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Brain Economics:

Housekeeping Routines in the Brain

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The specific function of scientific explanation is ...to turn the unexpected, as far as possible, into the expected.

Stephen Toulmin

1.1 Brain Economics

Any everyday activity is composed of a succession of different tasks. For instance, for many of us the typing of a sentence in an electronic document requires pressing keys on a keyboard and checking the screen to see whether the pressed keys correspond with the sentence that must be typed. No matter how simple, any task requires that sensory input received from the outside be elaborated (i.e., understood, compared, etc.) before executing an action (or response). When composing a sentence, the words retrieved from the writer's memory form the input for the task, and the representation of the words must be held in working memory before the letters composing the words are matched with the letters keys on the keyboard. When the position on the keyboard of the key corresponding to the input letter has been found, the finger which will execute the response must be selected. When the response finger has been selected the action to push the key will be initiated, and, finally the correspondence between the input text and the typed one must be visually checked.

Information processing is generally assumed to require processing resources, which may be defined in terms of general-purpose processing units (Hockey, 1997), or a commodity of limited availability which enables or energizes performance on a task, such as the various form of memory capacity, or communication channels (Norman & Bobrow, 1975). Availability of processing resources affects the speed and accuracy with which a task can be executed. Support for the existence of processing resources comes from demonstrations of poor performance when resources normally available for a task are pulled away by another task. For example, driving a car and simultaneously conversing with the passenger is possible under normal traffic conditions.

However, performance on one or both tasks may degrade depending on the demands of the concurrent task, resulting in a disrupted conversation when driving in a busy city center or in poor driving performance when the conversation gets more intriguing (see, e.g., Wickens, 1984).

Driving while conversing is an example of multitasking behavior. Multitasking is commonly used to study the allocation of processing resources, or how attention is divided between two or more tasks (Kahneman, 1973). One of the assumptions supporting the energetic concept of resources is that if the resources demands do not exceed the available supply, several tasks can be performed simultaneously (Kinsbourne & Hicks, 1978). The ability to execute several tasks simultaneously does not depend solely on the availability of processing resources, but also on the allocation policy with which the available supply is distributed across the tasks. The ability to allocate resources at appropriate times is defined as efficient timesharing (Salthouse & Miles, 2002), and it implies that the processing resources needed to execute one of the tasks are allocated to the specific task at the appropriate time, thereby effectively preventing the different tasks from drawing from the same resource pool concurrently (Salthouse & Miles, 2002). Timesharing can be inefficient when the resources necessary to perform both tasks are drawn from the same resource pool simultaneously and the available limit is reached, thereby impeding or delaying task execution (Wickens, 1984).

Another type of dual-task interference is structural interference (see, e.g., Broadbent, 1958). Interference is structural when the same process (e.g., response selection) is recruited simultaneously by two different tasks. This type of interference has been studied extensively with the psychological refractory period (PRP, e.g., Smith, 1967) paradigm in which two tasks, each requiring a speeded response, are to be executed (for reviews see Pashler, 1994; Jolicoeur, 1999). The temporal separation between the stimuli for the two tasks is systematically varied between long (e.g., 1500 ms) and short (e.g., 150 ms). The typical outcome is an increment in the response time to the second stimulus when it follows the first within a short interval. The delay in the reaction time has been interpreted as the result of a structural bottleneck (Broadbent, 1956) which lies at the stage of response selection. A bottleneck is a stage in the sequence of information processing which obstructs the flow of information processing for one task when it is already being used by another task.

The PRP effect is robust, and is still present when tasks requiring different stimulus or response modalities are combined (e.g., Creamer, 1963; Borger, 1963; Pashler

1994; Jolicoeur 1999; but see Greenwald 1972, 2003). Moreover, the effect does not disappear upon extended practice (Dutta & Proctor, 1992; Proctor & Dutta, 1993).

An alternative account for the PRP effect attributes it to executive control (Meyer & Kieras, 1997). Meyer and Kieras suggested that the fixed sequential order in the execution of the two tasks imposed by the task instructions explains the PRP effect more effectively than the response-selection bottleneck theory. The account proposed by Meyer and Kieras, named executive-process interactive control (EPIC), diverges from the response-selection bottleneck approach by arguing that the PRP effect reflects a strategic bottleneck adopted by participants to defer the execution of the second task until the first has been accomplished, rather than a fundamental structural bottleneck.

That multiple-task performance can be constrained by sharable energetic resources (or general capacity, see e.g., Kahneman, 1973), in addition to non-sharable structural bottleneck stages or processes, is supported by a large number of studies showing that the cognitive load associated with a secondary task can have a graded effect on the performance on the primary task. In a classic study, Allport, Antonis, and Reynolds (1972) reasoned that it is not necessary that two different tasks share the same structure or function to interfere with each other, but the scarce availability of general processing resource should be sufficient to induce performance costs. Allport et al. tested this assumption, showing first that the simultaneous execution of two task decreased performance levels, and, second, that dual-task performance was even more impaired if the two tasks shared a common structure than if they did not. Allport et al. asked their participants to divide their attention between a shadowing task and a task of remembering words. The shadowing task consisted of repeating spoken messages as they were presented, and it was performed only to pose a general load on cognitive processing, which should have a 'general' detrimental effect on performance. The memory task consisted of reporting if a word presented visually or auditorily (the presentation was dichotic) belonged to a set of already presented words. Allport and colleagues predicted that the shadowing task would interfere less with the visual memory task than with the auditory memory task because the simultaneous presentation of two auditory stimuli added a structural interference in the processing of sensorial input to the already present capacity load posed by the concurrent shadowing task.

Memory performance was better in the absence of the shadowing task, suggesting that the shadowing task per se drew resources away from the memory task, independently of the modality of the stimulus presentation. When the shadowing had to be performed simultaneously with the memory task, performance was poorer for words

presented auditorily than visually. This suggests structural interference at the level of the phonological loop. In fact, when the words to be compared were presented in the visual modality, Allport et al.'s (1972) participants executed the comparison using visual characteristics of the words displayed (e.g., the number of letters, the presence of repeated letters, or small marks on the slides used to display the words) and ignoring the verbal characteristics (e.g., semantic or phonological properties), therefore bypassing the phonological loop. In conclusion, these results sustained the claim that resources had a general 'energetic' connotation because performance costs were present when the tasks had to be performed simultaneously, and it showed that these performance drops were not exclusively related to structural interference because performance was worsened when the tasks combination also shared a structure.

The study of Allport et al. (1972) was one of the first to indicate that multitasking interference can result from more complex interactions involving specific structures, processes, or resources (Navon & Gopher, 1979). In his *multiple resources theory*, Wickens (1984) proposed that processing resources are represented by three dichotomous dimensions: processing stages (perceptual-cognitive and response processes), processing codes (verbal and spatial), and input-output modalities (visual/auditory and manual/vocal, respectively). While this proposal was not meant to provide a complete picture of resource-dependent processing in the brain, it has served to provide a reasonable coherent and simple explanation, and indeed prediction, of patterns of interference, or lack thereof, between many different task combinations (Sanders, 1997). Despite such successes, the resource framework has been criticized and several additions, next to structural bottlenecks, or alternative theoretical accounts have been proposed. Navon (1984) argued that the graded trade-offs in multiple-task performance might be due to demand characteristics rather than real limits to available resources. Others have pointed to the critical role of strategic resource allocation that must be managed by another coordinating process (e.g., Baddeley's, 1986, executive control or Gopher's, 1992, attentional control) that might be tightly associated with the executive processes subserved by prefrontal cortex (Duncan & Owen, 2000).

Within the framework of cross-talk models, dual-task interference is explained in terms of different forms of outcome conflict, in which one task may produce outputs, throughputs, or side effects that are harmful to the processing of the other task (Navon & Miller, 1987, 2002). An appealing feature, for present purposes, of the latter two proposals is that they lend themselves more easily than the more abstract resource concept to an interpretation of dual-task performance interference in terms of neuronal

crosstalk or interference or in terms of dynamic competition for neuronal workspace.

1.1.1 Individual differences and resources

The concept of resources, considering its multiple aspects and various links with higher level functions, is considered by some to be analogous to Spearman's g-factor (see, e.g., Sanders, 1997). The study of processing resources through the observation of individual differences in task performance can thus be considered a way to study resource management. Task performance depends on the resources available to an individual but also on how these resources are allocated to the different operations necessary to fulfill the task. For example, it has been hypothesized that individuals with higher IQ are capable of more efficient timesharing than individuals of lower IQ, because they employ a more efficient overall task structure (see e.g., Damos & Wickens, 1980; Kramer, Larish, & Strayer, 1995; Kramer, Larish, Weber, & Bardell, 1999).

Another source of individual differences which affects task performance is the level of familiarity with the task at hand. With sufficient practice, the operations necessary to execute the task will be performed more quickly and accurately, reducing interference and temporal overlap with other tasks. As a consequence of this automation processes, the execution of these operations becomes less subject to voluntary control, which can be interpreted as if fewer resources are required to execute the tasks (Schneider & Shiffrin, 1977).

Spelke, Hirst, and Neisser (1976) reported an example in which task automation following extensive practice (i.e., 17 weeks) on a task can be interpreted in terms of a reduction in the resources required to perform the task. Spelke et al. showed a reduction of interference in the task of automatic writing (for a review see Koutstaal, 1992) in which participants read short stories while writing down spoken words. Participants' performance at the beginning of the experiment was very poor, however after practicing automatic writing for an hour a day for seventeen weeks, participants were able to execute the task approximately as quickly as when performing only one of the two tasks. Broadbent (1982, see also Welford, 1980) proposed that, rather than automaticity of task execution, the results of Spelke et al. (1976) could be better accounted for by switching of attention between the two tasks. Nonetheless switching from one task to another is time consuming, it could facilitate dual task execution if participants developed a strategy of efficient response-buffering by which the response to one of the tasks is hold until it cannot be executed without compromising

the performance on the other task, in other words this approach could be thought of as sophisticated timesharing. Rather than attempting to disentangle if the best account for performance improvements as a consequence of task practice results from efficient timesharing (e.g., Broadbent, 1982) or economization of resources (e.g., Spelke et al., 1976) it is important to note that task performance improves as a function of practice, and it is therefore connected with resource management or resources per se.

Practice effects are even stronger when familiarity with a task has been acquired outside the experimental laboratory. For example a highly skilled typist can perform several tasks simultaneously (e.g., shadowing or reciting nursery rhymes) while typing words, whereas the performance in the same tasks of less skilled typists is likely to be more error prone, if possible at all (Shaffer, 1975). Individuals who are more familiar with a certain task or who have practiced for longer periods are likely to perform better than persons who encounter the problem for the first time. For example, experienced taxi drivers have a very detailed mental map of the city they drive in; thus it is likely they will be more capable than a naive person, such as a tourist, of finding alternatives routes when traffic is heavy (e.g., Grabner, Stern, & Neubauer, 2003; Woollett, Glensman, & Maguire, 2008). Yet, the acquisition of a specific ability is not a 'direct' source of individual differences as, for example, IQ would be, because extensive practice on a task is independent from the amount of resources that a person has available to resolve it.

If learned skills are not directly linked to the concept of resources, there is a temporal aspect to the ability of learning a new task or transferring acquired knowledge to new situations which can be related to efficient resources management and individual differences. In fact, if one person is faster than another in learning a skill or in transferring consolidated knowledge to a new skill, it can be assumed that one has more resources available or is more flexible in allocating resources. Evidence showing individual differences in transferring knowledge to a new situation was provided in a study by Grabner et al. (2003), who showed that for individuals who are equally familiar with a certain task (e.g., driving a taxi), individuals with lower cognitive abilities are less able to transfer acquired skill into a new task than are individuals with higher cognitive abilities. Grabner et al. studied the abilities of relatively high IQ and low IQ experienced taxi drivers with respect to learning new maps. After a period of familiarization with the map the two groups of taxi drivers were questioned about routes in the familiar environment (their city) and in the novel one (routes in an artificial map). The two groups of experienced taxi drivers did not differ on the familiar

task, but did differ in the novel task of memorizing routes in the artificial map (for evidence of individual differences in transferring time-sharing skill, see Ackerman, Scheider, & Wickens, 1984; Somberg & Salthouse, 1982).

1.1.2 Will the last be first?

One of the reasons that resource demands are studied is to determine possible sources of interference between tasks or task components so that training techniques can be developed to resolve or avoid the interference and therefore improve task performance (Polson & Friedman, 1988). Mathews, Hunt, and MacLeod (1980) presented evidence suggesting that appropriate instructions on the execution of the sentence verification task (Clark & Chase, 1972) can abate IQ differences. Mathews et al. (1980) tested the persistence of IQ-related differences when the strategies to solve the task were controlled for. The authors, in two separate sessions, explicitly instructed participants on the use of the two different strategies, the imagery one which was found in a study by (MacLeod, Hunt, & Mathews, 1978) to be used by high IQ individuals and consisted in visualizing an image of the sentence before proceeding to the comparison, and the linguistic one which was used by the group with low IQ and consisted in reiterating the sentence when the figure was displayed. The results showed no differences in accuracy between the two groups nor between the two strategies, which sustain the claim that individual differences in performance can be reduced, or even eliminated, with appropriate training.

Another example of how appropriate training may benefit human performance is a study by Kramer et al. (1995) in which it was tested whether training elderly persons to divide their attention more effectively could help them overcome the age-related deficit in rapidly re-deploying attention across different tasks. Elderly persons are not as efficient in dividing their attention as younger individuals, therefore it may be advantageous to devise a training method which could help elderly persons to divide their attention between tasks in a more effective way. Kramer et al. provided on-line feedback about performance on a monitoring task performed simultaneously with an alphabet arithmetic task to help their participants to re-distribute their attention better across the two tasks. In the monitoring task six different gauges had to be monitored and participants had to push a button when one of the gauges reached the digit 9 or a higher number. The state of the gauges could be checked by pushing a button and would remain displayed on an indicator for 1.5 s. Simultaneously participants had to perform “alphabet arithmetic” in which equations such as “H - 3 = E” must

be verified (where letters correspond to their ordinal position in the alphabet, e.g., A = 1, B = 2, ..., Z = 26). Two groups of elderly individuals participated in the study, one group received feedback to divide their attention equally between the two tasks, whereas the other was trained to divide their attention with a variable-priority strategy (i.e., participants were to dedicate 20% of their attention to one task and 80% to the other). Training with the variable-priority strategy led to better performance and better transfer of timesharing skill to a new situation.

The previous examples support the idea that differences in human performance may be reduced if accurate management of processing resources or optimization of timesharing are achieved through appropriate training. However, performance improvement does not consist solely of reducing differences between persons of different abilities, but can also aim to exploit the abilities or capabilities of information processing of any person, as, for example, by studying a task that is already performed and investigating if it is possible to develop new strategic solutions which are more efficient than the ones currently used.

Research by Seagull and Gopher's (1997) illustrates how individuals can be instructed to integrate different sources of information to better perform the complex task of piloting a helicopter. Seagull and Gopher (1997) studied the effect of instructing helicopter pilots to strategically restructure two tasks to increase task performance thus improving timesharing efficiency. They devised a training program which instructed helicopter pilots to use more effectively their helmet-mounted displays, displays which pilots avoided using because to collect peripheral information through these displays head movements are necessary and head movements may cause a loss of orientation. However, collecting peripheral information improves pilots' abilities to focus on a specific point, which may be useful, for instance, to avoid a collision or to spread the field of view in order to gain a broader perspective of the surroundings. Pilots who followed the training devised by Seagull and Gopher eventually outperformed the performance of the pilots who had not received the specific training.

Formulating schemas or guidelines to configure tasks optimally in terms of workload as well as in terms of interference or integration with other tasks will increase human performance (Polson & Friedman, 1988; Seagull & Gopher, 1997). However Polson and Friedman warned that such improvements will be possible only if the factors which affect human performance are determined. This includes, for example, the rigorous definition of which resources are involved in the execution of a particular task, how resources are recruited across multiple tasks, if a particular environment

may influence which resources are required or recruited, which variables interact in resource management, and how different task components interact in task execution. Also, it should not be forgotten that, as suggested by (Salthouse & Miles, 2002), the different abilities of each participant (e.g., individual differences in resource availability but also in task proficiency) must be taken into account when analyzing resource allocation policies. This type of research could lead to the development of specific training programs to acquire specialized skills as the ones devised by Gopher and collaborators (see e.g., Seagull & Gopher, 1997; Erev & Gopher, 1999; Kramer et al., 1995; Gopher, 1992; Gopher, Weil, & Bareket, 1989), which may help economizing resources in information processing, and perhaps boost the limited potential of lower IQ individuals.

1.1.3 A physical/neural counterpart for resources

Kinsbourne and Hicks (1978) proposed that resources are a generalized commodity reflected by functional cerebral space. Functional cerebral space is any cerebral area used to accomplish a mental operation and it depends on the specifics of localization of functions in the brain. What cerebral areas (or space) is used is determined by the processing requirements of the task at hand. For example, language areas are used when language production is involved (Ojemann, Ojemann, Lettich, & Berger, 1989; Ojemann, Fried, & Lettich, 1989) and areas specific for the elaboration of spatial information when the task requires mental rotation (Cohen et al., 1996). In Kinsbourne and Hicks's view, the functional topographic map (or arrangement) of the cerebral cortex can be used as a basis to explain dual task interference. The topographical organization of the cerebral cortex (Penfield & Rasmussen, 1950) refers to the spatial correspondence between the origin of the sensorial stimulation and the cerebral areas receiving it (e.g. in the cerebral cortex the sensory information from the hand is represented next to sensory information coming from the arm, i.e., somatotopically). According to this view, the simultaneous execution of two tasks would be hampered if the tasks involve partially overlapping or topographically nearby cerebral circuits (note that this view bears a distinct resemblance to crosstalk models of dual-task interference, Navon & Miller, 1987, 2002).

Polson and Friedman (1988) revisited multiple resource theory (Wickens, 1984) and the theory of functional cerebral space (Kinsbourne & Hicks, 1978) with their hypothesis that there are two primary resources pools, represented by the two cerebral hemispheres. This hypothesis was substantiated by results from studies on cere-

bral specialization that showed that the simultaneous execution of two tasks requiring complementary hemispheres interfered less than two tasks that involved the same hemisphere.

Other proposals for possible neural correlates of mental resources are found in studies investigating neural differences in information processing. These studies have focused on correlates of brain activity which could help interpreting individual differences in tests measuring cognitive abilities (e.g., IQ tests). Brain activity has been operationalized as cerebral glucose metabolism (or consumption of energy) as measured through positron emission tomography (PET, see e.g., Haier et al., 1992), level of brain activation as revealed by functional magnetic resonance imaging (fMRI, see e.g., Jaeggi et al., 2007), or amplitude of specific brain rhythms as quantified using electroencephalography (EEG, see e.g., Neubauer, Freudenthaler, & Pfurtscheller, 1995). The assumption behind these studies is that brain use requires brain activation, and that lower activation reflects more efficient brain use, a concept that is referred to as neural efficiency (Vernon, 1993).

The neural efficiency theory was proposed by Vernon (1993) based on a large body of literature which consistently showed that individuals with high cognitive abilities used their brain more efficiently as reflected by, for example, lower brain activations, when performing a task at a comparable level than individuals with low cognitive abilities. Vernon substantiated this idea with evidence showing more restricted patterns of brain activity in high than in low cognitive abilities individuals (measured by PET (see e.g., Haier & Bembow, 1995), EEG (see e.g., Neubauer et al., 1995), or fMRI (see e.g., Gray et al., 2005)) and that transmission of information was faster in individuals with high than low cognitive abilities (as revealed by nerve conduction velocity studies, see e.g., Vernon & Mori, 1992). In the context of neural efficiency, the notion of resources can be associated with neuronal activity, and the efficient use of resources is reflected by the reduced neural activity in individuals with higher cognitive abilities as compared to those with lower cognitive abilities.

Although the neural efficiency perspective has been supported by a number of studies, many of these studies reported a difference in brain activity between two groups of individuals without addressing the cause of the difference (see e.g., Jausovec & Jausovec, 2004a, 2005a). It must be noticed that differences in brain activity between individuals with high or low cognitive abilities do not unequivocally substantiate the conclusion that these differences reflect differences in neural efficiency. An alternative interpretation could be a higher level of automaticity of performance of one group

compared to that of the other. Petersen, Mier, Fiez, and Raichle (1998) showed that practice not only significantly reduced the amount of activation in a cerebral area, but also shifted the cerebral areas involved in task execution toward task-dependent areas. It can therefore be hypothesized that practice could account for the reduction in brain activity between individuals of different cognitive abilities if individuals with higher abilities are faster in devising and automating strategies to solve the task (for evidence substantiating this claim see e.g., Gevins & Smith, 2000; Grabner et al., 2003).

Shifts in brain activation as reported by Petersen et al. (1998) could also reflect that participants used a different strategy to solve the task. For example, Reichle, Carpenter, and Just (2000) showed that brain activation patterns of individuals executing a sentence verification task (Clark & Chase, 1972) reflected the strategy employed by the participants. The sentence verification task can be performed with two strategies (see MacLeod et al., 1978), one requiring verbal-linguistic abilities (i.e., predominantly located in the left hemisphere) the other spatial-imagery abilities (i.e., predominantly located in the right hemisphere). Reichle and collaborators instructed their participants to execute the task with one or the other strategy to observe if the patterns of their participants' brain activations were located mostly on the right hemisphere when the imagery strategy was used and in the left hemisphere when the linguistic strategy was used. Their results showed a strategy-dependent hemispheric activation, which supports the claim that the use of different strategies can induce different brain activity. These results also points to the possibility that individual differences in brain activation patterns between individuals of different IQs may reflect the adoption of different strategies to solve the same task.

Duncan et al. (2000) proposed a somewhat different perspective on the relation between brain activity and cognitive abilities. Using PET, they showed that prefrontal recruitment was an increasing function of the amount of g required by the task, and was not specifically related to the precise nature of the task. This evidence is consistent with the notion that prefrontal cortex implements a general capacity for top-down or executive control, and may account for the fact that substantial dual-task costs are generally observed for combinations of relatively difficult tasks that both require executive control.

Evidence for lower-level neural correlates of mental resources can be found in a study by Diamond, Scheibel, Murphy, and Harvey (1985) which showed that neurons and glial cells in the cerebral cortex of an outstanding scientist (i.e., Albert Einstein) had a smaller ratio in comparison with control individuals. Neurons and glial cells are

the two main types of cells which constitute the nervous system (for an introduction see Bear, Connors, & Paradiso, 2008). Neurons are the functional unit of the nervous system which through electrochemical impulses receive and transmit information to other cells. Glial cells sustain the neurons and constitute the sheath (i.e. myelin) which increases the speed and power of pulse propagation within a neuron (Bullock, Moore, & Fields, 1984). Einstein's neurons were supported by a higher number of glial cells than those of the control individuals. This could account for the outstanding cognitive ability of Einstein because a higher number of glial cells per neuron may reflect more sophisticated or efficient neural circuits (Colombo, Reisin, Miguel-Hidalgo, & Rajkowska, 2006; Fields, 2008a, 2008b; Kreutzberg, Klatzo, & Kleihues, 1992).

The ratio of neuron:glial cells may represent a plausible low-level neural correlate of mental capacity or efficiency. Myelination, the process by which myelin improves the connections between neurons, is a dynamic process by which white matter structure is modified by impulse activity or, in other words, use of a brain area modifies its connectivity similarly to the effect of physical exercise on muscles. Acquisition of skill modifies the structure of white matter, as has been shown for professional musicians (e.g., Bengtsson et al., 2005), working memory tasks (e.g., Nestor et al., 2007), cognitive development (e.g., Liston et al., 2006), reading skills (e.g., Gold, Powell, Xuan, Jiang, & Hardy, 2007), and IQ (e.g., E. M. Miller, 1994). For example, a recent study by Schmithorst, Wilke, Dardzinski, and Holland (2005) using diffusion tensor imaging (DTI; a relatively new MRI technique which reproduces the brain's neural tracts and connections, see Filler et al., 1991), showed higher brain connectivity, as reflected by the volumes of regional white matter, in children of higher as compared to lower cognitive abilities (see also, Posthuma et al., 2002, for similar evidence in an fMRI study with adult individuals).

1.2 A brief overview of EEG-based reflections of mental resources

EEG is a method for the visualization of temporal changes in brain activity, in optimal recording conditions temporal resolutions of 1 ms can be reached, which permits to observe the online processing of information (Luck, 2005b). On the other hand EEG spatial resolution is poor because the signal measured by an electrode reflects the summed contribution of many different electrical sources; as a consequence it is difficult to define univocally the internal generator for a given EEG pattern, therefore impeding the identification of the neurocognitive process eliciting it (Regan, 1989).

The EEG is composed of three types of cerebral activities which depends on the occurrence or absence of an experimental condition or event (Tallon-Baudry & Bertrand, 1999; Herrmann, Grigutsch, & Bush, 2005). Spontaneous background activity is by definition uncorrelated with the experimental condition. Induced activity is correlated with the experimental condition, but it is not precisely phase-locked to the onset of the condition or an event, in contrast to evoked activity that is by definition phase-locked. Evoked activity is generally quantified by means of event-related potentials (ERPs). Each type of activity has been linked to mental resources in the literature, and these linkages will be selectively reviewed for each type of activity.

1.2.1 Event-related potentials

As several recent reviews of the relationships between specific ERP components and mental resources are already available (e.g., Kok, 1997), the present discussion will be limited to those components that are directly relevant to the research reported in this thesis.

N2pc. If a participant is instructed to search for a target item (e.g., a red bar) among several distractor items (e.g., green bars) a negative-going deflection 200-300 ms post-stimulus that is located primarily at posterior scalp sites contralateral to the horizontal position of the target item can be observed (i.e., N2pc, N2-posterior-contralateral, Luck & Hillyard, 1994a). Luck and Hillyard (1994a) showed that the N2pc reflects the focusing of attention onto a potential target item, in the attempt to select the relevant item, whereas Eimer (1996) suggested that the N2pc may reflect the suppression of the irrelevant items. The N2pc is also elicited by non-targets that resemble targets, but not by nontargets that differ from the relevant target in a perceptually salient manner (Luck & Hillyard, 1994a). It is generally accepted that the N2pc reflects attentional capture by a target event (see e.g., Kiss, Velzen, & Eimer, 2008; Lien, Ruthruff, Goodin, & Remington, 2008). Whether the N2pc may also, or perhaps primarily, reflect a spatial shift of attention to the position of the target is more controversial (Woodman & Luck, 1999, 2003; Kiss, Velzen, & Eimer, 2008). More specific evidence linking N2pc to resource-limited information processing comes from several studies that have found the N2pc to be largely absent when the second target in an attentional-blink paradigm remained undetected (Dell'Acqua, Sessa, Jolicoeur, & Robitaille, 2006; Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006a; Robitaille, Jolicoeur, Dell'Acqua, & Sessa, 2007).

P3. The P3 (or P300) component is a positive-going deflection that is located primarily at parieto-central scalp sites and is elicited by relevant target events (Donchin, 1981). Its amplitude is highly dependent on the probability and general informativeness of the eliciting event, suggesting that it may reflect the amount of information provided by and extracted from the event (R. Johnson, 1986). A substantial body of evidence from both single-task and dual-task studies is consistent with the related notion that P3 amplitude reflects primarily limited perceptual-central resources that are mobilised by target categorization (for review, see Kok, 1997).

1.2.2 Frequency-domain EEG components and mental resources

Human EEG activity is composed of rhythmical activity which is associated with general mental states. The most dominant oscillation, which was also the first one to be discovered (Berger, 1929), is characterized by a periodicity of approximately 10 Hz and is called alpha-band activity. The term alpha refers to the fact that it was the first rhythm to be discovered; Berger (1929) used the first letter of the Greek alphabet for the first rhythm he discovered and the second (beta, 12-30 Hz) for the second. Subsequently gamma was used for the rhythm in the 30-80 Hz, delta was attributed to the oscillations below 4 Hz, and theta for the rhythm in the 4-8 Hz.

A very general way to link specific EEG frequency bands with specific cognitive demands is based on the observation of intervals of synchronization (enhanced presence) and desynchronization (diminished presence) of a certain rhythm. Synchronization indexes a state of cortical rhythmicity, whereas desynchronization refers to the interruption of rhythmicity. For example, (Nunez, Wingeier, & Silberstein, 2001) showed that alpha desynchronization correlated with mental effort, such that the alpha rhythm (8-12 Hz) decreased with increased mental effort – in contrast the theta rhythm (4-8 Hz) increased with increased mental effort. Thus, alpha-band and theta-band activity may show an opposite, but not necessarily unrelated, dependency on momentary mental effort.

The alpha rhythm. The EEG oscillations measured from a participants sitting quietly in a dimly illuminated room roughly resemble a 10 Hz sinusoidal activity. This rhythmicity increases in amplitude approximately one or two seconds after that the participant is asked to close his eyes and it will be temporarily suppressed immediately after he opens his eyes again. This 10 Hz rhythm with highest amplitude in the posterior part of the brain is known as alpha rhythm (Berger, 1929). The alpha rhythm

has been associated with an idling state of the nervous system (Adrian & Matthews, 1934) because decrease of alpha rhythm is generally observed when a participant gets involved in any kind of task (for a review see Pfurtscheller, Stancak, & Neuper, 1996). Only recently N. R. Cooper, Croft, Dominey, Burgess, and Gruzelier (2003) reinterpreted the functional significance of the alpha rhythm not as an idling state but as an inhibitory process of task-irrelevant cerebral areas. The claim of Cooper and collaborators was based on previous evidence showing that the alpha rhythm increases when performing an imagery task (Ray & Cole, 1985) or when it is necessary to suppress processes which may conflict with the execution of the task at hand (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999).

Many studies have provided evidence consistent with the view that a reduction in the amplitude of the alpha rhythm reflects increase mental effort (e.g., A. P. Anokhin, Lutzenberger, & Birbaumer, 1999; A. Anokhin et al., 1992; Hanslmayr, Sauseng, Doppelmayr, Schabus, & Klimesch, 2005; Jausovec & Jausovec, 2004a, 2005b; Jausovec, Jausovec, & Gerlic, 2001; Jausovec & Jausovec, 2000; Klimesch, 1997; Neubauer et al., 1995; Nunez et al., 2001). Some studies, however, have found alpha amplitude to be increased with focusing of attention (Kelly, Lalor, Reilly, & Foxe, 2006), inhibition of irrelevant information (Toffanin, Johnson, Jong, & Martens, 2007), and top-down control (Klimesch, Sauseng, & Hanslmayr, 2007). The hypothesis that increments in alpha rhythm reflect inhibition of irrelevant task areas has been further exploited in two studies where increments of alpha rhythm were artificially induced using repetitive transcranial magnetic stimulation (rTMS, Klimesch, Sauseng, & Gerloff, 2003) or neurofeedback (Hanslmayr et al., 2005) in order to reduce the input from task-irrelevant areas – such induced increments in alpha rhythm were associated with improved performance in a mental rotation task. Taken together, the evidence may indicate that the relation between mental effort and alpha-band activity is a complex one, with the results depending on the ratio of activation of relevant versus inhibition of irrelevant cortical areas and the site of registration. This strongly suggests that more attention to the cortical distribution of alpha-band activity in relation to the processing requirements of the task is warranted.

The beta rhythm. EEG oscillations within 13-30 Hz are defined beta rhythm, which is distributed primarily in the central brain regions. The beta rhythm has been related to motor action (e.g., movement, the intention to move, or sensorial stimulation, Pfurtscheller & Berghold, 1989; Neuper & Pfurtscheller, 1996), which results in a

desynchronization of the rhythm in motor cortex contralateral to the limb to move and, possibly, synchronization, reflecting motor idling, in ipsilateral motor cortex (Pfurtscheller et al., 1996). Tallon-Baudry, Bertrand, and Fischer (2001) have found the beta rhythm to be also related to memory retrieval.

The gamma rhythm. EEG oscillations within 30-80 Hz are defined gamma rhythm. Engel, Fries, and Singer (2001) have reported that the gamma rhythm is associated with higher cognitive functions such as the perceptual binding (C. M. Gray, König, Engel, & Singer, 1989), the maintenance of working memory (Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002), and selective attention (Fries, Reynolds, Rorie, & Desimone, 2001). Tallon-Baudry and Bertrand (1999) have linked induced gamma activity to the generation of an object representation from the different features represented in different parts of the brain. Melloni et al. (2007) proposed that long-range synchronization of gamma rhythm is the neural process mediating conscious perception.

An alternative interpretation of the gamma rhythm has been proposed by Chen and Herrmann (2001) after noticing the special interrelation between alpha (8-12 Hz), beta (13-30 Hz), and gamma (30-80 Hz) rhythms, which may suggest that these rhythms are harmonics or subharmonics of one another. Already Haenschel, Baldeweg, Croft, Whittington, and Gruzelier (2000) suggested that the beta rhythm may be a subharmonic of the faster gamma rhythm. Chen and Herrmann (2001) suggested that both alpha and beta rhythms may represent subharmonics of gamma oscillation after observing the coexistence of beta, gamma, and alpha rhythm after sensorial stimulation. However, it remains unclear how that hypothesis can account for the fact that many studies have found these rhythms to show qualitatively different dependencies on such factors as task, condition and mental effort (see e.g. Jausovec & Jausovec, 2005a).

The delta and theta rhythms. EEG oscillations within 0-4 Hz or 4-8 Hz are defined delta and theta rhythm, respectively. The delta rhythm has usually been related to deep sleep (Steriade, Nunez, & Amzica, 1993). The theta rhythm has been related to cognitive effort (Nunez et al., 2001) and to working memory functions (Jensen & Tesche, 2002), such that an increase in theta synchronization is functionally related to high cognitive effort or to the maintenance of more objects in working memory. (Bastiaansen, Berkum, & Hagoort, 2002b, 2002a) showed a linear and positive relationship between amplitude of theta and working memory load. Jausovec and Jausovec (2004b)

showed a relationship between theta amplitude and cognitive abilities. Their participants performed a figural n-back (Gevins & Smith, 2000) in which a colored (i.e., black, blue, brown, yellow, green, gray, purple, and red) form (i.e., a square or circle) had to be compared to the one that had appeared previously while counting the number of squares displayed. The theta rhythm was synchronized for a longer time (i.e., 1000-2000 ms) in individuals of lower than higher cognitive abilities (100-500 ms), suggesting that lower-ability individuals put more effort into executing the task.

1.2.3 Steady state evoked potentials and frequency tagging

Steady-state evoked potentials (SSEP) are evoked potentials (EP) to rapid repetitive stimulation (Regan, 1989). Regan (1989, p. 35) distinguished EP from SSEP because of the transient nature of the first ones: “The averaged transient EP can be regarded as a true transient response to the extent that the relevant brain mechanisms are in their resting states before each successive stimulus, and return to their resting state before the next stimulus. This requirement implies that the EP to any given trials does not depend on any previous trial.” On the other hand, when SSEP are considered they should not be idealized as a perfect repetition of the same EP waveform in time, but as a series of EP constituted by discrete frequencies with constant amplitude and phase.

After its introduction the SSEP method had been amply used in fundamental physiological research (see e.g., Derrington & Lennie, 1984), with questions ranging from the generators of the synchronous response characteristic of the SSEP response (see e.g., Stephen, Ranken, & Aine, 2006), its dependency on frequency of the eliciting stimulus (see e.g., Herrmann, 2001), to what methodology is been suited to localize the source of the resonance phenomenon (see e.g., Srinivasan, Bibi, & Nunez, 2006). However, such questions never were very interesting for cognitive scientists who were focused on aspects of information processing and attention rather than on the physiological properties of the response of rods and cones to flickering patterns (see e.g., Levitt, Schumer, Sherman, Spear, & Movshon, 2001). For this reason, the SSEP method was for a long time ignored by the cognitive scientist, until the first report of a meaningful functional relationship between SSEP amplitude and allocation of attention by Morgan, Hansen, and Hillyard (1996).

The motivation behind Morgan et al. (1996) study was to devise a technique which could unravel the brain mechanisms involved in visual selective attention and simultaneously overcome the limitations imposed from the recording of EP. One constraint in EP research is that, due to their transient nature, EP are evoked by stimuli which have

an abrupt onset, and which must follow one another with a fairly long interstimulus interval to avoid temporal overlap of successive EPs. Typically, visuo-spatial attention experiments require to selectively attend a stimulus or location. However, abrupt onsets of irrelevant items may cause attentional capture (Yantis & Jonides, 1990), making it difficult to ignore that stimulus.

Morgan et al. (1996) reasoned that a possible way to overcome the effect of attentional capture by an onset stimulus (stimulus transient) was to display stimuli on a background that was flashing constantly. The presentation of repeatedly flashed stimuli was also the main characteristic of the SSEP method devised by Regan (1966a, 1966b), which lead the authors to try to adapt Regan's method to study the brain mechanism underlying selective attention. Morgan et al. devised an experiment in which participants were presented with two streams of alphanumeric characters (the randomized presentation of the letters A through K and the digit 5) each superimposed on a background square that rapidly alternated between white and black (each square had a specific frequency, i.e., 8.6 or 12 Hz). Participants' task was to detect the digit 5 embedded in the stream of letters any time it appeared in the stream to be attended. Participants were informed that the two streams were displayed against a flickering background and were told that the flickering was irrelevant for the execution of the task. The two streams were displayed at the left and right of a fixation mark; the characters followed one another at a rate of six per second.

Morgan et al. (1996) showed that the amplitude of the SSEP was modulated by visuo-spatial attention; it increased when attention was directed toward the location and decreased when attention was drawn away from it. Additionally, the obtained high signal-to-noise ratio of the SSEP, due to its precise definition in frequency domain suggested two other advantages of the SSEP over the EP method. The first advantage concerns the relative "immunity" of the SSEP method from artifacts such as muscles (EMG) and eye movements which frequently force the exclusion of participants from the data set because their EEG trace is destructively contaminated by artifacts (for an introduction to artifacts-related problems in psychophysiological research see Luck, 2005b). The second advantage concerned the ability to perfectly discriminate between the SSEPs associated with the attended and unattended locations, as these were tagged by different frequencies.

These initial results established the SSEP method as a useful and powerful psychophysiological tool to investigate mechanisms of perception and attention, and has given rise to a number of subsequent studies (see, e.g.: Belmonte, 1998; Cosmelli et

al., 2004; Russo & Spinelli, 1999a, 1999b; Hillyard et al., 1997; Kelly et al., 2006; Kim, Grabowecy, Paller, Muthu, & Suzuki, 2007; Malinowski, Fuchs, & Muller, 2007; Morgan et al., 1996; M. M. Muller, Picton, et al., 1998; M. M. Muller, Malinowski, Gruber, & Hillyard, 2003; M. M. Muller & Hillyard, 2000; Pei, Pettet, & Norcia, 2002; Srinivasan, Russell, Edelman, & Tononi, 1999; Srinivasan et al., 2006; Wang, Clementz, & Keil, 2007, and others). The method seems especially suitable in studies where competition between simultaneously displayed stimuli is addressed such as, for example, conscious perception in binocular rivalry (Tononi, Srinivasan, Russell, & Edelman, 1998). Binocular rivalry consists of experiencing alternating perceptions of two simultaneously displayed incongruent visual stimuli, each presented to one eye. Tononi and collaborators (1998) used SSEP (measured using magnetoencephalography, or MEG) to show that the conscious percept of a stimulus was associated with a broadly distributed and coherent pattern of neural activity. Given the power of the SSEP to trace neural activity associated with each of the rivaling stimuli throughout the brain, they referred to the method “frequency tagging”. In the present thesis, we sought to employ these compelling advantages offered by the SSEP method to investigate mechanisms of focused and divided attention, both within modalities and across modalities.

1.3 Linking dynamics of resources management to brain rhythms: How does the human brain deal with difficult situations?

Dual-task paradigms permit the study of how resources are allocated to one or another task because the execution of multiple tasks results in interference when they compete for limited resources (Kahneman, 1973). Important questions are: what information has priority, how is priority attributed, and how can multiple tasks be simultaneously accomplished?

In this thesis questions were approached in a threefold manner. The first approach involved observing individuals with different levels of cognitive abilities to investigate whether correlations exist between higher cognitive abilities and brain activity as measured by EEG. In the second approach an innovative methodology (frequency tagging) was used to visualize the dynamics of the brain resource allocation policy when multiple tasks are performed simultaneously and attention is divided between them. In the third approach the neurological correlates of attentional disengagement (see Posner & Petersen, 1990) was investigated. Attentional disengagement is the

process through which attention is released from a previous objective to focus on the next one. The identified neurological correlate constitutes a significant development in the study of the time course, dynamics, and interplay of the processes involved in attentional control, especially with regard to top-down influences.

The management of resources and the dynamics of resource allocation occur on the fly. Therefore, to capture the time course of these changes at a neurophysiological level, a technique which permits the observation of changes in brain activity millisecond by millisecond must be employed. Electroencephalography (EEG) is a neuroimaging technique which allows to observe the very rapid changes in brain states which may correlate dynamic resource management in the brain.

In Chapter 2 EEG was used to investigate individual differences in resource management. EEG was measured in two groups with different levels of cognitive abilities (i.e. high vs. low IQ). While participants performed a sentence verification task using the same strategies, possible IQ-related and strategy related differences in brain rhythms were studied.

Chapter 3 and 4 focused on EEG changes, in a specific frequency range as determined by a frequency tag, between single- and dual-task performance and between attending one versus multiple sources of information to establish a more direct link between allocation of resources and EEG. Chapter 3 addressed the competition for resources within the visual modality, where two locations had to be monitored simultaneously, or one attended and the other ignored. Chapter 4 addressed the same questions and the same methodology using a cross-modal paradigm (i.e., stimuli were presented auditorily and visually).

Chapter 5 puts to a direct test the possible existence of a distinct disengagement-related waveform following the N2pc, which is an event-related potential linked to the automatic capture of attention. The existence of this component may provide an important tool for studying attentional control.

Chapter 2

Rethinking Neural Efficiency: Effects of Controlling for Strategy Use

The question is not what you look at, but what you see.

Henry D. Thoreau

Abstract

Neuroimaging studies have shown that neural activation patterns differ as a function of intelligence (IQ). However, these studies were conducted without controlling for the strategy used by the different IQ groups. We tested this hypothesis by recording electroencephalograms from 14 low ($89 < IQ < 110$) and 14 high ($121 < IQ < 142$) IQ individuals as they performed a sentence verification task, first with a linguistic and then an imagery strategy. Behavioral data showed that the strategies were used as instructed and higher IQ individuals tended to perform better. Analyses of the EEG rhythms in terms of instantaneous amplitude and power (event related desynchronization (ERD) in upper alpha (9.5-12.5Hz) and theta (4-6Hz) bands) showed that the use of different strategies evoked different activation patterns, but that these patterns did not differ between the two IQ groups, suggesting that care should be taken in attributing differences in neural processing to intelligence level. However an IQ-related correlate was found in ERD in the preparation interval. Thus, although processing patterns during task performance seem to depend more on the strategy used to perform the task than on IQ differences, preparation for task processing may depend on IQ.

2.1 Introduction

Theories of intelligence and intelligence testing have been a part of modern society for more than 100 years (Hunt, 1995; Sternberg, 2003). In the last 20 years, thanks to the development of neuroimaging techniques, investigation of the biological bases of intelligence (i.e. differences in brain and neural functioning) has gained increasing interest and has enjoyed considerable success. One theory that has evolved

from research on the neural underpinnings of intelligence is the neural efficiency theory (see, Vernon, 1993, for a review). Neural efficiency describes the negative correlation between brain activity under cognitive load and intelligence. It is indexed by both a lack of processing activity in brain areas irrelevant for good task performance and a more focused use of specific, task-relevant areas (Jausovec & Jausovec, 2001, 2004a; Neubauer et al., 1995).

The introduction of neural efficiency theory has given rise to a new approach to the study of intelligence in which imaging techniques are used to study differences in task performance, including the use of the electroencephalogram (EEG; Gevins & Smith, 2000) or functional magnetic resonance imaging (fMRI; J. R. Gray et al., 2005) for studying performance in working memory tasks, measuring nerve conduction velocity to examine individual differences in the performance of speed of information processing tasks (e.g., Vernon & Mori, 1992), measuring EEG during administration of fluid intelligence tests (e.g., Jausovec & Jausovec, 2003), measuring neural activity in simple speeded-processing tasks with fMRI scanning (Rypma et al., 2006), or using positron emission tomography (PET) during mathematical reasoning tasks (Haier & Benbow, 1995).

A consistent pattern emerging from these studies is that relatively high IQ individuals (HIQ) differ from relatively low IQ individuals (LIQ) in terms of a differential suppression of frontal area activity, with high IQ individuals generally relying on parietal regions and LIQ using both parietal and frontal regions during task performance. Such topographical patterns have led to the suggestion that LIQ and HIQ individuals differ in the use of neural circuits, especially non-frontal ones (see, e.g., Jausovec & Jausovec, 2005b). However, Duncan and collaborators (e.g., Duncan et al., 2000) suggest an alternative interpretation of differences in intelligence. They propose that the frontal lobe, the seat of executive control, is the neural base of general intelligence. Duncan et al. (2000) based this assumption on PET evidence showing that frontal area recruitment was an increasing function of the amount of *g* (where *g* represents “general intelligence” or Spearman’s *g*) required by the task.

The assumptions that the frontal lobe is critical in intelligence (Duncan et al., 2000) and that the performance of higher intelligence individuals is associated with lower levels of frontal-lobe activation (as suggested by the neural efficiency theory, e.g., Jausovec & Jausovec, 2005b) may seem contradictory. However, it may be that the two patterns of findings simply reflect two timepoints in the development of skilled performance. Performing any but the simplest task requires discovery or learning of a

strategy to solve it, and executive control plays an important role in strategy choice and deployment (Koechlin, Ody, & Kouneiher, 2003). The finding of Duncan et al. (2000) that increasing the difficulty of a task resulted in increased recruitment of frontal areas may reflect an increase in time spent devising a strategy for performing the task. If tasks are well learned or do not impose heavy cognitive demands on the performer, frontal area activation would be expected to be relatively low. This would be in line with the relative frontal suppression shown by higher IQ individuals in the studies that are taken to support the neural efficiency theory: Absence of frontal activation in HIQ individuals could reflect that the task load was within the capabilities of the participant and that the strategy used to perform the task had been established. Lower IQ individuals, on the other hand, could be assumed to be actively involved in the solution of the task, as reflected by a broader and longer activation of brain areas.

Two specific predictions follow from the view that frontal lobe recruitment depends on both intelligence and the familiarity with the task. One prediction is that HIQ individuals will show a high activation level in the frontal lobe at the beginning of the testing session as they engage in an active search for the best strategy to solve the task. Once they have settled on a strategy, a shift to non-frontal areas should occur. Lower IQ individuals, on the other hand, will often fail to fully automate task instructions or to develop a strategy for performing the task, with the result that activation patterns will remain relatively constant throughout the testing session. In line with this prediction, Gevins and Smith (2000), found that, in comparison to low ability individuals, high ability individuals displayed more frontal activity in the early stages of task performance during a spatial version of a n-back working memory task (in which the spatial position of a letter stimulus was to be compared with the position of the first item displayed or the item presented one or two items back), activity that gradually shifted to parietal sites. The authors argued that the shift to parietal sites reflected the automation of processing (see also Koch et al., 2006). Low ability individuals, in contrast, relied on the frontal lobe for the duration of the test (for similar findings, see Jausovec & Jausovec, 2004a).

A second prediction is that differences between HIQ and LIQ individuals should disappear when both groups have practiced until reaching an equal performance level. One way in which these hypotheses can be tested is by looking at event-related desynchronization (ERD). ERD shows robust correlations with mental effort (Nunez et al., 2001), such that the alpha rhythm (8-12 Hz) decreases (note that an amplitude decrement reflects desynchronization) with increases in mental effort whereas the frontal

theta band (4-8 Hz) tends to increase (note that amplitude increment reflects negative desynchronization¹) with increases in mental effort. In other words, in a state of relaxation or “idling” state, alpha waves are of a relatively high amplitude or synchronized. A change to a more active state desynchronizes the alpha rhythm. With regard to ERD, neural efficiency theory predicts that HIQ individuals, who require less effort to perform a task, will show less desynchronization in the alpha band, as well as less negative desynchronization of the theta band in comparison to LIQ individuals. A study by Grabner et al. (2003) supported the hypothesis that differences in ERD between HIQ and LIQ individuals will disappear when the task performed is familiar to both groups. The authors showed that patterns of ERD of two groups of relatively HIQ or LIQ experienced taxi drivers differed while performing the novel task of memorizing routes on an artificial map, but not on the familiar task of thinking about routes to take in their own city. These findings support the hypothesis that development of an efficient strategy, and the correlated activation or deactivation of the frontal lobe, plays a role in intelligence differences.

Despite the promises of neural efficiency theory in explaining differences in intelligence at a neural processing level, a number of studies have failed to support the theory. For example, Klimesch (see, e.g., Klimesch, 1997, 1999) studied performance in long-term memory tasks, such as semantic and episodic memory tasks, while measuring EEG. Computation of ERD revealed a larger desynchronization in the upper alpha band (10-12 Hz) and a larger negative desynchronization of the theta band for good as compared to poor memory performers, which is just the opposite of what neural efficiency theory would predict.

Differences in activation patterns between IQ groups have often been interpreted as differences in neural efficiency. However, as suggested by studies such as those of Klimesch, such a conclusion may not be warranted. Jausovec and Jausovec (2005b) presented an analysis of studies investigating neural efficiency theory, dividing them into studies that support the neural efficiency theory and studies that do not. Jausovec and Jausovec (2005b) attributed the discrepancies found between these studies to the restricted number or narrowness of the frequency bands used (e.g., exclusive analysis of theta and alpha bands, or restricting the analysis field to solely the upper components, that is, between 10-12 Hz in the alpha band), or to the poor temporal resolution of the measurements performed (e.g., PET and ongoing EEG do not provide good

¹Note that, in the literature, negative value of ERD are frequently referred to as event related synchronization (ERS), however to be consistent only the term ERD, and its polarity (i.e., positive or negative), will be used.

temporal resolution). A closer inspection of the studies surveyed in Jausovec and Jausovec (2005b) brings two other critical points to the fore. First, the IQ ranges used were relatively narrow (many investigations were restricted to individuals with average or high intelligence, e.g., university students). Second, and perhaps more importantly, the strategies with which the task could be performed were not controlled for. Gevins and Smith (2000) (see also, Jausovec & Jausovec, 2004a, 2005b; Neubauer, Fink, & Schrausser, 2002) suggested that higher ability subjects tend to better identify strategies needed for the solution of the task at hand. The use of different strategies in the two groups could account for the observed differences in brain activation.

Differences in strategy use have, to our knowledge, not been explicitly investigated in studies of brain use as a function of intelligence. However, it has been shown that ability differences as measured by standard psychometric tests can be related to strategy differences, see, e.g., Sternberg and Weil (1980) for strategy differences in solving transitive inference problems, Mathews et al. (1980) for sentence verification, L. A. Cooper and Regan (1982) for mental rotation problems. Because people differing in ability also tend to adopt different strategies for performing tasks – or do so at different times in performance – it is possible that strategy use has been a confounding factor in the study of neural processing correlates of intelligence. Our goal was to determine whether intelligence-related differences in neural processing would be found when strategy was controlled for.

2.2 Experiment

In order to test whether intelligence-related differences in neural processing would still be found when task performance strategy is controlled for, we had LIQ and HIQ individuals perform the sentence verification task (SVT, Clark & Chase, 1972) under two instructional conditions (Mathews et al., 1980). The task requires participants to judge whether a sentence describing the spatial relation of two symbols correctly matches a following picture (e.g., whether the sentence “star is below plus” matches the picture of a star below a plus). In the linguistic strategy condition, the sentence was to be read as quickly as possible without sacrificing understanding and then compared to the picture to determine whether or not the sentence matched the picture, whereas in the imagery strategy condition, stimuli and relations described in the sentence were to be represented as a visual image and then compared to the picture. We chose to present the linguistic strategy condition first for all subjects to reduce the chance that subjects

would use an imagery strategy even when the instructions are to use the linguistic strategy (see, e.g., MacLeod et al., 1978; Mathews et al., 1980, for evidence that individuals with high spatial abilities preferentially use an imagery strategy).

Additionally, we modified the traditional SVT in two ways in order to support the use of the linguistic strategy. First, because Tversky (1975) showed that an imagery strategy was more likely to be used when there was a temporal separation between the display of the sentence and the display of the picture, we used a 0-ms interval between the presentations of the sentence and the picture. Second, unexpected stimuli (stimuli not mentioned in the sentence) were introduced into the set of stimuli. Unexpected pictures discourage the use of imagery recoding when the linguistic strategy is supposed to be used (Kroll & Corrigan, 1981). For example, on a trial in which a heart above a star is displayed after the sentence “plus is above star”, imagining a plus above a star is an inefficient strategy. To prevent differences observed at the EEG level from being attributed to a difference in the materials used, unexpected pictures were also used in the imagery strategy condition².

Throughout the experiment, EEG was recorded with a 64-channel system. Time-frequency analysis, using Morlet wavelets, was used to compute instantaneous amplitude and power for EEG frequencies ranging from 4 to 75 Hz (for details, see Tallon-Baudry & Bertrand, 1999; Gladwin, Lindsen, & Jong, 2006). These instantaneous values, reflecting dynamics of cerebral processing, were analyzed for main effects of IQ and strategy and for possible interactions of these factors.

2.2.1 Methods

Participants. A total of 37 right-handed native Dutch speakers, with normal or corrected-to-normal visual acuity, and no history of neurological problems, were tested in an initial session consisting of intelligence testing and practice with the SVT. Participants were recruited through advertisements and reported no cognitive disabilities (including reading or writing deficits), did not use medications or drugs that can impair task performance, and were right handed and younger than 45 years old. Of the 37 par-

²Introduction of unexpected pictures discouraged the use of the imagery strategy but did not exclude it. Imaging a picture that represents a negative sentence is difficult. Imaging an affirmative sentence has a unique outcome, which can be compared with only one figure, whereas there are five possible positive matches with a negative sentence. One strategy is to imagine the one picture which does not represent the sentence (i.e., gives a false response). Negative sentences can be imaged by imaging the elements and relation contained in the sentence and responding “False” if that image matches the picture. This strategy was verbally explained during the presentation of the first negative sentence trial in the practice session for the imagery strategy.

ticipants who participated in the initial session, two were excluded for failing to meet the accuracy criterion of 80% correct in the SVT and seven chose not to continue in the experiment. Of the remaining 28 participants, two groups were formed, matched on age and sex (see Neubauer, Grabner, Fink, & Neuper, 2005; Neubauer & Fink, 2003, for implications of sex differences and the neural efficiency hypothesis), leaving 14 participants per group. The high IQ group contained individuals (aged 19-38, mean = 25.4, 7 females) with a university level of education and a relatively high intelligence (IQ = 121-142, mean = 127.7). The low IQ group included individuals (aged 18-37 years, mean = 21.9, 7 females) mostly having an intermediate vocational level of education, and a relatively low intelligence (IQ = 89-110, mean = 101.7).

Intelligence test. Intelligence was measured by a shortened version of the Groningen Intelligence Test (Luteijn, 1966; Luteijn & Ploeg, 1983). The Groningen Intelligence Test is a test of general intelligence used in the Netherlands much as is the Wechsler Adult Intelligence Scale (Wechsler, 1981). Five of the nine subtests, administered in a fixed order, were used, including the vocabulary test, the spatial ability test, the mental arithmetic test, the verbal analogies test, and the verbal fluency test. In the vocabulary subtest, participants are asked to indicate which of five alternative words is synonymous with a given word. The spatial ability subtest requires participants to indicate which two-dimensional shapes from a larger set are needed to exactly fill up a given space on the test page. In order to do this, the shapes need to be mentally rotated. In the mental arithmetic subtest, participants are asked to complete as many sums of three two-digits numbers as possible within one minute. The verbal analogies subtest is a multiple choice test in which the participant must indicate which of five alternatives is related in the same way to a given word as words in an example are related. Each of these subtests included 3 practice items and at least 20 test items. The verbal fluency subtest requires participants to produce as many words as possible in a given category, within one minute. This subtest was done twice, once with animals, and subsequently with professions as the given category. Test administration took approximately 45 min. IQ was computed using the Groningen Intelligence Test norms corrected for sex³.

³Because of the relevance of sex differences for neural efficiency (see e.g., Neubauer et al., 2005) we normalized IQ for sex differences. Using uncorrected norms would have led to the same group composition and slightly different ranges. Using uncorrected norms the IQ of the HIQ group ranged from 120 to 143 (mean 128.60) and that of the LIQ group from 90 to 115 (mean 103.79)

Stimuli and apparatus. Stimuli generation and response collection were controlled using a program created with E-prime 1.1 (Psychology Software Tools Inc., Pittsburg, USA) and running on a Pentium IV CPU equipped with a 17-inch monitor with a refresh rate of 100 Hz. Stimuli were presented in black on a white background. Sentences were presented in 20-point Courier New font and pictures were constructed by combining two symbols in a vertical arrangement subtending 1.2° of visual angle at a viewing distance of approximately 60 cm. Symbols were a heart, star, and a plus (each 8.5 mm high and 7.5 mm wide); only one symbol of each type could appear in a given display. Sentences were constructed to describe the relationship of the two symbols, varying the symbols (heart, star, or plus), the order of the two symbols (which symbol was mentioned first), the polarity of the sentence (affirmative or negative, e.g., “heart is below plus” vs. “heart is not below plus”), and the markedness of the term describing the spatial relation of the two symbols (e.g., “plus is above star” vs. “plus is below star”). A picture was considered “unexpected” if it contained an element not mentioned in the sentence. All sentences were presented in Dutch, for which the words heart (hart), star (ster), and plus (plus) all have four letters. Combinations of sentences and pictures resulted either in a true or false response (truth value). Sentences varied accordingly to polarity and truth value. Because the use of unexpected pictures introduced a higher number of true-negative (TN) and false-affirmative (FA) items compared to the number of false-negative (FN) and true-affirmative (TA) items (a ratio of 5:1), FN and TA items were presented five times each and TN and FA items one time each for a total of 240 trials.

Procedure. The experiment consisted of three sessions carried out on three separate days. In the first session, which took approximately 90 minutes, the intelligence test was administered and participants completed a familiarization phase in which they performed 36 trials of the SVT and were allowed to ask questions. They were then instructed to use the linguistic strategy in an additional practice session. Practice blocks consisted of 24 trials each. If participants made errors repeatedly, the appropriate response to the specific trial was explained, or the participant was advised to slow down to enhance accuracy. In each practice block a minimum accuracy level of 80% had to be achieved, participants who failed to reach that criterion received as many practice blocks as necessary to reach the accuracy criterion. On average one to five practice blocks were necessary to achieve the criterion. A practice session, also with accuracy criterion, was also included before each experimental session. In the second session,

which took approximately 90 minutes, participants performed the SVT using the linguistic strategy while EEG was measured. After a break of approximately 15 minutes they were then instructed on how to use the imagery strategy and were given an additional practice session. In the third session, which took approximately 90 minutes, participants performed the SVT using the imagery strategy while EEG was recorded.

At the start of each trial, a fixation cross was displayed in the middle of the screen for 1,500 ms, and was then presented in bold for another 500 ms to alert the participant to the imminent presentation of the sentence. The sentence remained in view until the participant pressed the space bar, after which it was immediately replaced by a picture that either matched or did not match the description given by the sentence. The time between onset of the sentence and the press of the space bar, referred to as comprehension RT (CRT), was recorded for later analysis. Participants were instructed to press the “S” key on the computer keyboard when the sentence was true (i.e., when it provided a correct description of the picture) and to press the “L” key when the sentence was false (i.e., when it did not provide a correct description of the picture). The time between onset of the picture and the true/false response, referred to as verification RT (VRT), was also recorded, as were errors in sentence verification. Performance feedback was presented on each trial (the word “correct” or “incorrect” presented in Dutch at fixation for 500 ms), after which a 1,500 ms fixation cross was displayed in the middle of the screen before the next trial.

EEG recording. The EEG was recorded using a tin 64-channel electro-cap (Electro-cap International Inc., Eaton, Ohio, USA). All scalp positions in the International 10-20 System were used, with additional sites located midway between the 10-20 locations (Sharbrough et al., 1991) and four electrode positions 10% inferior to the standard parieto-occipital electrodes (PO9, O9, PO10, O10; see Figure 1). The amplifier was a REFA 8-72 (Twente Medical Systems, Enschede, The Netherlands). Brain electrical activity was amplified 20,000 times with a digital FIR lowpass filter with a cutoff frequency of 135 Hz. Data were digitized to 22-bit accuracy at a rate of 500 Hz and stored on a hard disk for subsequent off-line analysis. Electrophysiological inputs were configured as a reference amplifier: All channels were amplified against the average of all connected inputs. Two electrodes were connected to the mastoids, the average of which served as an off-line reference for the EEG signal. An electrode on the sternum was used for the patient ground. HEOGL, HEOGR, VEOGL+, VEOGL- recorded the bipolar input for the EOG. Electrode impedances were kept below 5 K Ω

for all the electrodes during the experiment. Data acquisition was controlled through Brain Vision Recorder (version 1.03, BrainProducts GmbH, Munchen, Germany).

2.2.2 Data analysis

Behavioral data analysis. Sentence comprehension and picture verification RTs less than 200 ms or greater than 3 standard deviations above the mean (computed per participant) were considered outliers and were removed from the data set. Less than 1% of trials were eliminated.

EEG data analysis. Preprocessing of the data was executed with Brain Vision Analyzer (BrainProducts GmbH, Munich, Germany). Data were downsampled to 250 Hz, referenced to the average of the two mastoids, and then filtered with a time constant of 1 s and a high cut-off of 100 Hz (Butterworth Zero Phase Filters, at 24 dB/oct). The EEG trace was globally corrected for DC drifts (Hennighausen, Heil, & Rosler, 1993) using an interval of 400 ms (200 ms before and after either sentence or picture onset). Eye blink artifacts were corrected using the ocular correction algorithm of Gratton, Coles, and Donchin (1983). Epochs of 9.5 s each were segmented including the 3.5 s preceding and the 6 s following the stimulus onset (either the sentence or the picture). Epochs on which responses were incorrect or RTs longer or shorter than 3 standard deviations (SDs) from the mean were excluded from the analysis. Using this procedure, a total of 5.74% of the trials, ranging from .41% to 9.43%, $SD = 5.48$ trials per participant, were removed. Data were visually inspected for artifacts and bad segments were removed. Baseline correction was applied using the 100-ms interval before stimulus onset.

Instantaneous amplitudes. (IAs) of the pre-processed epochs were computed for each trial, by means of a convolution with a complex Morlet wavelet (for details, see Gladwin et al., 2006; Tallon-Baudry & Bertrand, 1999).

Formally,

$$IA(t, f) = |w(t, f) * s(t)| \quad (2.1)$$

where $s(t)$ is the original EEG data of one channel and $w(t, f)$ is a suitably normalized, complex form of the Morlet wavelet:

$$w(t, f) = \left(\frac{1}{\sqrt{\sigma_f} * \sqrt{\pi}} * \exp \left(\frac{-0.5}{2\pi\sigma_{ft}} * \exp(i2\pi ft) \right) \right) \quad (2.2)$$

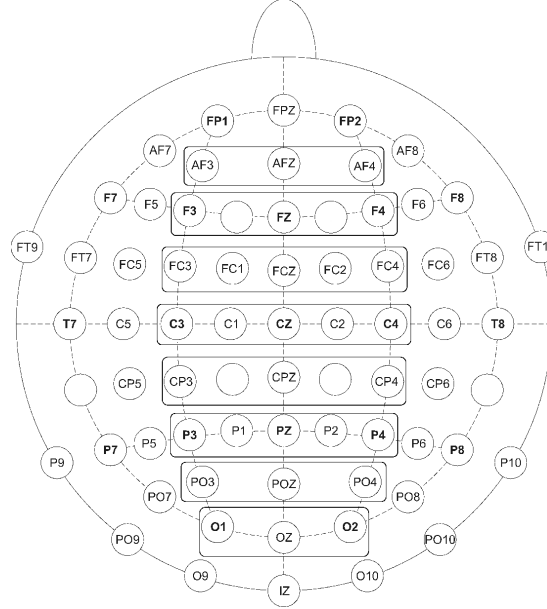


Figure 2.1: The electrode clusters used for time-frequency and ERD analyses. Data from outlined electrodes was averaged to form regions of interest (ROI). Those ROIs labeled (nasion to inion): antero-frontal; frontal; centro-frontal, central, centro-parietal, parietal; parieto-occipital; occipital.

where f is the center frequency of the wavelet and σ_f the standard deviation of its Gaussian envelope in the frequency domain. Averaged IAs were computed by averaging across trials.

Twenty-two Morlet wavelets with center frequencies in the range from 4 to 75 Hz and different uncertainty parameters, σ_f , were used. The 22 frequencies (with uncertainty parameter within brackets) were 4 (1), 6 (1), 7 (1), 8 (1), 9 (1), 10 (1), 12 (2), 14 (2), 16 (2), 18 (2), 20 (2), 23 (3), 26 (3), 30 (4), 35 (4), 40 (4), 45 (4), 55 (4), 60 (4), 65 (4), 70 (4), and 75 (4). A notch filter at 50 Hz with a standard deviation of 1 Hz was used to remove the possible influence of residual line current (50 Hz). The IAs over groups of electrodes were averaged to create the following regions of interests (see Figure 2.1): antero-frontal (AF3, AFz, AF4); frontal (F3, Fz, F4); frontocentral (FC3, FC1, FCz, FC2, FC4); central (C3, C1, Cz, C2, C4); centro-parietal (CP3, CP1, CPz, CP2, CP4); parietal (P3, P1, Pz, P2, P4); parieto-occipital (PO3, PO1, POz, PO2, PO4); and occipital (O1, Oz, O2). Matlab (The MathWorks Inc., 1984) and SPSS (SPSS Inc., 1989) were used for statistical testing and visualization. The data were smoothed in the frequency domain by averaging across three consecutive wavelets and in the temporal domain by using a low-pass filter (passband 0-1.5 Hz, 40 dB cutoff at 2.5 Hz). This degree of smoothing was chosen in an attempt to deal with possible intersubject

variability in the precise time-frequency location of effects (see e.g., Klimesch, 1999).

Prior to statistical analysis, IA data were log-transformed in order to normalize them across participants. As a first step in the statistical analysis, we performed a global test, that is, a test across all possible combinations of time, frequency, and region of interest, for any statistically significant main or interaction effects of IQ and strategy. The false discovery rate (FDR) procedure (Benjamini & Hochberg, 1995) was used to control for the effects of the large number of comparisons involved in these tests. The alpha level for the FDR procedure was set at .05 (for an average of 5% false alarms).

Frequency bands that showed significant and potentially interesting effects in the global, FDR-based analysis, were examined further with an analysis of ERD within each of these frequency bands. Following convention, ERD was computed using instantaneous power (i.e., the square of the instantaneous amplitude), according to the formula:

$$\%ERD(t) = \frac{R - A(t)}{R} * 100 \quad (2.3)$$

where R represents mean power during the reference interval (from 2 to 0.5 s preceding sentence onset, averaged across trials) and A(t) the instantaneous power, also averaged across trials. Changes in power are thus represented as a percentage of the reference/baseline values, where positive ERD values indicate power decreases (indicating cortical activation) and negative ERD values indicate power increases⁴ (reflecting cortical deactivation).

The time-course of ERD was computed and represented for the same regions of interest used in the analysis of instantaneous amplitude (anterofrontal, frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital, occipital).

2.3 Results

2.3.1 Behavioral results

Reaction times. The behavioral analysis suggested that the participants were able to follow the instructions to use each strategy at the appropriate time in that the patterns of CRTs and VRTs were similar to those that have been used to distinguish between the two strategies in previous experiments (e.g., MacLeod et al., 1978; Mathews et al., 1980). In particular CRT was shorter using the linguistic strategy

⁴In line with this convention (i.e., negative ERD reflects power increase) negative ERD was plotted upward.

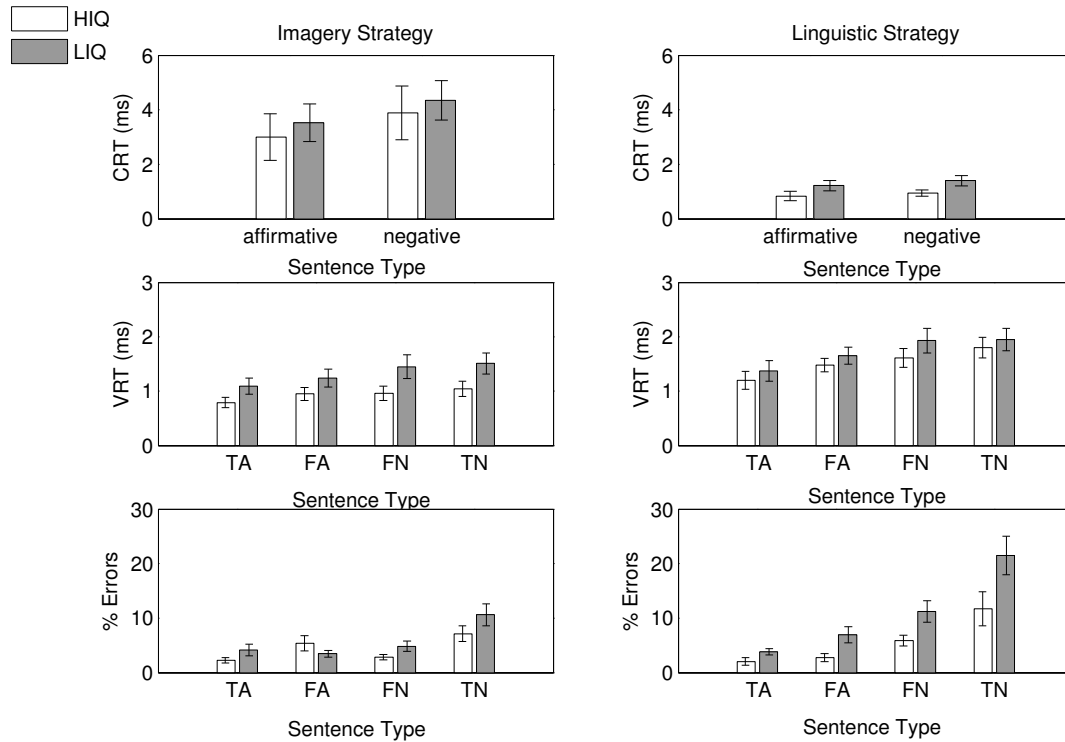


Figure 2.2: From top to bottom: CRTs, VRTs, and percentage of errors for the imagery and the linguistic strategy conditions (left and right panels respectively). In the upper panels CRT (in seconds) is displayed as a function of sentence type (affirmative and negative). In the middle panel VRT (in seconds) are displayed as a function of trial type (True Affirmative, False Affirmative, False Negative, and True Negative). White bars represent HIQ individuals, grey bars LIQ individuals.

(1,100 ms) than when using the imagery strategy (3,691 ms). The critical Polarity x Truth Value x Strategy interaction was significant for VRT. According to MacLeod et al. (1978) and others (e.g., Mathews et al., 1980) the use of the linguistic strategy should result in a Polarity x Truth Value interaction due to the fact that negative sentences, being linguistically more complex, need more processing than affirmative sentences. Furthermore, sentence and picture representations can be more easily compared when the two are congruent (Gough, 1965). Thus, the nature of the Polarity x Truth Value interaction is such that true affirmative (TA) trials are responded more quickly than false affirmative (FA) trials, but false negative (FN) trials are easier than true negative (TN) trials (Carpenter & Just, 1975). With the imagery strategy, the latencies for affirmative trials are comparable to negative trials (with no main effect of polarity), because the complexity of the negative sentences is resolved at the time that the representation of the sentence is created. However, FN and TA responses are faster

than the TN and FA ones. Because the speed of response is irrespective of whether the sentence is affirmative or negative the Polarity x Truth Value interaction is absent.

The left and right histograms in the upper part of Figure 2.2 show CRTs for the two groups of participants for the imagery and linguistic strategy conditions respectively. The CRTs were subjected to a mixed ANOVA with strategy (linguistic vs. imagery) and polarity (affirmative vs. negative) as within-subject factors and group (HIQ vs. LIQ) as a between-subjects factor.

A general advantage for the HIQ group was observed, but the difference between the two groups was not significant ($p > .2$). The main effect of strategy was significant, with CRT being faster in the linguistic than in the imagery strategy condition ($F(1, 26) = 47.25, p < .001, MSe = 3,973,451$). The Group x Strategy interaction was not significant, ($p > .8$), suggesting that both groups executed the task according to the given instruction. Participants were faster reading affirmative sentences than negative sentences ($F(1, 26) = 90.8, p < .001, MSe = 39,357$). The Polarity x Strategy interaction ($F(1, 26) = 48.56, p < .001, MSe = 73,265$) reflected that this difference was more evident in the imagery strategy condition, where negative predicates had to be fully comprehended before visual images could be generated. Neither the Polarity x Group nor the Strategy x Polarity x Group interaction ($p > .6$) was significant.

The left and right histograms in the middle part of Figure 2.2 show VRTs for the two groups of participants for the imagery and linguistic strategy conditions respectively. These data were analyzed with a mixed ANOVA with strategy (imagery vs. linguistic), polarity (affirmative vs. negative), and truth-value (true vs. false) as within-subject factors, and group (HIQ vs. LIQ) as a between-subjects factor. Overall the HIQ group was significantly faster than LIQ group in verifying the picture ($F(1, 26) = 5.1, p < .04, MSe = 965,996$). Verification RT was shorter in the imagery than in the linguistic strategy condition ($F(1, 26) = 57.8, p < .001, MSe = 243,974$). Responses to true trials were faster than responses to false trials ($F(1, 26) = 10.67, p < .003, MSe = 23,865$) and responses to affirmative sentences were faster than those to negative sentences ($F(1, 26) = 141.5, p < .001, MSe = 39,357$); the Polarity x Truth Value interaction ($F(1, 26) = 41.7, p < .001, MSe = 29,198$) was also significant. The Strategy x Polarity x Truth Value interaction ($F(1, 26) = 5.85, p < .02, MSe = 18,491$) suggests that the two groups were executing imagery and linguistic strategy as instructed. The Strategy x Polarity interaction ($F(1, 26) = 17.77, p < .001, MSe = 25,626$) is consistent with differences in strategy use (see Reichle et al., 2000). Reichle et al. (2000) stated that the variables polarity and truth-value affected performance more

in the linguistic than the imagery strategy condition, giving reliable Strategy x Polarity and Strategy x Truth Value interactions. However, we failed to find the Strategy x Truth Value interaction ($p < .2$). Only one interaction with group, the Polarity x Group interaction ($F(1, 26) = 6.21$, $p < .02$, $MSe = 39,357$) was found, all other $ps > .2$.

Accuracy. The overall mean percent error, shown in the left and right histograms in the bottom part of Figure 2.2 (imagery strategy condition on the left and linguistic strategy condition on the right), was low. Moreover, no evidence of speed-accuracy trade-off was found. Percent error was analyzed with a mixed ANOVA with strategy (imagery vs. linguistic), polarity (affirmative vs. negative), and truth-value (true vs. false) as within-subject factors, and group (HIQ vs. LIQ) as a between-subjects factor. The HIQ group made fewer errors than the LIQ group ($F(1, 26) = 6.5$, $p < .02$, $MSe = 33$), and more errors were made with the linguistic strategy than the imagery strategy ($F(1, 26) = 20.03$, $p < .001$, $MSe = 10$). Moreover the two factors interacted ($F(1, 26) = 7.78$, $p < .01$, $MSe = 10$) such that that the percentage of errors in the linguistic strategy condition was nearly twice that of the imagery strategy condition for the LIQ group (10.7% vs. 5.7%, respectively) but not for the HIQ group (5.5% vs. 4.4%, respectively). Fewer errors were made with affirmative than negative sentences ($F(1, 26) = 49.61$, $p < .001$, $MSe = 12$) and with false than true trials ($F(1, 26) = 10.25$, $p < .003$, $MSe = 12$). The Polarity x Truth Value interaction ($F(1, 26) = 29.3$, $p < .001$, $MSe = 11$) was also significant, reflecting strategy related differences as reported in the analysis of the VRTs, as was the Strategy x Polarity interaction ($F(1, 26) = 28.45$, $p < .001$, $MSe = 7$). Sentence polarity had a smaller effect in the imagery as compared to the linguistic strategy condition. Apart from the Group x Strategy x Polarity x Truth Value interaction ($F(1, 26) = 4.98$, $p < .03$, $MSe = 5$), no interaction with strategy was significant ($p > .1$). Together with the above reported Group x Strategy x Polarity x Truth Value interaction, the Group x Polarity interaction ($F(1, 26) = 5.05$, $p < .03$, $MSe = 13$) was significant; no other interaction with group was significant ($ps > .25$)⁵.

⁵Separate analysis of performance data based on only verbal or spatial ability, respectively, yielded generally the same pattern of results. However, for the error rates, verbal ability was found to have a bigger effect on percentage error (2.5% vs. 5.4% for high vs. low verbal ability participants) than was spatial ability (3.5% vs. 4.4% for individuals with high vs. low spatial ability).

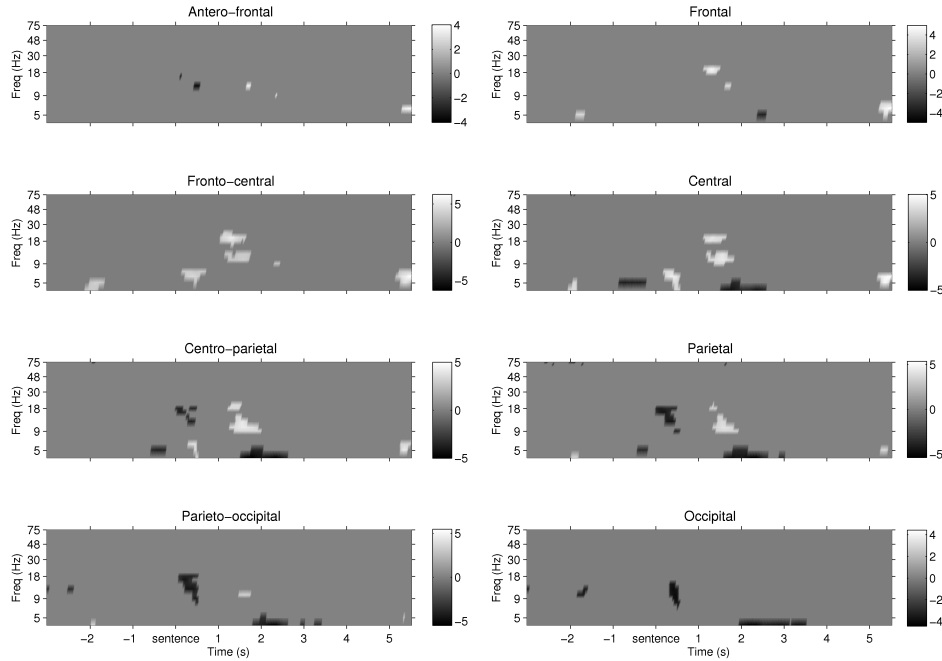


Figure 2.3: Thresholded FDR-map showing significant amplitude differences between imagery and linguistic strategy conditions at sentence onset (sentence). Each subplot is a time-frequency plot showing data points at which the difference was significant according to the FDR procedure. Time and frequency are plotted in the horizontal and vertical axes respectively. Each subplot refers to one of the ROIs shown in Figure 2.1. The cut-off t -value for these results, given by the FDR procedure, was 3.04.

2.3.2 Electrophysiological results

Instantaneous amplitude. The IA data for all eight regions of interests (ROIs; anterofrontal, frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital, occipital) were subjected to the FDR procedure. Three tests were performed, one for a main effect of IQ, one for a main effect of strategy, and one for an interaction of IQ and strategy. All tests were performed separately on the segments time locked to the onset of the sentence and to the onset of the picture. Only the tests for strategy differences yielded significant results. Even when alpha was raised to levels as high as .2 (indicating a willingness to accept an average of 20% of false positives), no significant main effects of IQ or IQ x Strategy interactions were found. Figures 2.3 and 2.4 show FDR thresholded t -maps for the comprehension and verification intervals, respectively. Figure 2.3 shows strategy differences in the sentence-onset epochs

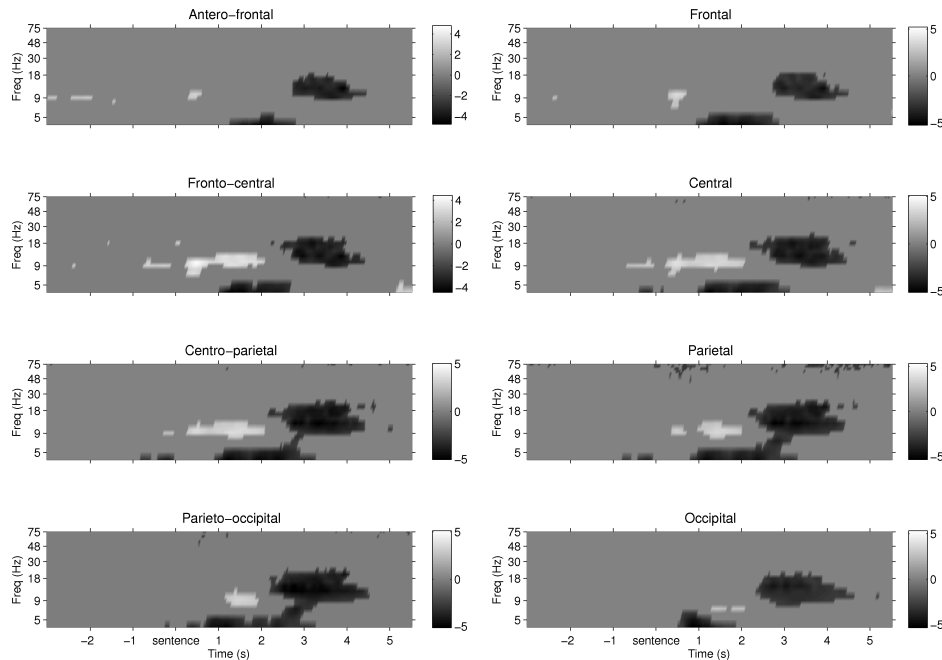


Figure 2.4: Thresholded FDR-map showing significant amplitude differences between imagery and linguistic strategy conditions at picture onset (picture). Each subplot is a time-frequency plot showing data points at which the difference was significant according to the FDR procedure. Time and frequency are plotted in the horizontal and vertical axis respectively. Each subplot refers to one of the ROI shown in Figure 2.1. The cut-off t -value for these results, given by the FDR procedure, was 3.22.

($t(26) = 3.04$; $p < .001$; where t represents the minimum threshold t -value and p the associated significance level). Figure 2.4 shows the strategy differences in the picture-onset epochs ($t(26) = 3.22$; $p < .001$). As can be seen in Figure 2.3, there were three main areas of significant strategy-related differences. First, in the alpha frequency range (8-12 Hz), IAs were higher in the imagery than in the linguistic strategy condition. The effect appeared to consist of two components with different topography. The first, occurring within 300-900 ms after sentence onset, was visible from frontal to parietal sites; the second, within 1-2 s after sentence onset, was visible from fronto-central to parieto-occipital sites. Second, in the theta frequency range (4-8 Hz), IAs were higher in the linguistic than in the imagery strategy condition. The effect appeared to consist of two components with different topography. The first component, occurring within 700-1,500 ms after sentence onset, was visible from frontal to occipital sites; the second, occurring within 1-3 seconds after sentence onset, was visible

from antero-frontal to parieto-occipital sites. Third, in the mu-beta frequency range (8-20 Hz), IAs were higher in the linguistic than the imagery strategy condition. This effect was broadly distributed across the scalp with a region-dependent time-course: Posterior areas had an earlier onset (approximately 2.5 s) than anterior areas (approximately 3 s); offset was approximately 4 s after sentence onset, independent of the region.

Figure 2.4 shows six areas of significant strategy-related differences. Approximately 1 s before picture onset, in the theta frequency range (4-6 Hz), IAs were higher in the linguistic than in the imagery strategy condition, and distributed from central to parietal areas. Within 500 ms after picture onset, in the higher alpha and lower beta frequency range (10-18 Hz), IAs were higher in the linguistic than in the imagery strategy condition, and distributed from antero-frontal to posterior areas. Within 1 s after picture onset, in the theta frequency range (4-8 Hz), IAs were higher in the imagery than in the linguistic strategy condition, and distributed from fronto-central to centro-parietal areas. Between 1-1.5 s after the onset of the picture, in the beta frequency range (18-24), IAs were higher in the imagery than in the linguistic strategy condition, and distributed from frontal to parietal regions. Between 1-2 s after picture onset, in the mu frequency range (9-13 Hz), IAs were higher in the imagery than in the linguistic strategy, and broadly distributed across the scalp. From 2-3.5 s after picture onset, in the theta frequency range (4-6 Hz), IAs were higher in the linguistic than the imagery strategy condition, and broadly distributed across the scalp.

The strategy-related effects revealed in the initial, global analysis were selectively subjected to further tests using more circumscribed ERD analyses targeted at specific, relevant frequency bands. In particular, ERD analysis was targeted at the theta and upper alpha bands. Although the initial results of the ERD analyses also showed substantial strategy-related differences in the beta band (16-26 Hz) as well as in the associated mu band (9-13 Hz with a scalp distribution centered at parietocentral locations), subsequent analyses showed such differences to be straightforward consequences of the well-known fact that mu/beta rhythms strongly desynchronize prior to and during response execution (e.g., Gladwin et al., 2006) and the fact that RTs were very different for the two strategies. For these reasons, these latter effects were not further explored.

In light of our research objective regarding IQ-related effects, we decided to maintain the distinction between IQ-groups in these follow-up analyses despite the fact that no IQ-related effects were present in the global analysis. This is justified because IQ-

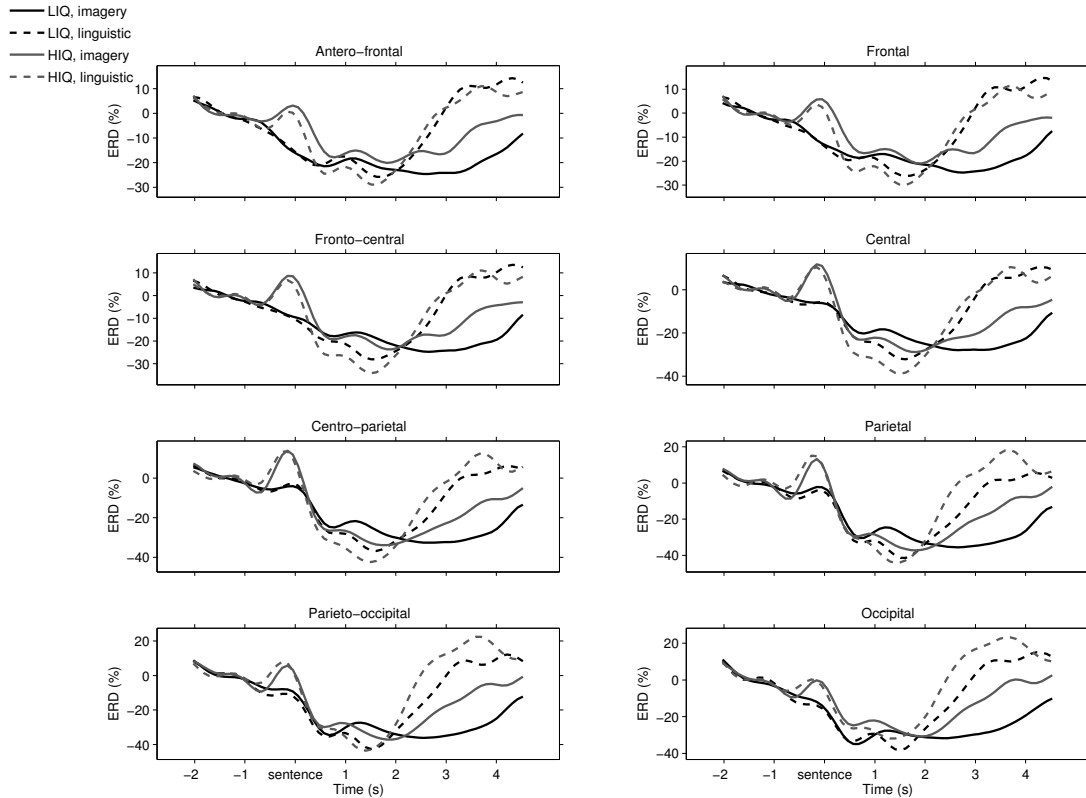


Figure 2.5: Alpha ERD time courses for HIQ and LIQ groups in the imagery and linguistic strategy conditions at sentence onset (sentence), for each ROI. Time and percent ERD are plotted in the horizontal and vertical axis respectively.

related effects on cerebral dynamics in the present study are likely to be subtle, given that subtle effects could be missed when correcting for a large number of multiple comparisons as implemented in the FDR procedure, and might have a much better chance to show up in more targeted analyses. We focus on those frequency bands that showed large strategy-related effects, reasoning that these would also be the ones most likely to show IQ-related differences.

Alpha ERD. Because ERD differences between groups or tasks may in some cases reflect differences in power in the reference interval rather than differences in power in the test interval (Doppelmayr, Klimesch, Pachinger, & Ripper, 1998), we first tested for possible baseline relative differences in alpha (9.5-12.5 Hz) power between the two groups. No IQ-related differences in baseline alpha power were found ($p > .8$). Figure 2.5 shows the percent ERD in the alpha frequency band for both groups in the

two strategy conditions, relative to the sentence onset. Consistent with the patterns shown in Figure 2.3, alpha ERD between 0.5 to 2 s after sentence onset was higher in the linguistic than in the imagery strategy condition. The time course of the alpha ERD observed in Figure 2.5 in the interval between 2 to 4 s after sentence onset is also consistent with the results shown in Figure 2.3, such that in the linguistic strategy condition the desynchronization of the alpha rhythm gradually decreased, whereas in the imagery strategy condition desynchronization was high for a longer period. Note that no IQ-related differences in alpha ERD were apparent in these two intervals. However, in the 300 ms preceding the sentence onset an IQ-related difference was observed: LIQ individuals showed a positive desynchronization whereas HIQ individuals showed a negative desynchronization ($F(1, 26) = 4.89, p < .03, MSe = 77$). This latter effect did not interact with strategy ($p > .7$), suggesting that it is a relatively “pure” IQ-related difference. Figure 2.6 shows the alpha ERD for the epoch time locked to the picture onset. Consistent with the results shown in Figure 2.4, ERD time course at picture onset was generally comparable between strategies. Alpha desynchronization was higher at picture onset for the imagery than for the linguistic strategy condition, and substantially reduced at the end of the verification processing; this reestablishment of the post-processing alpha rhythm happened earlier for the imagery than the linguistic strategy. No IQ-related differences were apparent.

An additional analysis of alpha ERD was performed using time intervals similar to the ones used by Neubauer et al. (1995). Neubauer et al.’s event-related periods were: (a) from 1.0 to 0.5 s before sentence onset (pre-stimulus interval); (b) from 250 to 125 ms before the CRT; (c) from 125 to 375 ms after the CRT; and (d) from 250 to 125 ms before the VRT. Similar ERD temporal intervals were estimated considering sentence onset and response executions. The averaged power in the upper alpha band was subjected to a mixed ANOVA with ROI (antero-frontal, frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital, occipital), strategy (imagery vs. linguistic), and time interval (preceding CRT, after CRT, preceding VRT) as within subjects factors, and group (HIQ vs. LIQ) as a between subjects factors. The pre-stimulus interval was excluded from the analysis because its values were close to baseline and the increased variance due to its extreme values would have biased the outcome of the ANOVA (see Figure 2.7). The time course of percent ERD differed between the two groups, as reflected by the Time Interval x Group interaction ($F(2, 52) = 4.08, p < .02, MSe = 576$). No other tests yielded evidence for IQ-related differences in ERD (all $ps > .2$). Percent ERD increased with the time spent on the trial ($F(2, 52) = 28.6,$

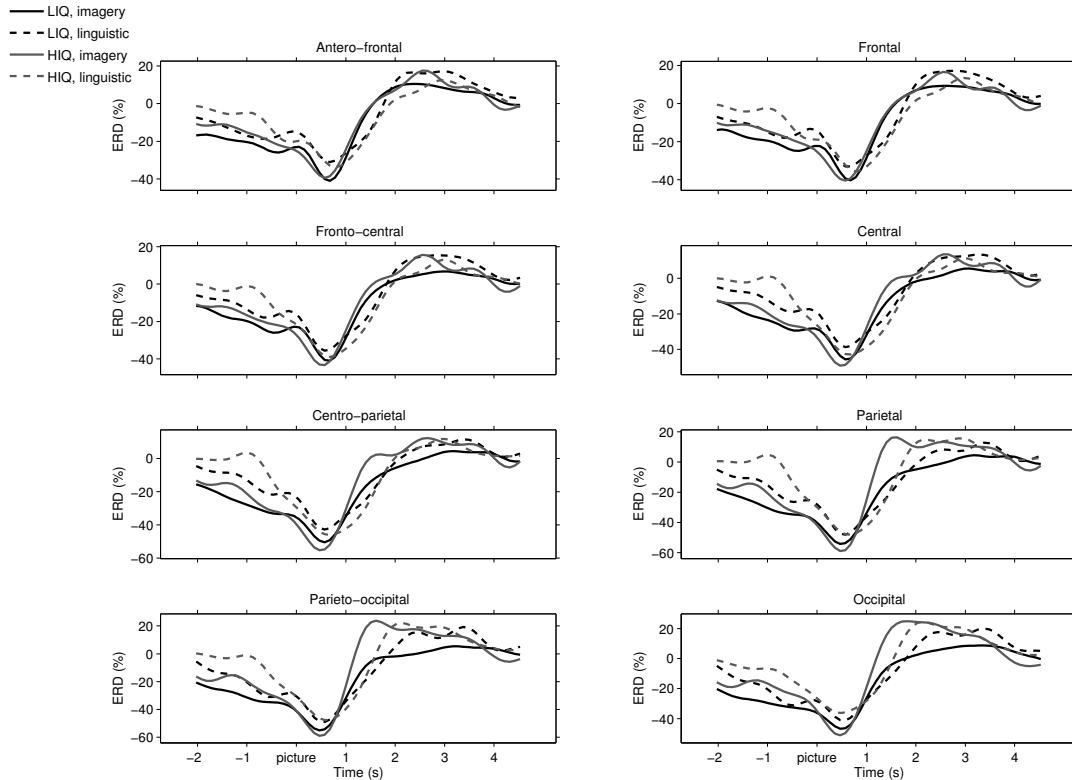


Figure 2.6: Alpha ERD time courses for HIQ and LIQ groups in the imagery and linguistic strategy conditions at picture onset (picture), for each ROI. Each subplot refers to one of the regions in the electrode cluster in Figure 2.1. Time and percent ERD are plotted in the horizontal and vertical axis respectively.

$p < .001$, $MSe = 576$), was higher in the posterior regions than in the anterior regions ($F(7, 182) = 11.01$, $p < .001$, $MSe = 492$), and its spatial distribution differed as a function of time (Time Interval \times ROI interaction ($F(14, 364) = 10.01$, $p < .001$, $MSe = 47$)) increasing slowly but consistently at the frontal regions and showing an abrupt increment followed by a steep decrement in the posterior regions (see Figure 2.7). With regard to strategy differences, ERD amplitude was lower in the linguistic than in the imagery strategy condition ($F(1, 26) = 15.98$, $p < .001$, $MSe = 1,719$) independently of ROI or time interval (both $ps > .2$). However, the ROI \times Time Interval \times Strategy interaction ($F(14, 364) = 3.27$, $p < .01$, $MSe = 17$), shown in Figure 2.7, reflects that topography and time course of percent ERD were affected by the strategy used. Between strategies differences in ERD time course were more pronounced at the VRT interval where changes in ERD were more marked in the linguistic than in

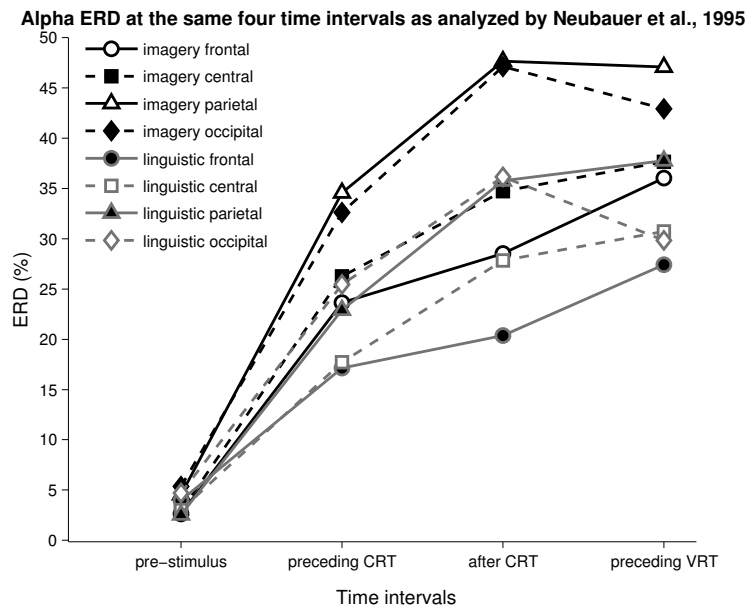


Figure 2.7: Time course and topography of the alpha ERD with time intervals similar to the ones of Neubauer et al. (1995). Percent ERD is plotted as a function of time interval (specified in the results section), for the imagery strategy condition (solid lines) and for the linguistic strategy condition (broken lines). Note that, for clarity, pairs of ROIs were averaged together to create the following ROIs: “frontal” is the average of antero-frontal and frontal, “central” is the average of fronto-central and central, “parietal” is the average of centro-parietal and parietal, and “occipital” is the average of parieto-occipital and occipital.

the imagery strategy condition. Moreover, in the VRT interval, ERD time course at central and occipital locations crosses over between the two strategies.

In summary, the topography and time course of alpha ERD were affected by the strategy used, and ERD was generally higher with the imagery strategy than the linguistic strategy. In general, the two groups showed a similar pattern in that the ERD time course did not differ for the IQ groups, except at the interval before the onset of the sentence. Analysis of the ERD in the analogous time intervals as those used by Neubauer et al. (1995) yielded a substantial difference at a strategy level but no IQ-related differences.

Theta ERD. Figures 2.8 and 2.9 show the theta ERD for epochs time-locked to the onset of the sentence and the picture, respectively. No IQ-related differences in baseline theta power were found ($p > .3$). In order to distinguish between so-called evoked and induced changes in theta power, analysis of theta ERD was performed both with

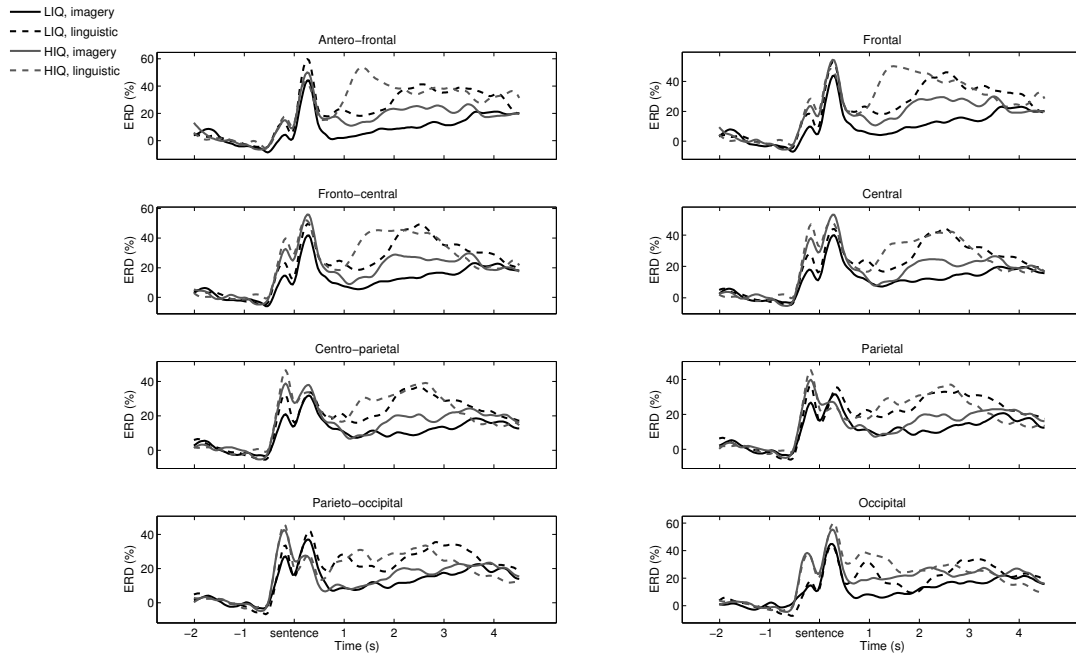


Figure 2.8: Theta ERD time courses for HIQ and LIQ groups in the imagery and linguistic strategy conditions at sentence onset (sentence), for each ROI. Time and percent ERD are plotted in the horizontal and vertical axis respectively.

and without a correction for average ERP (see Tallon-Baudry & Bertrand, 1999, for an extensive discussion regarding this issue). Though this produced somewhat different overall time courses for theta ERD, it did not affect any differences related to strategy or IQ. For this reason, we only report the results for ERD computed from instantaneous power uncorrected for ERP. In Figure 2.8, consistent with the results shown in Figure 2.3, between 0.5 and 3 seconds after sentence onset, theta ERD was lower in the linguistic than in the imagery strategy condition. IQ related differences, independent from strategy effects (Group x Strategy interaction $p > .16$), were found during the 0.5 s warning interval preceding sentence onset, where theta desynchronization was lower for HIQ than LIQ individuals ($F(1, 26) = 5$, $p < .03$, $MSe = 3,510$). Given the timing of this ERD decrement relative to the onset of the warning stimulus and the following sentence, this would seem to reflect preparatory activity. A test for IQ-related differences in theta ERD in the interval between 1 to 2 seconds after sentence onset did not yield significant results ($p > .2$). Figure 2.9 shows, consistent with the results shown in Figure 2.4, that in the interval from 2 to 4 seconds after picture onset, theta ERD was lower in the linguistic than in the imagery strategy condition. Interestingly, in the interval between 0.5 to 2 seconds after picture onset, there seems to be a

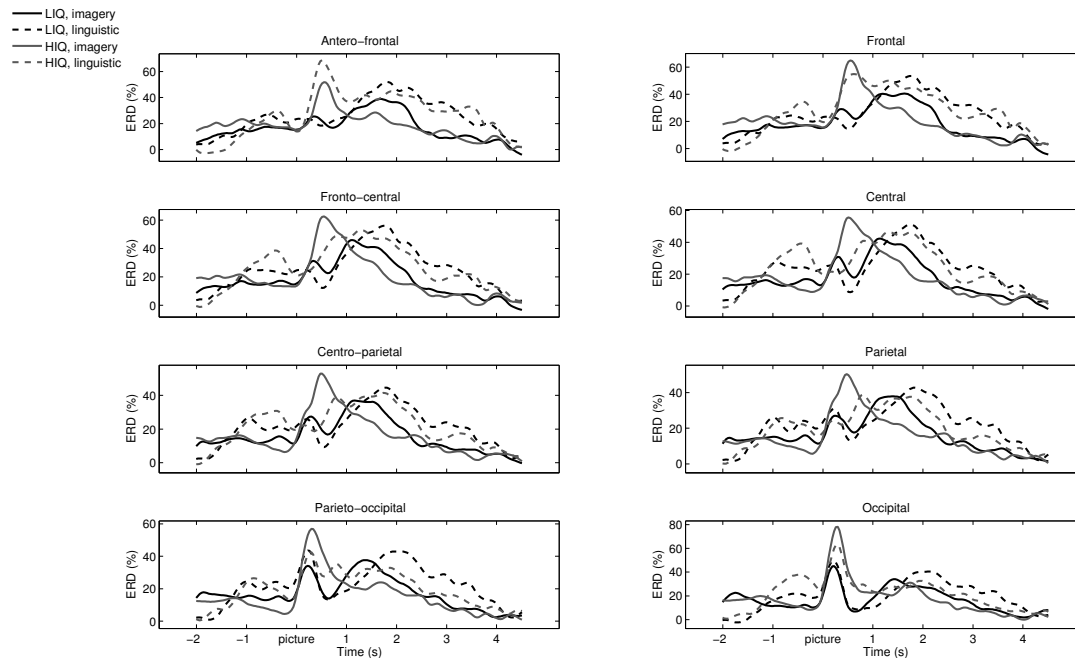


Figure 2.9: Theta ERD time courses for HIQ and LIQ groups in the imagery and linguistic strategy conditions at picture onset (picture), for each ROI. Time and percent ERD are plotted in the horizontal and vertical axis respectively.

remarkable similarity between the peak latencies of negative theta desynchronization and mean RT across groups and strategies, with differences in the peak latencies being closely proportional to differences in RT; this is clearest at parietal sites. This suggests that the differences in theta ERD following picture onset are most readily explained in terms of differences in processing speed.

2.4 Discussion

The primary aim of this study was to investigate whether previously documented IQ-related differences in degree and pattern of neural activation during SVT performance (Neubauer et al., 1995) persist when the strategies used in task performance are controlled by means of explicit instructions. To this end, EEG was measured while groups of LIQ and HIQ individuals performed the SVT using either a linguistic or a spatial-visual (imagery) strategy.

Analysis of the behavioral data suggested that both IQ groups used the two distinct strategies according to instruction. Most importantly, CRT (sentence comprehension

time) was much shorter in the linguistic as compared to the imagery condition and polarity of the sentence had a major effect on CRT only in the imagery condition. Both results indicate more extensive processing of the sentence prior to onset of the picture in the imagery condition. Interestingly, no significant IQ-related effects on CRT were obtained.

More evidence of appropriate strategy use was obtained in the analysis of VRT. VRT was substantially shorter in the imagery condition than in the linguistic condition. Even more importantly, a significant Polarity x Truth Value x Strategy interaction was found for VRT, which, according to several authors (i.e., MacLeod et al., 1978; Mathews et al., 1980), satisfies the litmus test for the distinction between the linguistic and imagery strategies. VRT was slower and more error prone for the low IQ group, especially for the more difficult trials in the linguistic condition (e.g., true-negative trials). However, there was no Polarity x Truth Value x Strategy x IQ interaction. Overall, the behavioral data strongly indicate that both groups performed the task according to the instructed strategy and suggest a modest overall advantage of HIQ over LIQ individuals with respect to both speed and accuracy of task execution.

A global analysis of IA across a wide range of EEG frequency bands and aggregated electrode positions revealed no significant IQ-related differences, whereas several strategy-related effects were obtained in the theta band and the upper alpha frequency band. A more focused analysis of the time course of these latter effects, in terms of ERD, showed a substantial and widely distributed decrease of upper-alpha power and increase of theta power during task execution, consistent with the suggestion of Nunez et al. (2001) that alpha power is reduced but theta power enhanced during effortful processing. In general, the difference in the temporal profiles of power changes in these two frequency bands as a function of strategy, and, hence, the strategy-related differences in the overall analysis, are probably best interpreted as a straightforward consequence of the substantial differences in dynamics and overall duration of processing between these strategies as reflected in the RT results. Qualitative differences in processing between the two strategies may also have contributed to the different ERD profiles. However, even if present, such contributions are difficult to separate from, and are likely to have been overshadowed by, the differences between strategies in overall duration of processing in the present study.

The lack of IQ-related differences in upper-alpha ERD during SVT performance in the present study contrasts with the findings of Neubauer et al. (1995). Neubauer et al. found significantly stronger upper-alpha ERD at frontal sites for LIQ as compared

to HIQ individuals during SVT performance. Although Neubauer et al. did not control for possible strategy differences between IQ groups, the present results show that strategy-related differences in upper-alpha ERD are not limited to frontal regions but widely distributed across the scalp, which makes it unlikely that a confounding of IQ and strategy in the Neubauer et al. study can fully account for the differences between our study and theirs. A more plausible account for these differences is suggested by the fact that participants in our study received relatively little SVT training as compared to the much more extensive practice given to the participants in Neubauer et al.'s study (note that these participants had also taken part in a previous study using the SVT conducted by Neubauer & Freudenthaler, 1994). Whereas the limited practice in the present study may have prevented task automation in either IQ group, the more extensive practice given in the Neubauer et al. (1995) study may have enabled their HIQ participants, but not LIQ participants, to achieve a high level of automation in SVT performance. As task automation has been linked to reduced involvement of frontal regions in task performance (Koch et al., 2006; Owen, Evans, & Petrides, 1996), we suggest that different amounts of SVT practice between the two studies provide a plausible, but admittedly speculative, explanation of the difference in results regarding IQ-related differences in frontal upper-alpha ERD. This possibility deserves further systematic study.

Whereas no IQ-related differences in EEG power were found during actual task execution, two differences were obtained during the 0.5 s warning or preparation interval preceding sentence onset. First, a phasic enhancement of theta power during the warning interval, found most prominently at fronto-central sites, was present in both groups, but was found to be significantly stronger in the HIQ group. Second, HIQ, but not LIQ, individuals showed a broadly distributed phasic enhancement of upper-alpha power during the warning interval. A similar change was reported in Neubauer et al. (1995) for the interval between sentence offset and picture onset, where a 500 ms blank interval was placed. This interval could be interpreted as a preparatory period for the execution of the sentence-picture comparison. Interestingly, higher amplitudes of fronto-central theta rhythm during the preparation interval in task-switch paradigms have been linked to enhanced quality or effectiveness of advance preparation (Gladwin et al., 2006). As advance preparation in task-switch paradigms has been argued to require successful retrieval and maintenance of task goals and task sets (Mayr & Kliegl, 2000), Gladwin et al.'s (2006) findings seem consistent with results linking theta rhythm to processes involved in memory retrieval and working memory

(Klimesch, 1999; Gevins & Smith, 2000). Thus, the stronger phasic enhancement of theta power found in HIQ individuals, might indicate more adequate, or more adequately timed, preparatory activity in these individuals.

The finding of a concurrent phasic enhancement of upper-alpha power in HIQ individuals may seem paradoxical, given the traditional view of alpha synchronization as a cortical “idling” process (Pfurtscheller et al., 1996). However, more recent evidence has suggested an alternative interpretation, in which alpha synchronization is thought to reflect active inhibitory control of task-irrelevant brain regions (N. R. Cooper et al., 2003; Klimesch, 1999). From this perspective, phasic alpha synchronization during the warning interval in HIQ individuals might reflect enhanced inhibition of task-irrelevant brain regions, which has been suggested to be a critical component in the configuration and maintenance of selective task sets (Monsell, 1996, 2003). In other words, it may be a reflection of the active process of focusing on the task and thus inhibiting task-irrelevant brain regions (Klimesch et al., 1999), or of the suppression of the flow of irrelevant information (Jensen, Gelfand, Kounios, & Lisman, 2002; see also Fink, Grabner, Benedek, & Neubauer, 2006, for considerations along this line). This evidence that HIQ individuals may have been able to achieve better preparatory control prior to stimulus onset is consistent with the behavioral results indicating overall superior SVT performance by HIQ as compared to LIQ individuals.

That preparatory set may be a crucial determinant of quality of task execution is also suggested by a series of studies linking accuracy of subsequent memory retrieval to brain activity (induced by trial-by-trial cuing of relevant stimulus information) prior to stimulus presentation (see, e.g., Otten, Henson, & Rugg, 2002, for evidence using fMRI; Otten, Quayle, Akram, Ditewig, & Rugg, 2006; Padilla, Wood, Hale, & Knight, 2006, for evidence using event-related brain potentials). These findings were interpreted in terms of effects of the quality of the cued task set on the quality of encoding. The present results suggest that an interesting topic for future studies would be to look for IQ-related differences in the quality of such flexible and selective cue-evoked memory encoding.

In summary, we failed to find the negative correlation between brain activation and intelligence predicted by the neural efficiency theory. We did find major differences in spatio-temporal activation patterns between linguistic and imagery strategy conditions, which highlights the need to control for potential confoundings of intelligence and strategy use in individual differences research. More particularly, it is important to prevent differences in IQ from being confounded with differences in expertise. Fi-

nally, whereas we did not find IQ-related differences in brain activation during actual task execution, we did obtain suggestive evidence that HIQ and LIQ individuals differed in the quality and timing of preparation immediately preceding SVT execution. The generality of the latter finding, and its potential relation to neural efficiency theory, might be fruitful topics for future research.

Chapter 3

Using Frequency Tagging to Quantify Attentional Deployment in a Visual Divided Attention Task

A corar e cagar as s'immerda i garit
Idiomatic translation: “Doing two things at the same time
will result in a mess.”

Proverb of Ferrara

Abstract

Frequency tagging is an EEG method based on the quantification of the steady state visual evoked potential (SSVEP) elicited from stimuli which flicker with a distinctive frequency. Because the amplitude of the SSVEP is modulated by attention such that attended stimuli elicit higher SSVEP amplitudes than do ignored stimuli, the method has been used to investigate the neural mechanisms of spatial attention. However, up to now it has not been shown whether the amplitude of the SSVEP is sensitive to gradations of attention and there has been debate about whether attention effects on the SSVEP are dependent on the tagging frequency used. We thus compared attention effects on SSVEP across three attention conditions—focused, divided, and ignored—with six different tagging frequencies. Participants performed a visual detection task (respond to the digit 5 embedded in a stream of characters). Two stimulus streams, one to the left and one to the right of fixation, were displayed simultaneously, each with a background grey square whose hue was sine-modulated with one of the six tagging frequencies. At the beginning of each trial a cue indicated whether targets on the left, right, or both sides should be responded to. Accuracy was higher in the focused- than in the divided-attention condition. SSVEP amplitudes were greatest in the focused-attention condition, intermediate in the divided-attention condition, and smallest in the ignored-attention condition. The effect of attention on SSVEP amplitude did not depend on the tagging frequency used. Frequency tagging appears to be a flexible technique for studying attention.

3.1 Introduction

Attention allows the selection of relevant objects from a cluttered scene, enhancing the perception or processing of a stimulus or a particular location. The neu-

ral mechanisms underlying it have been broadly investigated, with questions ranging from the locus of the control mechanisms for deciding what must be attended (see, e.g., Mehta, Ulbert, & Schroeder, 2000; O'Connor, Fukui, Pinsk, & Kastner, 2002; Vanduffel, Tootell, & Orban, 2000; Yingling & Skinner, 1976), to how the cognitive system trades off resources between different events (see, e.g., Desimone & Duncan, 1995; Kastner, Weerd, Desimone, & Ungerleider, 1998; Kok, 1997). A number of different techniques have been used to address how and when selectivity is expressed in the brain. For example, electroencephalography (EEG) has been used to show that the amplitude of the visual evoked potential associated with a stimulus is enhanced when the stimulus is presented in an attended rather than in an unattended location (for a review, see, Hillyard, Teder-Salejarvi, & Munte, 1998). Similarly, intracellular recordings in monkeys have shown that attended stimuli evoke increased neural synchronization in the gamma frequency range (35-90 Hz, see, e.g., Fries et al., 2001) relative to unattended stimuli, and functional magnetic resonance imaging (fMRI) in humans has shown enhanced stimulus-evoked activity when participants were attending to a stimulus or spatial location (for a review, see, Yantis & Serences, 2003).

A promising and increasingly popular technique to investigate the neural correlates of selective attention is frequency tagging. Frequency tagging is a method based on the steady state visual evoked potential (SSVEP; Regan, 1989) measured using EEG¹. The SSVEP is made up of the physiological responses evoked by series of sensorial stimulations. For example, the sudden appearance of a bright object (e.g., a white square) on a black computer screen evokes a response whose amplitude is highest in the primary visual cortex. If the stimulation is repeated with a fast enough frequency, the EEG trace will display a steady-state response with the same frequency as the presentation rate of the oscillating objects. While the SSVEP (and its auditory analog, the auditory steady-state response) was originally thought to result from periodic superimposition of early-latency evoked responses (Galambos, Makeig, & Talmachoff, 1981; Regan, 1989), recent evidence tends to support the hypothesis that the oscillatory response, at least for sufficiently high frequencies (> 6 Hz) reflects a separate neural oscillation that is driven by the periodic stimulus (Ross, Herdman, & Pantev, 2005a).

Besides having frequency characteristics similar to the visual stimulation, the amplitude of the SSVEP is enhanced when attention is directed to the stimulus as compared to when that stimulus is ignored (M. M. Muller, Picton, et al., 1998). This last

¹The same technique can be used with magnetoencephalography (MEG).

property constitutes the strength of the frequency tagging technique: Because it is possible to use specific, different tagging frequencies for a number of different spatial locations in a visual display, it is possible to see in the EEG response which locations participants have attended and which they have ignored.

Morgan et al. (1996) and Hillyard et al. (1997) were among the first to demonstrate that SSVEPs could be used to study attention. They induced SSVEPs by presenting two squares that oscillated between black and white with two different frequencies at two different target locations (left and right on a computer screen). Two streams of alphanumeric characters were simultaneously displayed superimposed on the oscillating squares and participants, after having been instructed to attend to either the left or the right stream, emitted a speeded response any time the digit “5” was displayed in the stream that was to be attended. Consistent with the suggestion that the SSVEP is sensitive to the degree of attention deployed, analysis of the electrophysiological data showed that the SSVEP evoked from the attended side had a higher amplitude than the SSVEP evoked from the ignored stream.

In the experiments of Hillyard et al. (1997); Morgan et al. (1996), attention was “all-or-none”, leaving open the question of whether the SSVEP is sensitive to gradations of attention across spatial locations. It has been shown that SSVEP amplitude is increased at attended versus unattended locations when two locations are to be attended (Muller et al., 2003; see also Malinowski et al., 2007). M. M. Muller et al. (2003) used four streams of symbols displayed horizontally with two locations to the left and two to the right of fixation, and asked their participants to attend to two of the locations simultaneously. Participants had to attend either the two locations in the left hemifield, the two locations in the right hemifield, or to either the left-most location and the third location from the left or the second location from the left and the right-most location. Participants were to respond whenever the digit 8 appeared simultaneously in both of the to-be-attended locations.

M. M. Muller et al. (2003) contrasted the conditions in which two locations in the same hemifield were to be attended with the conditions in which a to-be-ignored location was between the to-be-attended locations to test whether attention could be independently allocated to two locations. They reasoned that when a to-be-ignored location was situated between two to-be-attended locations, the amplitude of the SSVEP to that location would be enhanced if it were not possible to divide attention across two non-contiguous locations. Consistent with a multiple-spotlight hypothesis, no differences in SSVEP amplitude to the unattended locations as a function of location

were found. The study of M. M. Muller et al. (2003) (see also; Malinowski et al., 2007) shows that attention can act as multiple spotlights at multiple locations, and that SSVEP reflects this attentional deployment. However, because no comparison was made with a single focus of attention, it is not possible to say whether the amplitude of the SSVEP can be used as an index of the amount of attentional resources allocated to one versus two locations.

Amplitudes of early event-related brain potentials (ERPs, i.e., N1 and P1) have been shown to be linearly related to the amount of attention allocated to two competing items (Mangun & Hillyard, 1990), and that attention effects on early ERP components (in particular the N1 and N2) and those on the SSVEP are positively correlated (M. M. Muller & Hillyard, 2000). Here, we test whether the amplitude of the SSVEP is sensitive to attentional allocation by extending the paradigm used by Hillyard et al. (1997) – in which participants had to focus on one stream of items presented on an oscillating square while ignoring a second stream – by adding a divided-attention condition in which both streams were to be attended.

In addition to determining whether the SSVEP is sensitive to division of attention, we investigated the influence of different tagging frequencies on the SSVEP. Regan (1989) suggested that the complex pattern of activity related to an unpatterned flickering light may be related to the contributions of different functional subsystems which preferably respond to stimulation frequencies in the low (5-12 Hz), medium (12-25 Hz), or high (30-50 Hz) frequency ranges. The subsystems are sensitive to the physical properties of the stimulation, such as the luminance or color of the flickering. In addition, these subsystems are distinguished by other factors, such as the time between the onset of the flickering and the electrophysiological response associated to it, the topographical distribution of the EEG response to the flicker, and the properties of the fundamental and second harmonic (or frequency-doubled) EEG responses to the flicker suggest that different neural populations contribute to the response to flicker stimulation. Therefore different flicker frequencies may generate different, or affect in a different manner, the SSVEP (see also, Herrmann, 2001).

In spite of documented differences in flicker sensitivity (Herrmann, 2001; Regan, 1989), it appears that the visual system can be entrained by a wide range of frequency tags (Stephen et al., 2006), with the effect of attention generally being an increase in amplitude of the SSVEP. Increases in amplitude of the SSVEP as a function of attention have been reported for a broad range of frequencies and for a broad range of attention tasks (e.g., Belmonte, 1998, who used 8.9 Hz; Kim et al., 2007, who used

12.50 and 16.67 Hz; Kelly et al., 2006, who used 9.45, 10.63, 14.17, and 17.01 Hz; Hillyard et al., 1997; Morgan et al., 1996; who used 8.6 and 12 Hz; Muller et al., 1998; Muller & Hillyard, 2000, who used 20.8 and 27.8 Hz). However, up to now only one study of which we know has studied systematically the dependency of the effects of attention on the tagging frequency used. In this study Ding, Sperling, and Srinivasan (2006) induced SSVEPs by simultaneously presenting two circular arrays of disks, one at fovea the other at periphery. The onset and offset of one of the two arrays served as the frequency tag (i.e., the oscillation intended to evoke the SSVEP). On each trial participants were instructed to direct their attention toward the array that was frequency tagged or away from it. Each trial was tagged with one of 15 different frequencies in the range between 2.5 and 20 Hz. The participant's task was to emit a response any time that a triangle appeared within the to-be-attended search array.

For nearly all of the tagging frequencies used, Ding et al. found the usual enhancement in SSVEP amplitude in the focused relative to the ignored condition. However, for tagging frequencies within the lower alpha band (8-10 Hz), an increase in SSVEP amplitude to the peripheral array when attention was focused on the foveal array was found. On the basis of this finding Ding et al. concluded that the attention effect on the SSVEP response may depend on the tagging frequency used (Ding et al., 2006), and suggested that different frequencies recruit specific cortical networks. Because the result of Ding et al. (2006) of a lack of enhancement of attention on SSVEP amplitude when an attended object was flickering within the lower alpha rhythm range conflicts with the usual findings reported in the literature (i.e., an increase in SSVEP amplitude associated with attended stimuli, see e.g., Morgan et al., 1996; M. M. Muller & Hillyard, 2000), we included frequencies in the lower alpha range in our investigation of the effects of frequency on the attention effect on the SSVEP. In total we used six different tagging frequencies (8, 9.5, 10.5, 13, 17, and 23 Hz).

3.2 Experiment

Participants performed a speeded target-detection task in which a variable number of targets (the digit 5) were embedded among each of two streams of letters presented on sine-modulated monochrome background squares. The two streams were presented simultaneously to the left and right hemifields, with targets appearing asynchronously and equiprobably in either the left or right streams. Attention was cued on a trial-to-trial basis to the left, right, or both streams. Each background square was "tagged"

with one of six different frequencies. In addition to measuring the SSVEP evoked by each of the frequencies, ERPs elicited by targets were measured and the amplitudes of the components associated with effects of attention (P2, N2, and P3) were correlated with the attention effect on the SSVEPs. Response accuracy and reaction time (RT) were also measured.

3.2.1 Method

Participants. Fourteen healthy individuals (7 males) between the age of 20 and 30 (mean = 24.3, s.d. = 4.9) volunteered for the experiment and received € 18 for their participation. All had normal or corrected-to-normal vision. The study adhered to the Declaration of Helsinki and was approved by the local ethics committee. Informed consent was obtained from all participants.

Stimuli and apparatus. Stimuli were generated with the Matlab Psychtoolbox (Brainard, 1997) and displayed on a monitor with conventional raster graphics (800 x 600 pixels with a 144-Hz refresh rate) and a 17-inch screen. Stimuli were the distractor letters “A” through “K” and “P” and the target number “5”. Two sequences of 60 distractors and targets (presented for 166 ms each for a total stream length of 10 s) were displayed on each trial, one in the left and one in the right visual field, 5.7° lateral to a central fixation point. The stimulus sequences were randomized, with the constraint that repetitions and simultaneous presentation of a given character in the left and right display were not allowed. Characters were drawn in a blue (RGB: 0, 0, 255) Tahoma font, with a font size of 48 (corresponding to a width of 1.4° and a height of 1.9° of visual angle), and were presented serially in the same spatial location at a rate of 6 characters per s, with no interstimulus interval. In each sequence, the distractor letters A through K were each presented 5 times. Targets were not displayed in the first or last 500 ms of the stream presentation and were displayed with a minimum inter-target interval of 1 s in order to minimize the chances of overlap between target-related ERP components. Note that the inter-target interval applied across streams such that targets were never present in both streams at the same time. In the focused-attention conditions (attend left or attend right) 2, 3, or 4 targets were displayed on each side (for a total of 4, 6, or 8 targets). In the divided-attention condition (attend to both sides and respond to targets on both sides) 2, 3, 4, 6, or 8 targets were displayed on each trial. For the purposes of analysis, the unattended stream of the focused-attention condition is referred to as the ignored-attention condition. In order to equate stream length

across trials, the letter “P” was added to the stream in place of a target as necessary. With the exception of the three-target condition (in which two targets appeared on one side), potential targets were equally divided between the two sides of presentation.

An SSVEP for frequency tagging was induced by presenting a oscillating square (9.46° of visual field) centered at the location of each alphanumeric stream. The hue of each square oscillated sinusoidally from black (RGB: 0, 0, 0) to white (RGB: 255, 255, 255) with tagging frequencies of 8 and 9.5, 10.5 and 13, or 17 and 23 Hz for the left and right squares, respectively. Tagging frequencies were always presented in the abovementioned pairs²; side of presentation of the frequencies was factorially combined with attention condition and number of targets displayed. Three tagging frequencies (8 9.5, and 10.5) were chosen in the alpha range and the other frequencies were chosen so as not to include harmonics of these three frequencies while covering a relatively broad range of frequencies. The blue hue of the target-distractor streams was sine-modulated (from RGB: 0, 0, 0; to 0, 0, 255) with the same oscillation frequency (and phase) of the background square. In contrast with previous studies (e.g., Morgan et al., 1996; M. M. Muller et al., 2003; Malinowski et al., 2007) we chose to modulate the contrast of the stimulus stream in keeping with the modulation of the background square. This was done primarily to minimize the impact of the 6-Hz stimulus presentation rate on the perception of the background square.

Procedure. Participants were first instructed how to direct their attention to the left or to the right side without moving their eyes. Participants accommodated their chin on a chin rest at a distance of 60 cm from the display monitor. To minimize saccades or eye movements toward the attended side, participants were familiarized with the influence of eye movements and eye blinks on an on-line EEG recording. During this familiarization session, participants systematically moved their eyes from 1 to 10 degrees from center in 10 increasing steps, and from 10 to 1 degrees in 10 decreasing steps. After each movement the experimenter pointed out the changes in the electrooculogram (EOG) trace to the participants. Eye movements were monitored for the duration of the experiment using the EOG channels. Before the experimental trials commenced, each participant practiced the task in the focused-attention condition until a response accuracy criterion of 80% was reached (on average, 15 trials were sufficient to reach

²A pilot study (N = 6) showed that SSVEP amplitudes to higher frequency tags were smaller when a low frequency tag was present than when paired with a higher frequency tag. We therefore avoided pairing low with high frequency tags. This procedure also ensured that the difference between frequency tags was not salient to the subject.

the criterion). During the practice session participants received feedback on their performance. A trial started with the presentation for 1 s of one or two red (RGB: 127, 0, 0) “arrows” (“<”, “>”, or “<>”) which indicated how attention should be directed (to the left, right, or both sides, respectively). After a 250-ms blank interval, and 750 ms before the presentation of the letter streams, a red fixation cross appeared in the center of the screen and remained on display for the duration of the trial (10 s). Participants were to direct their attention as indicated by the cue and to press any key on the computer keyboard whenever they detected the number “5” on an attended side. Participants were not informed as to the number of targets that would be displayed on each trial. After the presentation of the two sequences of alphanumeric characters, the red fixation cross remained in view for 1 s, after which the trial ended. No feedback regarding performance was given. Each trial was self paced. For each combination of number of targets in each attentional condition (2, 3, or 4 in the focus left condition, 2, 3, or 4 focus right condition, 2, 3, 4, 6 or 8 in the divided-attention condition) and tagging frequency (8, 9.5, 10.5, 13, 17 or 23), 3 trials were presented, resulting in 54 trials each for the focused-left- and focused-right- (and ignored-left- and ignore-right-) attention conditions and 90 trials for the divided-attention condition (198 trials in total). The entire experiment lasted approximately 1.5 h.

EEG recording. The EEG was recorded using an electro-cap with 64 tin electrodes (Electro-cap International Inc., Eaton, Ohio, USA). All scalp positions in the International 10-20 System were used, with additional sites located midway between the 10-20 locations (Sharbrough et al., 1991) and six electrode positions 10% inferior to the standard parieto-occipital electrodes (FT9, PO9, O9, FT10, PO10, O10). The amplifier was a REFA 8-72 (Twente Medical Systems, Enschede, The Netherlands). Brain electrical activity was amplified 20,000 times with a digital low-pass filter with a cutoff frequency of 135 Hz. Data were digitized to 24-bit accuracy at a rate of 500 Hz and stored on a hard disk for subsequent off-line analysis. Electrophysiological inputs were configured as a reference amplifier: All channels were amplified against the average of all connected inputs. Two electrodes were connected to the mastoids, the average of which served as an off-line reference for the EEG signal. An electrode on the sternum was used for the subject ground. To monitor the electrooculogram (EOG), activity was recorded as bipolar input from the left and right horizontal eye channels (HEOGL and HEOGR) and from the vertical channels positioned above and below the left eye (VEOGL+, VEOGL-). Electrode impedances were kept below 5 K Ω for all

the electrodes during the experiment. Data acquisition was controlled through Brain Vision Recorder (version 1.03, BrainProducts GmbH, Munich, Germany).

ERPs data processing. Epochs of 1.2 s were segmented starting 200 ms before and until 1 s after target onset. Epochs in which artifacts or vertical eye movements and blinks exceeded $\pm 80 \mu\text{V}$ of electrode activity, and epochs in which horizontal eye movement exceeded $\pm 30 \mu\text{V}$ of electrode activity, were excluded from further analysis (an average of 17.5% of segments was removed which left 182, 237, and 220 epochs for the analysis of the focused-, divided- and ignored-attention condition respectively). Because horizontal eye movements toward target locations after target onset could bias the interpretation of the ERPs, visual inspection on the averaged horizontal eye channel was performed. According to Lins, Picton, Berg, and Scherg (1993), a horizontal eye movement of more than $3 \mu\text{V}$ propagates at posterior sites for less than $0.1 \mu\text{V}$. To exclude epochs contaminated from eye movements after target onset, visual inspection of the averaged horizontal eye movement channel for activity above $\pm 3 \mu\text{V}$ was performed separately for each participants for each side of presentation and attention condition. None of the participants included in this dataset performed eye movements above the $\pm 3 \mu\text{V}$ threshold.

The 200-ms interval before target onset served as baseline. Only segments corresponding to a correct response (i.e., to a “hit” if the target was to be attended and was responded to or a “correct rejection” if the target was to be ignored and was not responded to) were considered. Segments were averaged and filtered (cut-off frequency = 26 Hz at 12 dB / Oct Butterworth zero-phase low-pass filter) before computing the mean voltage of the ERPs within a specified time window centered on the peak of interest. Grand-average waveforms (see Figure 2) served as a reference to set the time windows from which each ERP deflection was estimated. Because the target onset was not phase-locked to the frequency tag, the possible effect of the different frequency tags on the target-locked ERPs should average out; for this reason tagging frequency was not included as a factor in the analysis of the ERPs (Russo & Spinelli, 1999a). The time window for the P2 component was set between 240-280 ms, for the N2 component between 325-355 ms, and for the P3 component between 440-600 ms.

Steady-state visual evoked potential (SSVEP) data processing. For computation of the SSVEP data were re-referenced to the average of the two mastoids. To exclude the possibility that eye movements toward the cued location could contribute to the en-

hancement of the amplitude of the SSVEP response, activity exceeding 3 μV in the averaged horizontal eye channel was checked for (Figure 3.5 in Appendix 2 representing the Grand-average EOG for the three instructional conditions shows that none of the participants showed such activity). Epochs, 10 s long from the onset to the offset of the oscillating square, were classified according to the presentation side (left vs. right), the attention condition (focused, divided, or ignored), and frequency (8, 9.5, 10.5, 13, 17, or 23 Hz). Epochs were then visually inspected for the presence of artifacts, and eye blinks were corrected using the algorithm of Gratton et al. (1983). All trials of each frequency were concatenated, yielding 90-s epochs (10 s x 9 trials, with 3 trials for each of the three target combinations (2, 3, or 4 targets)) in the focused-left- and in the focused-right-attention conditions, and a 150-s epoch (10 s x 15 trials, with 3 trials for each of the five target combinations (2, 3, 4, 6 or 8 targets)) in the divided-attention condition. In order to minimize contamination due to the stabilization time period of the band-pass filter, these epochs were copied twice and concatenated yielding a sequence of sufficient length to permit the distinction of frequencies with a resolution of 0.0037 Hz in the focused-attention condition and of 0.0022 Hz in the divided attention condition. The data thus obtained were filtered using a Gaussian filter centered on the tagging frequencies with a standard deviation of 0.01 Hz applied to the fast Fourier transform. After filtering, the second epoch of the concatenated sequence was kept and the first and third were discarded. To increase the reliability of the averaging process data were segmented in 1-s epochs and averaged together. Amplitudes of the SSVEPs were estimated by computing the square root of the variance of the averaged epochs.

To obtain a more robust estimate of the SSVEP, the amplitudes of a spatially contiguous group of electrodes having the highest amplitudes were averaged. These were the occipito-temporal electrodes contralateral to the side of presentation of the frequency tag. Before the averaging procedure, electrodes at posterior sites (using the central line, i.e., posterior to Cz), which is where the response to the tagging frequency is highest (Regan, 1989), were selected and sorted according to amplitude. Starting with the highest amplitude electrode, each next electrode was added to the current cluster or was used as the seed of a new cluster if it was not spatially contiguous to the previous electrode. The first (in order of amplitude) cluster of size 2 or greater (with a maximum of 8) was used for averaging, yielding the SSVEP amplitude for the specific condition.

For each subject, the SSVEP response was computed separately for each fre-

quency, attention condition, and side. Given that the amplitude of an SSVEP depends on the tagging frequency (Regan, 1989), SSVEP amplitudes were normalized by dividing each amplitude by the average value obtained in the three attention conditions. This normalization procedure was performed separately for each subject, frequency, and side.

3.3 Results

For all ANOVAs of behavioral and EEG data, Greenhouse-Geisser epsilon correction was used to adjust p-values, whenever applicable.

3.3.1 Behavioral results

Responses in the target-detection task were classified as hits, false alarms, or misses. Hits were defined as the first responses in the time window from 200 to 800³ ms following the occurrence of a target at a to-be-attended location. Subsequent responses in this time window, as well as responses outside this window, were designated false alarms (less than 0.01% on average). Errors of selective attention, indicated by responses to targets displayed on the to-be-ignored side, were also considered false alarms (less than 0.04% on average). The failure to respond to a displayed target within the 200-800-ms time window was considered a miss. In the behavioral analysis, only the percentage of hits and the RTs were considered. The behavioral data are shown in Figure 3.1. The upper panels of Figure 3.1 display the percentage of hits. Data were subjected to a repeated measures ANOVA with attention condition (focused vs. divided), side (left vs. right), and tagging frequency (8, 9.5, 10.5, 13, 17, or 23 Hz) as factors. Targets were detected more accurately in the focused- than in the divided-attention condition ($F(1, 13) = 7.89$, $p = 0.015$, $MSE = 938.47$, $\eta_p^2 = 0.38$). Targets displayed on the left side were detected more accurately than those displayed on the right ($F(1,13) = 5.46$, $p = 0.036$, $MSE = 2337.83$, $\eta_p^2 = 0.29$). The Attention Condition x Side interaction was significant ($F(1, 13) = 14.15$, $p = 0.002$, $MSE = 934.06$, $\eta_p^2 = 0.52$). The effect of side was more pronounced in the divided-attention condition, as shown in the upper left panel of Figure 3.1. The tagging frequency affected the accuracy of target detection ($F(5, 65) = 3.63$, $p = 0.018$, $MSE = 223.65$, $\eta_p^2 = 0.21$);

³The same analysis was performed excluding latencies greater than 2 SD above or below the mean for a given participant to avoid extreme values. The results of the two analyses yielded congruent outcomes.

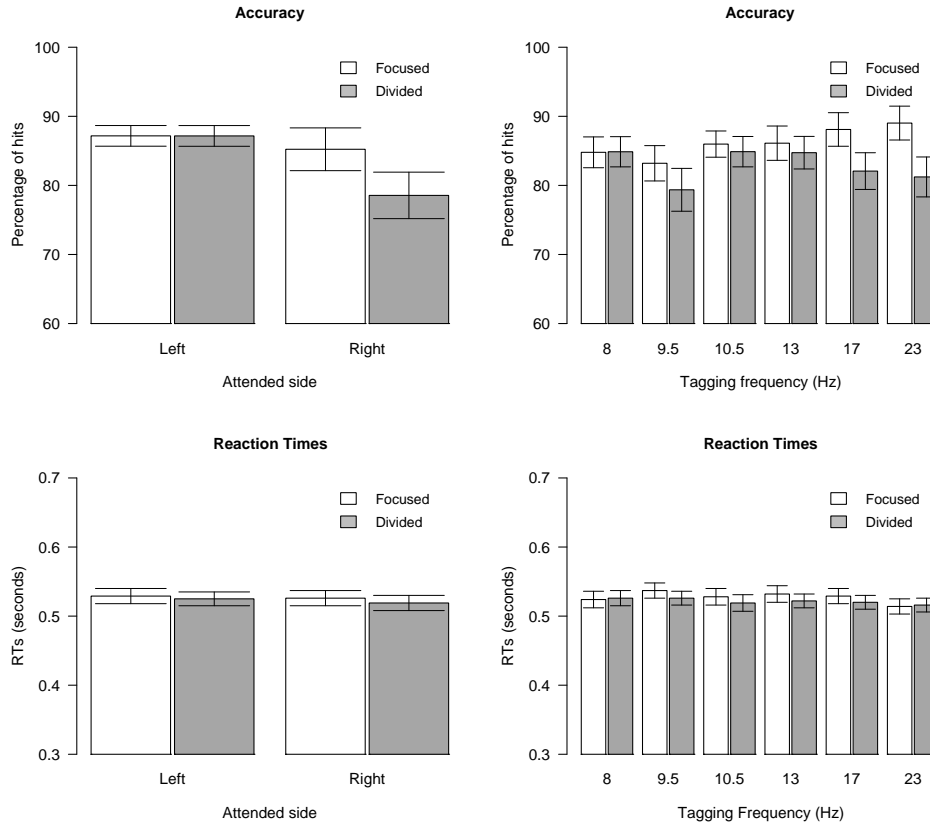


Figure 3.1: Percentage of hits (upper panels) and reaction times (lower panels) in the target detection task. Panels on the left show performance as a function of attended side (left vs. right) and attention condition (focused vs. divided), and panels on the right show performance as a function of frequency tag (8, 9.5, 10.5, 13, 17, and 23) and attention condition (focused vs. divided). Error bars show the standard error of the mean.

accuracy was 84.82, 81.28, 85.43, 85.42, 85.08, and 85.12% for the tagging frequencies 8, 9.5, 10.5, 13, 17, and 23 Hz, respectively. Pairwise comparisons (Bonferroni corrected) revealed a significant difference between accuracy for the 9.5 Hz and 8 Hz ($p = 0.044$) tagging frequencies and for 9.5 Hz and 13 Hz ($p = 0.007$). The difference between the 9.5 Hz and 23 Hz frequencies was not significant ($p = 0.07$). The Attention \times Frequency interaction was not significant ($F(5, 65) = 3.09$, $p = 0.055$, $MSE = 296.58$, $\eta_p^2 = 0.19$). From Figure 3.1, the focused-divided difference seems to increase steadily with increasing tagging frequency (with a possible exception of the 9.5 Hz). Contrasts performed on the Attention \times Frequency interaction confirmed such a significant linear relationship ($F(1, 13) = 8.17$, $p = 0.013$, $MSE = 427.3$, $\eta_p^2 = 0.39$). No other effect reached significance (all $ps > 0.2$).

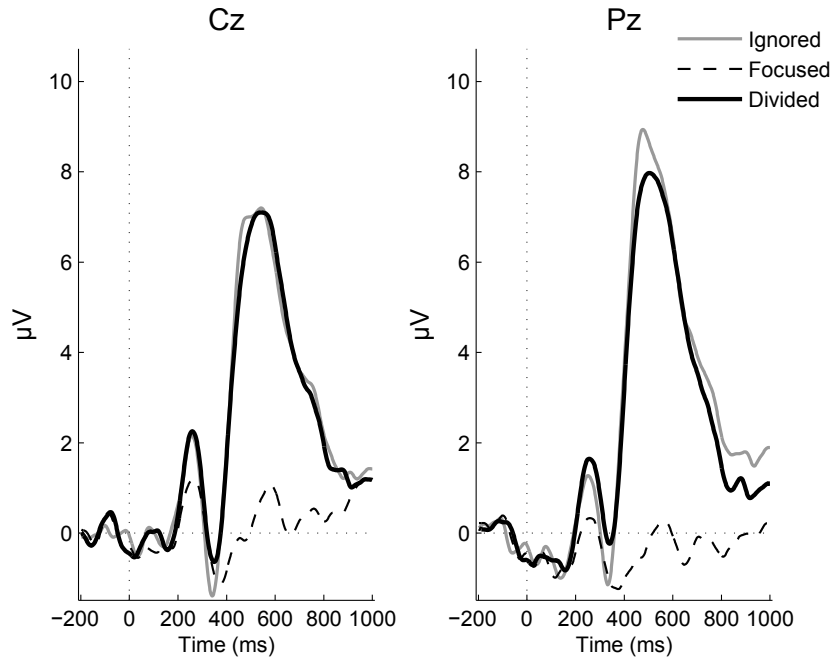


Figure 3.2: Event-related potentials at Cz and Pz, in the focused-, divided-, and ignored-attention conditions time-locked to target onset. Amplitudes were computed at Cz for P2 and N2 components, Pz for the P3 component. Positive ERP values are plotted upwards.

Reaction times (RTs) are displayed in the lower panels of Figure 3.1. Reaction times were submitted to a repeated measures ANOVA with attention condition (focused vs. divided), side (left vs. right), and tagging frequency (8, 9.5, 10.5, 13, 17, or 23 Hz) as factors. Tagging frequency had an effect on RT ($F(1, 5) = 3.17$, $p = 0.022$, $MSE = 0.002$, $\eta_p^2 = 0.19$); RT was 525, 531, 524, 527, 525, and 515 ms for the tagging frequencies 8, 9.5, 10.5, 13, 17, and 23 Hz, respectively. Pairwise comparisons revealed significantly faster RTs with the 23-Hz than the 9.5-Hz tagging frequency ($p = 0.036$; Bonferroni corrected). No other effect on RT approached significance.

3.3.2 Electrophysiological results

ERP amplitudes. The grand-averaged target-elicited ERPs at Pz and Cz for the three attention condition (focused, divided, and ignored) are shown in Figure 3.2. Note that the P1 and N1 components are largely missing, probably due to the interference caused by the rapidly flickering backgrounds. The panels show the modulation of the amplitude of the P2 and P3 components as a function of attention, however ERPs amplitudes did not differ between focused and divided attention. Statistical tests were

based on the electrodes for which the responses were largest. For the P2 and N2 components this was at Cz, and for the P3 component this was at Pz. The amplitudes of each of these ERP components as a function of attention were tested with separate repeated measure ANOVAs with attention condition (focus, ignore, divide) and side (left vs. right) as within subjects factors. P2 component amplitude (240-280 ms after target onset) was affected by the attention condition ($F(2, 26) = 4.37$, $p = 0.04$, $MSE = 13.6$, $\eta_p^2 = 0.25$). Pairwise comparisons (Bonferroni corrected) were performed to compare the three attention conditions, but did not yield significant differences. Polynomial contrasts showed a linear trend between attention condition and P2 component amplitude ($F(1, 13) = 6$, $p = 0.029$, $MSE = 13.6$, $\eta_p^2 = 0.32$). The nature of this linear contrast between P2 component amplitude and attention was further tested with a t-test, but where P2 component amplitudes in the focused- and divided-attention conditions were averaged together and compared to the ignored-attention condition. P2 component amplitude was significantly higher in the focused- divided- than in the ignored-attention condition ($t(1, 13) = 2.47$, $p = 0.028$). No other factors influenced the amplitude of the P2 component (all $ps > 0.4$). The N2 component (325-355 ms after target onset) was not significantly affected by any of the factors (all $ps > 0.1$). The P3 component (440-600 ms after target onset) amplitude was affected by the attentional condition ($F(2, 26) = 103.5$, $p < 0.001$, $MSE = 968.1$, $\eta_p^2 = 0.89$). Pairwise comparisons (Bonferroni corrected) of the attention conditions showed that P3 component amplitude was significantly higher in the focused- than in the ignored-attention condition ($p < 0.001$) and in the divided- than in the ignored-attention condition ($p < 0.001$), but did not differ between the focused- and the divided-attention condition ($p > 0.2$). No other factor influenced the amplitude of the P3 component (all $ps > 0.1$).

SSVEP amplitude. The amplitude of the SSVEP was tested with a repeated measures ANOVA with attention condition (focus, ignore, and divide), side (left vs. right), and frequency (8, 9.5, 10.5, 13, 17, or 23 Hz) as within-subject factors. The amplitude of the SSVEP was affected by attention condition ($F(2, 26) = 11.78$, $p = 0.001$, $MSE = 1.1$, $\eta_p^2 = 0.48$) such that amplitudes were higher in the focused-attention condition (1.086^4) than in the divided-attention condition (0.986^4) and in the ignored-attention condition (0.932^4) (see Figure 3.3). This linear trend was confirmed in a

⁴The values reported for these amplitudes are scale-free because when data are normalized they lose their dimensions.

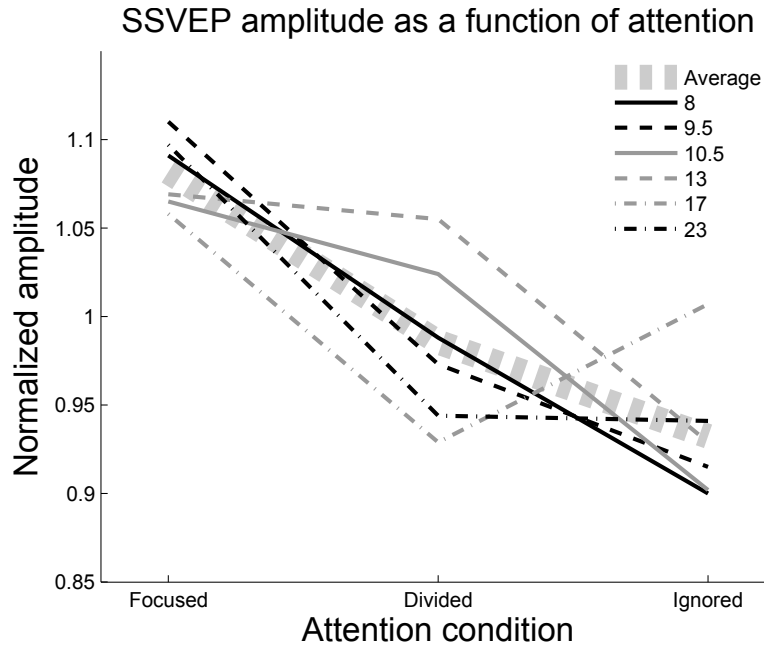


Figure 3.3: Normalized SSVEP amplitude as a function of tagging frequency.

trend analysis ($F(1,13) = 14.81$, $p = 0.002$, $MSE = 1.54$ $\eta_p^2 = 0.53$). Additionally tests of attentional effects on SSVEP amplitudes using pairwise comparisons (Bonferroni corrected) showed that the amplitude of the SSVEP in the focused-attention condition was significantly higher than in both the divided- ($p = 0.013$) and ignored-attention conditions ($p = 0.006$). SSVEP amplitude differences between the ignored- and divided-attention conditions were not statistically significant ($p > 0.1$). As should be expected from the fact that SSVEP amplitudes were normalized across frequencies, tagging frequency did not have an effect on the amplitude of the SSVEP ($p > 0.7$), nor did it interact with attention condition ($p > 0.7$). No other effects on SSVEP amplitude approached significance (all $ps > 0.1$).

Although both performance data and SSVEP amplitude suggests graded attention allocation across conditions, it could be argued that subjects adopted an attention-switching strategy in the divided attention condition, either within or across trials (J. Miller & Bonnel, 1994; VanRullen, Carlson, & Cavanagh, 2007). This attention-switching possibility was explicitly addressed using a mixture modeling approach based on the distributions of instantaneous amplitudes in the various conditions. The theoretical basis of this approach and the detailed results of the various tests are presented in the Appendix 3.5. To summarize, the results seem to argue strongly against

Pearson Correlation	9.5 Hz	10.5 Hz	13 Hz	17 Hz	23 Hz	P2	N2	P3
8 Hz	0.444	0.481	0.483	0.030	0.029	- 0.143	- 0.259	- 0.059
9.5 Hz		0.749**	0.563*	0.696**	- 0.462	- 0.156	- 0.312	- 0.224
10.5 Hz			0.359	0.568*	- 0.215	- 0.139	- 0.094	0.006
13 Hz				0.063	- 0.326	0.229	- 0.362	0.061
17 Hz					- 0.516	- 0.139	0.023	- 0.052
23 Hz						0.081	0.013	0.017
P2							0.510	0.774**
N2								0.632*

Table 3.1: Correlation between ERP amplitude (for the P2, N2, and P3 components) and the normalized SSVEP amplitude for each of the tagging frequencies. Two stars (**) superscript to a number indicate that the correlation is significant at the 0.01 level (2-tailed), one stars indicates a correlation significant at 0.05 level (2-tailed).

the idea that performance and SSVEP amplitude in the divided-attention condition can be accounted for in terms of within- or between-trial probabilistic switching between the two streams. Thus, participants do seem to have distributed attention as instructed. It is important to point out, however, that we cannot exclude the possibility of people having switched attention between locations at higher frequencies than our analysis procedure was sensitive to (e.g., > 2 Hz). Though we feel that this possibility is unlikely, we note that the idea that attention might rely on a rapid, intrinsically periodic sampling process has recently been advocated (VanRullen et al., 2007).

Correlational analyses. Correlational analyses were performed to examine the attentional effects on the ERP components and SSVEP. Attentional effects were estimated by computing the difference in amplitude in the focused- and ignored-attention conditions of the raw⁵ P2, N2, and P3 components of the ERP and of the normalized SSVEP for each of the tagging frequencies. Differences were based on the electrodes showing the highest amplitude for each ERP component and tagging frequency. The results of the correlation analyses are shown in Table 3.1. Although not always significant, the attentional effects were positively correlated across tagging frequencies, with the exception of the 23 Hz (see Table 3.1). Attention effects on ERP components were also positively correlated. However, there were no significant correlations between the attention effects as measured by the SSVEP and ERP.

⁵Normalized amplitudes of the ERPs components did not yield any difference to the outcome of this analysis.

3.4 Discussion

An experiment in which participants were to detect target digits embedded in a stream of letter distractors presented on an oscillating background was conducted to investigate the effects of visuospatial attention on SSVEP amplitude. Focused- and divided-attention conditions were compared to determine whether the SSVEP is sensitive to gradation of attention. Six different tagging frequencies were used in order to investigate possible dependencies on tagging frequency of attentional effects on SSVEP amplitude.

Participants detected fewer targets in the divided- than in the focused-attention condition, but RTs were similar in the two conditions. An apparent bias to attend left, especially in the divided-attention condition, was revealed by higher hit rates for left- than for right-side targets (for similar results see Hollander, Corballis, & Hamm, 2005). The difference in hit rate in the divided- and focused-attention conditions tended to increase with increasing tagging frequency, reflecting a combination of higher accuracy in the focused condition and lower accuracy in the divided condition as a function of increasing tagging frequency. These differences may reflect subtle perceptual effects caused by interactions between the frequency of RSVP presentation (6 Hz) and the frequency of the intensity modulation of both the alphanumeric characters and the background. Importantly, such interactions may have critically depended on the fact that the characters were intensity modulated in phase with the background. However, the nature of such interactions and how these might result in opposite effects on target-detection performance in the focused-attention and divided-attention conditions, remains to be understood. As discussed in some detail below, differential involvement of parvocellular and magnocellular visual pathways for low and high tagging frequencies may be responsible, at least in part, for these effects of tagging frequency on overt performance (see also Kim et al., 2007).

Across attentional conditions, the pattern of results for the P2 and P3 components amplitude were the same. Both components showed a lower amplitude in the ignored condition than in the focused- and divided-attention conditions, which did not differ. The finding that P2- and P3-component amplitude was essentially the same for all correctly reported targets—whether in the divided- or in the focused-attention condition—suggests that the P2 and P3 components reflect the outcome of attentional selection rather than top-down biasing effects on visual processing that mediate or cause visuospatial attentional selectivity (see Mangun & Hillyard, 1990). In other

words, the P2 and P3 components are associated with higher processing stages such as identification of specific properties of the target items which are unaffected by the amount of perceptual resources allocated to target selection.

SSVEP amplitude in the focused-attention condition was substantially larger for the attended than for the ignored stimulus stream, in line with results from numerous recent SSVEP studies (see: Belmonte, 1998; Cosmelli et al., 2004; Russo & Spinelli, 1999a, 1999b; Hillyard et al., 1997; Kelly et al., 2006; Kim et al., 2007; Malinowski et al., 2007; Morgan et al., 1996; M. M. Muller, Picton, et al., 1998; M. M. Muller, Teder-Salejari, & Hillyard, 1998; M. M. Muller et al., 2003; M. M. Muller & Hillyard, 2000; Pei et al., 2002; Srinivasan et al., 1999, 2006; Wang et al., 2007, and others). An important, novel, finding in the present study is that SSVEP amplitude in the divided condition fell in between those in the focused and ignored conditions. It is important to point out that we explicitly addressed the possibility that this result might be explained in terms of within- or between-trial switching of attention in the divided attention condition, and found that the evidence argues against this possibility (see Appendix 3.5). This suggests that, unlike P2 and P3 components, SSVEP amplitude may reflect gradations of visuospatial attention or, more precisely, the graded allocation of capacity-limited top-down modulation or biasing of visual processing across multiple locations or objects.

Evidence for graded effects of attention on SSVEP amplitude was also found in a recent study of Andersen, Hillyard, and Muller (2008). They showed that the amplitude of the SSVEP associated with an amplitude-modulated object increased linearly and additively with the number of target-defining features that it contained (i.e., two, one, or none). They interpreted this result as evidence for parallel additive amplification of physiological responses across two or more visual dimensions (e.g., orientation and color). Note that their results do not address the issue of whether distributing or biasing top-down attention across multiple dimensions comes with a divided-attention cost. Our results do address this latter issue, but for the case of spatial attention, and show that division of attention across multiple locations is reflected by a reduction in SSVEP amplitude. Thus, the two studies provide somewhat complimentary results regarding graded effects of attentional control and attentional effects on SSVEP amplitude.

Tagging frequency did not significantly modulate the attention effects on SSVEP amplitude. In the case of the difference in SSVEP amplitudes for the focused- and ignored-attention conditions, this lack of dependency is in line with a range of studies

using different tagging frequencies but showing similar attention effects on SSVEP amplitude (e.g., Belmonte, 1998, who used 8.9 Hz; Kelly et al., 2006, who used 9.45, 10.63, 14.17, and 17.01 Hz; Kim et al., 2007, who used 12.50 and 16.67 Hz; Hillyard et al., 1997 and Morgan et al., 1996, who used 8.6 and 12 Hz; Muller et al., 1998a; Muller et al., 1998b; and Muller & Hillyard, 2000, who used 20.8 and 27.8 Hz). The present results do not support the suggestion of Ding et al. (2006) that attentional effects on SSVEP amplitude depend on the specific attentional network that is recruited by a particular tagging frequency. It should be noted that Ding et al.'s suggestion was based on only a subset of their overall results, limited to one of four experimental conditions and to 2 of the 15 tagging frequencies that were used.

Correlational analyses of the difference in amplitudes for the focused- and ignored-attention conditions between the late ERP components (P2, N2, P3) revealed that attentional effects for the various ERP components were positively correlated. The same was true for the SSVEP amplitudes associated with the different tagging frequencies, with the exception of 23 Hz⁶. In contrast, the correlations between effects on ERP amplitudes on the one hand and SSVEP amplitudes on the other were all weak and nonsignificant, regardless of the precise way in which these amplitude differences were quantified or normalized.

Similar evidence that effects of visuospatial attention on the amplitudes of late ERP components are independent from those on the amplitudes of SSVEPs was reported by M. M. Muller and Hillyard (2000). These authors did, however, obtain significant positive correlations between attentional effects on the amplitude of early ERP components (N1, N2) and the amplitude of SSVEPs. In the present study, we were unable to reliably measure the amplitudes of early ERP components. The likely reason for this is that, unlike in the M. M. Muller and Hillyard (2000) study, target onset was not phase locked to the tagging frequency. This lack of phase locking probably resulted in a substantial amount of jitter in the latency of the early evoked components. For instance, target onset could occur at a time when the luminance of both the background and letter were near zero. Such jitter would result in early components in the ERPs being lost in the averaging process. The lack of correlations between attentional effects on late ERP-component amplitude and SSVEP amplitude, are consistent with the idea that different EEG measures reflect different and dissociable aspects of visuospatial selectivity. SSVEP amplitude (as well as that of the N1 and P1 components; see Mangun & Hillyard, 1990) seems to reflect the graded top-down modulation or

⁶Correlations pattern was generally positive although not all the correlations were significant.

biasing of visual processing at different locations in the visual field. In contrast, later ERP components reflect the effects or outcome of top-down processing, such as target categorization for the P3 component (e.g., Mangun & Hillyard, 1990; Kok, 1997), or enhancement of task-relevant information for the P2 component (e.g., Freunberger, Klimesch, Doppelmayr, & Holler, 2007).

A seemingly anomalous aspect of the results was the lack of correlation of the attentional effects on SSVEP amplitude at 23 Hz with those at the lower tagging frequencies. A possible reason for this pattern of correlations may be that only the magnocellular processing system but not the parvocellular system is sensitive to flicker frequencies above 20 Hz (Derrington & Lennie, 1984; Levitt et al., 2001). Thus, whereas the attentional effects on SSVEP at the lower frequencies are likely to reflect a mixture of attentional modulations of parvocellular and magnocellular processing, those at 23 Hz are likely exclusively due to attentional modulation of magnocellular processing. That the relative contribution of the two systems is relevant to the outcomes of this experiment is suggested by Yeshurun and Levy (2003) evidence that spatial attention may have different effects on processing in parvo- and magnocellular pathways. This conclusion is based on the finding that spatial attention enhances spatial resolution but reduces temporal resolution.

Yeshurun and Levy (2003) argue that these opposite effects of attention on spatial and temporal resolution can be explained most parsimoniously in terms of spatial attention enhancing parvocellular processing and inhibiting, either directly or indirectly, by means of competitive interactions between parvo- and magnocellular pathways, magnocellular processing. The overall effects of attention on SSVEP amplitude at 23 Hz do not support the idea that spatial attention inhibits magnocellular processing (otherwise the attention effect would be smaller since only the relatively inhibited magnocellular system would contribute to performance). Instead, the present results seem to indicate generally facilitative effects of spatial attention on parvo- and magnocellular processing.

An enhanced parvocellular contribution at frequencies below 20 Hz may also help explain the finding that the difference in accuracy between the focused- and divided-attention conditions increased with increasing tagging frequency. As tagging frequency increases, the limited temporal sensitivity of the parvocellular pathway results in a gradual transition in perception from a stimulus (alphanumeric character and background) that clearly flickers at the lowest frequency (8 Hz) but that is perceptually stable at the highest frequency (23 Hz). This perceived stability may have increased

the parvocellular pathway's contribution to target detection at the higher tagging frequency.

If focused spatial attention results in relatively more parvocellular than magnocellular processing at attended locations, this beneficial effect of higher tagging frequencies on target detection in the parvocellular pathway should be expected to be considerably higher in the focused as compared to the divided-attention condition. While this perspective can account for larger differences in performance between focused- and divided-attention conditions at higher tagging frequencies, it fails to explain why, as our results suggest, target detection in the divided-attention condition seems to deteriorate as tagging frequency is increased.

In conclusion this study showed that the amplitudes of the SSVEP and ERP are functionally related to the deployment of attention to stimuli. Attention effects were such that amplitudes in the focused-attention condition were higher than the amplitudes in the ignored-attention condition both for SSVEPs and ERPs. However, although attention effects were consistent between amplitudes of ERP components and SSVEP at the different tagging frequencies, correlations between the two were not significant. More interestingly, this study showed that dividing attention between two locations is associated with a reduction in the amplitude of the SSVEP, showing that SSVEPs are sensitive to gradation of attention. For the ERPs, however, there were no differences between focused and divided attention conditions, providing further support for the claim that SSVEPs and ERPs reflect physiological responses associated with distinct attentional mechanisms. The consistency of the effects of attention on the SSVEP across tagging frequencies suggests that the frequency tagging procedure can be applied flexibly in a range of paradigms.

3.5 Appendix 1: Switching or sharing in divided attention?

Both the within-trial and the between-trial versions of the attention-switching hypothesis of divided attention imply that the distributions of SSVEP instantaneous amplitude for the left and right locations in the divided-attention condition, computed either within or between trials, should consist of a binary mixture of the corresponding distributions for the focused and ignored conditions. As explained below, this allows us to compute a predicted variance for the instantaneous amplitude in the divided-attention condition from those in the focused-attention condition and the ignored-attention condition. Comparing this predicted variance to the empirically obtained variance provides a test of whether a mixture is actually present, that is, whether people did not divide attention but switched between locations.

The variance of a binary-mixture distribution, σ_{Mix}^2 , is known to obey the following equation (Falmagne, Cohen, & Dwivedi, 1975):

$$\sigma_{Mix}^2 = x * \sigma_1^2 + (1 - x) * \sigma_2^2 + x * (1 - x) * (\bar{A}_1 - \bar{A}_2)^2 \quad (3.1)$$

where σ_1^2 and σ_2^2 are the variances of the two basis distributions, \bar{A}_1 and \bar{A}_2 the corresponding means, and x the mixing probability. The third term on the right side of equation 3.1

$$x * (1 - x) * (\bar{A}_1 - \bar{A}_2)^2 \quad (3.2)$$

is generally referred to as the inflation factor. In the present application, the divided-attention condition provides the mixture distribution, the focused condition provides the first basis distribution (σ_1^2) and the ignored condition the second basis distribution (σ_2^2). It is important to note that the binary mixture distribution is a bimodal distribution. The inflation factor represents the impact of this bimodality on overall variance and this impact increases as a function of the difference in mean between the two basis distributions. Because the mean amplitudes in the focused and ignored condition differed substantially, the inflation factor should represent a sizable contribution to overall variance (σ_{Mix}^2). If, contrary to what the mixture model assumes, people did not switch attention between locations but truly divided attention between locations as instructed, the actual amplitude distribution would be unimodal and its variance should therefore be overestimated by the mixture model.

Equation 3.1 was used to predict the variance of instantaneous amplitudes in the divided-attention condition separately for each combination of location (left or right)

and tagging frequency (8, 9.5, 10.5, 13, 17, or 23), separately for each participant. Following the definitions of the basis distributions, the mixing probability, x , represents the probability that attention happened to be focused on that particular location and frequency when it was presented in the divided-attention condition. Because results were subsequently averaged across all possible combination of frequency and location, we assume x to be close to .5, that is, at chance level.

For these analyses, trials were 14-s epochs starting 2 s before the onset of the frequency tag and ending 2 s after the offset of the frequency tag. Epochs were then filtered with a Gaussian filter centered on the tagging frequency with a bandwidth of 0.1 Hz for the between-trial tests and 0.75 Hz for the within-trial tests. Instantaneous amplitude was estimated through Hilbert transformation of the filtered signal. \bar{A}_1 and \bar{A}_2 in Equation 3.1 were estimated by computing mean instantaneous amplitudes for single trials in the focused and ignored conditions (excluding the first and last 3 s of the epoch (leaving epochs of 8 s) to compensate for the stabilization period of the Gaussian filter), and then averaging across the single trials. Between-trial variances for all attention conditions were computed from estimates of single-trial mean amplitudes. Within-trial variances were computed across the same epochs (8 s) and then averaged across trials.

Equation 3.1 was used to compute predicted variance for the divided-attention condition from the estimated mean amplitudes and variances in the focused and ignored conditions. In order to normalize these predicted values before further analysis, the ratio between the empirical and estimated variance was computed ($\sigma_{Mix}^2 : \sigma_{Empirical}^2$), separately for each tagging frequency, location, and posterior electrode (i.e., posterior to Cz). To enhance robustness, ratio values were first averaged across the posterior electrodes, then, log-transformed ratio values were averaged across all combinations of tagging frequency and location (consistent with the assumption that the overall value of x in Equation 3.1 must be close to .5). Note that if people attended or facilitated processing at both locations by switching between them, either on a within-trial or a between-trial basis, predicted and empirical variances would be expected to be very similar and the average ratio value should be close to 1. On the other hand, if people did not actually attend both locations by switching between them, the inflation factor in Equation 3.1 would cause an overestimation of the true variance, given that we obtained consistent amplitude differences in the focused and ignored conditions (\bar{A}_1 and \bar{A}_2 in Equation 3.1). This overestimation would result in ratio values ($\sigma_{Mix}^2 : \sigma_{Empirical}^2$) larger than 1. Therefore, if ratio values would be found to

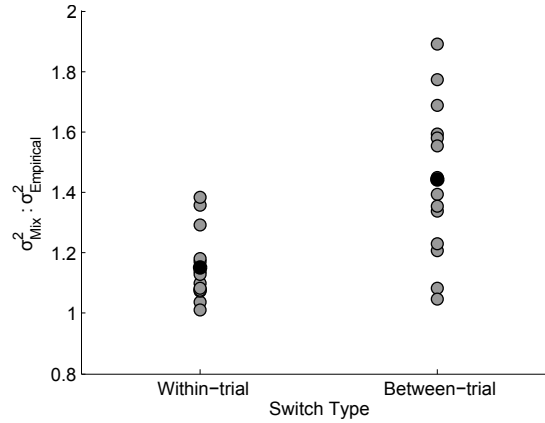


Figure 3.4: Spread of the ratio between the empirical and estimated variance ($\sigma^2_{Mix} : \sigma^2_{Empirical}$) across participants for the within- and between-trial switches (grey dots). For both within- and between-trial switches the mean values (black dots) are larger than 1.

be substantially and significantly larger than 1, this would strongly argue against the attention-switching idea.

Figure 3.4 shows the ratio $\sigma^2_{Mix} : \sigma^2_{Empirical}$ for SSVEP instantaneous amplitude for within-trial and between-trial switches for all individual participants and the average across all the participants. For the between-trial ratio values, a t-test revealed that the ratio values were significantly different from 1 ($t(13) = 6.53$, $p < .001$). For the within-trial ratio values, the same test also yielded a significant difference ($t(13) = 4.87$, $p < .001$ – the fact that the latter values tend to be much smaller than the ratio values in the between-trial case is due to the fact that $\sigma^2_{Empirical}$ is much greater in the within-trial case). The results of this analysis establish a consistent and sizable overestimation of the actual variance of SSVEP amplitude in the divided-attention condition, and would thus seem to argue strongly against the idea that performance and SSVEP amplitude in this condition can be accounted for in terms of within- or between-trial probabilistic switching between the two streams. Thus, with the possible exception of a small subset of participants, people do seem to have distributed attention as instructed⁷. It is important to point out, however, that we cannot exclude the possibility of people having switched attention between locations at higher frequencies than our analysis procedure was sensitive to (e.g., > 2 Hz). Though we feel

⁷We also found no evidence for attentional switching during the divided attention condition using a correlational approach based on a procedure developed by Andersen and coworkers (2008). The approach is based on the notion that attentional switching between the left and right locations should cause correlations in SSVEP amplitude for the left and right location in the divided-attention condition to be considerably more negative than those obtained in the focused condition. No such systematic and reliable differences were however obtained.

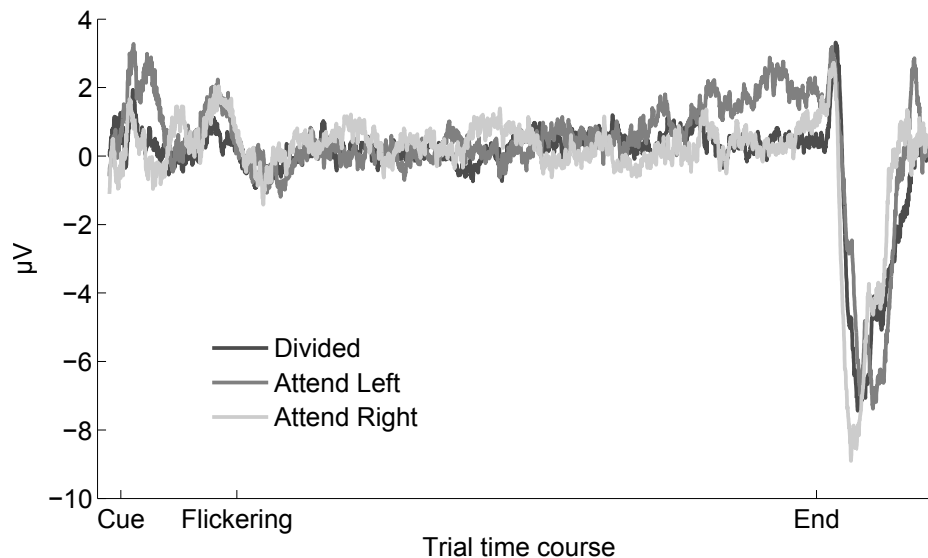


Figure 3.5: Grand-average EOG for the three instructional conditions (divided, attend left, attend right). The abscissa represents the trial duration, from the onset of the cue (2 s before flickering/RSVP onset), to the end of the flickering.

that this possibility is unlikely, we note that the idea that attention might rely on a rapid, intrinsically periodic sampling process has recently been advocated (VanRullen et al., 2007).

3.6 Appendix 2: Control of eye movements artifacts

Both ERPs and SSVEPs crucially depend on the eccentricity of the stimuli with, for example, bigger ERP amplitudes in response to stimuli that are closer to the fovea (Regan, 1989). Especially with trials of long duration (e.g., 10 s), the actual eye position may not be exactly on the fixation cross for the whole trial length, but may slightly deviate towards an attended target. As a result of such a fixation deviation the “attended” stimulus is closer to the fovea than the “unattended” one.

To prevent the influence of such EOG fluctuation into the EEG activity, participants were carefully instructed not to move their eyes and their EOG was monitored on-line. The grand averages of the EOG recordings in each of the three instructional conditions (divided, attend left, attend right) is shown in the Figure 3.5.

It is evident that eye movements (EOG fluctuations) were minimal. The amplitude of the EOG never exceeds 2 μ V, which according to Lins et al. (1993) will not significantly influence the EEG activity at the back of the head, where the SSVEPs

were measured.

Chapter 4

Dynamic crossmodal links revealed by steady-state responses in auditory-visual divided attention

There is no good reason to assume that the brain is organized in accordance with the concepts of folk psychology.

Cornelius H. Vanderwolf

Abstract

Frequency tagging has been often used to study intramodal attention but not intermodal attention. We used EEG and simultaneous frequency tagging of auditory and visual sources to study intermodal focused and divided attention in detection and discrimination performance. Divided-attention costs were smaller, but significant, in detection than in discrimination. The auditory steady-state response showed no effects of attention at frontocentral locations, but did so at occipital locations where it was evident only when attention was divided between audition and vision. Similarly, the visual steady-state evoked potentials at occipital locations were substantially enhanced when attention was divided across modalities. Both effects were equally present in detection and discrimination. We suggest that both effects reflect a common cause: An attention-dependent influence of auditory information processing on early cortical stages of visual information processing, mediated by enhanced effective connectivity between the two modalities under conditions of divided attention.

4.1 Introduction

Selective attention plays an important role in managing the continuous stream of incoming sensory information. By focusing attention on currently relevant information, the processing system is biased towards processing this information relative to currently less relevant and potentially conflicting or interfering information (Deco & Zihl, 2006; Desimone & Duncan, 1995). Attention can be focussed on a single source (e.g., object or location) but can also be divided across multiple information sources. These different modes of attention are referred to as focussed and divided attention.

Performance in divided-attention studies is usually interpreted in terms of a trade-off between the relative amount of attention allocated to each task or source and the performance on each task. When a task is resource limited, performance is expected to improve as a monotonic function of the relative amount of attention allocated to the task. Performance tradeoffs between two concurrent tasks can be orderly represented in an “Attention Operating Characteristic” (AOC) which plots the joint performance on two tasks as a function of the attentional instructions (see e.g. Bonnel & Hafter, 1998; Sperling & Melcher, 1978; Norman & Bobrow, 1975).

Divided-attention costs can vary depending on both the features of the stimulus and the type of response to be made (Duncan, 1980). Bonnel, Stein, and Bertucci (1992) and Bonnel and Hafter (1998) showed that such costs can also depend on the nature of the task – concurrent target detection tasks did not yield statistically significant performance tradeoffs whereas strong tradeoffs were found for concurrent target discrimination tasks. Bonnel et al. (1992) and Bonnel and Hafter (1998) interpreted their results in terms of a hierarchical processing model (Hoffman, 1979; Duncan, 1981): Detection tasks depend on a relatively low level capacity-free processing stage, whereas discrimination additionally requires a higher level capacity-limited stage.

The formal distinction between detection and discrimination of targets has been debated in the literature (see e.g., Brawn & Snowden, 2000; Kawahara, Lollo, & Enns, 2001). We follow the distinction made by Kawahara and collaborators, which seems most compatible with the procedures used by Bonnel and coworkers (1992, 1998). They proposed that detection is involved when an observer is asked to distinguish between a uniform stimulus and a stimulus that contains a non-uniformity or discontinuity in space or time. Only the presence or absence of the non-uniformity is to be reported, not its identity. By contrast, discrimination (also referred to as identification) requires the observer to identify the nature of the discontinuity.

The notion that detection performance is not capacity-limited has not gone unchallenged. Several studies found target-detection performance to be enhanced when target location was cued in advance, suggesting that detection can be affected by attentional mechanisms (Muller & Humphreys, 1991; Hawkins et al., 1990; Downing, 1988; see also Lappin and Uttal, 1976). Bonnel et al. (1992) argued that such results do provide evidence that target detection can be affected by spatial uncertainty but do not undermine their proposal that detection performance is capacity free when, as in their own studies, spatial uncertainty has been removed.

In the present study, we followed the procedure of Bonnel and Hafter (1998), em-

ploying concurrent crossmodal auditory and visual detection or discrimination tasks with fixed stimulus locations and with several different attention allocation instructions. The tasks involved either detecting or discriminating a small and brief upward or downward change in tone volume in the auditory task and in stimulus brightness in the visual task. This particular procedure was chosen for several reasons. The data presented by Bonnel and Hafter (1998, Table 4) do seem to show effects of instructed attention allocation on performance even for concurrent detection. While these effects may have been due, at least in part, to participants matching performance to instructed relative attention (see e.g., Navon, 1985), they might also reflect subtle but theoretically important capacity limitations in detection performance. Related to this point, participants may have become aware that different attentional policies impacted discrimination performance more than detection performance, and this may have led them to adopt less differentiating attention allocation policies in detection conditions. To address the possibility of different attentional strategies in crossmodal detection and discrimination, we recorded electroencephalographic (EEG) activity and used event-related potentials (ERPs) and, in particular, steady-state responses (SSEPs) to gain information regarding the attentional mechanisms operative in the various experimental conditions. Finally, we chose to study intermodal rather than intramodal focused and divided attention in order to benefit from and contribute to the recent surge of research interest and findings regarding crossmodal perception and attention (see e.g., Driver & Noesselt, 2008; Macaluso & Driver, 2005; Stein & Stanford, 2008)

Using steady-state responses for studying auditory-visual intermodal attention. The auditory steady-state response (ASSR) refers to oscillatory EEG or MEG activity with constant amplitude and phase at the frequency of a periodic eliciting stimulus. The ASSR can be elicited by stimuli such as sequences of clicks, Gaussian tone pulses, or amplitude-modulated tones, and its amplitude is typically found to be maximal at stimulation frequencies around 40 Hz (Ross et al., 2005a). While the ASSR was originally thought to result from periodic superimposition of middle latency evoked responses (Galambos et al., 1981), recent evidence tends to support the hypothesis that the ASSR reflects a separate neural oscillation that is driven by the periodic stimulus (Ross et al., 2005a). Converging evidence from several neuroimaging studies and patient studies has shown the primary auditory cortex (medial portion of Heschl's gyrus) to be the main source of the 40-Hz ASSR (Gutschalk et al., 1999; Ross, Picton, & Pantev, 2002; Ross, Herdman, & Pantev, 2005b; Simpson, Hadjipapas, Barnes,

Furlong, & Witton, 2005)

While the functional meaning of the ASSR remains unclear, an interesting hypothesis is that its amplitude may index sensory gain control in primary auditory cortex (Giard, Fort, Mouchetant-Rostaing, & Pernier, 2000). Some studies have found effects of attention on the 40-Hz ASSR amplitude, for intramodal auditory selective attention (Skosnik, Krishnan, & O'Donnell, 2007; Gander, Bosnyak, Wolek, & Roberts, 2007) as well as for auditory-visual intermodal selective attention (Ross, Picton, Herdman, & Pantev, 2004), but such effects have not always been found (Linden, Picton, Hamel, & Campbell, 1987). A key feature of studies that obtained positive effects of attention on ASSR amplitude may be that they used tasks that required focused attention to the stimulus rhythm, or carrier frequency, eliciting the ASSR (Saupe, Widmann, Bendixen, Muller, & Schroger, 2009). Whether such effects can also be found when the stimulus rhythm is incidental to the task to be performed, and thus merely serves as a frequency tag for quantification of the ASSR, is uncertain – one of the aims of the present study is to assess this possibility for the case of auditory-visual intermodal attention.

The visual counterpart to the ASSR is the steady-state visual evoked potential (SSVEP Regan, 1989), which is found with amplitude-modulated or flickering visual stimuli across a wide range of frequencies (Herrmann, 2001). In a recent elegant study, two main cortical sources of a 12-Hz SSVEP were established: a main source in the primary visual cortex (V1) and a secondary source in the motion sensitive areas (MT/V5, Russo et al., 2007). This suggests the possibility that SSVEP amplitude may index sensory gain control in primary visual cortex. Positive effects of intramodal selective attention on SSVEP amplitude have been reported in many studies that employed different paradigms such as visuospatial attention or selective color-based processing (see e.g., Morgan et al., 1996; M. M. Muller, Teder-Salejarvi, & Hillyard, 1998; Hillyard et al., 1997; Malinowski et al., 2007; Ding et al., 2006; Pei et al., 2002). In a visuospatial divided-attention task, SSVEP amplitude for frequencies ranging from 8 to 23 Hz exhibited a graded dependency on attention, with substantially larger amplitudes for attended as compared to unattended locations and intermediate amplitudes when attention was divided across locations (Toffanin, Jong, Johnson, & Martens, 2009). In contrast to the many studies that used the SSVEP to investigate neural mechanisms of intramodal visual attention, we are not aware of any studies that used this measure to investigate effects of intermodal attention on visual information processing.

The present study. ASSR amplitude and SSVEP amplitude may provide useful indices of sensory gain control in early cortical auditory processing and visual processing, respectively. In the present study, we used these measures to investigate effects of intermodal auditory-visual selective or divided attention on early modality-specific cortical processing in detection or discrimination. The almost exclusive emphasis on steady-state responses may require some explanation, as we seem to have ignored the much more extensive and arguably better developed literature on the use of event-related potentials (ERPs) in the investigation of intramodal and intermodal attention (for review, see Driver & Noesselt, 2008; Macaluso & Driver, 2005). The reasons for this are mostly practical. The use of the frequency-tagging technique in the present study turned out to have abolished the short-latency and mid-latency ERP components (P50, C1, N1, P1, P2, N2), preventing any analyses of such components (for similar effects, see Skosnik et al., 2007; Ross et al., 2005b). Such devastating effects on early ERP components seem consistent with the notion that these components reflect phase resetting of ongoing EEG activity rather than an evoked additive neural response (Ross et al., 2005a). The apparent incommensurability of the SSEP and ERP techniques may be responsible for the fact that they seem to have made little useful contact in the literature (for an exception, see M. M. Muller & Hillyard, 2000). In the Discussion section, we will relate the findings of the present study to some key findings of effects of crossmodal attention on ERP components.

The auditory stimulus consisted of a 40-Hz amplitude-modulated tone and the visual stimulus of a 24-Hz luminance-modulated colored square, both presented simultaneously for 2.5 seconds at approximately the same central location. Participants judged visual and auditory stimuli to share a common spatial source – thus, crossmodal selective attention could not be achieved by means of spatial selective attention to one or the other source of stimulation (Eimer & Schroger, 1998). Auditory and visual targets consisted of a brief (125 ms) decrease or increase of the mean loudness of the tone and of the main brightness of the colored square, respectively. Participants had to detect the presence of targets in the detection task, and had to identify the direction of change (decrease or increase) in the discrimination task. In different attention conditions, they were instructed to selectively attend to one and to ignore the other modality (100% auditory or 100% visual), or to divide their attention across modalities (20-80%, 50-50%, or 80-20% auditory-visual).

As relevant prior data regarding intermodal attention effects on ASSR and SSVEP amplitudes in the literature are either inconsistent or largely absent, the present study

must be deemed exploratory. However, some possible outcomes will be briefly discussed. One possibility is that intermodal attention effects on ASSR and SSVEP amplitude are mediated by largely the same neural structures and mechanisms as those underlying intramodal attention effects (Talsma & Kok, 2002). In that case, graded effects of intermodal attention, similar to the graded effects of visuospatial attention on SSVEP amplitude reported by Toffanin and coworkers (2009), might be expected. Moreover, such effects might depend on whether the task involves detection or discrimination.

On the other hand, recent empirical and theoretical developments regarding crossmodal influences on modality-specific brain regions may suggest a very different outcome (for review, see Driver & Noesselt, 2008; Stein & Stanford, 2008), especially with regard to the distinction between divided-attention and focused-attention conditions. Many studies have found multisensory influences even in relatively low-order, early regions of sensory cortex (for review Ghazanfar & Schroeder, 2006). Such influences may underlie multisensory effects on perceptual judgments, and are subject to constraints of spatial and temporal proximity or overlap between incoming signals from different sensory modalities (Macaluso & Driver, 2005). Possible mechanisms underlying crossmodal influences include rapid feedforward integration, thalamic influences, direct connections between primary cortices, and feedback from multisensory regions to sensory-specific brain areas (Driver & Noesselt, 2008). Apart from spatial and temporal constraints, which are likely to be fulfilled in the present study, crossmodal influences on modality-specific brain regions may also depend on attentional factors. Talsma, Doty, and Woldorff (2007) found crossmodal modulation of the auditory P50 only when participants attended to both audition and vision, and stated “We thus conclude that when attention is directed to both modalities simultaneously, auditory and visual stimuli are integrated very early in the sensory flow of processing (~ 50 ms poststimulus). Attention appears to play a crucial role in initiating such an early integration of auditory and visual stimuli. When only one modality is attended, the integration processes appear to be delayed.” (Talsma et al., 2007, p. 689). This idea suggests the interesting possibility of crossmodal effects on ASSR and SSVEP amplitudes, where these effects may be particularly evident in the divided-attention conditions. More specifically, crossmodal interactions may manifest in two possibly related ways in divided-attention conditions. First, in these conditions 40-Hz activity, which specifically tags auditory input, may show up also at posterior occipital sites, whereas 24-Hz activity may show up at frontocentral, auditory sites. Second, cross-

modal interactions may serve to enhance sensory gain in low-order auditory and visual cortices, thus suggesting the possibility that ASSR and SSVEP amplitudes might actually be enhanced in divided-attention as compared to focused-attention conditions. Again, such effects may depend on whether the task involves detection or discrimination.

4.2 Experiment

4.2.1 Method

Participants. Ten healthy right-handed students (3 males) between the age of 19 and 23 (mean = 21.1; sd = 1.5) participated as paid volunteers. All volunteers had normal or corrected-to-normal vision. The study adhered to the Declaration of Helsinki and was approved by the local ethics committee. Informed consent was obtained from all participants. Due to technical malfunctioning, EEG data for one participant were lost.

Stimuli and apparatus. Visual stimuli were presented on a 17 inch CRT screen graphics (800 × 600 pixels with a 144-Hz refresh rate). Auditory stimuli were presented through a single loudspeaker placed at the top center of the computer monitor used for visual presentation; participants judged visual and auditory stimuli to share a common spatial source. The auditory stimulus was presented at 65 dB, measured at the location of the participants' ears. Stimuli were generated with the Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). Participants accommodated their chin on a chin rest at a distance of 65 cm from the display monitor. The computer keyboard was used for the participants' responses.

The visual stimulus was a 4x4 cm (subtending 3.52° of visual angle) oscillating yellow square presented at the center of the screen. The luminance oscillation was created by changing the red and green values of the RGB values of the square according to a 24 Hz sine wave while the blue value of the RGB value was kept at zero. The mathematical description of the red and green values at time t is:

$$col(t) = b + m \cdot b \cdot \sin(2 \cdot \pi \cdot f \cdot t) \quad (4.1)$$

where b is the base value of the colors (125), m the modulation value (0.6), and f the modulation frequency (24 Hz). The visual target was an increase or decrease in the base value (b) for a period of 125 ms (three cycles of a 24 Hz sine wave).

The auditory stimulus was a 500 Hz sine wave with 100% amplitude modulation at 40 Hz. The auditory target was an increase or decrease in the maximum volume of the tone for a period of 125 ms (exactly 5 cycles of a 40 Hz sine wave). To avoid any clearly perceptible discontinuities at target onset and offset, auditory target onset always coincided with the modulated amplitude being at or near its minimum value.

For both the visual and the auditory stimulus modulation onset was at $t = 0$. This was done to insure that the modulation was time/phase locked on every trial.

Experimental design. All the participants performed both the detection and the discrimination tasks which were administered in separate sessions with a week between sessions. Task order was counterbalanced across participants.

The event structure of a trial is illustrated in Figure 4.1 (Panel A). A trial started with a presentation of a grey square in the center of the screen for 2000 ms – darkening of the square during the last 1000 ms indicated the upcoming presentation of the stimuli. After this warning period, the amplitude-modulated auditory and visual stimuli were presented for 2500 ms. During this 2500 ms period visual and auditory targets were presented. If a trial contained targets in both modalities, the targets were presented at the same time. In 80% of the trials, the targets were presented between 1000 and 2000 ms. In the other 20%, the targets were presented between 300 and 1000 ms. The latter trials served to force participants to remain focused during the entire interval and were excluded from analysis, ensuring a sufficiently long pre-target interval on the remaining analyzed trials for the SSEP to develop and stabilize (Ross et al., 2005b).

In the detection task, participants were instructed to indicate whether a visual and/or an auditory target was present. Target probability for each modality was 50%, with a random half of targets being a decrease in volume or luminance and the other half a decrease. Target presence and target type was randomly determined on each trial and independently for the two modalities.

In the discrimination task, auditory and visual targets were presented on each trial. Participants had to indicate if the target was a decrease or an increase in the volume of the tone or luminance of the square. Target type was randomly determined on each trial and independently for the two modalities.

Both tasks were administered in five different attentional conditions. Two conditions were focused-attention conditions where participants were instructed to focus their attention fully on one of the modalities (100% auditory or 100% visual). In the

other three attention conditions they had to divide attention between the two modalities. Three different distributions of attention were used: 80% attention visual and 20% attention auditory, 50% visual and 50% auditory, and 20% visual and 80% auditory. Each of these conditions was administered in two consecutive blocks of 60 trials. The order of the attention conditions was determined by a reduced order five Latin square in such a way that participant number six received the same condition order as participant number one. The order of the conditions was the same in the detection and the discrimination tasks for each participant.

Participants were prompted to respond after the 2.5 second period of stimulus presentation had expired. As Bonnel and Hafter (1998) found no effects of response order in a similar paradigm, participants were prompted to respond to the dominant modality first, by pushing one of two buttons labeled as ‘no’ and ‘yes’ in the detection task and as ‘up’ and ‘down’ in the discrimination task. In the two focused attention conditions the name of the attended modality served as the single prompt to respond. In the divided attention conditions participants were consecutively prompted to respond for each modality. The response for the dominant modality was made first in the 80/20 and the 20/80 conditions, and in the 50/50 condition response order was alternated between participants with, for each participant, opposite orders being used in the detection and the discrimination tasks. Responses for the auditory modality were made with the left hand and for the visual modality with the right hand.

Training. Each session started with a short explanation of the task to be performed, followed by a training that involved 100 trials of practice in each of the two focused attention conditions. Only stimuli and targets in the relevant modality were presented in these practice runs. During each practice run, a staircase tracking algorithm adjusted the target intensity (i.e. the volume difference between the baseline tone and the target tone or the luminance difference between the baseline square and the target square) to achieve an 80% accuracy level ($d' = 1.7$). The resulting target intensities were used in the experimental part of the session. Note that this procedure aimed to equate performance accuracies in the focused attention conditions across all combinations of task and modality.

EEG recording and electrode placement. EEG was recorded using a common reference amplifier: All channels were amplified against the average of all connected inputs. Electrical activity measured at the electrodes was amplified 20.000 times and

digitally filtered using a low pass FIR filter with a cutoff value of 140 Hz. The EEG signals were recorded using Brain Vision Recorder (Brain Products GmbH, Munich, Germany). EEG signal was digitized at 500 Hz with a resolution of 0.02 μ V.

A 70-electrode cap (Electro-cap International Inc, Eaton, Ohio, USA) was used for placement of the tin electrodes. All scalp positions in the International 10-20 System were used, with additional sites located midway between the 10-20 locations (Sharbrough et al., 1991) and six electrode positions 10% inferior to the standard parieto-occipital electrodes (FT9, PO9, O9, FT10, PO10, O10). Two additional electrodes were placed on the left and right mastoid for offline re-referencing of the EEG signal, and the ground electrode was placed on the sternum. Eye movements were monitored via bipolar recordings of the electrooculogram (EOG). For the horizontal EOG the electrodes were placed at the left and right external canthi and for the vertical EOG the electrodes were placed above and beneath the middle of the left eye. All inter-electrode impedances were kept below 5 K Ω for the EEG electrodes and 10 K Ω for the EOG electrodes.

4.2.2 Data analysis

Only trials where the target was presented after the first second of the stimulation interval were used for analysis (80% of the trials). This ensures that the SSEP was well-developed and had stabilized by the time the target was presented.

Behavioral data. Dprime (d') values were calculated from hit and false alarm rates for each subject and each experimental condition, using standard procedures (Macmillan & Creelman, 2005):

$$d' = z(H) - z(F) \quad (4.2)$$

where $z(H)$ and $z(F)$ are the the z-transformations of the hit rate and the false alarm rate respectively. Dprime values were subsequently subjected to repeated-measures analysis of variance (ANOVA). For all ANOVA's of behavioral and EEG data, Greenhouse-Geisser epsilon correction was used to adjust p-values, whenever applicable.

Electrophysiological data. All signals were re-referenced to the average of the mastoids. A 0.1 Hz high-pass filter (12 dB/oct slope) was applied to correct for slow wave fluctuations in signal amplitude. Ocular correction was performed using the method

developed by Gratton et al. (1983). All data was visually inspected for artifacts after segmentation.

ERPs. For the ERP analysis, segments of 1000 ms were made starting 200 ms prior to target onset on trials where responses were correct. A baseline correction was performed using the 200 ms interval preceding target onset. Segments were averaged and then smoothed with a 9 Hz low-pass filter (48 dB/oct slope). For the detection task, ERPs were calculated for each attention condition, separately for trials containing only a visual target, only an auditory target, or both targets. For the discrimination task, where every trial contained both a visual and an auditory target, ERPs were calculated for each attention condition. Because early components, including the N2, could not be reliably identified in the ERPs (see Figure 4.3), presumably due to the use of the frequency tagging technique¹, analysis was restricted to peak amplitude and latency values of the P300 component at Cz. These values were determined by simple peak picking in the 350-750 ms interval following target onset.

SSEPs. The procedure used to estimate ASSR and SSVEP amplitude is illustrated in Figure 4.1 (Panels B and C). We used segments of 8000 ms that began 3000 ms before the start of the 2500 ms stimulation interval during which the amplitude-modulated auditory and visual signals were presented. Segments were averaged over trials, separately for each combination of task and attention condition, resulting in auditory or visual steady-state evoked potentials (SSEPs; Figure 4.1, panel B). Instantaneous amplitudes (IAs) were then computed in two steps. First, SSEPs were filtered, using FFT and a narrow Gaussian band-pass filter defined by a center frequency f (the driving frequencies of the visual and auditory stimuli, 24 or 40 Hz, respectively) and a standard deviation $\sigma(f)$ (0.2 Hz). Instantaneous amplitudes of the filtered SSEPs were computed by means of (the absolute value of) the Hilbert transform (Figure 4.1, panel C). This procedure is formally equivalent to computing instantaneous amplitude by means of a convolution with a complex Morlet wavelet², (for details, see Gladwin

¹Early ERP components also failed to become evident at any electrode position when the cutoff of the low-pass filter was set at 20 Hz.

²For the complex Morlet wavelet, frequency resolution ($\sigma(f)$) and time resolution ($\sigma(t)$) are reciprocally related as follows: $\sigma(f) \cdot \sigma(t) = 1/(2\pi)$. Small values for $\sigma(f)$ provide a desirably narrow focus on the driving or tagging frequency, but also result in a loss of temporal resolution in computing instantaneous amplitude. Because stimulation extended across a 2500 ms interval, during which SSEP amplitude may be assumed to remain fairly constant (see Figure 4.1), some loss of temporal resolution could be tolerated but up to a limit. Based on computer simulations, we determined that a value of 0.2 Hz for $\sigma(f)$ – corresponding to $\sigma(t) \approx 0.8$ s – provided a near-optimal

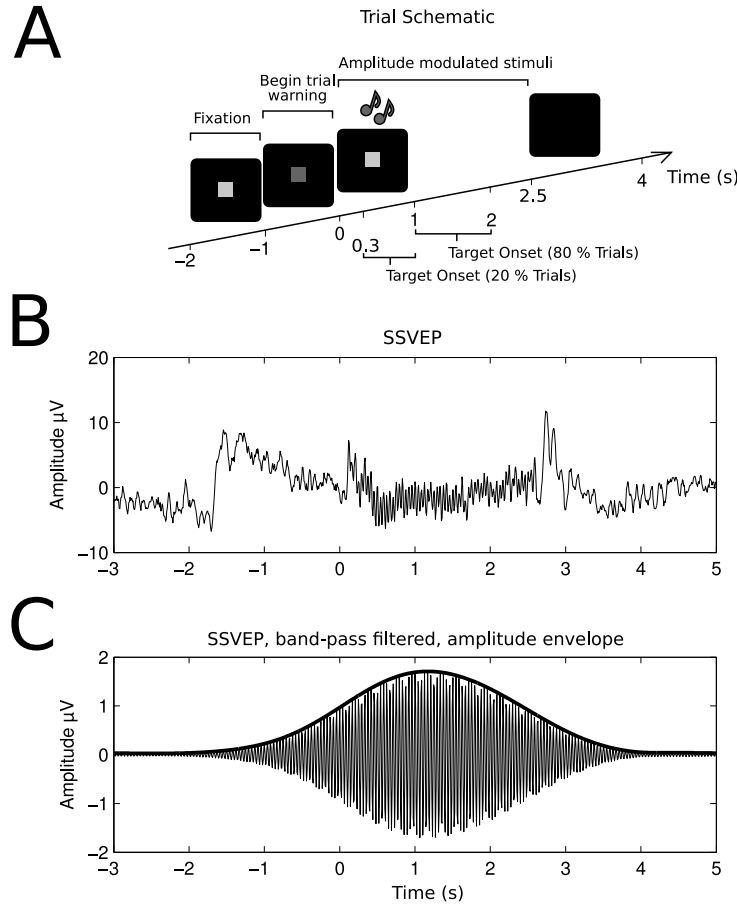


Figure 4.1: **Panel A.** Schematic of trial procedure. A grey square was displayed for 1 s in the center of the screen and darkened for another second indicating the upcoming presentation of the 2.5 s amplitude-modulated auditory and visual stimuli. Targets could be presented in the visual and/or auditory modality. To ensure that participants deployed attention on the modulated stimuli for the whole trial duration, targets were presented between 1 and 2 s in 80% of the trials, or between 0.3 and 1 s in the remaining 20%. Only trials with targets between 1 and 2 s were analyzed. When targets were presented in both modalities they appeared simultaneously. **Panel B** and **C** depict the procedure for computing ASSR and SSVEP amplitude. In this example SSVEP amplitude is computed for a specific channel (PO3) in one of the conditions for an individual participant. **Panel B:** The SSVEP obtained by averaging across all available trials. Onset of the frequency tags is at $t = 0$, and an oscillatory EEG response can be seen to develop quickly and last until offset of the tags ($t = 2.5$). The large component at $t = -2$ is related to onset of the visual warning stimulus. **Panel C:** SSVEP amplitude envelope obtained through Hilbert transform after narrow band-pass filtering ($f = 24$ Hz, $\sigma(f) = 0.2$ Hz). Mean SSVEP amplitude was computed across the interval 1–1.5 s after stimulus onset.

compromise between the opposing requirements of frequency specificity and temporal specificity in the present study.

et al., 2006; Tallon-Baudry & Bertrand, 1999). SSEP amplitude was computed as the average amplitude across the 1000-1500 ms interval following onset of the 2500 ms stimulation interval.

Average scalp distributions of ASSR and SSVEP amplitudes were computed for each combination of task and attention condition. For each subject, normalized scalp distributions were computed by dividing the amplitude at each electrode by the maximum amplitude across all electrodes (McCarthy & Wood, 1985). Normalized amplitudes were then averaged across participants. Values for individual electrodes of the average scalp distributions vary between 0 and 1, with high values indicating consistently high relative SSEP amplitudes across participants for that electrode and low values indicating consistently low relative SSEP amplitudes.

The procedure used to estimate SSEP amplitude as outlined above, i.e., time-domain averaging across trials to produce an SSEP followed by frequency-domain estimation of SSEP amplitude, renders the nature of possible attentional effects on SSEP amplitude ambiguous. Such effects could reflect veridical and consistent effects on SSEP amplitude at the level of single trials (i.e., veridical effects on sensory gain control) but could also reflect attentional effects on intertrial coherence of the phase relation between the driving oscillatory stimulation and the resulting EEG activity (Ding et al., 2006; Kim et al., 2007). To address this possibility, we computed SSEP amplitude for single-trials, using the procedure detailed above, and then averaged these values across trials. By definition, average SSEP amplitude estimated in this way cannot be sensitive to degree of intertrial phase coherence. Therefore, if attention primarily affects such phase coherence, attentional effects on SSEP amplitude should no longer be present. In fact, attentional effects computed this way were virtually identical to those obtained with the former method of estimating SSEP amplitude. We therefore conclude that the attentional effects on SSEP amplitude, computed with the former method and to be reported below, almost certainly reflect genuine effects of attention on sensory gain control.

4.3 Results

4.3.1 Behavioral results

Averaged d' -values for each combination of modality (auditory, visual), task (detection, discrimination), and attention condition (100%, 80%, 50%, and 20% – note that

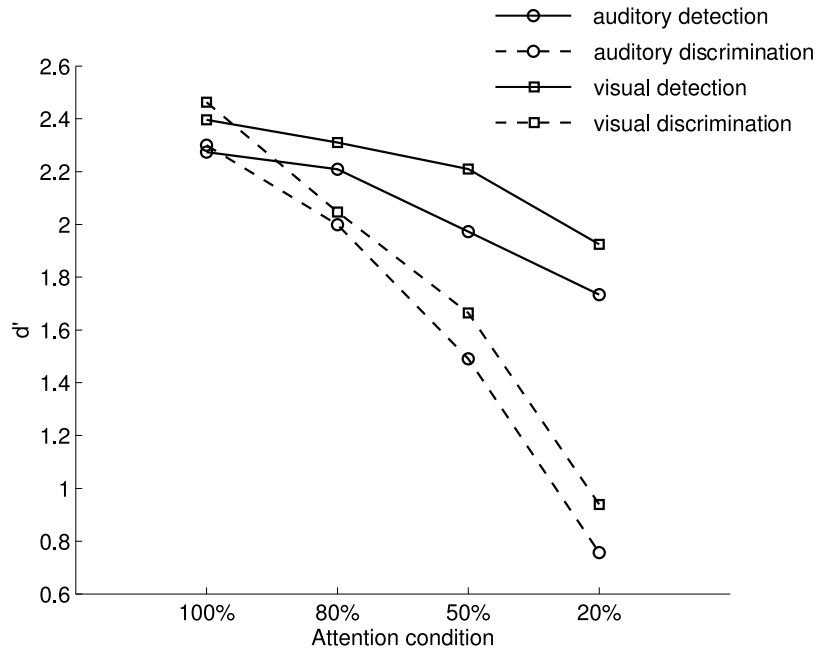


Figure 4.2: Performance accuracies (d') as a function of attention condition for each combination of target modality (auditory, visual) and task (detection, discrimination). Attention condition refers to the instructed proportion of attention to be allocated to the target modality (100% thus refers to the focused-attention conditions).

no responses were given in the 0% condition) are presented in Figure 4.2. Note that our procedure for adjusting target intensity during training in order to achieve comparable levels of performance in the focused-attention (100%) condition for all combinations of modality and task, seems to have been quite effective. Divided-attention costs on performance were much stronger for discrimination than for detection, but some costs seem to be present also for detection. A $2 \times 2 \times 4$ (task \times modality \times attention) repeated measures analysis of variance (ANOVA) yielded significant main effects of task, $F(1, 8) = 6.4$, $p < .05$, and attention, $F(3, 24) = 74.9$, $p < .001$, and a significant interaction of task and attention, $F(3, 24) = 14.0$, $p < .001$. A separate analysis on the results for detection yielded a significant main effect of attention, $F(3, 24) = 18.8$, $p < .001$.

4.3.2 Electrophysiological results

ERPs. ERPs at electrode Cz and time-locked to target onset are shown in Figure 4.3, for all attention conditions in the detection and discrimination tasks. Note that these

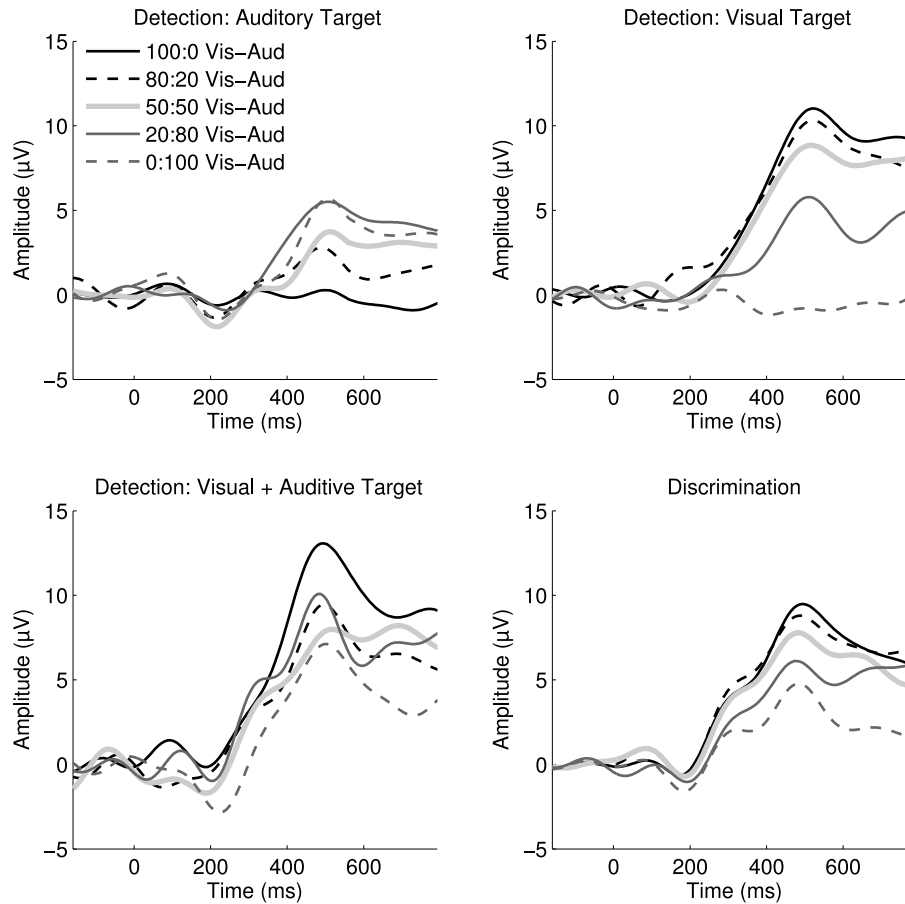


Figure 4.3: ERP waveforms at Cz. Target onset is at $t = 0$. The upper and lower left panels display the waveforms in each attention condition separately for each of the three possible target types in the detection task (auditory-only, visual-only, auditory + visual). The lower right panel shows the waveforms for the discrimination task.

ERPs were computed from correct trials only. Separate panels show the ERPs associated with the three possible target events in the detection task: visual-only, auditory-only, and visual+auditory. The waveforms are dominated by the P300 that started after about 300 ms, whereas most of the earlier ERP components are hardly visible – as suggested earlier, this latter phenomenon is likely to result from the usage of frequency tagging in both modalities. Analysis of ERP waveforms was therefore restricted to peak P300 amplitude in the 400–800 ms interval.

The first analysis focused on P300 amplitudes for visual-only and auditory-only targets in the detection task. A repeated-measures ANOVA with target type (visual vs. auditory) and attention condition (recoded to indicate attention to the target type

ranging from 0 to 100%) as within-subject factors yielded main effects of target type, $F(1, 8) = 11.6$, $p < .01$, and attention condition, $F(4, 32) = 18.3$, $p < .001$, and a significant interaction, $F(4, 32) = 3.1$, $p < .05$. Pairwise comparisons between the attention conditions showed no significant differences between the 100%, 80%, and 50% conditions, significant differences between each of these three conditions and both the 0% and 20% conditions, and a significant difference between the 0% and 20% conditions. Thus, visual targets elicited larger P300 components than auditory targets, and, with the exception of the 20% condition, the effect of attention on P300 amplitude was approximately all-or-none.

Inspection of Figure 4.3 suggests that P300 amplitudes for bimodal targets in the detection task may roughly correspond to the sum of amplitudes for visual-only and auditory-only targets in that task. An analysis designed to test for possible differences between amplitudes for bimodal targets and the sum of unimodal targets yielded no significant differences. This result is consistent with the notion that the P300 response to bimodal targets in detection is composed of the linear sum of independent P300 responses to each of the constituent unimodal target events (Teder-Salejarvi, McDonald, Russo, & Hillyard, 2002; Talsma & Woldorff, 2005)

P300 amplitudes for bimodal targets in detection and discrimination were analyzed in a repeated-measures ANOVA with task and attention condition as within-subject factors. Apart from the main effects of attention condition, this analysis yielded as a new result a borderline significant main effect of task, $F(1, 8) = 4.5$, $p < .07$, reflecting somewhat smaller P300 amplitudes when the task required discrimination as compared to detection.

SSVEP. Averaged topographical maps of the 24 Hz SSVEP amplitude are shown in Figure 4.4, for all combinations of task and attention condition. These maps show a pronounced and consistent maximum at the most posterior electrodes. Also evident, for detection and discrimination, are the increased values at these electrodes for divided-attention as compared to the focused-attention conditions. Statistical analysis of SSVEP amplitude was based on the average amplitudes computed across the four electrodes where this amplitude, averaged across all task by attention condition combinations, was maximal. This subset of electrodes was determined separately for each participant, but showed a high degree of consistency across participants, containing only electrodes at posterior occipitoparietal locations. Estimates of the signal-to-noise ratio (SNR) of SSVEP amplitudes that were used in statistical analysis were computed

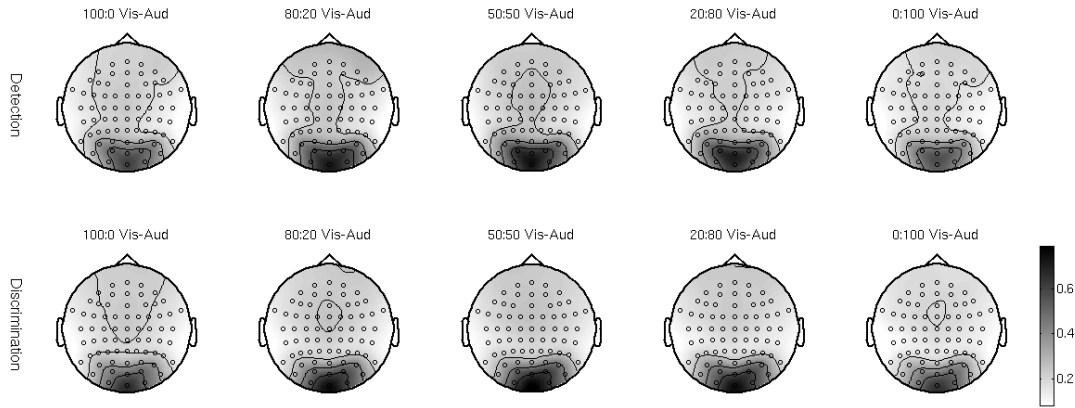


Figure 4.4: Topographic maps of the steady-state visual evoked response (24 Hz). The upper panel depicts separate maps for each attention condition in the detection task; the lower panel does so for the discrimination task. Higher values represent higher average normalized amplitudes across participants at that location.

in the following way. We used exactly the same procedure as that used for computing the 24 Hz response, but now centered the Gaussian filter at 22 Hz or 26 Hz. Dividing the 24 Hz amplitude estimate, averaged across all task x attention condition combinations, by the average of the 22 and 26 Hz estimates, similarly averaged across experimental conditions, provides an estimate of the frequency specificity, or SNR, of the 24 Hz SSVEP amplitude. Values of this estimate across participants ranged from 11.5 to 48.3, with an average of 28.4, indicating excellent frequency specificity for SSVEP amplitude estimation.

To accommodate the substantial individual differences in SSVEP amplitude, values were normalized for each participant by dividing by the average value across all ten (task x attention condition) conditions. Figure 4.5 shows normalized mean SSVEP amplitude as a function of task and attention condition. For both detection and discrimination, SSVEP amplitude increased markedly from focused-attention to divided-attention conditions, culminating at the 50-50% condition. Amplitudes also appear to be slightly larger in the 100%-visual as compared to the 100%-auditory condition. A repeated-measures ANOVA with task and attention condition as within-subject factors yielded only a main effect of attention condition, $F(4, 32) = 8.5$, $p < .001$. Polynomial contrast analysis showed this effect to be explained completely by the quadratic contrast, $F(1, 8) = 24.2$, $p < .001$ – the linear contrast did not approach significance, $F(1, 8) = 1.5$, $p > .26$.

To assess the relation between SSVEP amplitude and performance accuracy, SSVEP

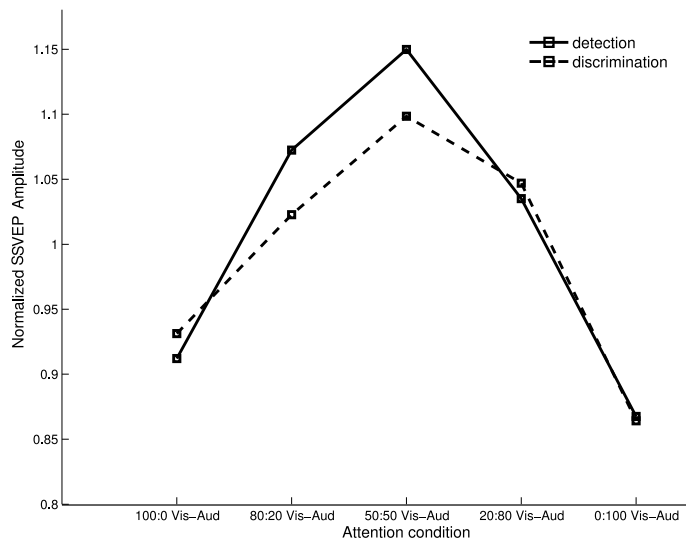


Figure 4.5: Average normalized amplitudes of the steady-state visual evoked potential, for all attention conditions and separately for detection and discrimination.

amplitude was computed separately for correct trials and incorrect trials, and separately so for visual targets and auditory targets and for detection and discrimination. In order to have a sufficient number of trials for stable estimates of SSVEP amplitude, errors were pooled across attention conditions – corresponding ‘pooled’ values for correct trials were obtained by weighted averaging of the amplitudes for individual attention conditions, with the weights corresponding to the relative frequency of errors in each condition. For each participant, the resulting values were normalized by dividing by the average value of ‘correct’ amplitudes across the four combinations of task and target modality. The results of this analysis, averaged across participants, are shown in the left panel of Figure 4.6. Amplitudes seem somewhat smaller for detection as compared to discrimination. Amplitudes for auditory targets appear to be somewhat larger for errors than for correct responses in both detection and discrimination, whereas an opposite but more pronounced effect seems to be present for visual targets. A repeated-measures ANOVA with correctness, task, and target modality as within-subject factors yielded a significant main effect of correctness, $F(1, 8) = 9.0$, $p < .02$, and a significant interaction of correctness and target modality, $F(1, 8) = 10.9$, $p < .015$. Separate analyses for visual and auditory targets yielded a significant main

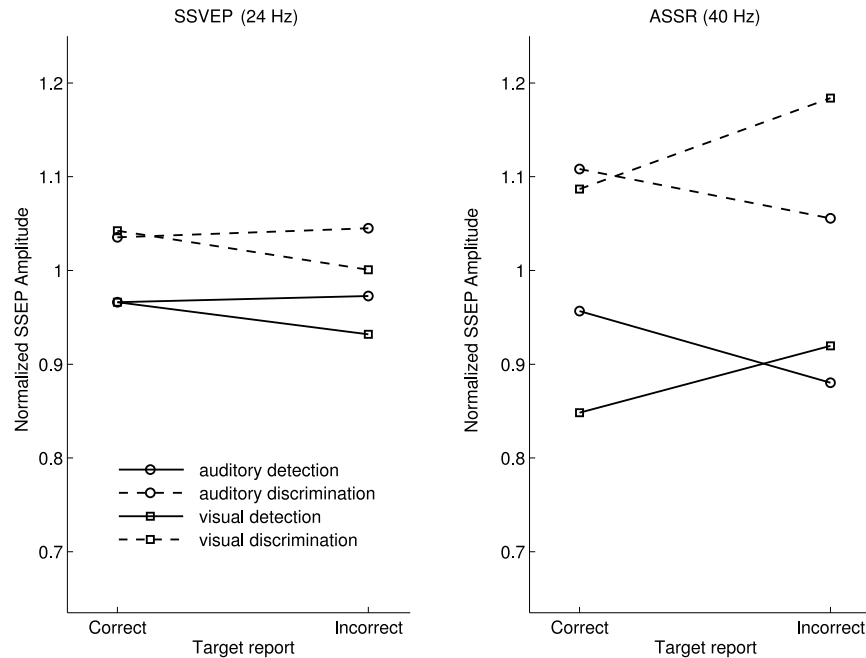


Figure 4.6: Normalized amplitudes of the steady-state visual evoked potential (SSVEP; left panel) and auditory steady-state potential (ASSR; right panel), as a function of correctness of the target response, target type (auditory, visual), and task (detection, discrimination).

effect of correctness for visual targets, $F(1, 8) = 22.2$, $p < .002$, but not for auditory targets, $F(1, 8) = 4.1$, $p < .10$.

ASSR. Averaged topographical maps of the 40 Hz ASSR amplitude are shown in Figure 4.7, for all combinations of task and attention condition. Replicating previous results, these maps show ASSR amplitude to be largest across a fairly wide fronto-central region (see e.g., Saupe et al., 2009). As for the SSVEP, statistical analysis of ASSR amplitude was based on the average value computed across the four electrodes where this amplitude was maximal – all 36 electrodes (9 participants \times 4 electrodes) used in this computation had a frontocentral location. Following the same procedure as described above for SSVEP (24 Hz) amplitude, but now with 38 and 42 Hz as the bracketing frequencies, yielded for the 40-Hz ASSR amplitude an SNR range of 2.6 to 10.0, with an average of 5.5. These values indicate acceptable and useful frequency specificity for ASSR amplitude.

ASSR amplitudes were normalized, using the same procedure as that described earlier for SSVEP amplitude. A repeated-measures ANOVA with task and attention condition as within-subject factors yielded no significant effects (all p 's > 0.17).

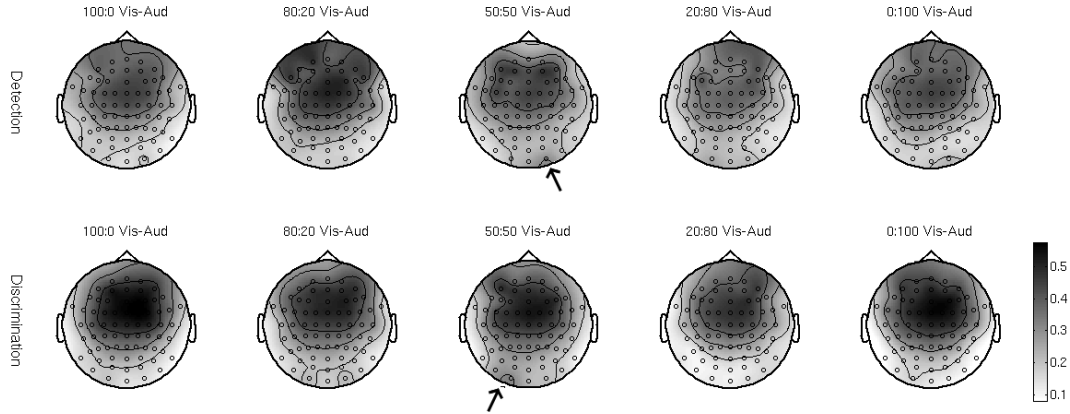


Figure 4.7: Topographic maps of the auditory steady-state response (40 Hz). The upper panel depicts separate maps for each attention condition in the detection task; the lower panel does so for the discrimination task. Higher values represent higher average normalized amplitudes across participants at that location. Arrows point to the emergence of the 40 Hz response at posterior locations during the 50-50% divided-attention condition.

A possible relation between ASSR amplitude and accuracy for auditory and visual targets was analyzed in the same way as previously outlined for SSVEP amplitude. The results of this analysis, averaged across participants, are shown in the right panel of Figure 4.6. Amplitudes were somewhat smaller for detection as compared to discrimination. More importantly, amplitudes for auditory targets appeared to be smaller for errors than for correct responses in both detection and discrimination, whereas the opposite effect seems to be present for visual targets. A repeated-measures ANOVA with within-subject factors correctness, task, and target modality yielded as the only significant effect an interaction of correctness and target modality, $F(1, 8) = 10.1$, $p < .02$. Separate analyses at each level of target modality failed to show significant effects of correctness (all p 's $> .13$). Thus, these results suggest an opposite but weak relation between ASSR amplitude and performance accuracy for auditory targets and visual targets. Note that these latter effects are almost the mirror image of those found for SSVEP amplitude depicted in the left panel of Figure 4.6.

Close inspection of the topographical maps in Figure 4.7 reveals a slightly enhanced presence of 40 Hz activity at posterior occipital electrodes for the 50-50% divided-attention condition in both detection and discrimination. Because such an effect would be of considerable theoretical significance but the observation is post hoc, we analyzed it in detail. We averaged ASSR amplitude across the three most posterior electrodes (O9, Iz, O10), as the effect seems most prominent at those electrodes –

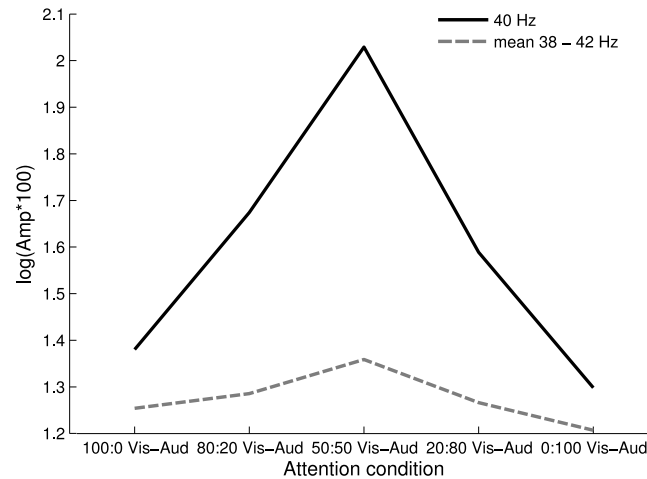


Figure 4.8: Mean log-transformed amplitude of the 40 Hz response at posterior occipital locations, as a function of attention condition. The amplitude of the 38/42 Hz response serves as an important control to assess possible influences of EMG artifacts and gamma-band EEG activity. See text for further explanation.

very similar results were obtained when we used the same set of four electrodes used for computing SSVEP amplitude. Because the amplitudes involved are very small (less than $0.1 \mu\text{V}$) and to accommodate the very substantial individual differences, we also averaged amplitudes across detection and discrimination to enhance robustness and then log-transformed them (using the natural logarithm). Because the posterior electrodes are prone to EMG artifacts, and the 50-50% divided-attention condition might be considered the most challenging one and lead participants to tense up, it is possible that the effect represents an EMG artifact. In addition, the effect might reflect enhanced gamma activity in background EEG at posterior sites under more challenging conditions (Fell, Fernandez, Klaver, Elger, & Fries, 2003). To explicitly check for these alternative explanations, we used exactly the same procedure used to compute 40 Hz amplitudes to compute amplitudes at two neighboring frequencies, 38 and 42 Hz, and then averaged across these two frequencies. As both EMG activity and gamma-band EEG activity have broad spectra, we reasoned that such activities should be equally evident at those neighboring frequencies, thus providing an appropriate check for the possibility that such activities might underlie the 40 Hz effect at posterior sites.

Average (log-transformed) ASSR (40 Hz) amplitudes and corresponding mean 38-42 Hz amplitudes are presented in Figure 4.8, as a function of attention condition. The ASSR amplitude is slightly larger than the 38/42 Hz control value at

the focused-attention conditions, but this difference is substantially increased at the divided-attention conditions and is maximal at the 50-50% condition. The relatively small attention effects on the 38/42 Hz control amplitude that can be seen might reflect a modest contribution of EMG or gamma-band activity to the attentional effects on ASSR amplitude, but might also reflect leakage of 40 Hz activity to neighboring frequencies due to nonlinear neural interactions. Repeated-measures ANOVA with component (40 Hz, 38/42 Hz) and attention condition as within-subject factors yielded main effects of component, $F(1, 8) = 14.0$, $p < .01$, and attention condition, $F(4, 32) = 7.3$, $p < .005$, and a significant interaction of these factors, $F(4, 32) = 5.4$, $p < .01$. Polynomial contrast analysis revealed that the latter effects involving attention condition were almost completely explained by the quadratic contrast ($F(1, 8) = 13.8$, $p < .01$, for the main effect of attention condition, and $F(1, 8) = 11.6$, $p < .01$, for the interaction). Analysis of simple effects showed that the effect of attention was significant for the 40 Hz component ($p < .001$), but not for the 38/42 Hz component ($p > .15$). These results seem to provide compelling evidence that the enhanced presence of 40 Hz activity at posterior sites in divided-attention conditions represents genuine neural activity at occipital sites that is specifically associated with the auditory input stream.

Inspired by this latter effect, we also undertook several analyses aimed towards identifying possible attention-dependent SSVEP (24 Hz) activity at frontocentral electrodes, which could not be explained in terms of volume conduction from the primary occipital sources of the SSVEP. None of these produced even a hint of a possible presence of such effects.

4.4 Discussion

In the present study we explored the effects of bimodal divided attention on performance during auditory-visual detection and discrimination, using a paradigm similar to that developed by Bonnel and coworkers (1998). The behavioral results showed clear dual-task costs when attention had to be divided between the auditory and visual modalities for discrimination performance and also, though the costs were substantially smaller, for detection performance. These results replicate earlier results by Bonnel and coworkers (1998) who, as we argued before, also seem to have obtained divided-attention costs in detection performance when, as in the present study, target intensity was adjusted in such a way that overall performance levels were approxi-

mately equated for the focused-attention conditions in the detection and discrimination tasks. Thus, the present evidence fails to support the notion that auditory-visual bimodal detection and discrimination are mediated by qualitatively different processing stages, a pre-attentive capacity free stage in detection and an attention-dependent capacity limited stage in discrimination (Bonnell et al., 1992; Bonnell & Hafter, 1998). Instead, the evidence seems more consistent with the notion that bimodal detection is in fact subject to capacity limitations but that these limitations are generally less severe than those delimiting dual-task performance with auditory-visual discrimination tasks.

Results from a study by Kawahara et al. (2001), who used an attentional-blink paradigm, further substantiate this view. They found an attentional blink (i.e., impaired detection of the second target when it followed the first target within 100 to 500 ms, see Raymond, Shapiro, & Arnell, 1992) when the second target had to be identified but not when it had to be detected – an attentional blink in detection performance was obtained only when the stimuli were highly degraded. These results also suggest that detection is subject to capacity limitations but that such restrictions become manifest in performance only when detection is sufficiently difficult in terms of signal to noise ratios.

The fact that divided-attention costs were much smaller for detection than for discrimination, even when performance in the two tasks was equated in the focused-attention conditions, might be explained in terms of a steeper performance-resource tradeoff for discrimination than for detection (Norman & Bobrow, 1975). In the present study we sought to address an alternative, but compatible, account – that people may tend to adopt less differentiating attention allocation policies in detection conditions, perhaps because they become aware that different allocation policies may impact performance in concurrent detection less than that in concurrent discrimination. We will discuss the results for the various electrophysiological measures in detail below, but the fact that attentional effects on all these measures were remarkably similar for detection and discrimination, fails to provide any support for this alternative account.

Event-related potentials. Because the various early-onset ERP components were either absent in the present study or too small to allow for useful analysis, only the P300 component could be considered. The absence of early ERP components might be attributed to two, not mutually exclusive, factors. On one hand, the target events

in the present study were difficult to detect or discriminate and may thus have had insufficient signal power to reliably or strongly evoke these components. Alternatively, or additionally, the use of frequency tagging may have interfered with the generation of early ERP components. This possibility is strongly indicated for the auditory modality by elegant recent work by Ross and coworkers (2005). They found that the P1-N1-P2 response elicited by a brief noise burst was largely obliterated when the noise burst was superimposed upon a continuous 40 Hz amplitude-modulated background tone, especially when, as in the present study, both were presented binaurally. For the visual modality, concurrent recording of the SSVEP (at 20.8 and 27.8 Hz) and transient ERPs was successfully accomplished by M. M. Muller and Hillyard (2000). A potentially important difference is the fact that target onset was phase-locked to the tagging frequency in their study but not in the present one. This lack of phase locking is likely to have caused a substantial amount of jitter in the latency of the early ERP components in the present study. For instance, when target onset occurred at a time when the modulated luminance was at or near a minimum as compared to a maximum, these components must have surely been delayed. Such jitter would cause early ERP components to be considerably attenuated in the averaging process (Toffanin et al., 2009).

In the detection task, mean P300 amplitude, which was computed across correctly detected targets only, was larger for visual-only targets than for auditory-only targets. More important, P300 amplitude on single-target trials was found to scale systematically with instructed attention allocation – as more attention was allocated to one modality, P300 amplitude increased for targets in that modality while it decreased for targets in the other modality. These results are in agreement with findings by previous studies that also showed an increase of P300 amplitude as a function of attention allocation (e.g. Mangun & Hillyard, 1990; Hoffman, Houck, MacMillan, Simons, & Oatman, 1985; Wickens, Kramer, Vanasse, & Donchin, 1983; Isreal, Chesney, Wickens, & Donchin, 1980). Such results have been interpreted in terms of P300 amplitude reflecting the resource distribution of a limited capacity processing system (Hoffman et al., 1985). However, others have argued that P300 amplitude is closely tied to the behavioral outcome, and might reflect the effects of attentional selection rather than the attentional modulation and selection of relevant information itself, with the latter causal processes being reflected by earlier ERP components such as the P1 and N1 (Mangun & Hillyard, 1990; Toffanin et al., 2009). Consistent with this latter notion, the effects of relative attention allocation on P300 amplitude were distinctly nonlinear,

with relatively large and similar amplitudes in the 100%, 80%, and 50% conditions, a smaller amplitude in the 20% condition, and an essentially absent P300 in the 0% condition. Thus, it is questionable whether the attentional effects on P300 amplitude can provide any more direct information on the allocation of attention across the two modalities than what is provided by effects on overt behavior. Interestingly, P300 amplitude for bimodal targets closely equaled the summed amplitudes for unimodal targets – this might suggest that at the level of processing indexed by the P300, there is little or no overhead cost associated with the requirement to divide attention in bimodal detection (Bonnell et al., 1992; Bonnell & Hafter, 1998).

In the discrimination task, targets in the different modalities were always presented simultaneously. Consistent with the larger amplitudes for visual-only targets than for auditory-only targets in the detection condition, P300 amplitude in the discrimination condition steadily increased as more attention was allocated to the visual modality. When compared to the P300 amplitudes for bimodal targets in the detection condition, amplitudes in the discrimination condition were somewhat smaller. As bimodal targets were far less common in the detection condition, this latter effect may reflect the well-known effect of probability on P300 amplitude (R. Johnson, 1984, 1986).

Frequency tagging: ASSR and SSVEP. Several aspects of the results from frequency tagging were unexpected and, we suggest, quite remarkable. First, ASSR amplitude (40 Hz) at frontocentral electrodes, where the amplitude exhibited a clear maximum, showed no significant effects of intermodal attention. The lack of a difference between the focused-auditory and focused-visual conditions replicates earlier findings (Linden et al., 1987) and reinforces the notion that such a difference may be found only when the target event is defined in terms of a change in the tagging frequency itself (see Ross, Herdman, Wollbrink, & Pantev, 2004, for evidence using MEG, and Saupe et al., 2009, for evidence using EEG).

ASSR amplitude fluctuates from trial to trial. Such fluctuations were found to predict performance accuracy, with high ASSR amplitude being associated with accurate performance with auditory targets but with inaccurate performance with visual targets. Though these results are only correlational, it is tempting to infer a causal relationship where ASSR amplitude indexes relative preparedness to process auditory as compared to visual information. The contrast with our failure to find effects of intermodal attention instructions on ASSR amplitude may be more apparent than real. The correct-incorrect distinction may simply provide a more powerful contrast than that

provided by the various attention conditions – after all, different attention instructions had significant but relatively mild effects on performance accuracy. Furthermore, even the correct-incorrect contrast failed to produce significant effects on accuracy when visual targets or auditory targets were considered separately. The combined results may point to a subtle, but theoretically significant, relation between (EEG-based) ASSR amplitude and relative processing bias towards auditory versus visual sources of information, which requires considerable power to detect. This perspective makes it understandable why and how such power is enhanced when the target is defined in terms of a change in the tagging frequency itself (Ross, Herdman, Wollbrink, & Pantev, 2004). Our only reservation with this solution to boost power is that it would seem to do away with the very elegance and promise of frequency tagging as a technique that can provide a continuous window on perceptual information processing in the brain without influencing or interfering with such processing.

Clear attention effects on ASSR amplitude were found at posterior occipital sites, where the 40 Hz response was markedly stronger in divided-attention as compared to focused-attention conditions. It is important to note that these effects were very small in absolute size, approaching, but not exceeding, the resolution limits of our EEG recording system. These effects are unlikely to reflect either EMG artifacts or gamma-band EEG activity, as they were not found, or were much smaller, at neighboring frequencies (38/42 Hz). Neither can they be due to passive volume conduction from primary ASSR sources in auditory cortex, as no significant attention effects were found there. By exclusion then, as the 40 Hz frequency specifically tags the auditory input stream, the enhanced 40 Hz response at occipital sites in divided-attention conditions must be taken to reflect an enhanced influence of auditory input or auditory processing on neural activity in occipital cortex. To our knowledge, this is the first demonstration of an unambiguous attention-dependent influence of auditory information on occipital activity using EEG (Talsma et al., 2007, may have demonstrated such an influence of visual information on auditory regions). The nature of such an enhanced influence in divided-attention conditions remains to be clarified. The fact that ASSR amplitude at anterior-central sites showed no attention effects would seem to rule out the possibility that the effects at posterior sites are due to a stronger neural drive (as opposed to passive volume conduction) from auditory regions, presumably primary auditory cortex, in divided-attention conditions. Rather, these effects might reflect stronger effective connectivity from auditory to visual cortical areas in divided-attention conditions. That issue will be discussed in more detail later.

SSVEP amplitude (24 Hz) exhibited a clear maximum at posterior occipital sites, with a highly favorable signal-to-noise ratio. Attention effects on posterior SSVEP amplitude resembled those found for ASSR amplitude at posterior sites, with higher amplitudes obtained in divided-attention conditions as compared to focused-attention conditions and with both effects being fully accounted for by the quadratic contrast in polynomial contrast analyses. We stress that almost identical attention effects were obtained when SSVEP amplitude was computed in a way that rendered it completely insensitive to possible attention-related differences in intertrial phase coherence (see Methods). Thus, these effects on SSVEP amplitude almost certainly reflect genuine effects on sensory gain control (Kim et al., 2007).

SSVEP amplitude in the focused-visual condition did not differ from that in the focused-auditory condition. This lack of an effect of intermodal selective attention contrasts strongly with the many positive findings of clear intramodal visuospatial attention effects on SSVEP amplitude, also in studies that used tagging frequencies similar to the 24 Hz used in the present study (M. M. Muller & Hillyard, 2000; M. M. Muller, Teder-Salejarvi, & Hillyard, 1998; M. M. Muller, Picton, et al., 1998; Morgan et al., 1996; Toffanin et al., 2009). The latter findings have generally been interpreted in terms of modulation of sensory gain control in primary or secondary visual cortex, and this interpretation is corroborated by evidence from numerous fMRI studies of visuospatial attention (Kastner et al., 1998; Russo, Martinez, & Hillyard, 2003; Tootell et al., 1998). Several recent fMRI studies of auditory-visual intermodal attention have also found evidence for enhanced activity in modality-specific cortical areas associated with the attended modality in conjunction with diminished activity in cortical areas associated with the unattended modality (for a recent example and overview, see J. A. Johnson & Zatorre, 2005, 2006). Importantly, these cortical areas are typically found not to include primary auditory and visual cortex (e.g. J. A. Johnson & Zatorre, 2005, 2006; Shomstein & Yantis, 2004). As occipital SSVEP has been associated with sources in primary visual cortex (Russo et al., 2007), the fact that evidence from fMRI studies indicates that effects of selective intermodal attention are largely restricted to secondary or higher visual cortical areas, may thus be consistent with the lack of selective intermodal attention on SSVEP amplitude in the present study.

As noted before, the enhanced SSVEP amplitude in divided-attention conditions resembles the results for ASSR amplitude (40 Hz) at occipital sites, and we suggest that both effects may share a common cause: Enhanced effective connectivity from auditory to visual cortex in divided-attention conditions so that activity in auditory

cortex can affect, directly or indirectly, activity in visual cortex during crossmodal auditory-visual attention. The central idea here is that enhanced 40 Hz activity at occipital sites serves the critical function of unambiguously indexing such enhanced effective connectivity, but that 40 Hz activity itself constitutes only a small portion of total neural activity in auditory cortex that, once effective connectivity has been established, can exert a more general influence on neural activity levels and patterns in visual cortex. If SSVEP amplitude is assumed to reflect sensory gain control in primary visual cortex (Russo et al., 2007), the present findings would seem to provide strong evidence for an influence of auditory information processing on early cortical stages of visual information processing.

In the present study, we failed to obtain any evidence for a reverse attention-dependent influence from visual information processing on auditory information processing. This might point to a truly asymmetric interaction between vision and audition under the conditions of the present experiment, or it could be due to limitations of the measures and techniques we used to find evidence for such a reverse influence. Seemingly consistent with the former possibility, Giard and Peronnet (1999), in what could arguably be considered an auditory-visual divided-attention task, found influences of auditory information on occipital activity to be both earlier (~ 50 ms) and stronger than the reverse influences.

It is important to point out that the effects of intermodal attention on SSVEP amplitude were very similar for detection and discrimination. Apart from serving as a useful indication of the robustness of the present results, this similarity also serves to indicate that attentional strategies and mechanisms are likely to have been largely the same in detection and discrimination. Attention-dependent crossmodal links of the type demonstrated here might have important functions in supporting flexible multi-sensory integration. The tasks we used in the present study, with target events in one modality being independent of and unrelated to those in the other modality, provided no basis for useful multisensory integration, begging the question of whether and how such links may have influenced task performance. We have interpreted SSVEP amplitude to reflect sensory gain at low levels of cortical visual processing, but the positive functional connotations of the concept of sensory gain may be reason to reconsider that interpretation. As noted earlier, recent evidence tends to support the hypothesis that the ASSR reflects a separate neural oscillation that is driven by the periodic stimulus (Ross et al., 2005a). If we apply the same hypothesis to the SSVEP, it becomes possible to see how input from auditory processing regions, even when it carries no

useful information – and thus should be considered noise – may raise the level of background activity in early visual cortex and thereby enhance SSVEP amplitude as background activity is entrained by, or feeds, the neural oscillation. However, a higher level of background activity, or noise, would not necessarily facilitate the processing of discrete visual events, and would perhaps be more likely to actually hamper such processing. Thus, attention-dependent crossmodal links, by enabling crosstalk, may have contributed to divided-attention costs in performance in the present study (Navon & Miller, 2002). The more important and general point is that tasks, such as the ones used here, that provide little or no possibilities for useful multisensory integration, may nevertheless be powerful tools to establish potential neural mechanisms underlying such integration. To assess the functional significance of such mechanisms requires the complementary use of tasks or paradigms that allow for useful types and degrees of multisensory integration.

Multisensory integration: ERPs and SSEPs. The SSEP is easily quantified in the frequency domain and knowledge about the neural generators of the ASSR and SSVEP greatly enhance their utility in assessing neural activity in specific cortical regions. Two major sources of the SSVEP have been identified in primary visual cortex and in the motion-sensitive area MT/V5 – in addition, activity in mid-occipital and ventral occipital region appear to make minor contributions to the SSVEP (Russo et al., 2007). Together with the posterior occipital distribution of the SSVEP in the present study, this has led us to interpret SSVEP amplitude to index neural activity in early regions of visual cortex. While several studies have identified primary auditory cortex as the main source of the ASSR, a recent study analyzed sources by means of PET and found six sources of the ASSR, including temporal, frontal, and parietal regions as well as regions in the brain stem and cerebellum (Reyes et al., 2005). Given the evidence, it seems reasonable to associate ASSR amplitude primarily with neural activity in early regions of auditory cortex.

The regional specificity of ASSR and SSVEP in conjunction with the fact that their temporal resolution is inherently poor, imply that these measures do not allow for a chronometric analysis of brain activity across different cortical areas. Several possible mechanisms underlying crossmodal influences have been proposed, including rapid feedforward integration, thalamic influences, direct connections between primary sensory cortices, and feedback from multisensory regions to sensory-specific brain areas (Driver & Noesselt, 2008). We believe that the present results, while

providing clear evidence for attention-dependent crossmodal influences, are mute regarding the issue of underlying mechanisms, because of this inherent limitation of the SSEP measure. In contrast, the high temporal resolution of ERPs combined with the high spatial resolution of fMRI, can provide a picture of the sequential activation of cortical areas during perceptual processing. Some interesting results that demonstrate the potential of this technique and speak to underlying neural mechanisms are already available, for both intramodal attention (e.g., Russo et al., 2003) and intermodal attention (e.g., McDonald et al., 2003; see Driver & Noesselt, 2008, and Macaluso & Driver, 2005, for a more extensive overview). The present results indicate that bimodal frequency tagging may amply compensate for the loss of temporal resolution by providing great sensitivity and power to detect tonic and subtle changes in regionally specific background neural activity related to crossmodal influences. Frequency tagging and evoked potentials thus seem to represent somewhat complementary techniques, which probably can be used profitably as such in EEG/MEG research on intermodal attention and intersensory interactions.

Chapter 5

P4pc: An Electrophysiological Marker of Strategic Attentional Disengagement

If there is hope of exploring causal control of brain systems by mental states, it must lie through an understanding of how voluntary control is exerted over more automatic brain systems.

Michael I. Posner

Abstract

The processing of successive targets requires that attention be engaged and disengaged. Whereas the N2pc can be seen as an electrophysiological signature of attentional engagement, no event-related potential component has been linked to attentional disengagement. This may be due to the fact that most studies using N2pc required search for only one target. Here, we used an RSVP paradigm with multiple targets in a stream to force swift disengagement of attention from a target after it has been processed. A distinct disengagement-related waveform following the N2pc, which we called the P4pc, was found. This marker may provide an important tool for studying attentional control.

5.1 Introduction

Several event-related brain potential (ERP) measures have been functionally linked to visual-spatial attention (Luck, 2005a). Among these, the N2pc (N2-posterior-contralateral) component, typically observed 200-300 ms poststimulus at posterior electrodes contralateral to the side of a laterally presented visual target, has been associated with the selection of target stimuli and/or the suppression of nontargets (see, e.g. Kiss, Velzen, & Eimer, 2008; Luck & Hillyard, 1994a, 1994b).

When multiple targets are possible, either simultaneously or in close temporal proximity, attention must be disengaged from processed targets to allow attentional selection of other targets (Posner & Petersen, 1990). Attentional disengagement can be triggered by the onset of another stimulus (see, e.g. Hopfinger, 2005) or used in

a strategic, top-down manner, in anticipation of possible simultaneous or subsequent targets. No ERP component has yet been identified that may serve as a marker of attentional disengagement in the way that the N2pc serves as a marker of attentional engagement, perhaps because in most of these studies the use of single targets rendered swift disengagement unnecessary.

Lien and colleagues (2008) found that an N2pc evoked by an uninformative lateralized cue was followed within 100 ms by a positive component. They suggested that this ‘reversed N2pc’ might represent a compensatory shift of attention to correct for erroneous capture by the cue, and this interpretation was recently supported by (Seiss, Kiss, & Eimer, 2009). However, the notion that the N2pc reflects a shift of spatial attention instead of, or in addition to, attentional engagement has been disputed (Kiss, Velzen, & Eimer, 2008), leaving open the possibility that the reversed N2pc could reflect attentional disengagement rather than, or in addition to, a compensatory shift of attention. In the present study we put this possibility to a direct test.

We asked participants to detect multiple targets embedded in two lateralized rapid serial visual presentation (RSVP) streams, dividing attention between the two streams or focusing on one stream. We expected similar N2pc components for relevant targets in the focused- and divided-attention conditions (Kiss, Velzen, & Eimer, 2008), and because attentional capture should be followed by swift attentional disengagement, we expected to find a ‘disengagement component’ following the N2pc for targets in both conditions. As no shift of spatial attention is necessary in the focused-attention condition, finding such a component in that condition would challenge the notion that a reversed N2pc exclusively reflects corrective shifts of attention. We predicted that this component would be larger in the divided-attention than in the focused-attention condition for two reasons. First, as compared to the focused-attention condition, disengagement from a target in the divided-attention condition serves the additional purpose of restoring spatial attention to a divided state. Second, the average time separating two subsequent targets was shorter in the divided-attention condition. These differences can reasonably be expected to produce stronger, and perhaps also earlier, effects of top-down attentional disengagement in the divided-attention condition.

5.2 Experiment

5.2.1 Method

Participants. Fourteen healthy individuals (7 males) between the ages of 20 and 30 (mean 24.3 years, s.d. 4.9) participated in the experiment. The study adhered to the Declaration of Helsinki and was approved by the local ethics committee. Informed consent was obtained from all participants.

Stimuli and apparatus. Stimuli were presented on a 17" CRT monitor (800 x 600 pixels at 144-Hz). Stimuli were the distractor letters "A" through "K" and "P" and the target number "5". Two sequences of 60 distractors and targets were displayed on each trial, one in the left and one in the right visual field, 5.7° lateral to a central fixation point against a flickering background. The flickering background was included to test a secondary hypothesis not central to the thesis of the present work (see Toffanin et al., 2009). The stimulus sequences were randomized, with the constraint that repetitions and simultaneous presentation of a given character in the left and right display were not allowed. Characters were displayed in a blue (RGB: 0, 0, 255) Tahoma 48-point font (corresponding to a width of 1.4° and a height of 1.9° of visual angle), and were presented serially in the same spatial locations at a rate of six characters per s, with no inter-stimulus interval. In each sequence, the distractor letters A through K were each presented five times. Targets were not displayed in the first or last 500 ms of the stream, never appeared in pairs, and were separated from one another with a minimum inter-target interval of 1 s. The 1-s interval between target onsets was chosen to ensure that the N2pc and subsequent components triggered by target onsets did not overlap (see Figure 5.1 for a trial schematic). In the *focused-attention* conditions (attend left or attend right) 2, 3, or 4 targets were displayed on each side (for a total of 4, 6, or 8 targets). In the *divided-attention* condition (attend to both sides and respond to targets on both sides) 2, 3, 4, 6, or 8 targets were displayed on each trial. In order to equate stream length across trials, the letter "P" was added to the stream in place of a target as necessary. For the purposes of analysis, the unattended stream of the focused attention condition is referred to as the *ignored-attention* condition. With the exception of the three-target trials (in which two targets appeared on one side), potential targets were equally divided between the two sides of presentation.

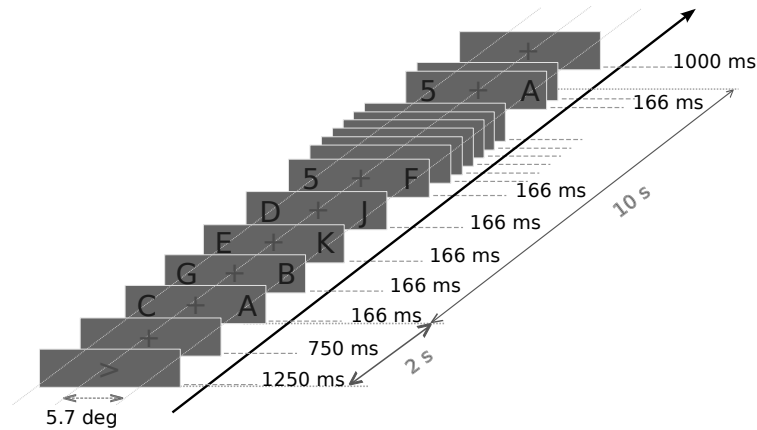


Figure 5.1: Schematic of a trial in which attention had to be focused on the RSVP displayed at the right location. A cue (the ‘>’ sign) was displayed for 1250 ms, and replaced by the fixation cross for 750 ms. Two RSVP streams (60 items each) were then displayed one to the left (5.7°) and one to the right of fixation with a presentation rate of 6 Hz. Participants had to respond to the digit 5 only when it appeared at the cued location. At the end of the RSVP display the fixation cross remained displayed for 1 second.

Procedure. Participants first received instructions on how to direct their attention to the left, right or both sides without moving their eyes and to respond as soon as detecting the digit 5 on the side or sides to be attended. A chin rest was used to ensure a constant viewing distance of 60 cm. Before the experimental trials began, each participant practiced the task in the focused-attention condition until a response accuracy criterion of 80% was reached (in general, 15 trials were sufficient to reach the criterion). A trial (see schematic in Figure 5.1), started with the presentation for 1 s of one or two red (RGB: 127, 0, 0) “arrows” (“<”, “>”, or “<>”) which indicated how attention should be directed (to the left, right, or both sides, respectively). After a 250-ms blank interval, and 750 ms before the presentation of the letter streams, a red fixation cross appeared in the center of the screen and remained on display for the duration of the trial (10 s). Participants pushed any key on the computer keyboard whenever they detected the number “5” on an attended side. Response hand was counterbalanced across participants.

Participants were naive as to the number of targets that would be displayed on each trial. After the presentation of the two sequences of alphanumeric characters, the red fixation cross remained in view for 1 s, after which the trial ended. No performance feedback was given. Eighteen trials were presented for each combination of number of targets in each attentional condition resulting in 54 trials for each of the focused and ignored attention conditions (54 focus left - ignore right, 54 focus right - ignore

left) and 90 trials for the divided attention condition. The entire experiment lasted approximately 1.5 h.

EEG recording. The EEG was recorded using an electro-cap with 64 tin electrodes. All scalp positions in the International 10-20 System were used, with additional sites located midway between the 10-20 locations and six electrode positions 10% inferior to the standard parieto-occipital electrodes (FT9, PO9, O9, FT10, PO10, O10). Averaged mastoids served as an off-line reference for the EEG signals. An electrode on the sternum was used for the subject ground. To monitor the electrooculogram (EOG), activity was recorded as bipolar input from the left and right horizontal eye channels and from the vertical channels positioned above and below the left eye.

ERP data processing. Epochs of 1 s were segmented starting 200 ms before and ending 800 ms after target onset. Only segments corresponding to a correct response (i.e., to a “hit” if the target was to be attended and was responded to or a “correct rejection” if the target was to be ignored and was not responded to) were considered. Epochs in which artifacts or vertical eye movements and blinks exceeded $\pm 80 \mu\text{V}$ of electrode activity and epochs in which horizontal eye movement exceeded $\pm 30 \mu\text{V}$ of electrode activity were excluded from further analysis (an average of 17.5% of segments was removed which, on average, left 182, 237, and 220 epochs for the analysis of the focused-, divided-, and ignored-attention condition respectively). ERPs were visually inspected on the averaged horizontal eye channel for activity above $3 \mu\text{V}$ to detect possible eye movements. The same procedure was adopted to control for redirection of gaze toward the side to be attended after the onset of the cue. None of the participants included in this dataset performed eye movements above the $3 \mu\text{V}$ threshold.

The 200-ms interval before target onset served as baseline. Segments were averaged before computing the mean voltage of the ERPs within a specified time window centered on the peak of interest. Grand-average waveforms (see Panel A Figure 5.2) served as a reference to set the time windows from which each ERP deflection was estimated. The N2pc was computed by averaging waveforms ipsilateral to target presentation across hemispheres and subtracting them from the average of the contralateral waveforms. N2pc amplitude (see Panel A, Figure 5.2) was estimated by computing the mean activity between 220-320 ms after target onset; the following component (which we refer to as P4pc: Positive, 400 ms post-target, Posterior, Contralateral) was estimated by computing the mean activity between 340-430 ms after target onset.

5.3 Results

For all ANOVAs of behavioural and EEG data, Greenhouse-Geisser epsilon correction was used to adjust p-values, whenever necessary to correct for possible violations of sphericity.

5.3.1 Behavioral results

Responses within 200-800 ms after target onset were classified as hits. The effect of attention condition (focused vs. divided) on percentage of hits and reaction times was tested with a dependent samples t-test with attention condition as a within-subject factor. The percentage of hits was higher in the focused- (86.2%) than in the divided- (82.8%) attention condition ($t(13) = 2.81, p < .016$). False alarms to distractors (less than .01% on average) and to-be-ignored-targets (less than .04% on average) were rare. Reaction times to hits were not affected by attentional condition (mean reaction times were 527 and 522 ms for the focused- and divided-attention conditions, respectively, $p > .9$).

5.3.2 Electrophysiological results

ERP amplitudes. Panels B, C, and D of Figure 5.2 show the grand averages of the contralateral and ipsilateral waveforms for the focused- (Panel B of Figure 5.2), divided- (Panel C of Figure 5.2), and ignored-attention conditions (Panel D of Figure 5.2), and Panel A of Figure 5.2 shows the differential waveforms (N2pc and P4pc) at the electrodes where the N2pc was maximal (PO7 and PO8). Attentional effects on the N2pc (220-320 ms after target onset) and P4pc (340-430 ms after target onset) amplitudes were tested with a repeated-measures ANOVA with attention condition (focused-, ignored-, or divided-) as a within-subject factor.

N2pc amplitude was affected by attention ($F(2, 26) = 22.6, p < .001, MSE = 5.6, \eta_p^2 = .635$). Pairwise comparisons (Bonferroni corrected) revealed that N2pc amplitude was higher in both the focused- and divided-attention conditions than in the ignored-attention condition ($ps < .001$), but did not differ between the focused- and divided-attention conditions ($p > .9$). N2pc amplitude in the ignored-attention condition differed significantly from baseline ($t(13) = 6.14, p < .001$). No effects on peak latency were found.

P4pc amplitude was also affected by attention condition ($F(2, 26) = 8.7, p < .003$,

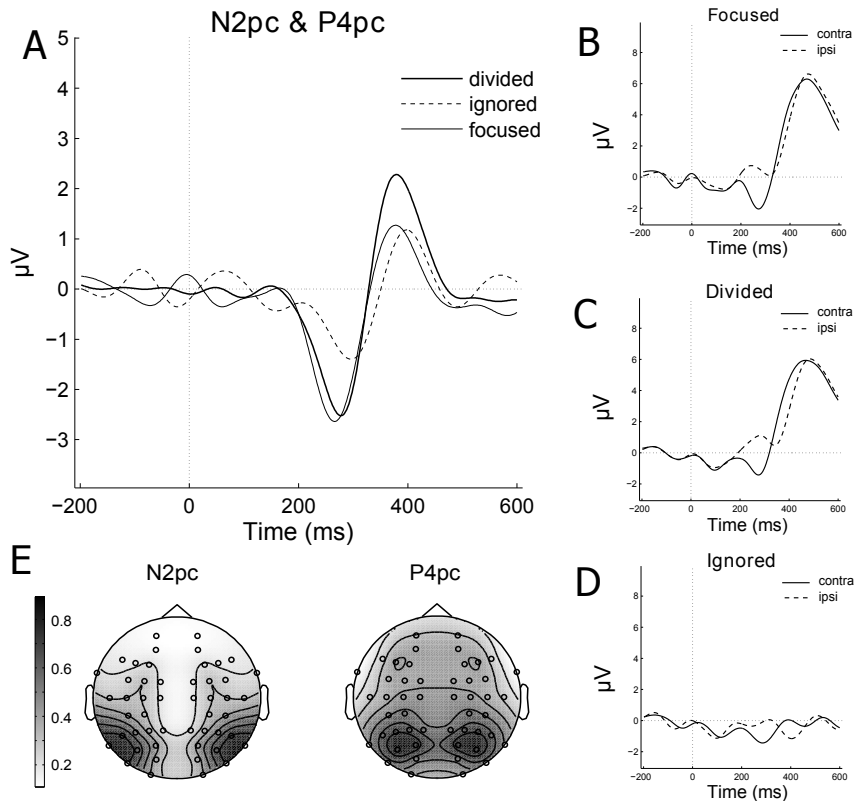


Figure 5.2: Panel A depict the differential waveforms, the N2pc and the P4pc, at electrodes PO7 and PO8. Panel E displays their rescaled topographies, in the divided-attention condition, note that the topographies in the focused- and ignored-attention condition were very similar to the one displayed here. Contra- and ipsi-lateral waveforms at PO7 and PO8 are shown in Panels B, C, and D, for the focused, divided, and ignored attention condition respectively. For display purposes N2pc and P4pc were filtered with a second-order (12 dB per octave) low-pass Butterworth filter with a cut-off frequency of 9 Hz. Note that to aid comparison of the N2pc and P4pc topographic maps, the polarity of the P4pc has been inverted.

MSE = 5, $\eta_p^2 = .4$). Pairwise comparisons revealed that P4pc amplitude was higher in the divided- than in either the ignored- ($p < .018$) or focused-attention condition ($p < .004$), and did not differ between focused- and ignored-attention conditions ($p > .9$). P4pc amplitude differed from baseline in both the focused- ($t(13) = 4.34$, $p < .002$) and ignored-attention conditions ($t(13) = 5.01$, $p < .001$). No effects on peak latency were found.

Scalp topographies of the N2pc and P4pc components are shown in Figure 5.2 Panel E. Topographies were obtained by mirroring the activity of the N2pc (left panel) and P4pc (right panel) across the two hemispheres. Differences in topographies were tested with an ANOVA with attention condition (focused-, divided-, or ignored-), elec-

trodes and components (N2pc or P4pc) as within-subjects factors. Before statistical testing, amplitudes were rescaled using a range normalization procedure (McCarthy & Wood, 1985). The ANOVA yielded main effects of electrode ($F(24, 312) = 31.2$, $p < .001$, $MSE = 16.6$, $\eta_p^2 = .71$) and component ($F(1, 13) = 24.9$, $p < .001$, $MSE = 7.1$, $\eta_p^2 = .66$). A significant Component \times Electrode interaction was obtained ($F(24, 312) = 8.4$, $p < .001$, $MSE = 3.6$, $\eta_p^2 = .4$), indicating different topographies for N2pc and P4pc¹. No other effects reached significance.

5.4 Discussion

Performance and EEG in focused-, divided-, and ignored-attention conditions with multiple targets were compared. Target detection accuracy was higher in the focused- than in the divided-attention condition, but no differences in detection speed between the conditions were observed. Attentional capture by targets elicited an N2pc, the amplitude of which was modulated according to instructional set (i.e., N2pc had the lowest amplitude in the ignored-attention condition). The N2pc was followed within about 110 ms by a second component of opposite polarity. The amplitude of this 'P4pc' component was higher in the divided- than in the focused- or ignored-attention condition.

The N2pc found for to-be-ignored targets indicates that targets in the irrelevant stream did capture attention, at least on a proportion of trials (for similar results, see Seiss et al., 2009). Interestingly, such targets completely failed to elicit a P300, suggesting a dissociation between target-selection processes reflected by the N2pc and target-categorization processes reflected by the P300 (Luck & Hillyard, 1994b). Significantly larger N2pcs were obtained for targets in the divided- and focused-attention conditions than for those in the ignored condition, reflecting modulated attentional capture as a function of instructions. No difference was found between the focused- and divided-attention conditions for N2pc amplitude, suggesting that the degree of target selection or attentional engagement in the divided- and focused-attention conditions was comparable. This finding replicates results by Kiss and coworkers (2008a) and supports their conclusion that the N2pc is unlikely merely to reflect lateral shifts of visuospatial attention (Woodman & Luck, 2003; Hickey, McDonald, & Theeuwes, 2006). It is also consistent with the relatively small (but significant) difference in

¹Because the overall differences in scalp topographies might reflect in large part differences at frontal location, we repeated the same analysis using only the 13 posterior electrodes. This analysis yielded similar results.

detection accuracy and lack of difference in detection speed between the conditions.

The P4pc showed a different pattern of results that seems well in line with the notion that it reflects attentional disengagement. P4pc amplitude was largest in the divided-attention condition and no significant differences in amplitude were found between the focused- and ignored-attention conditions. The presence of a significant P4pc in the focused-attention condition, in which there is no apparent need to shift attention to a different location, clearly indicates that disengagement as reflected by the P4pc does not need to involve such shifts. The larger P4pc in the divided-attention condition was predicted based on the idea that attentional disengagement in this condition serves the additional purpose of restoring spatial attention to a divided state after it has been captured by a target in one of the streams. This difference may also have been due in part to the average time separating two relevant targets being shorter in the divided-attention condition, making the need for swift disengagement more salient. The presence of a sizable P4pc for to-be-ignored targets, even when the N2pc indicated infrequent or weak attentional capture by such targets, seems consistent with the obvious need to disengage attention and redirect attention to the relevant stream after erroneous capture (see also Lien et al., 2008; Seiss et al., 2009).

Alternative interpretations. Whereas the present results are consistent with the notion that the P4pc reflects attentional disengagement, other interpretations are possible. In the following we will discuss a number of relevant studies that have investigated the N2pc component and either have or have not found evidence for a P4pc-like component, and consider whether their results are consistent with our interpretation or may suggest alternative ones.

Most N2pc studies have employed search paradigms with a single array that contained at most one target and relatively long intertrial intervals. Thus they imposed little need for swift attentional disengagement after the target had been processed and therefore no P4pc should have been triggered (see e.g. Kiss, Jolicoeur, Dell'acqua, & Eimer, 2008). As mentioned earlier, both Lien et al. (2008) and Seiss et al. (2009) found clear P4pc components that they interpreted as reflecting a corrective shift of attention after attention had been wrongly captured by an irrelevant cue or a stimulus in the irrelevant hemifield. This interpretation of the P4pc is supported by results from Woodman and Luck (1999; 2003; for a similar finding, see Hickey et al., 2006). Using a paradigm that promoted sequential shifts of attention either within or between hemifields, Woodman and Luck found a P4pc-like component, which they referred

to as an inverted N2pc, following an initial N2pc only for shifts between hemifields. Their results clearly show that shifts of visuospatial attention can contribute to what we call the P4pc component. As noted before, the presence of a significant P4pc in our focused-attention condition indicates that such spatial shifts cannot be the exclusive cause of the P4pc. However, because shifts of visuospatial attention after attentional capture by a target may have occurred in the divided- and ignored-attention conditions of our experiment, the larger P4pc amplitude in the divided-attention condition and the P4pc for to-be-ignored targets may have been caused, at least in part, by such shifts of attention.

Given that most N2pc studies have used search tasks in which the search array was displayed until response, the possibility that the P4pc in the present study somehow resulted from the targets being embedded in RSVP streams requires consideration. For instance, distractors in the RSVP paradigm act as masks, and the literature presents some suggestive evidence that the presence of a mask following a target may produce P4pc-like components in the ERP. For example, Brisson and Jolicoeur (2007a) used an auditory-visual psychological refractory period (PRP; e.g. Smith, 1967) task in which the second visual stimulus was masked, and they found a P4pc-like component following the initial N2pc. When they used a similar paradigm, but without the mask, they again found the N2pc but no subsequent P4pc-like component (Brisson & Jolicoeur, 2007b, for similar results see Experiment 4 and 5 in Leblanc et al., 2008). However, the combined results from three recent studies that measured the N2pc in an RSVP task strongly argue against the possibility that the present P4pc results represent artifacts due to targets being embedded in RSVP streams. Each of these studies (Dell'Acqua et al., 2006; Jolicoeur et al., 2006a; Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006b) focused on the N2pc elicited by the second of two targets, and each study found this N2pc component but, importantly, no subsequent P4pc component despite the fact that the second target was always followed by at least one distractor. The absence of the P4pc in these studies is consistent with the notion that this component reflects attentional disengagement. Because participants knew that a trial contained only two targets they also knew that no swift disengagement from the second target was necessary.

It could also be argued that the P4pc might merely reflect latency and/or amplitude differences in ipsi- and contralateral P300 (see Panels B, C, and D of Figure 5.2). However, the scalp distribution of P4pc in the present study was markedly different from, and more posterior than, that of P300. Also, a clear P4pc but no P300 was

present in the ignored-attention condition. Thus, like the N2pc, the P4pc seems to constitute a genuine component. The similarities between the occipitotemporal scalp topographies of the N2pc and P4pc suggest that the two components reflect opposite effects on neural activity in largely overlapping neural substrates in visual cortex (for similar results, see Woodman & Luck, 1999). The significant topographical differences between the two components may reflect that attentional engagement results from an interaction between top-down biasing information (for instance, in the focused condition a combination of target-defining features and relevant location) and bottom-up input (see e.g. Olivers & Meeter, 2008), whereas strategic disengagement can be initiated by strictly top-down means (e.g. Posner, Walker, Friedrich, & Rafal, 1984).

To summarize, as for the N2pc component, a potential contribution of visuospatial attentional shifts to the P4pc must be recognized, but as the present results indicate, such shifts cannot be the sole cause of these components (see also Kiss, Velzen, & Eimer, 2008). The hypothesis that the P4pc reflects, at least in large part, top-down attentional disengagement, can not only explain the present results, but also provides a reasonably coherent account of the presence or absence of this component in the ERP literature. The P4pc may provide an important tool for the investigation of the nature and dynamics of strategic control of visuospatial attention in complex visual environments with multiple spatially or temporally distributed sources of information.

Intellectual understanding is one of the best versions of the Golden Rule: Listen to others as you would have others listen to you. Precise demonstration of truth is important but not as important as the communal pursuit of it. Put in terms of Kant's categorical imperative, When addressing someone else's ideas, your obligation is to treat them as you believe all human beings ought to treat one another's ideas.

Wayne C. Booth

6.1 Strategic Resources Allocation: How More Isn't Less

The neural efficiency hypothesis (Vernon, 1993) states that more intelligent people can perform the same task as less intelligent individuals using less of their brain's processing capacity. Many studies (e.g., A. P. Anokhin et al., 1999; Jausovec & Jausovec, 2004a; Neubauer et al., 1995) have reported evidence supporting the neural efficiency hypothesis in the form of a negative correlation between brain activation and intelligence. However, none of these studies considered that different individuals may also adopt different strategies to perform the same task. Different strategies can lead to the same performance (so that no differences in response accuracy and/or speed are found), but may still yield differences in brain activation (e.g., Petersen et al., 1998). In this case, the differences in brain activation would be due to the adoption of different strategies but not to intelligence differences. The study reported in Chapter 2 was conducted to determine whether evidence for intelligence-related differences in neural processing would be found when strategy was controlled for.

The critical comparison in the experiment reported in Chapter 2 was between the levels of brain activity of groups of high- and low-IQ individuals performing a sentence verification task using the same strategy. It was reasoned that the neural efficiency hypothesis predicts that if the brain activity of the high-IQ group will be lower than that of the low-IQ group even when strategies are controlled for. A finding

of no differences in the level of brain activation between the two groups would favour the conclusion that individual differences in brain activities related to intelligence may have been confounded with differences in strategy choices.

Task performance was found to depend on the level of cognitive ability. The overall superior task performance of high cognitive ability individuals was evident in faster and more accurate performance relative to that of individuals of low cognitive ability. However, the patterns of brain activity emerging from the analysis of the EEG did not sustain the claims of the neural efficiency hypothesis, showing no differences between individuals of high and low cognitive abilities during the actual execution of the task. Electroencephalogram analysis did, however, show differences in spatio-temporal activation patterns which depended on the strategy with which the groups of participants had been instructed to perform the task. Taken together, the latter two findings highlight the need to control for potential confounding of intelligence and strategy use in individual differences research and suggest that differences in brain activity patterns emerging from groups characterized by different levels of cognitive abilities must be interpreted with caution.

Consistent with the superior behavioral performance of high cognitive abilities individuals, a specific phasic decrement in alpha ERD before the beginning of each trial was observed in individuals of high cognitive abilities, but was absent in individuals of low cognitive abilities. This phasic increment in alpha rhythm can, following the suggestion of previous researches that phasic increments in alpha rhythm reflect active inhibitory control of task-irrelevant brain areas (see e.g., N. R. Cooper et al., 2003; Klimesch, 1999) or the suppression of the flow of irrelevant information (see e.g., Jensen, Gelfand, Kounios, & Lisman, 2002; Fink, Grabner, Benedek, & Neubauer, 2006) be interpreted in terms of better preparatory control by higher ability persons. The increment in alpha power reported in Chapter 2 was observed prior to stimulus onset, independent of the strategy that had to be used to resolve the comparison, and especially because it was not directly linked with any of the processes required to perform the task, it was interpreted as active suppression of residual information pertaining to previous comparisons which could have interfered when executing the forthcoming comparison.

The absence of individual differences in EEG activity during task execution and of the presence of differences in EEG activity in the preparation interval suggests that individuals of high and low IQ may adopt different policies in the allocation of resources. This conclusion is supported from the high-IQ group's phasic increase in

alpha power during the preparation interval which, likely, reflects a process of adequate, or adequately timed, preparatory activity (see Jong, 2000). In conclusion, the findings reported in Chapter 2 suggest a link between temporal allocation of resources, individual differences, and brain activity, but suggest caution in interpreting individual differences in information processing as evidence of differences in processing efficiency. The absence of brain activity differences between the two IQ groups when executing the task using the same strategy suggests that being more intelligent does not imply that the brain is used less.

6.2 Attention Allocation Policy Millisecond-by-Millisecond

Chapters 3 and 4 used frequency tagging as a method to link behavioral measures of the amount of attentional resources allocated to a spatial location or a specific task to a physiological index. Frequency tagging is an EEG method based on the steady state evoked potential (SSEP; Regan, 1989) and is made up of a series of physiological responses to a frequency modulated stimulus. The SSEP is well-defined in the frequency domain because the presentation rate of the sensorial stimulation defines the frequency of the SSEP. SSEP amplitude is enhanced when attention is directed to the object inducing it as compared to when that object is ignored (M. M. Muller, Picton, et al., 1998). Frequency tagging is a profitable technique in comparison with traditional techniques of brain imaging such as fMRI or EEG and ERPs because it is relatively insensitive to noise, allows the quantification of sustained attention and keeps separate the electrophysiological responses associated with separate, simultaneously displayed, stimuli.

Chapter 3 is a report of an experiment designed to test whether the amplitude of the visual SSEP (SSVEP) is sensitive to the graduated deployment of attention necessary to distribute attention across two spatial locations (i.e., divided attention) or to fully focus on one spatial location and simultaneously ignore the other spatial location. Also, because it has been suggested that the attention effect on the SSVEP may depend on the tagging frequency used (Ding et al., 2006), six different frequencies were included to study the effects of frequency tagging on the attention effect on the SSVEP.

The results showed that the amplitude of the SSVEP elicited by the frequency tag was linearly related to the amount of attention deployed to a spatial location (i.e., it was highest in the focused- and smallest in the ignored-attention condition, with the divided-attention condition falling between the two). The gradual changes

in SSVEP amplitude were consistent with the participants' behavioral performance, which showed divided-attention costs when detection performance was compared between focused- and divided-attention conditions. The coherent pattern of attention effects on behavioral performance and physiological responses links SSVEP amplitude with the allocation of processing resources (in that SSVEP amplitude and target detection are highest when attention is fully focused on one location, gradually decrease when attention is shared between two locations, and are minimal when attention is fully focused on another location).

No evidence was found to support Ding et al. (2006) claim that the choice of tagging frequency influences the attention effect on SSVEP amplitude. Interestingly, it emerged that tagging frequency may affect behavioral performance (i.e., divided attention costs tended to increase as tagging frequency increased). This finding, combined with negative correlations between the attention effects on SSVEP amplitudes between high (e.g., 23 Hz) and low (below 17 Hz) tagging frequencies, was interpreted as evidence of differential contributions of the magno- and parvo-cellular systems to the perception of the flickering background used to induce the SSVEP. The magno- and parvo-cellular systems are sensitive to different ranges of temporal frequencies (see e.g., Levitt et al., 2001), with the parvo-cellular system being relatively blind to oscillation at high frequencies (i.e., above 20 Hz). It is thus likely that faster tagging frequencies were perceived as being more stable and uniform than lower frequencies, making target detection easier than in conditions where the tagging frequency was lower. However, the differential contributions of the magno- and parvo-cellular systems to the ability to detect a target were not systematically tested in Chapter 3 such that more research will be necessary to address whether there is a causal relationship between involvement of the separate visual systems and target detection.

Chapter 4 is a report of an experiment using frequency tagging in a cross-modal task with simultaneous auditory and visual stimuli to address from an electrophysiological perspective the longstanding controversy between accounts supporting the view of attentional resources as a general capacity (see e.g., Navon & Gopher, 1979) versus that of resources as modality specific and independent pools (e.g., Wickens, 1984). Moreover, the study aimed to (1) further explore the sensitivity of frequency tagging to attentional modulation by asking participants to divide their attention between an auditory and a visual object in different percentages (i.e., 100-0%, 80-20%, 50-50%) and (2) to establish if divided-attention costs in detection and discrimination tasks share a central locus or are traceable to different loci (e.g., perceptual limitations

for detection tasks and a central bottleneck for discrimination, see e.g., Duncan, 1980).

Gradual changes in SSEP amplitude as a function of attention allocation were found, supporting the view that SSEP amplitude is linked to the amount of attention allocated to an object or location. The effects of attention on SSEP amplitude were generally similar between the detection and discrimination tasks, suggesting that attentional strategies and mechanisms are likely the same in detection and discrimination tasks (see also, Bonnel et al., 1992; Bonnel & Hafter, 1998). The fact that the amplitude of the SSVEP was highest in the divided- as compared to the focused- and ignored-attention conditions can be interpreted as evidence supporting the multiple resources theory (Wickens, 1984), where different modalities have at their disposal independent resource pools. However, such a conclusion may be too hasty given that there were no attentional effects on the amplitude of the ASSR estimated from central electrodes, suggesting that the ASSR is not sensitive to attentional modulation (Linden et al., 1987; but see Ross, et al., 2004 or Saupe et al., 2009). It should be noted, however, that there could be other reasons for the absence of attention modulation such as, for example, the nature of the stimuli used (a recent study by Ross et al., 2005b, showed that the onset of single clicks presented to the auditory channel other than the one where the frequency tag was presented disrupted the ASSR).

Even though no evidence of attentional modulation of the amplitude of the ASSR at central electrodes was found, such effects were found for occipital electrodes. This suggests that there is interplay between visual and auditory information when both must be attended to (see e.g., Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Stein & Stanford, 2008). The evidence of interplay between auditory and visual information was, however, assymetric. No evidence of amplitude modulation in the SSVEP measured at auditory processing areas was found.

One of the most remarkable findings of the present research becomes evident when the results from Chapter 3 and Chapter 4 are combined. In both of these studies, divided attention costs were evident in terms of worse performances in the divided- than in the focused-attention condition. However, amplitude modulation of the SSVEP as a function of attention was not consistent across the two studies. In the experiment reported in Chapter 3, with two visual stimulus streams and an identification task, SSVEP amplitude in the divided-attention condition was between that of the focused- and ignored-attention conditions, whereas in the experiment reported in Chapter 4, with a visual and an auditory stimuli in both detection and discrimination tasks, SSVEP amplitude was highest in the divided-attention condition. This dissoci-

ation of performance and SSVEP amplitude suggests that the SSVEP is sensitive to more than resource allocation alone.

6.3 Resources and attention control

Chapter 5 addressed the role of top-down control on the allocation of attention, and, in particular, the disengagement of attention. Attention disengagement becomes especially relevant when successive targets must be processed and attention must be released from one item to focus on another (see e.g., Posner & Petersen, 1990). The presence of an ERP component reflecting the disengagement of attention was predicted based on the existence of an ERP component, the N2pc (N2-posterior-contralateral), linked to attentional capture (e.g., Kiss, Velzen, & Eimer, 2008). The N2pc can be assumed to reflect the engagement of attention to one object or location. Therefore an ERP component reflecting the disengagement of attention, if it exists, should follow the N2pc. Because disengagement is a process reflecting top-down control rather than being exogenously driven we designed an experiment where participants had to focus or divide attention between two locations. Although timely attentional disengagement is important in both focused- and divided-attention conditions, we predicted that this component would be smaller in the focused- than in the divided-attention condition because in the divided-attention condition spatial attention had to be restored to a divided state.

ERP analyses showed a target-elicited N2pc in all three attention conditions (focused, divided and ignored, where ignored is the location opposite to the location to be focused on), confirming that items that possessed target-defining features captured attention (Luck & Hillyard, 1994a) even when they appeared in the irrelevant stream. Interestingly, to-be-ignored items completely failed to elicit a P300, suggesting a dissociation between the target-selection processes reflected by the N2pc and the target-categorization processes reflected by the P300 (Luck & Hillyard, 1994a). Significantly larger N2pcs were obtained for targets in the divided- and focused- attention conditions than for those in the ignored condition, reflecting modulated attentional capture as a function of instructions. No difference was found between the focused- and divided-attention conditions for N2pc amplitude, which replicates the findings of Kiss, Velzen, and Eimer (2008) showing that the N2pc is not linked to spatial shifts of attention, and suggesting that the degree of target selection or enhancement in the divided and focused conditions was comparable. This finding is consistent with the

relatively small (but significant) difference in detection accuracy and lack of difference in detection speed between the conditions.

The P4pc showed a different pattern than that of the N2pc, but one that seems well in line with the notion that it reflects attentional disengagement. The largest P4pc amplitudes were found in the divided-attention condition and no significant differences in amplitude were found between the focused- and ignored-attention conditions. The presence of a significant P4pc in the focused-attention condition indicates that disengagement from a selected target can be purely time-based and does not need to involve moving attention to a different location. The larger P4pc in the divided attention condition was predicted based on the idea that attentional disengagement in this condition serves the additional purpose of restoring spatial attention to a divided state. This difference may also have been due in part to the average time separating two relevant targets being shorter in the divided-attention condition, making the need for swift disengagement more salient. The presence of a sizable P4pc for to-be-ignored targets, even when the N2pc indicated infrequent or weak attentional capture by such targets, seems consistent with the obvious need to disengage attention and redirect attention to the relevant stream after erroneous capture.

The evidence presented in Chapter 5 supports the claim that the P4pc component may provide an electrophysiological marker of strategic, top-down controlled disengagement of attention from lateralized visual targets. The availability of such a marker may provide an important tool for the investigation of the nature and dynamics of strategic control of visuospatial attention in complex visual environments with multiple spatially or temporally distributed sources of information.

English Summary

Short Summary

When resources (e.g., attention or memory) are scarce the human cognitive system must solve the economic problem of resource allocation. We used electroencephalography to examine the time course of the allocation of resources in the brain in hopes of revealing the routines adopted by the human-processing system when managing its resources. We first focused on individual differences in resource management. In this regard we found that individuals of low- and high-IQ did not differ in the amount of available resources. Rather they differed in the timing with which they allocate them, with high-IQ individuals choosing the most beneficial moment. We then examined resource allocation policies in dual-task situations. Using frequency tagging, a method which can provide distinct physiological responses for tasks that are executed simultaneously, we found that the amplitude of each response reflected the amount of resources allocated to a task. Moreover, the evidence suggested different allocation policies when multiple stimuli were presented within one modality (resource-sharing) versus when they were presented in different modalities (resource-addition). Finally, we examined the processes of active control which are involved in resources allocation. An electrophysiological marker for attention disengagement was identified, which has the potential to serve as an important tool for studying attention control.

Brain Economics: Housekeeping routines in the brain

Human performance is limited. This is obvious, for example, when driving a car and simultaneously conversing with a passenger. Whereas this is possible in normal traffic conditions, performance on one or both tasks will degrade as soon as the demands of the concurrent tasks change, resulting in a disrupted conversation when

driving in a busy city center or in poor driving performance when the conversation gets more intriguing (see, e.g., Wickens, 1984).

The observation that performance on concurrent tasks depends on the amount of attention allocated to the tasks led to the idea that, at any moment, the human system possesses a finite amount of processing resources to perform one or more tasks (see, e.g., Norman & Bobrow, 1975). Since the introduction of the concept of resources, numerous studies (for a review see, e.g., Sanders, 1997) have been conducted to better understand the economic principles guiding resource management in the human-processing system (see, e.g., Navon & Gopher, 1979).

A common approach to the study of performance costs on the execution of concurrent tasks is dual-task paradigms, which measure the interference between different tasks when they must be performed simultaneously and therefore compete for the available resources (see, e.g., Kahneman, 1973). Important questions addressed by these studies are: What task has priority? How is priority attributed? How can multiple tasks be simultaneously accomplished? Does a plausible neural correlate for the concept of resource exist?

In this dissertation the focus was on resource allocation policies and resource management, especially in trying to identify a plausible neural counterpart for the concept of resources and for the mechanisms involved in resource allocation. Because the management of resources and the dynamics of resource allocation occur on the fly, a technique which permits the observation of changes in brain activity millisecond by millisecond must be employed in order to capture the time course of these changes at a neurophysiological level. Electroencephalography (EEG) is a neuro-imaging technique which allows the observation of the rapid changes in brain states which may correlate to dynamic resource management in the brain.

Given that resource allocation is a complex problem, the study of its dynamics was approached in a threefold manner: (1) Investigating potential sources of resources allocation between individuals of different IQ, (2) developing an EEG technique to objectively measure the amount of brain resources allocated to two concurrent tasks, and (3) searching for an electrophysiological marker reflecting the processes of active control which govern the mechanisms of resources allocation.

In the first approach (reported in Chapter 2) individuals with different levels of cognitive abilities were tested in a simple cognitive task (the sentence verification task, see, e.g., Clark & Chase, 1972) to investigate whether correlations exist between higher cognitive abilities and brain activity as measured by EEG. Because individ-

uals of different IQ levels might adopt different resource allocation policies—which should not be mistaken with the development of different strategies to solve the task at hand—the experiment reported in Chapter 2 measured EEG while participants were rigorously instructed to perform the task using identical strategies.

The analysis focused on possible IQ-related and strategy-related differences in brain rhythms. Results showed that task performance depended on IQ level, with high-IQ individuals performing faster and more accurately than low-IQ individuals. The patterns of brain activity emerging from the EEG analysis showed no differences between individuals of high- and low-IQ individuals during the actual execution of the task. Some differences in spatio-temporal EEG patterns were present, but these depended on the strategy with which the groups of participants had been instructed to perform the task. Taken together, these findings highlight the need to control for potential confounding of intelligence and strategy use in individual differences research and suggest that differences in brain activity patterns emerging from groups characterized by different levels of cognitive abilities must be interpreted with caution.

Another interesting finding from the experiment reported in Chapter 2 was that there was a specific phasic increment in alpha rhythm before the beginning of each trial in high-IQ individuals, but not in low-IQ individuals. This phasic increment in alpha rhythm can be interpreted as a difference in preparation to the task between high- and low-IQ individuals. Because this increment in alpha power was observed prior to stimulus onset—independent of the strategy that had to be used to execute the task—and especially because it was not directly linked with any of the processes required to perform the task, it can be assumed to represent a genuine intelligence-related difference.

In Chapters 3 and 4 two experiments are reported in which resource management in the brain is studied using an approach which attempted to establish a more direct link between allocation of resources and EEG applying frequency tagging¹, an innovative methodology which permits to visualize the dynamics of resource allocation when multiple tasks are performed simultaneously and attention is divided between them. Chapter 3 addressed the competition for resources within the visual modality (i.e., unimodal attention), where two locations had to be monitored simultaneously,

¹Frequency tagging is a technique that quantifies a physiological response, the steady state evoked potentials, which is made up from the series of evoked responses associated with the repetitive presentation of a simple stimulus (e.g., a white square). Main advantage of the frequency tagging technique is that it is relatively insensitive to noise, allows the quantification of sustained attention, and keeps separate the electrophysiological responses associated with separate, simultaneously displayed, stimuli.

or one attended and the other ignored. Moreover, in Chapter 3 it was tested whether the hypothesis of Ding et al. (2006) that the attention effect on the amplitude of the steady-state visual evoked potential (SSVEP, which is the electrophysiological response measured when frequency tagging is employed) depended on the tagging frequency used. The results showed a linear relationship between the amplitude of the SSVEP elicited by the frequency tag and the amount of attention deployed to a spatial location, which implies the adoption of a resources-sharing policy in unimodal divided attention (see e.g., Bonnel & Miller, 1994). Moreover, these effects were independent on the frequency chosen to evoke the SSVEP.

The experiment reported in Chapter 4 used frequency tagging in a multimodal divided attention task in which auditory and visual stimuli were presented simultaneously, each stimulus evoking a steady state evoked response independent from the stimulus presented in the other modality. The experiment reported in Chapter 4 aimed to address from an electrophysiological perspective the controversy between accounts supporting the view of attentional resources as a general capacity (see e.g., Navon & Gopher, 1979) versus that of resources as modality specific, independent pools (see e.g., Wickens, 1984). Moreover, the study aimed to (1) further explore the sensitivity of frequency tagging to attentional modulation by asking participants to divide their attention between an auditory and a visual object in different percentages (i.e., 100-0%, 80-20%, or 50-50%) and (2) to establish if divided-attention costs in detection and discrimination tasks share a central locus or are traceable to different loci (e.g., perceptual limitations for detection tasks and a central bottleneck for discrimination tasks, see e.g., Duncan, 1980).

The results supported the view that SSVEP amplitude is linked to the amount of attention allocated to an object or location, showing gradual changes in SSVEP amplitude as a function of attention allocation. Absence of SSVEP amplitude differences between detection and discrimination tasks suggested that attentional strategies and mechanisms involved in these tasks may be the same (see also Bonnel et al., 1992; Bonnel & Hafter, 1998). Also, the attentional modulation of the amplitude of the auditory steady-state evoked potential at occipital electrodes, which register activity from the visual areas (see, e.g., Russo et al., 2007), suggested the presence of interplay between visual and auditory information when both must be attended to, which is a clear example of multisensory integration².

²Multisensory integration is reflected in enhanced sensitivity to environmental events when their occurrence is signaled simultaneously through more than one sensorial stimulus. For example, a train approaching is signaled

One of the most remarkable findings of the present research becomes evident when the results from Chapter 3 and Chapter 4 are combined. In both of these studies, divided attention costs were observed in terms of worse performances in the divided- than in the focused-attention condition. However, amplitude modulation of the SSVEP as a function of attention was not consistent across the two studies. In the experiment reported in Chapter 3, with two visual stimulus streams and an identification task, SSVEP amplitude in the divided-attention condition was intermediate to that of the focused- and ignored-attention conditions, whereas in the experiment reported in Chapter 4, with a visual and an auditory stimuli in both detection and discrimination tasks, SSVEP amplitude was highest in the divided-attention condition. The difference in SSVEP amplitude in divided attention condition between unimodal and multimodal tasks suggests that the SSVEP is sensitive to more than resource allocation alone and could be seen as support for Wicken's (1984) multiple-resources view of attention.

In Chapter 5 the focus was on voluntary aspects of the control of resources allocation and testing the existence of a neural correlate linked to the active process of attentional disengagement (i.e., the prompt release of attention from the object which has just captured attention when temporally close targets must be detected, see, e.g., Posner & Petersen, 1990). Because the capture of attention by a target is reflected by a specific event-related potential (ERP), the N2pc (N2-posterior-contralateral, see, e.g., Kiss, Velzen, & Eimer, 2008), the release of attention from a target should also be related to a specific ERP component. Chapter 5 reports such an ERP component after the N2pc, which we called P4pc, and interpret as a ERP-correlate of disengagement. The availability of such an electrophysiological marker may provide an important tool for the investigation of the nature and dynamics of strategic control of visuospatial attention in complex visual environments with multiple spatially or temporally distributed sources of information.

In conclusion, the work reported in this thesis links electrophysiological indexes to the processes involved in the management of resources. This link has been substantiated by (1) evidence showing that individual differences in resources allocation are linked to specific neural correlates, (2) providing a method to estimate the amount of resources allocated to concurrent tasks, and (3) identifying an electrophysiological marker of attention disengagement, a processes of voluntary attention control. These contributions will help to comprehend and reveal the economic routines behind human

both by the visual percept created by the train's shape and color, and by the auditory percept created by the train noise (for reviews see e.g., Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Rowland & Stein, 2008; Stein & Stanford, 2008).

cognitive behavior.

Nederlandse samenvatting

Vertaald uit het Engels door Marleen B. Schippers

Korte Samenvatting

Als het menselijke cognitieve systeem slechts beperkte hulpbronnen (zoals aandacht en geheugen) ter beschikking heeft, moet er een keuze gemaakt worden over de toekenning hiervan. We hebben gebruik gemaakt van elektro-encefalografie (EEG) om te onderzoeken wat voor routines de hersenen gebruiken om deze hulpbronnen toe te wijzen en te beheren. Als eerste hebben we ons gericht op de individuele verschillen in het beheer van hulpbronnen. Hierbij vonden we dat individuen met een laag of hoog IQ niet van elkaar verschilden in de hoeveelheid beschikbare hulpbronnen. Zij verschilden echter wel van elkaar voor wat betreft het moment waarop zij deze toewezen, waarbij proefpersonen met een hoog IQ dat op het meest optimale moment deden. Hierna hebben we onderzocht hoe de toewijzing van hulpbronnen verloopt gedurende het uitvoeren van een dubbele taak. Door gebruik te maken van frequentie markering, een methode die (onderling) verschillende fysiologische reacties kan onderscheiden voor simultaan uitgevoerde taken, zagen we dat de amplitude van elke reactie aangeeft hoeveel hulpbronnen waren toegewezen aan die taak. Bovendien suggereerden de resultaten dat er een verschillend manier van toewijzen plaatsvond als meerdere stimuli binnen n modaliteit gepresenteerd werden (gedeelde hulpbronnen), vergeleken met wanneer zij in verschillende modaliteiten gepresenteerd werden (samengevoegde hulpbronnen). Tenslotte onderzochten we de processen die zorgen voor het actieve beheer tijdens het toewijzen van hulpbronnen. We vonden een elektro-fysiologische markering die aangeeft wanneer de aandacht wordt losgekoppeld. Deze markering is in potentie een belangrijk nieuw hulpmiddel bij het bestuderen van het beheer van aandacht.

Hersen-economie: huishouden in het brein

Het vermogen van mensen om informatie te verwerken is beperkt. Dit wordt bijvoorbeeld duidelijk als we tijdens het besturen van een auto een gesprek voeren met een passagier. In normale verkeersomstandigheden is dat goed te doen, maar de prestaties op één of beide taken nemen af op het moment dat die veeleisender worden. Zo breekt de conversatie af tijdens het rijden in een druk stadscentrum of, als het gesprek erg interessant is, gaat iemand fouten maken in het verkeer (zie o.a., Wickens, 1984).

De vaststelling dat de prestatie op twee gelijktijdige taken afhankelijk is van de hoeveelheid aandacht die eraan gegeven wordt, heeft geleid tot het idee dat het menselijke verwerkingssysteem op elk moment slechts een beperkt aantal hulpbronnen ter beschikking heeft (zie o.a., Norman & Bobrow, 1975). Sinds de introductie van het concept 'hulpbronnen' zijn talloze experimenten uitgevoerd (voor een overzicht, zie Sanders, 1997) om de economische principes achter het beheer ervan in het menselijke verwerkingssysteem te begrijpen (zie o.a., Navon & Gopher, 1979).

Een veel gebruikte aanpak bij het bestuderen van de uitvoering van gelijktijdige taken is het paradigma van de dubbeltaak. Met dit paradigma worden de verstoringen van beide taken gemeten terwijl zij tegelijkertijd worden uitgevoerd en daardoor met elkaar strijden om de beschikbare hulpbronnen (zie o.a., Kahneman, 1973). Belangrijke vragen hierbij zijn: Welk taak heeft prioriteit? Hoe wordt deze prioriteit bepaald? Hoe kunnen twee taken tegelijkertijd uitgevoerd worden? Bestaat er een plausibele neurale correlaat voor het concept van hulpbronnen?

Dit proefschrift bestudeert zowel de strategieën in het toewijzen van hulpbronnen aan een bepaalde taak als het beheer van deze hulpbronnen. Met name wordt getracht een plausibele neurale correlaat te vinden voor de hulpbronnen en voor de mechanismen die de hulpbronnen toewijzen. Het beheer van hulpbronnen en de dynamiek van de toewijzing ervan vinden in erg korte tijd plaats. Om dit op neurofysiologisch niveau te kunnen volgen, is een techniek nodig die veranderingen in hersenactiviteit in de orde van grootte van milliseconden kan vastleggen. Elektro-encefalografie (EEG) is zo'n visualisatietechniek. Daarmee kunnen snelle veranderingen in neurale processen zichtbaar gemaakt worden die mogelijk samenhangen met het dynamische beheer van hulpbronnen in het brein.

Het toekennen van hulpbronnen is een complex probleem. Daarom is de studie naar de dynamiek ervan uitgevoerd in drie delen: (1) onderzoek naar verschillen in de

toekenning van hulpbronnen tussen individuen met een verschillend IQ, (2) ontwikkelen van een EEG techniek die de hoeveelheid hulpbronnen kan bepalen die worden toegekend aan twee gelijktijdige taken, en (3) onderzoek naar een elektrofysiologische markering voor de mechanismen van het beheer van hulpbronnen.

In de eerste aanpak (uiteengezet in hoofdstuk 2) werden individuen met verschillende cognitieve vaardigheden getest op een simpele cognitieve taak (de “sentence verification” taak, zie o.a., Clark & Chase, 1972). Hiermee werd onderzocht of er correlaties bestaan tussen hogere cognitieve vaardigheden en hersenactiviteit zoals gemeten met EEG. Omdat individuen met verschillend IQ verschillende toewijzingsstrategieën zouden kunnen gebruiken (niet te verwarren met verschillende oplossingsstrategieën van de taak zelf), werden de proefpersonen in het experiment van hoofdstuk 2 strikt geïnstrueerd om de taak uit te voeren met een identieke strategie.

De analyse was gericht op de relatie tussen hersenritmes enerzijds en IQ en gehanteerde strategie anderzijds. De resultaten lieten zien dat taakprestatie afhangt van het IQ, waarbij individuen met een hoger IQ sneller en beter presteren dan individuen met een laag IQ. De patronen van hersenactiviteit die tevoorschijn kwamen uit de EEG analyse lieten geen verschillen zien tussen individuen met een hoog en laag IQ gedurende de uitvoering van de taak. Er waren wel enkele verschillen in spatieel-temporale patronen, maar deze bleken afhankelijk van de strategie waarmee de proefpersonen waren geïnstrueerd om de taak uit te voeren. Samengevat laten deze bevindingen zien dat in onderzoeken naar individuele verschillen rekening gehouden moet worden met factoren als intelligentie en oplossingsstrategieën, omdat deze de experimentele condities kunnen beïnvloeden. Daarnaast laten ze zien dat verschillen in hersenactiviteit tussen groepen proefpersonen met verschillende cognitieve vaardigheden met de benodigde voorzichtigheid moeten worden geïnterpreteerd.

Een andere interessante bevinding van het experiment uit hoofdstuk 2 was de specifieke fasevermeerdering in het alfaritme voorafgaande aan elke taak in individuen met een hoog IQ, maar niet in individuen met een laag IQ. Deze fasevermeerdering in alfaritme kan worden geïnterpreteerd als een verschil in taakvoorbereiding tussen individuen met een hoog en met een laag IQ. Omdat deze vermeerdering in alfa-power aanwezig was vóór het begin van de stimulus, ongeacht de strategie die werd gebruikt om de taak uit te voeren, en vooral omdat het niet direct gekoppeld was aan de processen die nodig zijn om de taak uit te voeren, kan worden aangenomen dat het om een daadwerkelijk intelligentiegerelateerd verschil gaat.

In hoofdstukken 3 en 4 worden twee experimenten beschreven waarin geprobeerd

wordt een koppeling te leggen tussen het gemeten EEG-signaal en de toewijzing van hulpbronnen. Dit wordt gedaan door middel van frequentiemarkering³: een innovatieve methodologie die visualisatie van de dynamiek in toewijzing mogelijk maakt wanneer meerdere taken tegelijkertijd worden uitgevoerd en de aandacht is verdeeld tussen deze taken. Hoofdstuk 3 maakt gebruik van de competitie die ontstaat tussen hulpbronnen binnen de visuele modaliteit (unimodale aandacht) als twee verschillende locaties op een beeldscherm in de gaten gehouden moeten worden, of als één in de gaten gehouden moet worden en de andere genegeerd. Daarnaast wordt in hoofdstuk 3 de hypothese van Ding et al. (2006) getest. Deze hypothese zegt dat het effect van aandacht op de amplitude van de ‘steady state visual evoked potential’ (SSVEP is de elektrofysiologische reactie die gemeten wordt wanneer frequentiemarkering wordt gebruikt) afhankelijk is van de gebruikte markeringsfrequentie.

Resultaten laten een lineaire verhouding zien tussen de amplitude van de SSVEP opgewekt door de frequentiemarkering en de hoeveelheid aandacht gegeven aan een bepaalde locatie. Dit impliceert dat er een strategie wordt gevolgd waarbij de beschikbare hulpbronnen verdeeld worden tijdens het uitvoeren van taken van unimodale verdeelde aandacht (zie o.a., Bonnel & Miller, 1994). Daarnaast bleken deze effecten onafhankelijk van de frequentie die gebruikt was om de SSVEP op te wekken.

In het experiment beschreven in hoofdstuk 4 werd frequentiemarkering gebruikt in een aandachtstaak waarin auditieve en visuele stimuli tegelijkertijd werden aangeboden. Elke stimulus veroorzaakte hierbij een ‘steady state evoked response’ die onafhankelijk was van de stimulus in de andere modaliteit. Daarmee werpt dit experiment een elektrofysiologisch perspectief op de controverse tussen het idee dat aandachtsbronnen een vorm van algemene capaciteit zijn (zie, o.a., Navon & Gopher, 1979) en het idee dat bronnen modaliteitsspecifiek en onafhankelijk zijn (zie o.a., Wickens, 1984). Deze studie had nog twee doelen. Ten eerste het verder exploreren van de gevoeligheid van frequentiemarkering door modulatie van aandacht door het instrueren van proefpersonen om in verschillende verhoudingen hun aandacht te verdelen tussen de auditieve en visuele items (bv. 100-0%, 80-20%, of 50-50%). Ten tweede om vast te stellen of de kosten van verdeelde aandacht in taken als detectie en onderscheidingsvermogen een centrale plaats delen of dat ze herleid kunnen wor-

³Frequentiemarkering is een techniek die een fysiologische reactie, ‘steady state evoked potentials’, kwantificeert. Deze bestaat uit een serie evoked responses (opgewekte reacties) die geassocieerd zijn met de herhaalde presentatie van een simpele stimulus (bv. een wit vierkant). Het grootste voordeel van de frequentiemarkering techniek is dat het (1) relatief ongevoelig is voor ruis, (2) de langdurige aandacht kan kwantificeren, en (3) de elektrofysiologische reacties op onderling verschillende, maar gelijktijdige stimuli kan onderscheiden.

den tot verschillende plaatsen (zoals perceptuele beperkingen bij detectietaken en een algemene bottleneck voor onderscheidingstaken, zie o.a., Duncan, 1980).

De resultaten ondersteunen het idee dat de amplitude van de SSVEP gekoppeld is aan de hoeveelheid aandacht die toegewezen is aan een voorwerp of locatie: het blijkt dat geleidelijke veranderingen in SSVEP amplitude een functie zijn van de toekenning van aandacht. De afwezigheid van verschillen in de amplitude van de SSVEP tijdens detectie en onderscheidingstaken suggereert dat de strategieën en mechanismen van aandacht tijdens deze taken hetzelfde zijn (zie ook Bonnel et al., 1992; Bonnel & Miller, 1994; Bonnel & Hafter, 1998). De aandachtsmodulatie van de amplitude van de auditieve SSVEP bij de occipitale elektrodes, die activiteit van de visuele gebieden meten (zie o.a., Russo et al., 2007), suggereert dat er een samenspel is tussen visuele en auditieve informatie wanneer op beide gelet moet worden. Dit is een duidelijk voorbeeld van multisensorische integratie⁴.

Een van de meest opmerkelijke bevindingen van dit onderzoek wordt duidelijk als de resultaten van hoofdstuk 3 en hoofdstuk 4 gecombineerd worden. In beide experimenten werden de kosten van het verdelen van aandacht gezien in termen van slechtere prestaties in de verdeelde aandachtsconditie dan in de gerichte aandachtsconditie. Echter, de modulatie van de amplitude van de SSVEP als een functie van aandacht was niet consistent tussen beide experimenten. In het experiment van hoofdstuk 3, met twee stromen van visuele stimuli en een detectietaak, zat de hoogte van de amplitude van de SSVEP tijdens de verdeelde aandacht tussen die van de gerichte- en geëneerde aandachtscondities in. In het experiment van hoofdstuk 4 echter, met een visuele en een auditieve stimulus in zowel detectie- als onderscheidingstaken, was de amplitude het grootste in de verdeelde aandachtsconditie. Het verschil in SSVEP amplitude tijdens de verdeelde aandachtsconditie tussen unimodale en multimodale taken suggereert dat de SSVEP gevoelig is voor meer dan alleen het toekennen van hulpbronnen en kan worden gezien als een ondersteuning voor Wicken's (1984) idee van aandacht als bestaande uit meerdere hulpbronnen.

Hoofdstuk 5 gaat over de willekeurige aspecten van het toekennen van hulpbronnen en over een neurale correlaat die gekoppeld kan worden aan het proces van het loskoppelen van aandacht (d.w.z. het onmiddellijk wegnemen van aandacht van een

⁴Multisensorische integratie houdt in dat er een verhoogde sensitiviteit voor gebeurtenissen in de omgeving is als de aanwezigheid ervan gelijktijdig wordt signaleerd door meerdere sensorische kanalen. Een trein die aan komt rijden wordt bijvoorbeeld opgemerkt door zowel visuele perceptie van de kleur en de vorm van de trein als door auditieve perceptie van het lawaai van de trein (oor een overzicht, zie o.a., Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006; Rowland & Stein, 2008; Stein & Stanford, 2008).

voorwerp dat eerder de aandacht had in een taak waarin targets kort na elkaar moeten worden gedetecteerd, zie o.a., Posner & Petersen, 1990). Omdat het geven van aandacht aan een object een specifieke event-related potential (ERP) laat zien in het EEG signaal, de N2pc (N2-posterieur-contralateraal, zie o.a. Kiss, Velzen, & Eimer, 2008), ligt het voor de hand dat ook het wegnemen van aandacht van dat object gerelateerd is aan een specifieke ERP component. Hoofdstuk 5 beschrijft een ERP component na de N2pc, die we P4pc hebben genoemd. Deze wordt geïnterpreteerd als een ERP-correlaat van het wegnemen van aandacht. De aanwezigheid van zo'n elektrofysiologische markering kan een belangrijk hulpmiddel zijn voor het onderzoeken van de aard en dynamiek van het strategische beheer van visueel-spatiele aandacht in visueel complexe omgevingen met meerdere in ruimte en tijd verdeelde bronnen van informatie.

Het onderzoek dat in dit proefschrift beschreven wordt, koppelt elektrofysiologische indices aan processen die betrokken zijn bij het beheer van hulpbronnen. Dit wordt onderbouwd door (1) onze resultaten die laten zien dat individuele verschillen in de toekenning van hulpbronnen zijn gekoppeld aan specifieke neurale correlaten, (2) het beschikbaar stellen van een methode waarmee de hoeveelheid bronnen die toegekend zijn aan een taak kunnen worden gemeten, en (3) het vaststellen van een elektrofysiologische markering van het wegnemen van aandacht, wat een vrijwillig proces is. De economische principes van menselijk cognitief gedrag zijn daarmee beter te begrijpen en te onderzoeken.

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