent with earlier reports (Pulvermüller et al. 2001, Shtyrov and Pulvermüller, 2002), the MMN to words was larger than that to pseudowords, possibly reflecting the existence of memory traces for spoken words. Bilateral redundant stimulus presentation led to a further increase of the MMN to words relative to both unilateral stimulation modes. The bilateral redundancy gain was absent for pseudowords.

This result demonstrates that a bilateral advantage could be obtained in the auditory modality even when processing was not requiring attention. The binaural enhancement of MMN for words presents additional support for the word related MMN to be modulated by long-term memory traces for words rather than by differences in lexical status. We interpret the neurophysiological manifestation of a word-specific bilateral redundancy gain as evidence for interhemispheric cooperation in the automatic access to memory traces for

[2] The report of this experiment largely corresponds to the paper Endrass et al. (2004).

spoken words. Accordingly, word-related cortical networks distributed over both hemispheres allow summation of neural activity between and within hemispheres, thereby potentiating the word-related MMN.

2. Introduction

Behavioral studies on interhemispheric interaction showed that cognitive processing is improved in conditions with bilateral redundant stimulus presentation. If both hemispheres simultaneously receive the same stimulus information, processing becomes faster and more reliable compared with unilateral hemifield stimulation of the dominant hemisphere. In experiments using visual stimulus presentation, this bilateral redundancy gain was observed for simple visual stimuli (Minussi et al. 1998), consonant-vowel syllables (Marks & Hellige, 1999), words (Hasbrooke & Chiarello, 1998; Mohr et al., 1994, 1996; Yoshizaki, 2001), and familiar faces (Mohr et al., 2002; Schweinberger et al., 2003). The bilateral redundancy gain, which appears to be a general phenomenon elicited by a variety of stimuli, is especially pronounced when learned meaningful stimuli, such as words or familiar faces, are being processed. In contrast, the bilateral advantage was reduced or absent when processing of complex unfamiliar or meaningless stimuli such as pseudowords or unknown faces was required (Mohr et al., 1994, 1996, 2002; Schweinberger et al., 2003; Yoshizaki, 2001). The magnitude of the bilateral redundancy gain therefore reflects the existence of memory networks for learned stimuli. The putative underlying mechanism is the summation of activity in neuronal ensembles distributed over both hemispheres, which represent and process the learned meaningful stimuli (e.g., known words), but not for unknown ones (e.g., pseudowords) (Mohr et al., 1994; 2002). However, all earlier experiments revealing the bilateral redundancy gain used visual stimuli and required subjects to focus their attention on stimulus presentation (Mohr et al., 1994, 1996, 2001, 2002; Schweinberger et al., 2003; Yoshizaki, 2001). It is therefore unclear whether this robust behavioral effect is restricted to visual processing or it might also be obtained during auditory processing, and it is also unclear which role attention to stimuli plays in the generation of the effect.

To this end auditory stimulus presentation did not reveal a bilateral advantage regarding behavioral measures. Mohr et al. (2001) presented spoken words and pseudowords in monaural and binaural conditions while subjects performed a lexical decision task. Binaural word presentation did not significantly improve performance compared to monaural word or binaural pseudoword presentation. The absence of a bilateral advantage was explained either by low task difficulty, which reduced differences between presentation conditions, or by already bi-hemispheric stimulation in monaural conditions due afferent connections from each ear to the ipsilateral hemisphere. The bilateral advantage observed in behavioral studies is reflected by a significant decrease in reaction times and error scores in the bilateral condition relative to the best unilateral condition and has been interpreted to reflect cooperation between the two hemispheres rather than independent hemispheric operation or even interhemispheric inhibition (Mohr et al., 1994b; 2002).

To further test the hypothesis that the bilateral redundancy gain is a general indicator of the processing of familiar meaningful stimuli, it is necessary to look at possible neurophysiological correlates of the bilateral gain elicited by other than visual stimuli, if possible in a task where attention to stimuli is minimized. To this end, we here use a neurophysiological brain response called the Mismatch Negativity (MMN) and compare it between familiar and unfamiliar acoustic stimuli presented either to one or both ears.

The MMN is elicited by perceived auditory changes, typically the occurrence of an infrequent deviant stimulus among frequent standard stimuli. The MMN is a frontocentrally distributed ERP component peaking around 100 – 250 ms after stimulus onset. The MMN can be elicited in the absence of focused attention towards the acoustic input and it has therefore been postulated that it is to a large degree independent of attention (Näätänen and Winkler, 1999; Näätänen, 2001; Näätänen et al., 2001). Recent studies on electrocortical correlates of speech processing used the MMN paradigm, which is supposed to measure attention-independent, automatic processing of acoustic stimuli.

It could be shown that, in contrast to the MMN elicited by simple tones or noises, the MMN to language sounds, phonemes and syllables, shows laterality to the left dominant hemisphere (Alho et al., 1998; Rinne et al., 1999; Shtyrov et al., 1998; Shtyrov

et al., 2000). Rinne et al. (1999) showed, that the MMN for vowels was more strongly lateralized to the left hemisphere than for non-phonetic stimuli. The magnetic counterpart of the mismatch negativity (MMNm) to syllables was stronger in the left than in the right auditory cortex, indicating a left-hemispheric dominance in speech processing already at a preattentive level (Alho et al., 1998; Shtyrov et al., 1998). But laterality demised when syllables were combined with background noise. Shtyrov et al. (2000) found laterality of the MMNm dipole moment to differ with stimulus category: syllables were lateralized to the left hemisphere, slowly changing complex sounds were lateralized to the right hemisphere, and complex rapidly changing non-speech sounds (sharing acoustic properties with syllables) had no significant laterality. The left-hemispheric dominance for syllables was explained by long-term memory traces for the native speech sounds formed in the dominant hemisphere.

Interestingly, the MMN to phonemes of the subjects' mother tongue was larger than that to sounds of a foreign language (Dehaene-Lambertz, 1997; Näätänen et al., 1997). Pulvermüller et al. (2001) showed that syllables completing meaningful words elicit higher MMN amplitudes than syllables completing pseudowords in the Finnish language. This MMN enhancement to words was only observed in native speakers of Finnish and was absent in participants without any knowledge of Finnish. The main cortical source of the word-related MMN was localized in the left superior temporal lobe. This increase in MMN for words compared with pseudowords was interpreted as an enhancement of brain activity induced by word stimuli relative to that elicited by pseudowords. This activity incensement may be caused by the stored long-term memory traces of words. It was taken as evidence for the presence of memory traces for individual spoken words in the human brain. The memory traces are organized as strongly connected assemblies of cortical neurons, which become fully active, or ignite, when words are being processed (Pulvermüller et al. 2001, 2004). Activation of these memory traces may be a preattentive process operating in the absence of focused attention to stimuli (Näätänen, 2001).

Shtyrov and Pulvermüller (2002) replicated their finding in three different conditions: rare words presented among repetitive words or pseudowords, or pseudowords presented among words. Phonetic and phonological contrasts were identical in all conditions. Both conditions with word deviants elicited larger MMNs than the condition with pseudoword deviant. Enhanced word related MMN amplitudes were found

independent of the lexical status of standard stimulus (word or pseudoword). This indicates that the lexical status of the deviant is reflected by the MMN enhancement to word, whereas that of the standard stimulus was without significant effect.

The MMN to meaningful words presented as deviant stimuli was larger than that to meaningless pseudowords (Korpilahti et al., 2001; Pulvermüller et al. 2001), an effect which was independent of the lexical status of the standard stimulus (Shtyrov and Pulvermüller, 2002). The enhancement of the MMN to language elements, such as phonemes and words, relative to foreign sounds or pseudowords, was explained by stored long-term memory traces that would only exist for the learned items (Näätänen, 2001). If these memory traces are strongly connected neuronal ensembles distributed over both hemispheres, their existence should be equally reflected by the word-related MMN enhancement and by the bilateral redundancy gain (Pulvermüller et al. 2001, 2004; Pulvermüller and Mohr, 1996).

With the present study, we hoped to replicate the MMN enhancement to words in a language in which it has not been reported so far (German), and to find the first evidence for a neurophysiological reflection of the bilateral gain specific to spoken words. Words were predicted to show a larger MMN in the binaural condition, relative to monaural stimulation, whereas such electrophysiological bilateral gain was hypothesized to be absent or reduced to pseudowords.

3. Methods

Subjects

Seventeen healthy participants (7 females) took part in the present experiment and were paid for their participation. Their mean age was 25.4 years (SD=2.79) and all participants had 13 years of formal education. All subjects were right-handed according to the Edinburgh handedness questionnaire (Oldfield, 1971; mean handedness score was 91.2, SD=9.93). All subjects were native speakers of German and reported normal hearing and no psychopathological or neurological disorders in the past. All participants gave their written informed consent according to the Declaration of Helsinki and were told they could interrupt or abort the investigation at any time.

Stimuli

The stimuli of this experiment comprised the German word [ap] (written as “ab” and which means down) and the pseudoword [ak]. A female speaker recorded multiple repetitions of the two stimuli. Stimuli were carefully selected in order to optimize acoustic similarity between them. They were normalized to have equivalent peak sound energy, fundamental frequency (211 Hz) and duration (235 ms). In addition, the syllable bodies, voice onset times and durations of the final click were exactly matched. The acoustic waveforms of both stimuli are displayed in **Figure IV.D.1**, which shows that both stimuli consist of a syllable body of ~100 ms and a final plosion at 200 ms after syllable onset. Stimuli were analyzed and modified with Cool Edit 2000 (Syntrillium Software Corporation, Scottsdale, AZ, USA).

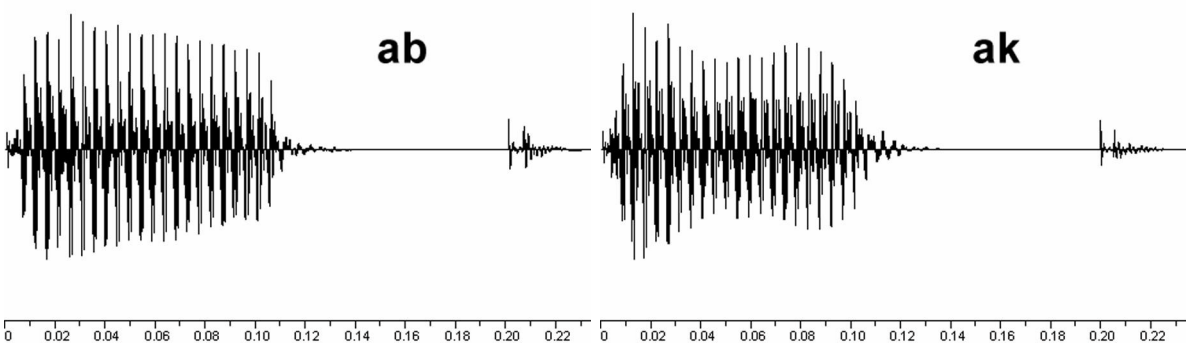

Figure IV.D.1. Acoustic waveforms of the stimuli used in the present experiment. The German word [ap] (“ab” in written German; left trace) and the pseudoword [ak] (right trace) are shown.

Procedure

Two stimulation conditions were applied: the word was used as the standard stimulus and the pseudoword as deviant in condition 1 and the reversed combination, with the pseudoword as standard and the word as deviant, was implemented in condition 2. In this design, the acoustic change, the main variable determine the MMN, was identical between conditions. Futhermore, this combination of conditions allowed determining the MMN by subtracting the event-related potential (ERP) to each standard stimulus from the ERP elicited by the same, physically identical deviant stimulus, so that possible physical differences between standard and deviant stimuli could be controlled for. All standard and deviant stimuli were presented to the left ear, to the right ear, or to both ears simultaneously. All stimuli were presented for 235 ms, followed by a silence interval lasting of 565 ms, resulting in an interstimulus (onset-to-onset) interval of 800 ms. In each of the two conditions, 2250 standard ($p = .833$) and 540 deviant stimuli ($p = .167$) were presented. The order of the two conditions was counterbalanced over subjects.

Stimuli were presented with the Experimental Runtime System software (BeriSoft Cooperation, Frankfurt, Germany) via headphones with a loudness of 60 dB above individual hearing threshold, which was determined for each individual separately before the experiment. All stimuli were presented in pseudo-random order with at least four and up to six standard stimuli between two consecutive deviant stimuli.

Data Acquisition

During experimental stimulation, subjects were seated in a comfortable chair in front of a computer screen watching a silent video film of their choice. They were instructed to ignore auditory stimulation and attend to the film. Three breaks were provided during the complete experimental session.

The EEG (electroencephalogram) was recorded with two 32-channel DC-amplifiers (SYNAMPS, Neuroscan, El Paso, USA) from 64 head positions referenced to CZ using an extended 10-20 system electrode cap (EasyCap, Falk Minow Services, Herrsching-Breitbrunn, Germany). Data were recorded with a sampling rate of 200 Hz and a bandpass of DC to 30 Hz. Impedances were kept below 5 kOhm. Data were recorded continuously

and stored for off-line analysis. After the experimental session, electrode positions were digitized using a 3D digitizer (Polhemus Inc., Colchester, USA).

Vertical, horizontal and blink electrooculograms (EOG) were recorded for later artifact correction following the MSEC (multiple source of eye correction) method (Berg and Scherg, 1994). After correction of eye movements, trials were averaged separately for each subject and condition across trials. Trials still containing artifacts with voltage variation exceeding 75 µV were omitted. Subjects were excluded from further analysis if less than 100 trials in one of the deviant conditions could be averaged.

A baseline correction was performed for each individual and each condition by subtracting the average scalp distribution during a 100 ms epoch prior to stimulus onset. After average referencing event-related potentials, electrode positions were corrected by spline-interpolation of the data sets from individually digitized electrode positions on a standardized electrode montage. If significant interactions of a stimulus- or presentation mode-related factor with a topographical variable were found in the statistical evaluation, the analysis was repeated after amplitude normalization according to McCarthy and Wood (1985). Only significant effects that survived this normalization and were also significant in the non-normalised “raw data” analysis are reported. In this case, the F- and p-values given are from the analysis of normalized data.

After calculating mean ERP amplitudes for each stimulus type, presentation condition, electrode and subject, the MMN was computed by subtracting the ERP response to standard stimuli from the response to the deviant stimuli. The MMN was obtained separately for the two stimulus conditions (word and pseudoword) and for the three auditory presentation modes (left ear, both ears and right ear). Although we tried to match the two stimuli as far as possible, it cannot be excluded that the remaining physical differences could influence the electrophysiological response and the MMN to the stimuli. Therefore, we determined the MMN for the two conditions by subtracting the ERP elicited by the standard stimulus from that elicited by the physically identical deviant stimulus (e.g. word-deviant minus word-standard).

Statistical Analysis

The maximum MMN response was observed over frontal and central areas. Therefore, statistical analyses were performed for 9 electrodes over frontal and central areas of both hemispheres (3 electrode lines: Fz, Cz and Cp and 3 electrode lines: left, central and right). Visual inspection of ERP curves showed two major components of the MMN response that suggested the calculation of mean amplitudes for three time windows (70 – 140, 180 - 260 and 290 – 360 ms).

Separate statistical analyses were calculated for all three time windows. Four-way ANOVAs were computed for the mean MMN amplitude calculated in a given time window with the following within-subject factors: Wordness (word vs. pseudoword), Ear (left, both vs. right ear stimulation), Gradient (frontal, fronto-central vs. posterior-central), and Laterality (left, central vs. right). P-Values were corrected by Greenhouse-Geisser epsilon if df > 1. If significant interactions or main effects of factors with more than 2 levels were found, one-sided t-tests were used for planned comparison tests.

Source Analysis

The source location for the MMN response was calculated (to determine the source of electrocortical activity) for each experimental condition. Source estimates of the MMN response were obtained for the averaged MMN response (across all subjects) in the three presentation conditions (left ear, right ear and both ears) for both stimulus categories (words and pseudowords) using the L2 Minimum Norm method implemented in BESA software (MEGIS Software GmbH, Munich, Germany). The signal-to-noise ratio (SNR) was at least 2. The SNR of the solution was estimated as a ratio of the signal power and average power in the pre stimulation baseline. Each channel was weighted individually taking into account its SNR. The obtained minimum-norm images were projected on the schematic cortex model using BESA software.

4. Results

Figure IV.D.2 shows event related potentials (ERPs) separately for standard and deviant stimuli, the three presentation conditions, and for words and pseudowords respectively. Evoked potential differences among standard word and pseudoword stimuli were small and not significant, whereas large differences among deviant stimuli were obtained. A MMN response was revealed by word and pseudoword stimuli in all three presentation conditions (see **Figure IV.D.3**). MMN response was increased when a word was presented in contrast to pseudoword presentation.

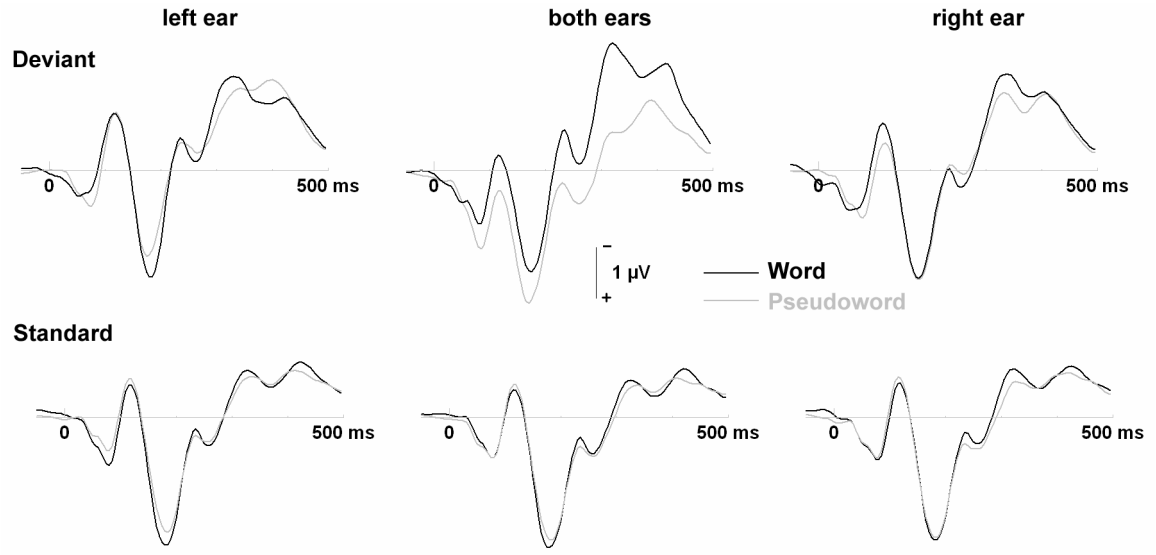

Figure IV.D.2. Mean Amplitudes of event-related potential (ERP) responses recorded at electrode Fz over the frontal lobes. ERPs to deviant (upper row) and standard stimuli (lower row) are displayed separately for words (black line) and pseudowords (grey line). Note the uniformity of ERPs to standard stimuli and the profound differences between conditions and stimuli in the ERPs to the deviant stimuli.

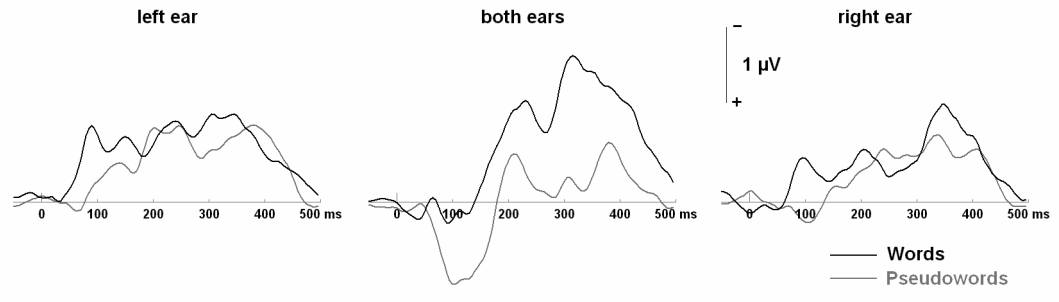

Figure IV.D.3. Mean MMN responses elicited by words (black lines) and pseudowords (gray lines) in the three presentation conditions recorded at electrode Fz.

Three time windows were selected for statistical analysis: 70 –140 ms, 180 – 260 ms and 290 to 360 ms. In the early time window, 70 - 140 ms (**Figure IV.D.4**) MMN peaked for the first time in monaural conditions and also differed for the first time between word and pseudoword stimuli. In the second time window, 180 - 260 ms (**Figure IV.D.5**), a MMN peak was obtained in the binaural condition with a pronounced difference between words and pseudowords, whereas no such difference was obtained in monaural conditions. The third time window, 290 - 360 ms (**Figure IV.D.6**), captures the maximum MMN response in all three presentation conditions. The MMN has a latency of ~100-200 ms and therefore the earliest interval can be related to the perception of the syllable onset, which may allow for some stimulus discrimination already. The second interval may be related to the perception of the end of the syllable body, where syllables and words can sometimes be identified although subjects would usually not be confident in identifying words at this stage. The third interval includes the MMN response from 90 to 170 ms after the final plosion (approx. 200 ms after stimulus onset), when subjects are usually confident in recognizing a word ending in a stop consonant (Warren and Marslen-Wilson, 1988). Earlier studies found the maximal word related MMNs in the range corresponding to this latest interval (Pulvermüller et al., 2001; Shtyrov and Pulvermüller, 2002), which is consistent with the present findings.

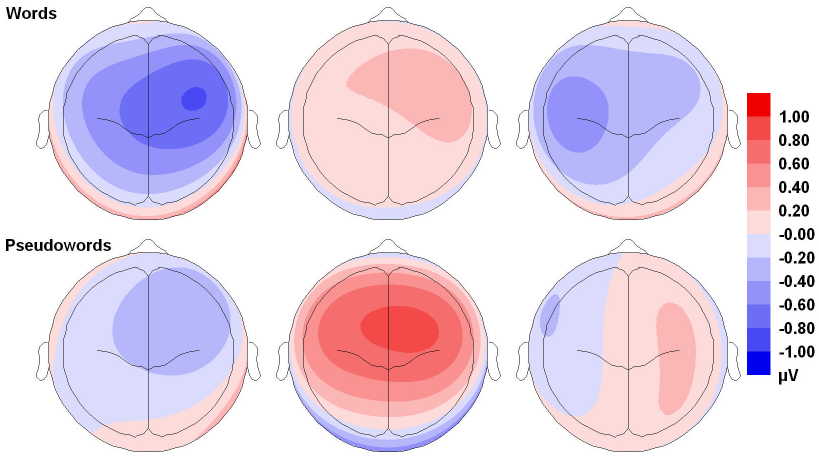

Figure IV.D.4. Grand average topographies (average reference) of the MMN response in the time window from 70 to 140 ms after stimulus onset.

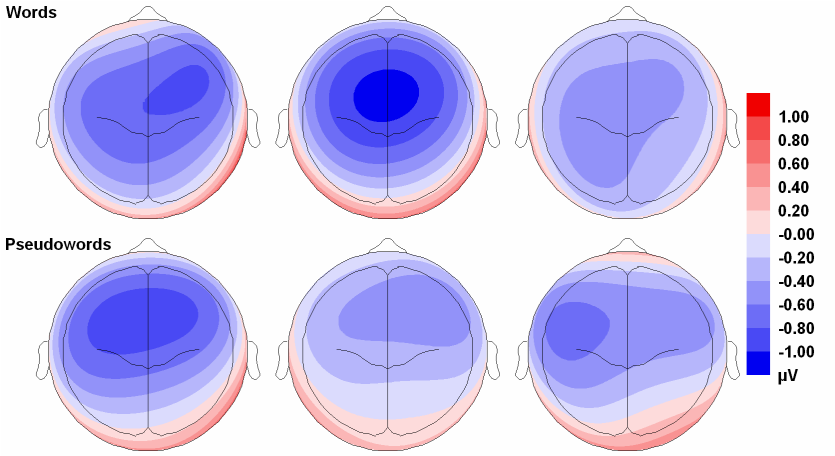

Figure IV.D.5. Grand average topographies (average reference) of the MMN response in the time window from 180 to 260 ms after stimulus onset.

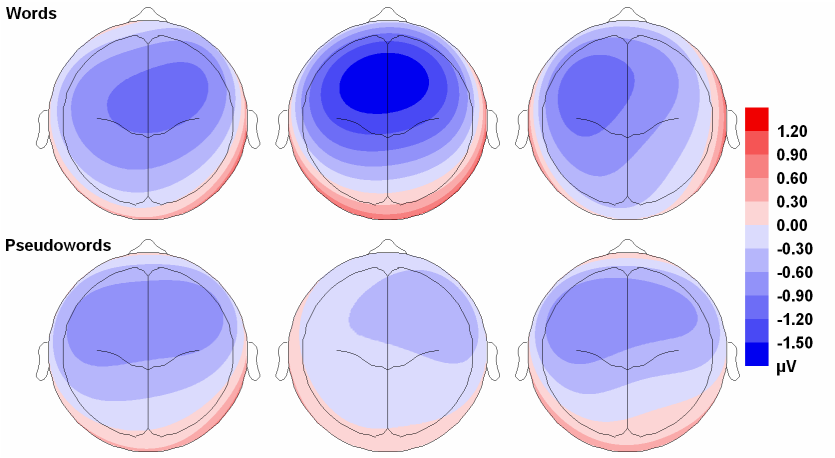

Figure IV.D.6. Grand average topographies (average reference) of the MMN response in the time window from 290 to 360 ms after stimulus onset. Note that in this time window, maximal average amplitudes of the MMN are larger for words than for pseudowords and that, there is an MMN enhancement to words only in the bilateral stimulation mode (relative to unilateral word stimulation).

Analysis of mean amplitudes in the time window between 70 and 140 ms (**Figure IV.D.4**) revealed a significant main effect of Wordness ($F(1,16)=6.84$, $p<0.02$) with word stimuli eliciting a larger overall MMN amplitude than pseudoword stimuli. Differences between the three presentation conditions (left, right vs. both ears) were also found ($F(2,32)=37.95$, $e=0.91$, $p<0.001$). Planned comparisons showed significant differences between left and right ear stimulation with a larger negativity in left ear condition ($t(16)=2.74$, $p<0.01$). Interestingly after monaural stimulation, more negative amplitudes were obtained than after binaural stimulation (left vs. binaural: $t(16)=10.22$, $p<0.001$; right vs. binaural: $t(16)=5.38$, $p<0.001$). In the binaural condition, no MMN response could be recorded in this time window. Differences in laterality between the three presentation conditions were indicated by a significant Condition x Laterality interaction ($F(4,64)=3.60$, $e=0.62$, $p<0.03$). Planned comparisons showed that the MMN was lateralized to the right hemisphere after left ear stimulation ($t(16)=1.76$, $p<0.05$) and to the left hemisphere after right ear stimulation ($t(16)=2.94$, $p<0.01$). Binaural stimulation elicited no amplitude difference between hemispheres.

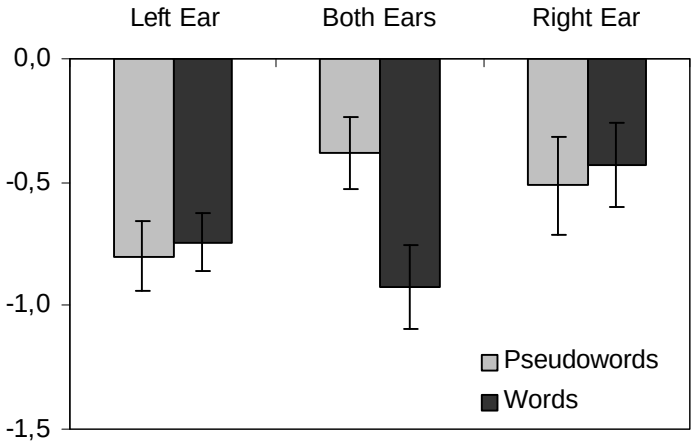

Figure IV.D.7. Mean MMN amplitudes are displayed for the second time window (180 – 260 ms), separately for word and pseudoword stimuli and the three presentation conditions (Wordness x Condition interaction). The binaural MMN was larger for words than for pseudowords, whereas monaural MMNs did not differ between words and pseudowords. Error bars indicate standard error of the mean.

In the second time window (form 180 to 260 ms, **Figure IV.D.5**) a significant Wordness x Condition interaction was found ($F(2,32)=8.34$, $e=0.98$, $p<0.01$). Planned comparisons for this interaction (**Figure IV.D.7**) indicated only in the binaural condition a larger MMN for word than pseudoword stimuli ($F(1,16)=8.82$, $p<0.01$). The MMN for pseudoword stimuli was more negative after left ear stimulation than after binaural stimulation ($t(16)=2.49$, $p<0.02$).

The latest time window (290 - 360 ms, **Figure IV.D.6**) revealed a significant Wordness x Condition interaction ($F(2,32)=5.76$, $e=0.99$ $p<0.01$; see also **Figure IV.D.8**). Planned comparisons indicated a MMN difference between word and pseudoword stimuli in the binaural condition ($t(16)=3.84$, $p<0.001$) with a larger MMN for word stimuli. For both monaural presentation conditions words elicited greater average MMNs than pseudowords but the difference did not reach significance. For word stimuli, the MMN was more negative after binaural stimulation than after monaural stimulation (right ear vs. both ears: $t(16)=2.05$, $p<0.03$; left ear vs. both ears: $t(16)=2.07$, $p<0.03$). For pseudoword stimuli, left ear MMN was more negative than binaural MMN (left ear vs. both ear: $t(16)=2.14$, $p<0.03$). This Wordness x Condition interaction showed that the MMN was more pronounced when words were presented binaurally in contrast to binaural presentation of pseudowords, but also compared with monaural word presentation. Additionally, a marginally significant main effect of Wordness ($F(1,16)=4.14$, $p<0.06$) was found with overall MMN for words being larger than for pseudowords. The Condition x Laterality interaction was also significant in this time window ($F(8,128)=2.8$, $e=0.72$, $p=0.051$). A lateralized MMN response was revealed only in the right ear condition ($t(16)=3.02$, $p<0.01$).

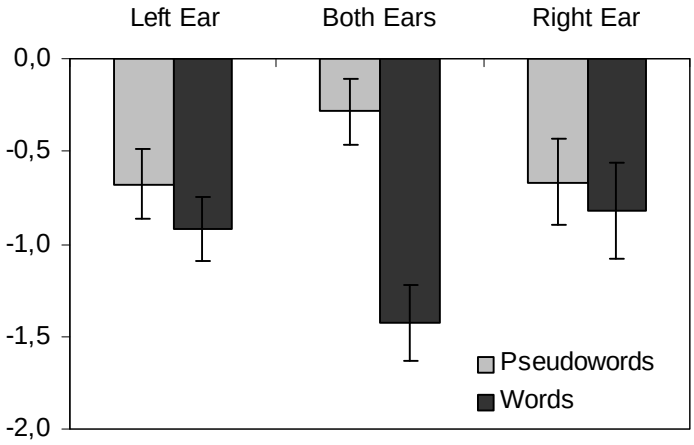

Figure IV.D.8. Display of the significant interactions of the factors Wordness and Condition found in the time window between 290 and 360 ms. The MMN amplitude was larger when words were presented binaurally in contrast to binaural presentation of pseudowords, but also compared with monaural word presentation. Error bars indicate standard error of the mean.

Source Analysis

Figure IV.D.9 depicts the minimum-norm estimates for the average MMN response over the left and right hemisphere for all conditions. The source distributions are displayed for the time point of the MMN peak in the binaural condition (at 345 ms). Minimum-norm estimates in all conditions are peaking at temporal regions of the cortex. The source distribution of the MMN in the unilateral conditions indicates that left ear stimulation elicited a stronger MMN response over the left hemisphere (RH) than over the left (LH) and the reverse, greater LH than RH MMNs, was found for right ear stimulation. The MMN source distribution in the binaural condition was more equally located over both hemispheres. Overall activity was more pronounced for word stimuli than for pseudoword stimuli. Especially, comparing the binaural condition with monaural conditions, activation for pseudowords in the binaural condition was reduced, whereas word stimulation produced strongest activation in the binaural condition.

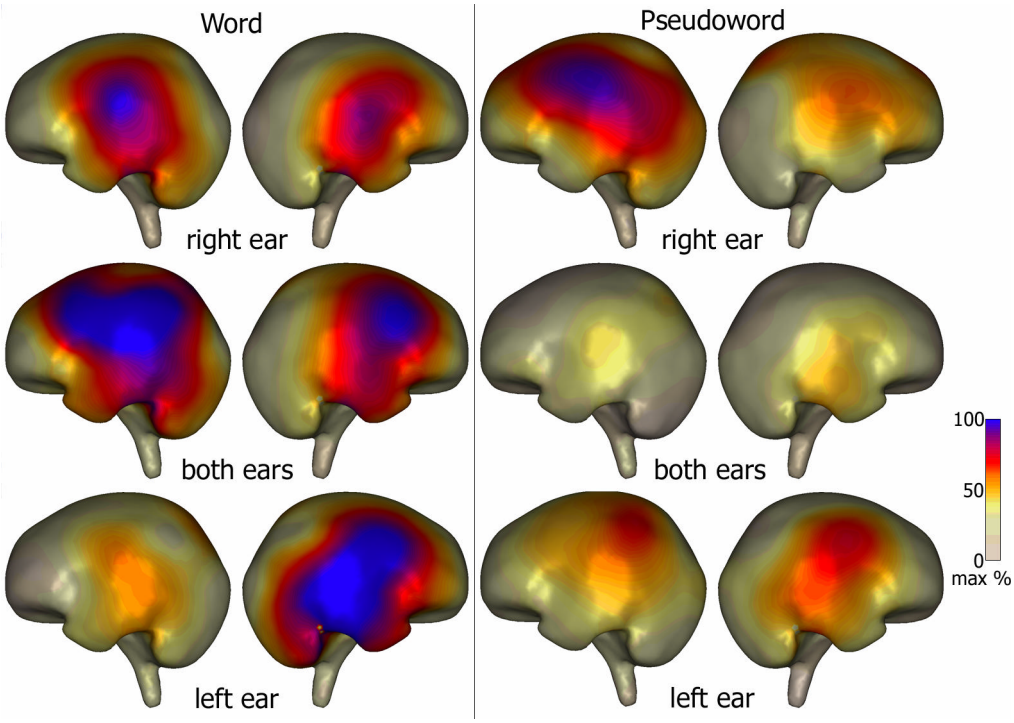

Figure IV.D.9. Display of the sources of MMN 345 ms after onset of word and pseudoword stimuli as revealed by L2 Minimum-Norm Estimates. Source distributions of the MMN response in words are on the left side and those to pseudowords on the right. Sources in the left and right hemispheres elicited by right ear stimulation alone, after redundant stimulation of both ears, and after left ear stimulation alone are presented from top to bottom. Note that words elicited more pronounced overall activation than pseudowords and that highest activation levels were revealed for binaurally presented words.

5. Discussion

The MMN elicited by spoken words and pseudowords was compared between left ear, right ear and binaural redundant stimulus presentation. The MMN was larger to words than to pseudowords, and, in addition, there was a significantly enlarged MMN in the binaural redundant condition compared with both monaural stimulation modes for the words only. Correspondingly, distributed source analysis using L2-Minimum-Norm Estimates indicated that the activity in the binaural word condition was generally increased and that it exhibited a more bi-hemispheric distribution compared with activity either in the pseudoword conditions or in both monaural word conditions.

Because the MMN is elicited by the acoustic contrast between a frequent standard stimulus and a rare deviant stimulus, it can reflect acoustic properties of this acoustic contrast, as it can be influenced by acoustic properties of the deviant stimulus. In the present experiments, the acoustic contrast was kept constant between conditions by using a "reversed" design where the standard stimulus of condition 1 was the deviant in condition 2 and vice versa. To rule out the possibility that acoustic properties of the stimuli influenced the MMN, we calculated the MMN by subtracting the event-related potentials to each stimulus presented as the standard from the ERP of the physically identical item presented as the deviant. Therefore, it is unlikely that the observed MMN differences are due to acoustic differences between word and pseudoword stimuli or by a difference in acoustic contrast between standard and deviant stimuli.

Our results confirm earlier reports that words presented in an oddball paradigm as deviant stimuli elicit larger MMN responses than pseudowords (Korpilahti et al., 2001; Pulvermüller et al. 2001, Shtyrov and Pulvermüller, 2002). However, in Pulvermüller and colleagues' (2001) studies, pseudowords were always used as standard stimuli while the lexical status of the deviant stimuli varied. There are therefore two competing explanations for the MMN enhancement to words these authors reported: It could have been caused either by the activation of cortical memory traces for words elicited by the deviant stimulus or by the lexical difference between word deviants and pseudoword standards (note again that pseudoword deviants were contrasted with pseudoword standard stimuli therefore implying the absence of a lexical contrast in this case). However, Shtyrov and Pulvermüller (2002) contrasted a word deviant with word and pseudoword standards and

could confirm the enhanced MMN to word deviants, irrespective of the lexical status of the standard stimulus. Therefore an explanation in terms of lexical contrasts between standard and deviant stimuli could not be supported. Our present data add to this evidence that the event-related potentials elicited by standard stimuli did not differ significantly between word and pseudoword stimuli (see Figure 2). In contrast, words elicited a clearly larger negativity than pseudowords when presented as deviants. In addition, the present design implemented a lexical contrast in both conditions (either word standard and pseudoword deviant or vice versa), thus excluding the possibility that lexical contrast was the critical factor. Our results are consistent with the proposal that the activation of pre-existing long-term memory traces is reflected by the enlarged MMN to words. Pseudowords may have elicited a smaller MMN because they do not have, and therefore did not activate, corresponding cortical cell assemblies. Furthermore, we could confirm that memory traces are activated early and even if subjects are instructed to ignore the language input and focus their attention elsewhere.

This is the first study revealing a bilateral redundancy effect for spoken word stimuli. Earlier, Mohr and colleagues (2001) had investigated whether there is a behavioral bilateral advantage during a lexical decision task with auditory word and pseudoword presentation. However, contrary to the findings during visual processing, word processing was not significantly improved by binaural redundant presentation compared with monaural presentation as revealed form behavioral data (Mohr et al., 2001). The absence of a bilateral advantage in this earlier experiment might have been due to a ceiling effect, because overall accuracy was already high in monaural conditions. In addition, spoken words unfold in time and there is a great deal of variability between stimuli (e.g., with regard to when stimulus information allows for word recognition) (e.g., Marslen-Wilson, 1987) and between subjects (when subjects feel confident that a word can be recognized and therefore press a button). This variability makes the behavioral correlates of spoken word recognition more variable than those of written words so that significant differences are less likely to occur, in particular if averages over numerous spoken word stimuli are calculates as in Mohr et al.'s (2001) study. In the present neurophysiological work, we investigated the underlying brain processes directly by looking at an early automatic brain response, and we focussed on one pair of stimuli exactly controlled for several acoustic features. The effects obtained may depend on such precise stimulus control.

In addition to the MMN enhancement to words, we found that MMN amplitude depended on the stimulation mode. Already 200 ms after stimulus onset, there was a significant interaction of the factors Stimulus type and Condition, and this significant interaction could be confirmed by the analysis of the largest MMN peak, around 300 ms after stimulus onset. There were larger MMNs to words than pseudowords after bilateral stimulation and an enhanced word MMN was present after bilateral stimulation relative to both monaural conditions. The two intervals where this interaction was significant may reflect different stages of the word recognition process. Words and syllables ending in a final stop consonant (such as [p] or [k]) can sometimes be correctly identified already at the end of the last syllable body (100 ms in case of the present stimuli), before the final plosion (200 ms). However, most subjects would only be confident in recognizing the respective words when they have heard the final plosion as well (Warren and Marslen-Wilson, 1988). These two time steps in the process of spoken word recognition have been called the isolation point (when subjects start to guess correctly what the upcoming word might be) and the recognition point (when subjects feel confident; Marslen-Wilson, 1987). The present data indicate that already at the isolation point stage, a bilateral redundancy gain occurs at the neurophysiological level. However, a greater and clearer effect can be seen later, with a 100-150 ms latency upon the word recognition point.

The word-specific MMN enhancement in the binaural condition relative to unilateral stimulation might be explained by summation of neural activity within word-related cell assemblies distributed over both hemispheres. Only in the word condition, a significant MMN enlargement was obtained while in the pseudoword condition the MMN was even reduced compared with monaural stimulation. During binaural stimulation, the memory traces for words would be activated twice at the same time so that summation effects might lead to an enhancement of MMN. Because of the incomplete crossing of the auditory pathway, auditory stimulation always leads to activation of both hemispheres. Therefore, we cannot decide, on the basis of the present data, whether the summation effects that putatively led to the word-specific MMN enhancement in the bilateral condition occurred within or between the hemispheres. On the basis of the bilateral advantage obtained for visually presented words, but not pseudowords, and for familiar faces, but not unfamiliar faces, Mohr et al. (1994, 1996, 2002) argued in favor of summation of neural activity between the hemispheres in strongly connected neuronal

ensembles distributed over both hemispheres. This explanation provides a possible interpretation for the present data as well.

In summary, the fact that only learned stimuli, such as words or familiar faces, elicit a bilateral advantage in behavioral tasks and a corresponding neurophysiological MMN increase can be explained within the cell assembly theory proposed by Hebb (1949). Accordingly, no summation effect can be obtained for complex unfamiliar stimuli, such as pseudowords or unfamiliar faces, as they do not have neuronal representation. In contrast, strong summation effects following redundant bilateral presentation can occur for stimuli that are cortically represented by distributed neuronal ensembles with strong internal connections (Pulvermüller and Mohr, 1996, Pulvermüller, 1999, Mohr et al. 2002). The binaural word related MMN enlargement (comparing to monaural presentation) provides additional support for the existence of long-term memory traces representing spoken words in the brain and is consistent with an interhemispheric summation effect caused by redundant stimulation of both hemispheres simultaneously.

V. General Discussion

The experiments presented in the present thesis were conducted to investigate interhemispheric processing with different designs and stimuli. Behavioral and neurobiological aspects of bihemispheric processing were examined. The conducted experiments were focused on the question of how processing is influenced by stimulating both cortical hemispheres in contrast to stimulating only one hemisphere. Further, it was intended to characterize the underlying neurophysiological processes with evoked potential and source analyses.

In the following section, the results of the different experiments are summarized. Thereafter, the results are discussed in terms of models of interhemispheric processing, particularly in terms of the neurobiological model based on Hebb's cell assembly theory (1949).

A. Summary of the Results on Behavioral Data (Experiment A – C)

It has been replicated that words gain form bilateral presentation. Higher accuracy and faster reactions were obtained after bilateral redundant stimulation compared to unilateral stimulation with only one stimulus (*experiment A and C*). Additional stimulation of the right hemisphere improved performance of word processing compared to exclusive stimulation of the left hemisphere, which is superior for linguistic processing (accuracy was enhanced by 10 % and reaction time by 50 ms approximately). This bilateral advantage was not found for pseudowords. In case of pseudoword presentation, bilateral performance resembled unilateral performance.

A bilateral advantage was also shown while object processing (*experiment B*). Objects were faster and more accurately processed when two redundant copies were bilaterally presented than when only one copy was unilaterally presented. In contrast, non-objects did not improve subject's performance after bilateral compared to unilateral presentation. Double stimulation with non-objects did not significantly change performance compared to single stimulation. Faster reactions were also found for double bilateral presentation of patterns compared to single unilateral presentation of patterns

during a stimulus detection task. The comparison of bilateral advantages from the object decision task and the stimulus detection task revealed that the magnitude of the bilateral advantage differentiated between tasks. The bilateral advantage for object was twice as high as for patterns and no bilateral advantage was revealed for non-objects.

In *experiment C* redundant stimulation in the bilateral condition was compared with double stimulation in the unilateral condition. Pseudowords gained neither from unilateral redundant nor from bilateral stimulation. Performance did not significantly change with increased number of identical stimulus copies. In contrast, both unilateral and bilateral redundancy influenced performance for words. Higher accuracy and faster reactions were found in bilateral condition compared to both unilateral conditions. The relevant comparisons for determination of the bilateral advantage were: one copy in each visual field vs. one copy in one visual field and two copies in each visual field vs. two copies in one visual field. Word processing also gained form redundant stimulation within one visual field / hemisphere as revealed from the comparisons between one copy in one or each visual field vs. two copies in one or each visual field. However, this redundancy advantage was obtained only on accuracy data, but not for reaction times. Further, the bilateral advantage was compared with redundancy advantage in the RVF condition, which is superior in word processing. Therefore, bilateral stimulation with one stimulus copy appearing in each visual field (BVF1) was compared with redundant stimulation within the RVF condition with two stimulus copies appearing in the RVF (RVF2). Both performance measures (accuracy and reaction time) turned out to be superior in the bilateral condition than in the redundant RVF condition.

B. Summary of the Results on Evoked Potential Data (Experiment A and D)

Evoked potential data for words and pseudowords during a lexical decision task revealed a significant Wordness x Presentation mode interaction (*Experiment A*). Bilaterally presented words elicited higher overall negativity than pseudowords in the time range from 160 to 200 ms. The bilateral advantage was further analyzed with the comparison between bilateral and RVF condition. The results indicated an interaction of Wordness x Presentation Mode with topography. Whereas words and pseudowords in the bilateral condition elicited larger negativity over parieto-occipital electrodes of the right hemisphere, only words elicited also larger negativity over the left hemisphere. The source analysis with minimum norm estimate provided additional support for the interpretation that cortical activity was increased in the bilateral word condition. Higher cortical activity was revealed for bilaterally presented words than for both unilateral word conditions. Whereas words in the bilateral condition elicited higher activity over both hemispheres, pseudowords caused higher activity only over the respective ipsilateral hemisphere. These differences were especially prominent over temporal brain regions.

The analysis of interhemispheric transmission time also revealed difference between words and pseudowords. Visual evoked potentials (N1 component) were analyzed for peak latency differences between hemispheres ipsilateral and contralateral to the stimulated visual field. Shorter latency differences (IHTT) were found for words presented to the LVF than for words presented to the RVF. In contrast, IHTT did not differ between LVF and RVF pseudoword condition and transmission times for pseudowords resembled those of words in the RVF condition. These findings indicate that words were faster transmitted from the right to the left hemisphere, than vice versa.

In *experiment D*, word and pseudoword stimuli were auditorily presented to the left ear, to the right ear or to both ears simultaneously. From evoked potential data, the mismatch negativity was determined for each condition. Overall MMN response was larger for words than for pseudowords. The three presentation conditions differed between each other. Words elicited a larger MMN in binaural than in monaural conditions, especially in the time range from 290 to 360 ms. In contrast, pseudowords had a smaller MMN in the binaural condition than words and than in monaural pseudoword conditions. Source analysis revealed that activity was higher for the binaural word condition than for any other

condition (**Figure IV.D.9.**). A significant activity enhancement for the bilateral condition was found only in the word condition, while activity was reduced for pseudowords.

C. Interpretation of the Present Findings

A differential bilateral advantage was revealed during a lexical decision task (*experiment A and C*). Bilateral presentation facilitated performance for words but not for pseudowords. This is a well-established phenomenon, which has been reliably found in healthy participants (Mohr et al., 1994b; 1996; 2000; Mohr and Pulvermüller, 2002; Zaidel and Rayman, 1994).

Word processing was improved when both hemispheres received the same information compared to stimulus presentation to the right hemisphere, but also compared to stimulation of the left hemisphere. Therefore, it has been suggested that the right hemisphere might contribute to lexical processing, when both hemispheres are engaged in task accomplishment (Mohr and Pulvermüller, 2002). This interpretation is consistent with the finding that the right hemisphere was also involved in language processing (Pulvermüller et al., 1995; Pulvermüller, 1999; Pulvermüller et al., 1999).

Most crucial for the interpretation of the bilateral advantage is the finding that no bilateral advantage was found for pseudowords. Additional presentation of a pseudoword has never been found to facilitate performance (Mohr et al., 1994; 1996; 2000; Mohr and Pulvermüller, 2002; Zaidel and Rayman, 1994). However, Hasbrooke and Chiarello (1998) did not confirm a differential bilateral advantage for words and pseudowords. Although they did not find a significant interaction, their data also showed that words gained more from bilateral processing than pseudowords. They suggested that the bilateral advantage might occur on different processing stages of the lexical processing: early pre-lexical processes, lexical access or post-lexical motor planning and execution. Since, the majority of findings on bilateral pseudoword processing did not reveal a bilateral advantage for these stimuli, it seems unlikely that the bilateral advantage during lexical decision tasks occurred on a pre-lexical processing stage. Furthermore, since the lexical status of the

presented stimuli (word vs. pseudoword) influenced bilateral processing, it might be suggested that the bilateral advantage occurs during lexical access.

Another relevant finding for interpreting the bilateral advantage was revealed from a split-brain patient. Mohr et al. (1994a) tested a split-brain patient who underwent a complete commissurotomy. This patient did not gain from bilateral word presentation during a lexical decision task. Consequently, it was suggested that the bilateral advantage depends on interhemispheric connections through the corpus callosum.

The bilateral advantage was supposed to occur only for meaningful stimuli, like words or familiar faces (Mohr et al., 1994; 1996; 2000; 2002; Mohr and Pulvermüller, 2002; Schweinberger et al., 2003; Zaidel and Rayman, 1994). Yoshizaki (2001) recently demonstrated the influence of visual familiarity on bilateral advantage with the Japanese script forms Katakana and Hiragana. Words are normally written in either script form. Yoshizaki (2001) presented meaningful words in both script forms, but only words presented in the proper script form were found to gain form bilateral presentation. According to this finding, it is possible that visual familiarity has an influence on the bilateral advantage.

In *experiment B* object processing was examined with bilateral stimulation. Line drawings were presented including meaningful, familiar objects and meaningless non-objects. A bilateral advantage was found for objects. Non-objects did not gain from bilateral stimulation. This result provides further support for the proposal that only meaningful stimuli gain from bilateral processing, whereas meaningless stimuli do not.

However, the bilateral advantage for objects (7 % in accuracy and 30 ms in reaction time) was smaller in magnitude than for words (*Experiment A and C*). In an earlier experiment, Mohr et al. (1994b) also reported a smaller bilateral advantage for words. Mohr and Pulvermüller (2002) argued that the bilateral advantage might be influenced by task properties, like task difficulty.

The assumption that only meaningful stimuli gain from bilateral stimulation is violated by findings from simple reaction tasks. For example, Minussi et al. (1998) demonstrated that reactions were faster, when a pattern appeared in both visual fields

compared to the appearance in only on visual field. Faster reactions for bilaterally presented patterns were also found in *experiment B.* This finding suggested that a bilateral advantage does not necessarily require the presentation of meaningful stimuli. It can also be obtained after meaningless pattern presentation. Therefore, it seems likely that the processing requirement of the experimental task plays an important role.

Tasks revealing a bilateral advantage for meaningful stimuli always required full stimulus identification, whereas simple reaction tasks did not. Lexical decision, familiarity decision, and object decision tasks require stimulus selection: word or pseudoword, familiar or unfamiliar, object or non-object. However, one could also argue that in decision tasks, there is always a target and a non-target stimulus present. Bilateral performance would therefore be facilitated after target presentation, but facilitation would not occur after non-target presentation. Schweinberger et al. (2003) contradicted this argument with an interesting result on unfamiliar face processing. They applied a task in which facial expressions of unfamiliar faces had to be classified in positive or neutral. The faces with positive facial expression might be regarded as target stimuli during this task. Bilateral presentation did not facilitate performance for positive or negative facial expressions.

The magnitude of the bilateral advantage was compared between the two tasks in *experiment B.* The bilateral advantage was larger for objects during the object decision task (33 ms) than for patterns during the simple reaction task (14 ms). Processing during the two tasks might depend on different processing levels and therefore differ in size. Whereas the simple reaction task requires only stimulus detection, the object decision task requires full stimulus identification and a decision. In turn, this result also supports the view that the bilateral advantage during a decision task might not rely on perceptual processes, because the bilateral advantage is smaller during simple reaction tasks, which should solely rely on perceptual processes.

It was intended to examine whether processing is differentially facilitated by unilateral stimulus redundancy and bilateral stimulus presentation with *experiment C.* The results indicated that both redundant presentation conditions improved performance for words. A unilateral redundancy gain (two vs. one copies in one visual field) and a bilateral advantage (one copy in each visual field vs. one copy in one visual field) were shown. Unfortunately, only accuracy but not processing speed gained from unilateral stimulus

redundancy, whereas bilateral redundancy influenced both performance measures (accuracy and reaction time). As earlier mentioned, pseudowords did not gain from bilateral stimulation. The present experiment also showed that neither unilateral nor bilateral redundant stimulation facilitated pseudoword processing. Unexpectedly, the magnitude of the bilateral advantage was higher than the magnitude of the unilateral redundancy gain for words. This indicated that performance gained from double stimulus presentation compared to single stimulus presentation. Furtermore, performance might be facilitated more by presenting the two copies in separate visual fields than by presenting them jointly to one visual field.

Mohr et al. (1996) conducted a similar experiment, however with a slightly different setup for stimulus presentation. Two identical stimuli were presented either unilaterally to the LVF or RVF, or bilaterally (one copy in the LVF and one copy in the RVF) in the upper or lower visual field, or two identical stimuli were presented in each visual field. They did not reveal a difference between unilateral redundant condition and bilateral condition (one copy in each visual field). Therefore, they argued that redundant stimulation facilitates word processing regardless of location of the second stimulus. The results of experiment C seem contradictory with the results of Mohr et al. (1996). From comparison between the two experiments, it is conceivable that the differences regarding the experimental setup might have caused different results. Duration of stimulus presentation was shorter in the present experiment (100 ms vs. 120 ms). This would explain lower accuracy scores found in the present study. The most obvious difference between the two experiments is the arrangement of stimulus presentation in the bilateral condition when one copy of a stimulus appeared in each visual field. While Mohr et al. (1996) showed the two stimuli either in the lower half or in the upper half of each visual field, the stimuli appeared vertically centered during *experiment C*.

Mohr and Pulvermüller (2002) designed an experiment with stimulus presentation in the upper or lower central visual field or in both positions simultaneously (Experiment 2). They also found a word specific redundancy gain for this task. However, they did not include central stimulation in that experiment but in another experiment (Experiment 5). Reaction times resembled for central stimulation and redundant stimulation in upper and lower visual field (approximately 620 ms vs. 630 ms). For this reason, it is possible that the bilateral presentation mode in *experiment C* of the present thesis also included some

unilateral redundancy due to vertically centered stimulation in addition to bilateral redundancy. This might have caused the superiority of bilateral stimulation over unilateral redundant stimulation. Further, this might also explain the small unilateral redundancy gain, because vertically centered presentation is compared with stimulus presentation in the upper and lower visual field.

The findings form *experiment C* in combination with the findings of Mohr et al. (1996) and Mohr and Pulvermüller (2002) would recommend a more complex design for the comparison between unilateral and bilateral redundancy (**Figure V.C.1**). Apart form the six presentation conditions of *experiment C* (one vertically centered copy vs. two copies in upper and lower visual field) it should also include stimulus presentation in either upper visual field or lower visual field. This assignment would obviate the influence of unilateral redundancy due to vertically centered stimulation and would allow the comparison between all conditions.

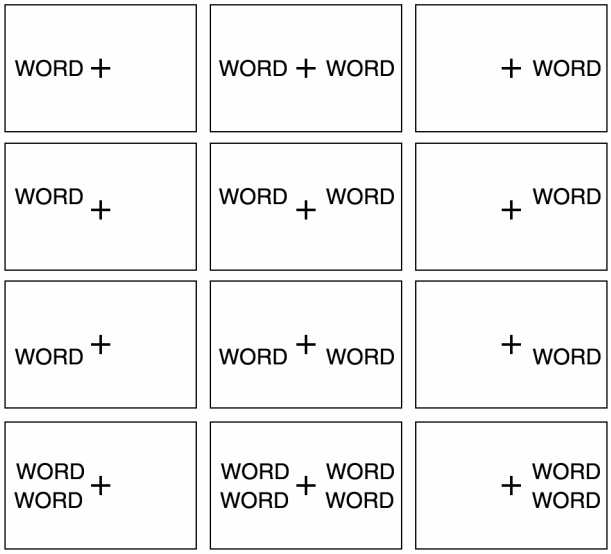

Figure V.C.1. A recommended experimental design is presented for the comparison between unilateral and bilateral stimulus redundancy.

Based on these arguments it remains unclear whether bihemispheric stimulus distribution is actually superior to unilateral redundant stimulus distribution. Performance after bihemispheric stimulation resembled performance after unilateral redundant stimulation, when the bilateral stimuli were placed either in the upper or lower vertical half of the respective visual field (Mohr et al., 1996). In contrast, bihemispheric performance

exceeded redundant unihemispheric performance, when the stimuli in bilateral condition were presented vertically centered (*Experiment C*).

In the context of *experiment A and D,* electrophysiological measures of bihemispheric processing were also collected. These experiments were supposed to reveal a neurophysiological equivalent of the bilateral advantage, which was repeatedly shown in behavioral data. Since performance gained form bilateral stimulation with words but not with pseudowords, it was expected that this difference should also be reflected in electrophysiological data.

In *experiment A* evoked potentials were recorded simultaneously with behavioral data. As already mentioned a bilateral advantage was found for word processing but not for pseudoword processing. This interaction was also obtained from evoked potential data and minimum norm analysis in the time range of the N1 component. Bilaterally presented words elicited more negative going amplitudes than bilaterally presented pseudowords. This difference was most pronounced over parieto-occipital brain regions. The bilateral word condition also differed form unilateral word presentation. Obviously, the bilateral condition differed from unilateral condition over the respective ipsilateral hemisphere. In unilateral conditions, activity is most pronounced over the hemisphere contralateral to the stimulated visual field due to the complete crossing of visual pathways. Therefore, it is not surprising that the respective ipsilateral negativity is more pronounced in bilateral condition, in which both hemispheres receive direct visual stimulation. More interesting is the difference between bilateral and unilateral conditions over the hemisphere contralateral to the stimulated visual field in unilateral condition. This difference was found over parieto-occipital regions for the comparison between bilateral and RVF condition. Whereas, evoked potential data are not reliable in spatial localization and in determination whether activity was increased or reduced minimum norm source analysis allows the interpretation of these circumstances. Bilaterally presented words elicited higher activity over temporal regions of both hemispheres compared to unilaterally presented words, and compared to bilaterally and unilaterally presented pseudowords. These results suggest that there is a neurophysiological equivalent of the bilateral advantage obtained form performance measures. Neuronal activity over temporal regions of both hemispheres is more pronounced after bilateral word stimulation.

Evoked potential data of *experiment A* were also used to determine interhemispheric transmission time after unilateral stimulation. As bihemispheric processing differed between words and pseudowords, a difference in interhemispheric transmission has been suggested. In fact, words were faster transmitted from the right to the left hemisphere, than pseudowords. Equal transmission times were found for the reverse direction.

In *experiment A* words revealed faster transmission form the right to the left hemisphere and higher left hemispheric activity (contralateral activity) in bilateral compared to the RVF condition. These findings suggest that this higher left hemispheric activity might be caused by information transmission form the right hemisphere in the bilateral condition, which was faster for words than for pseudowords.

In experiment D further support was obtained for a neurophysiological equivalent of the bilateral advantage. In contrast to earlier experiments on bihemispheric processing for redundant stimuli, the present experiment used auditory stimulus presentation in a passive listening task. This experiment examined therefore two more aspects of bilateral processing. Is it possible to excite the bilateral advantage in the auditory modality and without subject's attention?

Mohr et al. (2001) already examined bihemispheric processing with auditory word and pseudoword presentation to the left or to the right ear, or to both ears respectively. In this experiment binaural presentation of words and pseudowords failed to significantly alter responses compared to monaural stimulation. This task did not elicit a bilateral advantage, but right ear stimulation facilitated word processing compared to left ear stimulation. Mohr et al. (2001) gave two possible explanations for their findings. Due to very low task demands very high accuracy was revealed even in monaural conditions. Performance in this task might not gain form binaural stimulation because performance reached already its maximum in monaural conditions (ceiling effect). The other possible explanation arose from the incomplete crossing of auditory pathways. Whereas lateralized tachistoscopic visual presentation provides a reliable technique for unihemispheric stimulation of the contalateral hemisphere in the visual modality, monaural auditory presentation does not only stimulate the contralateral hemisphere but stimulates to a certain percentage the ipsilateral hemisphere as well. 30 – 40 % of the afferent fibers from each

ear reach the ipsilateral hemisphere. Therefore, bihemispheric stimulation might already have taken place during monaural auditory stimulation. Inconsistent with this explanation, they found a right ear advantage for word processing: when monaural stimulus presentation already stimulated both hemispheres, the two monaural conditions should not differ. Therefore, the first interpretation is favoured. This is also supported by the results of *experiment D*.

Neurophysiological activity was recorded for a word and a pseudoword during a passive listening task. Both stimuli were repeatedly presented either in monaural or binaural conditions. The mismatch negativity (MMN) was determined for words and pseudowords separately in the three presentation conditions. The MMN was more pronounced for the word stimulus compared to the pseudoword stimulus which was consistent with earlier studies (Pulvermüller et al., 2001; Shtyrov and Pulvermüller, 2002). Furthermore, a bilateral advantage was reflected by the significantly increased MMN for words after binaural stimulation compared to monaural stimulation. Minimum norm source analysis revealed higher cortical activity over temporal brain regions of both hemispheres for the binaural word MMN compared to monaural word MMN and compared to monaural and binaural pseudoword MMN. Since cortical activation was higher for binaurally presented words, it is concluded that there is an auditory equivalent of the bilateral advantage, observed in the visual modality. This results also indicated that the presence of a bilateral advantage did not depend on subject's attention directed to stimulus presentation.

Pulvermüller and colleagues (Pulvermüller et al., 2001; Shtyrov and Pulvermüller, 2002) explained the larger MMN for words compared with the MMN for pseudowords with activation within cortical memory traces existing for words but not for pseudowords. Since these activity differences are found for the MMN component, it has been argued that memory traces are activated at a very early processing stage and without directional attention. This has also been found to be true for the bilateral advantage. Binaural word presentation initiated the summation of activity within cortical cell assemblies, whereas binaural pseudowords presentation did not, because for this kind of stimuli cortical representations do not exist.

D. Implications for Interhemispheric Processing: Towards a Model of Interhemispheric Processing

In summary, the conducted studies yielded the following results: Bihemispheric processing facilitated processing of meaningful stimuli, like words and objects. In contrast, meaningless stimuli, like pseudowords and non-objects did gain from bilateral redundant stimulus presentation. Processing of words was also improved by unilateral redundant stimulation, whereas pseudoword processing was not improved. Therefore, it was suggested that redundant stimulation facilitates processing of meaningful stimuli, regardless of second stimulus location. Redundant processing aided processing more, when stimuli were divided between visual fields than when they were both presented to the same visual field. However, this result needs to be further tested with a more sophisticated experimental design regarding also upper vs. lower visual field differences. Furthermore, a bilateral advantage was also found in a simple pattern detection task. This bilateral advantage for patterns was smaller in magnitude compared to the bilateral advantage for objects.

Electrophysiological data provided further information about the nature of the bilateral advantage. In fact, bilaterally presented words elicited higher cortical activity than unilaterally presented words or pseudowords. Word related activity was increased over contralateral and ipsilateral hemispheres (relative to the unilaterally stimulated visual hemifield). This differential bilateral activity increase was demonstrated for visual and auditory word and pseudoword presentation.

E. How do the present findings fit with models of interhemispheric processing?

Since bilateral redundant stimulation facilitated processing of meaningful stimuli, models assuming interhemispheric inhibition are inappropriate to explain the present findings. The same is true for models which state independent processing, as performance in bilateral conditions was superior to *both* unilateral conditions. It is more useful to explain the present data in terms of a model stating improved processing after bihemispheric processing.

Different race models have been stated for explaining interhemispheric processing. Originally, Raab (1962) suggested that the two hemispheres were two independent but competing processors. The faster of the two processors initiates the response on bilateral redundant trials. Therefore, bilateral performance should be superior to unilateral performance. Miller (1982) and Mordkoff and Yantis (1991) modified the strict independent race model. They also assumed a race of hemispheric processing, but they suggested that there is a certain proportion of interhemispheric exchange, however on different stages of processing. All race models commonly predict superior processing when both hemispheres simultaneously receive stimuli than when stimuli are directed only to one hemisphere.

The present behavioral results do not falsify a race model explanation. According to this model, a bilateral advantage would be seen for any kind of stimuli. However, meaningless stimuli like non-objects and pseudowords did not reveal superior bilateral processing. One could argue that meaningless stimuli are really processed and pseudoword or non-object decisions are made when no word or object was recognized. In contrast, the electrophysiological findings are clearly contravening a strict independent race model because bilaterally presented words elicited higher contralateral cortical activation than unilateral conditions. When the hemispheres independently process stimuli, cortical activation over the hemisphere contralateral to the stimulated visual hemifield should not differ between unilateral and bilateral stimulation.

The race model assumption was also violated by the findings of Mohr et al. (1994a) and Schweinberger et al. (2003). A split-brain patient who underwent a complete

commissurotomy did not gain from bilateral stimulation with words or pseudowords (Mohr et al., 1994). Therefore, interhemispheric connections via the corpus callosum are required for the word specific bilateral advantage. Schweinberger et al. (2003) asked to classify facial expressions of unfamiliar faces, which were presented unilaterally and bilaterally. Whereas a bilateral advantage for familiar faces was obtained during a familiarity task, no bilateral advantage emerged during classification of facial expressions. The argument, that subjects did not really process one stimulus cannot account for these results, since neither positive nor neutral faces gained from bilateral stimulation. These results indicate that the occurrence bilateral advantage actually depends on the presence of meaningful stimuli and intact interhemispheric connection pathways. The absence of a bilateral advantage in combination with the results of Schweinberger et al. (2003) also falsify the interactive race models of interhemispheric processing, because a bilateral advantage is not always obtained after bilateral stimulation.

A neurobiological approach for the explanation of interhemispheric processing used the concept of transcortical cell assemblies (Pulvermüller and Mohr, 1996). According to Hebb (1949), cognitive concepts are represented in the brain as cell assemblies, which are supposed to be strongly interconnected neuron populations. Cell assemblies are distributed over large cortical regions and are assumed to comprise neurons of both hemispheres connected via the corpus callosum (transcortical cell assemblies). Cell assemblies are formed during learning mechanisms by frequent simultaneous activity of neurons.

Pulvermüller and Mohr (1996) suggested that a bihemispheric processing advantage should be obtained when neurons of both hemispheres were part of one cell assembly. After bihemispheric stimulation, an interhemispheric summation of stimulus specific activity takes place within cortical cell assemblies. This model is capable of explaining different aspects of interhemispheric processing.

The absence of the word specific bilateral advantage in a split-brain patient (Mohr et al., 1994a) supports the view that the interhemispheric connections running through the corpus callosum and the anterior commissure are responsible for superior bilateral processing. The interhemispheric summation of activity is prevented when the two hemispheres are not connected.

The presence of a differential bilateral advantage also supports the cell assembly approach. A bilateral advantage is obtained for meaningful stimuli only, whereas meaningless stimuli do not gain from bilateral presentation. This differential bilateral advantage has been reported form studies on lexical processing, face processing, and object processing, when full stimulus processing was required. In terms of the cell assembly framework, it is reasonable to obtain a bilateral advantage only for meaningful stimuli. According to this explanation, the existence of cortical cell assemblies is required for interhemispheric summation. Since pseudowords, unfamiliar faces, and non-objects are not represented in cortical cell assemblies, they do not elicit a bilateral advantage.

However, a bilateral advantage has also been reported during simple stimulus detection tasks. In the present thesis, a bilateral advantage was revealed by simple patterns. In contrast to decision tasks, these tasks do not require full stimulus identification but rather simple stimulus detection. This bilateral advantage fits well with the assumptions with race models of interhemispheric processing. Based on the difference in reaction time between detection tasks and decision tasks it has been argued that the two tasks might rely on different processing stages: Whereas stimulus detection tasks rely on simple perceptual processes, decision tasks rely on further cognitive processing, for example lexical processing. Minussi et al. (1998) demonstrated that early visual evoked potentials differed between bilateral and unilateral conditions. These results suggest neural coactivation mechanism rather than independent hemispheric processing. The magnitude of the bilateral advantage was found to be smaller during simple stimulus detection than during object decision (Experiment B). Cortical summation of activity might therefore not only occur within cell assemblies by meaningful stimuli but also on early perceptual processing when only stimulus detection is required. Minussi et al. (1998) reported summation effects prior to 130 ms after stimulus onset. In contrast, the word specific evoked potential summation effect occurred 160 to 200 ms after stimulus onset. This is consistent with the time course of cell assembly activation. From studies revealing word specific electrocortical responses around 200ms, it was suggested that cell assembly ignition might occur around 150 ms after sensory activation (Mohr and Pulvermüller, 2002; Pulvermüller, 1999). The summation of cortical activation during simple reaction tasks occurs prior to the ignition of cell assemblies and therefore does not depend on the presence of meaningful stimuli.

The specificity of cortical summation to meaningful stimuli is also supported by a unilateral redundancy gain (Experiment C). Words gained from unilateral redundant stimulus presentation whereas pseudowords did not. This result cannot be explained with the race model assumption. Double stimulation of only one hemisphere should not facilitate processing. In contrast, the cell assembly framework is able to explain this finding. Multiple presentations of meaningful stimuli should elicit summation of activity in interhemispheric cell assemblies regardless of stimulus location (Mohr et al. 1996). In contrast to earlier findings of Mohr et al. (1996), the present results indicate that performance on word processing gained more when the two stimuli were presented bilaterally than when they were presented unilaterally. This indicated that the location of stimulus presentation was relevant for the summation process. Possibly, bihemispheric stimulation activated a larger number of neurons within a cortical cell assembly and therefore improved performance more than unilateral stimulation. However, the vertically centered presentation of stimuli in bilateral condition and in unilateral nonredundant condition might also account for the obtained difference.

Summation of neuronal activity is the central argument for the explanation of a bilateral advantage within the cell assembly framework. This summation of activity was demonstrated in terms of superior behavioral performance in several experiments. Further evidence for the existence of neuronal activation summation was obtained from the electrophysiological experiments of the present thesis. A neurophysiological correlate of the bilateral advantage in behavioral experiments was obtained. Bilaterally presented words were accompanied by higher cortical activation compared to unilaterally presented words or pseudowords. The activity was increased over the hemisphere located ipsilateral to the unilaterally stimulated visual field. Even more interesting, bilateral activity was also higher over contralateral hemispheres, which are directly stimulated in unilateral conditions. This higher contralateral activation was explained to be caused by a summation of activity also including the activity of the ipsilateral hemisphere, which is not stimulated in unilateral conditions. Summation of cortical activity after bilaterally presented stimuli was found for visually and auditorily presented words. Pseudowords did not elicit higher contralateral activity in bilateral compared to unilateral conditions. Furthermore, it was demonstrated that this interhemispheric summation process did not require subject’s attention.

Reference List

Alho, K., Winkler, I., Escera, C., Huotilainen, M., Virtanen, J., Jääskeläinen, I. P., Pekkonen, E., & Ilmoniemi, R. J. (1998). Processing of novel sounds and frequency changes in the human auditory cortex: Magnetoencephalographic recordings. Psychophysiology, 35, 211-224.

Allen, M. (1983). Models of hemispheric specialization. Psychological Bulletin, 93, 73-104.

Baillet, S., Mosher, J.C., & Leahy, R.M. (2001). Electromagnetic Brain Mapping. IEEE Signal Processing Magazine, 18 (6), 14-30.

Banich, M.T. (1995). Interhemispheric interaction: Mechanisms of unified processing. . In: Kitterle, F.L. (Ed.). Hemispheric Communication: Mechanisms and Models. Hillsdale: Lawrence Erlbaum Associates.

Banich, M.T., & Belger, A. (1990). Interhemispheric interaction: How do the hemispheres divide and conquer a task? Cortex, 26(1), 77-94.

Banich, M.T., & Karol, D.L. (1992). The sum of the parts does not equal the whole: evidence from bihemispheric processing. Journal of experimental Psychology: Human Perception and Performance, 18, 763-784.

Belger, A., & Banich, M.T. (1998). Costs and benefits of integrating information between the cerebral hemispheres: A computational perspective. Neuropsychology, 12(3), 380-398.

Berg, P., & Scherg, M. (1994). A multiple source approach to the correction of eye artifacts, Electroencephalography and clinical Neurophysiology, 90, 229-241.

Berger (1988). Interhemispheric cooperation and activation in integration of verbal information. Behavioural Brain Research, 29(3), 193-200.

Bertero, M., de Mol, C., & Pike, E.R. (1988). Linear inverse problems with discrete data. II. Stability and regularisation. Inverse Problems, 4, 573-594.

Boles, D.B. (1979). Laterally biased attention with concurrent verbal load: Multiple failures to replicate. Neuropsychologia, 17, 353-361.

Boles, D.B. (1983). Hemispheric interaction in visual field asymmetry. Cortex, 19, 99-113.

Boles, D.B. (1987). Reaction time asymmetry through bilateral versus unilateral stimulus presentation. Brain and cognition, 6, 321-333.

Boles, D.B. (1990). What bilateral displays do. Brain and cognition, 12, 205-228.

Boles, D.B. (1994). An experimental comparison of stimulus type, display type, and input variable contributions to visual field asymmetry. Brain and Cognition, 24, 184-197.

Boles, D.B. (1995). Parameters of the bilateral input. In: Kitterle, F.L. (Ed.). Hemispheric Communication: Mechanisms and Models. Hillsdale: Lawrence Erlbaum Associates.

Braitenberg, V., & Pulvermüller, F. (1992) Entwurf einer neurologischen Theorie der Sprache. Naturwissenschaften, 79, 103-117.

Braitenberg, V. (1978). Cell assemblies in the cerebral cortex. In Heim, R.; Palm, G., eds. Theoretical approaches to complex systems (lecture notes in biomathematics, vol 21), Berlin: Springer; 171-188.

Braun, C.M.J. (1992). Estimates of interhemispheric dynamics from simple manual reaction time to extrafoveal stimuli. Neuropsychological Review, 3, 321-365.

Brown, B.S., Bjerke, M.D., & Galbraith, G.C. (1998). Interhemispheric transfer in normals and acallosals: latency adjusted evoked potential averaging. Cortex, 34, 677-692.

Brown, W.S., & Jeeves, M.A., 1993. Bilateral visual field processing and evoked potential interhemispheric transmission time, Neuropsychologia, 31, 1267-1281.

Brown, W.S., Jeeves, M.A., Dietrich, R., & Burnison, D.S. (1999). Bilateral field advantage and evoked potential interhemispheric transmission in commissurotomy and callosal agenesis. Neuropsychologia, 37, 1165-1180.

Brown, W.S., Larson, E.B., & Jeeves, M.A. (1994). Directional asymmetries in interhemispheric transmission time: evidence from visual evoked potentials, Neuropsychologia 32, 439-448.

Chiarello, C., & Nuding, S. (1987). Visual field effects for processing content and function words. Neuropsychologia, 25, 539-548.

Clarke, J.M., & Zaidel, E. (1989). Simple reaction times to lateralized light flashes. Varieties of interhemispheric communication routes. Brain, 112, 849-70.

Collins, M., & Coney, J. (1998) Interhemispheric communication is via direct connections. Brain and Language, 64(1), 28-52.

Coney, J. (1985). Dual hemispheric processing in a letter matching task. Perception & Psychophysics, 38(4), 331-342.

Cook, N.D. (1984). Homotopic callosal inhibition. Brain and Language, 23(1), 116-25.

Cook, N.D. (1986). The brain code: mechanisms of information transfer and the role of the corpus callosum. Methuen: London.

Corballis, M.C. (1998). Interhemispheric neural summation in the absence of the corpus callosum. Brain, 121, 1795-1807.

Davis, R., & Schmit, V. (1973). Visual and verbal coding in the interhemispheric transfer of information. Acta Psychologica, 37(4), 229-240.

Dehaene-Lambertz, G. (1997). Electrophysiological correlates of categorical phoneme perception in adults. NeuroReport, **8**, 919-924.

Dimond, S., & Beaumont, G. (1971). Use of two cerebral hemispheres to increase brain capacity. Nature, 232, 270-271.

Dimond, S., & Beaumont, G. (1972). Processing in perceptual integration between and within the cerebral hemispheres. British Journal of Psychology, 63(4), 509-514.

Eglin, M. (1987). Interference and priming within and across visual fields in a lexical decision task. Neuropsychologia, 25(4), 613-624.

Endrass, T., Mohr, B., & Pulvermüller, F. (2004). Enhanced mismatch negativity brain response after binaural word presentation. European Journal of Neuroscience, 19(6): 1653-1660.

Endrass, T., Mohr, B., & Rockstroh, B. (2002). Reduced interhemispheric transmission time in schizophrenia patients: Evidence from event-related potentials. Neuroscience Letters 320, 57-60.

Hagelthorn, K.M., Brown, W.S., & Amano, S. (2000). Normal development of bilateral field advantage and evoked potential interhemispheric transmission time. Developmental Neuropsychology, 18(1), 11-31.

Hamalainen, M.S., & Ilmoniemi, R.J. (1994). Interpreting magnetic fields of the brain: minimum norm estimates. Medical & Biological Engineering & Computing, 32 (1), 35-42.

Hasbrooke, R.E., & Chiarello, C. (1998). Bihemispheric processing of redundant bilateral lexical information. Neuropsychology, 12(1), 78-94.

Hatta, T., & Yoshizaki, K. (1996). Interhemispheric cooperation of left- and right-handers in mental calculation tasks. Laterality, 1, 299-313.

Hatta, T., Kawakami, A., & Kogure, T. (2002). Effects of type of cognitive demand on bilateral advantage in interhemispheric processing. Psychological Research, 66(2), 133-142.

Hauk, O., Berg, P., Wienbruch, C. Rockstroh, B., & Elbert, T. (1999). The minimum norm methode as an effective mapping tool for MEG analysis. In: R. Yoshimoto, M. Kotani, S. Kuriki, H. Karibe, N. Nakasato (Eds.), Recent Advances in biomagnetism. Tohuku University Press, Sendai, pp. 213-216.

Hauk, O., Keil, A., Elbert, T., & Mueller, M.M. (2002). Comparison of data transformation procedures to enhance topographical accuracy in time-series analysis of the human EEG. Journal of Neuroscience Methods, 113 (2), 111-122.

Hebb, D.O. (1949). The organization of behavior. A neurophysiological theory. New York: Willey.

Hellige, J.B. (1993). Hemispheric asymmetry: what's right and what's left? Cambridge, MA: Harvard University Press, 1993.

Hellige, J.B. (1996). Hemispheric asymmetry for visual information processing. Acta Neurobiologiae Experimentalis, 56, 485-97.

Hellige, J.B., & Michimata, C. (1989). Visual laterality for letter comparison: Effects of stimulus factors, response factors, and metacontrol. Bulletin of the Psychonomic Society, 27(5), 441-444.

Hellige, J.B., Jonsson, J.E., & Michimata, C. (1988). Processing from LVF, RVF and bilateral presentations: Examinations of metacontrol and interhemispheric interaction. Brain & Cognition, 7, 39-53.

Hellige, J.B., Taylor, A.K., & Eng, T.L. (1989). Interhemispheric interaction when both hemispheres have access to the same stimulus information. Journal of Experimental Psychology: Human Perception and Performance, 15, 711-722.

Iacoboni, M., & Zaidel, E. (1996). Hemispheric independence in word recognition: Evidence from unilateral and bilateral presentations. Brain & Language, 53(1), 121-140.

Iacoboni, M., Ptito, A., & Weekes, N.Y. (2000). Parallel visuomotor processing in the split brain: Cortico-subcortical interactions. Brain, 123(4), 759-769.

Jones, B. (1982). The integrative action of the cerebral hemispheres. Perception & Psychophysics, 32(5), 423-433.

Koivisto, M. (2000). Interhemispheric interaction in semantic categorization of pictures. Cognitive Brain Research, 9, 45-51.

Koivisto, M., & Revonsuo, A. (2003). Interhemispheric categorization of pictures and words. Brain & Cognition, 52(2), 181-191.

Korpilahti, P., Krause, C.M., Holopainen, I., & Lang, A.H. (2001). Early and late mismatch negativity elicited by words and speech-like stimuli in children. Brain and Language, 76, 332-339.

Kroll, J. F., & Potter, M. C. (1984). Recognizing Words, Pictures, and Concepts: A Comparison of Lexical, Object, and Reality Decisions. Journal of Verbal Learning and Verbal Behavior, 23, 39-66.

Larson, E.B., & Brown, W.S. (1997). Bilateral field interactions, hemispheric specialization and evoked potential interhemispheric transmission time. Neuropsychologia, 35, 573-581.

Levy, J., & Trevarthen, C. (1976). Metacontrol of hemispheric function in human split-brain patients. Journal of Experimental Psychology: Human Perception & Performance, 2(3), 299-312.

Levy, J., Heller, W., & Banich, M.T. (1983) Are variations among right-handed individuals in perceptual asymmetries caused by characteristic arousal differences between hemispheres? Journal of Experimental Psychology: Human Perception & Performance, 9(3), 329-359

Liederman J., & Meehan P. (1986). When is between-hemisphere division of labor advantageous? Neuropsychologia, 24(6), 863-74.

Liederman J., Merola J., & Martinez S. (1985). Interhemispheric collaboration in response to simultaneous bilateral input. Neuropsychologia, 23(5), 673-83.

Ludwig, T.E., Jeeves, M,A., Norman, W.D., & DeWitt, R. (1993). The bilateral field advantage on a letter-matching task. Cortex, 29(4), 691-713.

Luh, K.E., & Levy, J. (1995). Interhemispheric cooperation: Left is left and right is right, but sometimes the twain shall meet. Journal of Experimental Psychology: Human Perception & Performance, 21(6), 1243-1258.

Mackavey, W., Curcio, F., & Rosen, J. (1975). Tachistoscopic word recognition performance under conditions of simultaneous bilateral presentation. Neuropsychologia, 13(1), 27-33.

Marks, N.L, & Hellige, J.B. (1999). Effects of bilateral stimulation and stimulus redundancy on interhemispheric interaction. Neuropsychology, 13, 475-487.

Marslen-Wilson, W.D. (1987). Functional parallelism in spoken word-recognition. Cognition, 25, 71-102.

Marsolek, C.J., Nicholas, C.D., & Andresen, D.R. (2002). Interhemispheric communication of abstract and specific visual-form information. Neuropsychologia, 40, 1983-1999.

Marzi, C.A. (1999). The Poffenberger paradigm: a first, simple, behavioural tool to study interhemispheric transmission in humans. Brain Research Bulletin 50 (5-6), 421-422.

Marzi, C.A., Bisiacchi, P., & Nicoletti, R. (1991). Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. Neuropsychologia 29, 1163-1177.

McCarthy, G., & Wood, C. (1985). Scalp Distributions of event-related Potential: An Ambiguity associated with Analysis of Variance models. Electroencephalography and clinical Neurophysiology 62, 203-208.

McKeever, W.F., & Huling, M.D. (1971). Bilateral tachistoscopic word recognition as a function of hemisphere stimulated and interhemispheric transfer time. Neuropsychologia, 9(3), 281-288.

Miller, J. (1982). Divided Attention: Evidence for coactivation with redundant signals. Cognitive Psychology, 14, 247-279.

Minussi, C., Girelli, M., & Marzi, C.A. (1998). Neural site of the redundant target effect: electrophysiological evidence. Journal of Cognitive Neuroscience, 10, 216-230.

Mohr, B., Heim, S., Pulvermüller, F., & Rockstroh, B. (2001). Functional asymmetry in schizophrenic patients during auditory speech processing. Schizophrenia Research, 52, 69-78.

Mohr, B., & Pulvermüller, F. (2002). Redundancy gains and costs in cognitive processing: effects of short stimulus onset asynchronies. Journal of Experimental Psychology: Learning, Memory and Cognition, 28, 1200-1223.

Mohr, B., Landgrebe, A., & Schweinberger, S.R. (2002). Interhemispheric cooperation for familiar but not unfamiliar face processing. Neuropsychologia, 40, 1841-1848.

Mohr, B., Pulvermüller, F., & Zaidel, E. (1994b). Lexical decision after left, right, and bilateral presentation of content words, function words, and non-words: evidence for interhemispheric interaction. Neuropsychologia, 32, 105-124.

Mohr, B., Pulvermüller, F., Cohen, R., Rockstroh, B. (2000). Interhemispheric cooperation during word processing: evidence for callosal transfer dysfunction in schizophrenic patients, Schizophrenia Research, 46, 231-239.

Mohr, B., Pulvermüller, F., Mittelstädt, K., & Rayman, J. (1996). Multiple simultaneous stimulus presentation facilitates lexical processing. Neuropsychologia, 34, 1003-1013.

Mohr, B., Pulvermüller, F., Rayman, J., & Zaidel, E. (1994a). Interhemispheric cooperation during lexical processing is mediated by the corpus callosum: evidence from the split-brain. Neuroscience Letters, 181, 17-21.

Mordkoff, J.T., & Yantis, S. (1991). An interactive race model of divided attention. Journal of Experimental Psychology: Human Perception & Performance, 17(2), 520-538.

Mordkoff, J.T., & Yantis, S. (1991). An interactive race model of divided attention. Journal of Experimental Psychology: Human Perception & Performance, 17(2), 520-538.

Moscovitch, M., & Klein, D. (1980). Material-specific perceptual interference for visual words and faces: Implications for models of capacity limitations, attention, and laterality. Journal of Experimental Psychology: Human Perception & Performance, 6(3), 590-604.

Mullin, P.A., & Egeth, H.E. (1989). Capacity limitations in visual word processing. Journal of Experimental Psychology: Human Perception & Performance, 15(1), 111-123.

Näätänen, R. (2001). The perception of speech sounds by the human brain as reflected by the mismatch negativity (MMN) and its magnetic equivalent (MMNm). Psychophysiology, 38, 1-21.

Näätänen, R., Lehtokoski, A., Lennes, M., Cheour, M., Huotilainen, M., Iivonen, A., Valnio, A., Alku, P., Ilmoniemi, R.J., Luuk, A., Allik, J., Sinkkonen, J., & Alho, K. (1997). Language-specific phoneme representations revealed by electric and magnetic brain responses. Nature, 385, 432-434.

Näätänen, R., Tervaniemi, M., Sussman, E., Paavilainen, P. & Winkler, I. (2001). 'Primitive intelligence' in the auditory cortex. Trends in Neurosciences, 24, 283-288.

Näätänen, R., & Winkler, I. (1999). The concept of auditory stimulus representation in cognitive neuroscience. Psychological Bulletin, 125, 826-859.

Norman, W.D., Jeeves, M.A., Milne, A., & Ludwig, T. (1992). Hemispheric interactions: The bilateral advantage and task difficulty. Cortex, 28, 623-642.

Nowicka, A., Grabowska, A., & Fersten, E. (1996). Interhemispheric transmission of information and functional asymmetry of the human brain. Neuropsychologia, 34, 147-151.

Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9, 97-113.

Olk, B., & Hartje, W. (2001). The bilateral effect: Callosal inhibition or intrahemispheric competition? Brain & Cognition, 45(3), 317-324.

Ortmann, W.D. (1995). Hochfrequente deutsche Wortformen. Bde. 1 & 2, Goethe-Institut, Arbeitsstelle für wissenschaftliche Didaktik, München.

Poffenberger, A.T. (1912). Reaction time to retinal stimulation with special reference to the time lost in condition through nerve centers. Archives of Psychology, 23, 1-73.

Pollmann, S., & Zaidel, E. (1999). Redundancy gains for visual search after complete commissurotomy. Neuropsychology, 13(2), 246-258.

Pulvermüller, F. (1999). Words in the brain's language. Behavioral Brain Sciences, 22, 253-336.

Pulvermüller, F., Kujala, T., Shtyrov, Y., Simola, J., Tiitinen, H., Alku, P., Alho, K., Martinkauppi, S., Ilmoniemi, R.J., & Näätänen, R. (2001). Memory traces for words as revealed by the mismatch negativity. NeuroImage, 14(3), 607-616.

Pulvermüller, F., Lutzenberger, W., & Birbaumer, N. (1995). Electrocortical distinction of vocabulary types. Electroencephalography & Clinical Neurophysiology, 94(5), 357-370.

Pulvermüller, F., Lutzenberger, W., & Preissl, H. (1999). Nouns and verbs in the intact brain: Evidence from event-related potentials and high-frequency cortical responses. Cerebral Cortex, 9(5), 497-506.

Pulvermüller, F., & Mohr, B. (1996). The concept of transcortical cell assemblies: a key to the understanding of cortical lateralization and interhemispheric interaction. Neuroscience and Biobehavioral Reviews, 20, 557-566.

Pulvermüller, F., Shtyrov, Y., Kujala, T., & Näätänen R. (2004). Word-specific cortical activity as revealed by the mismatch negativity (MMN). Psychophysiology, 41, 106-112.

Raab, D.H. (1962). Statistical facilitation of simple reaction times. Transactions of the New York Academy of Sciences, 24(5), 574-590.

Rinne, T., Alho, K., Alku, P., Holi, M., Sinkkonen, J., Virtanen, J., Bertrand, O., & Näätänen, R. (1999). Analysis of speech sounds is left-hemisphere predominant at 100-150 ms after sound onset. NeuroReport, 10, 1113-1117.

Roland, P.E., Larsen, B., Lassen, N.A., & Skinhoj, E. (1980). Supplementary motor area and other cortical areas in organization of voluntary movements in man. Journal of Neurophysiology, 43(1), 118-136.

Rugg, M.D. (1982). Electrophysiological studies. In J.G. Beaumont (Ed.), Divided visual field studies of cerebral organization. London: Academic Press.

Rugg, M.D., Lines, C.R., & Milner, A.D. (1984). Visual evoked potentials to lateralized visual stimuli and the measurement of interhemispheric transmission time, Neuropsychlogia, 22, 215-225.

Rugg, M.D., Milner, A.D., & Lines, C.R. (1985). Visual evoked potentials to lateralised stimuli in two cases of callosal agenesis. Journal of Neurology, Neurosurgery & Psychiatry, 48(4), 367-373.

Saron, C.D., & Davidson, R.J. (1989). Visual evoked potential measures of interhemispheric transfer time in humans. Behavioral Neuroscience, 103(5), 1115-1138.

Schweinberger, S.R., Baird, L.M., Blümler, M., Kaufmann, J.M., & Mohr, B. (2003). Interhemispheric cooperation for face recognition but not for affective facial expressions. Neuropsychologia, 41, 407-414.

Seitz, R.J., & Roland, P.E. (1992). Learning of Sequential Finger Movements in Man: A Combined Kinematic and Positron Emission Tomography (PET) Study. European Journal of Neuroscience, 4(2), 154-165.

Sergent, J., & Myers, J.J. (1985). Manual, blowing, and verbal simple reactions to lateralized flashes of light in commissurotomized patients. Perception & Psychophysics, 37(6), 571-578.

Shtyrov, Y., & Pulvermüller F. (2002). Neurophysiological evidence of memory traces for words in the human brain. NeuroReport, 13(4), 521-525.

Shtyrov, Y., Kujala, T., Ahveninen, J., Tervaniemi, M., Alku, P., Ilmoniemi, R. J., & Näätänen, R. (1998). Background acoustic noise and the hemispheric lateralization of speech processing in the human brain: Magnetic mismatch negativity study. Neuroscience Letters, 251, 141-144.

Shtyrov, Y., Kujala, T., Palva, S., Ilmoniemi, R.J., & Näätänen R. (2000). Discrimination of speech and of complex nonspeech sounds of different temporal structure in the left and right cerebral hemispheres. NeuroImage, 12(6), 657-663.

Snodgrass, J.G., & Vanderwart, M. (1980). A Standardized Set of 260 Pictures: Norms for Name agreement, Image Agreement, Familiarity and Visual Complexity. Journal of Experimental Psychology, Vol. 6, No. 2, 174-215.

Van der Heijden, A.H., la Heij, W., & Boer, J.P. (1983). Parallel processing of redundant targets in simple visual search tasks. Psychological Research, 45(3), 235-254.

Warren, P., & Marslen-Wilson, W. (1988). Cues to lexical choice: discriminating place and voice. Percept Psychophys, 43, 21-30.

Weissman, D.H., & Banich, M.T. (2000). The cerebral hemispheres cooperate to perform complex but not simple tasks. Neuropsychology, 14, 41-59.

Yoshizaki, K., 2001. Effects of visual familiarity for words on interhemispheric cooperation for lexical processing. Cognitive Brain Research.. 12 (3), 409-414.

Zaidel, E. (1983). Disconnection syndrome as a model for laterality effects in the normal brain. In: Hellige, J. (Ed.). Cerebral hemisphere asymmetry: Method, theory and application. New York: Praeger.

Zaidel, E., & Rayman, J. (1994). Interhemispheric control in the normal brain: Evidence from redundant bilateral presentations. In: Umilta, C., & Moscovitch, M. (Eds.). Attention and performance 15: Conscious and nonconscious information processing, (vol. 15). Cambridge, MA: Cambridge University Press.

Zaidel, E., Clarke, J.M., & Suyenobu, B. (1990). Hemispheric independence: A paradigm case for cognitive neuroscience. In Scheibel, A.B., & Wechsler, A.F. (Eds.). Neurobiology of higher cognitive function. New York: Guilford.