Weighting Mechanisms Within and Across Modalities: Evidence from Event-related Brain Potentials

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CHAPTER I

Synopsis

General Introduction

In everyday life, our sensory systems are continuously confronted with a vast quantity of information. For instance, the human eye contains more than 100 million photoreceptors and each of these receptors provides information from 1 to 1000 impulses per second (Gegenfurtner, 2004). Thus, the visual sensory system alone produces a data volume of more than 2 gigabyte per second. From this enormous data pool (and in addition with the data of the remaining senses) we need to select relevant or salient information in order to determine an adequate response and to control its execution. Due to our inability to process all incoming information at once, we typically resolve this data overload while paying attention to individual objects of a scene, one after another. The question of which object will be selected first is assumed to depend on the dynamic interplay of two distinct types of attentional control mechanisms (Corbetta & Shulman, 2002). Selecting certain information (e.g., colour of one's own car) in advance that is relevant to current intentions can be described as *goal-driven*, controlled in a 'top-down' fashion. On the other hand, when our attention is automatically attracted by salient objects in the environment that 'pop out' from their surroundings (e.g., fire alarm), attention is thought to be *stimulus-driven*, controlled in a 'bottom-up' fashion. This functional distinction is widely accepted and builds the basis for recent theories modelling visual attention (e.g., Wolfe, 1994, 1998; Itti & Koch, 2001), even though, the idea of a two-component framework for attentional deployment dates back at least a century ago, when William James (1890) suggested 'active' and 'passive' modes of attention, respectively.

However, various visual search studies over the last two decades (e.g., Maljkovic & Nakayama, 1994; Found & Müller, 1996) demonstrated that the deployment of visual attention is not solely based on the interaction between these two, top-down and bottom-up, factors, but rather suggest (at least) one additional factor that needs to be considered. For instance the study by Found & Müller (1996) revealed that search performance on a given trial depends to a large amount on what was presented at the previous trial. This finding was based on the observation that participants reacted faster when the visual dimension of the singleton remained the same (color on trials *n* and *n-1*), as compared to a change of the dimension (color on trial *n* and orientation on *n-1*), across consecutive trials. This pattern of effects provided clear-cut evidence that, besides top-down and bottom-up factors[1], events of the immediate past (previous trial) play a crucial role for our current behaviour. The question of when and where such sequential effects are created within the human processing system is subject of the present thesis.

Visual search

Over the last three decades, the visual search paradigm became undoubtedly one of the most established and successful paradigms researchers have used (and still use) to investigate competing theories of visual attention. One reason for its popularity might be its high analogy to real search processes everyone accomplishes all the time. Real world examples include search for one's own car at the car park, search for the ball in a rugby game, or search for your luggage at the airport baggage claim. Inside the lab, visual search arrays are used to approximate this sort of real world situations. Bela Julesz was among the first scientists who used the visual search paradigm to study visual processing inside the lab (Julesz, 1975, 1981, 1986). He found that some target elements, or a group of target elements, embedded in a field of distractors could easily be segregated at first glance whereas other elements failed to 'pop-out' from their surroundings. Based on this observation, Julesz suggested that those target elements that can be effortlessly singled out from their neighbours could be considered as 'elementary' features for visual processing or 'textons' (van Rullen & Koch, 2005).

In the standard visual search paradigm (figure 1), subjects are asked to search for a target item (e.g., left tilted bar) amongst a variable number of distractor items (e.g., upright

[1] Other factors, such as *novelty* and *unexpectedness*, affecting attention are assumed to reflect an interaction between cognitive and sensory influences (Corbetta & Shulman, 2002).

bars). The total number of items in the display is referred to as display (set) size. Typically, in 50% of the trials a target appears and subjects are required to make a 'target-present/absent' decision as fast and accurate as possible. Accuracy or, more often, the time taken for these decisions (reaction time, RT) are the critical variables. If reaction time is the variable of interest, the display remains present until the subject's response.[2] Further, reaction time can be analyzed as a function of display size. The resulting slope (search rate) of the RT x display size function is assumed to index the cost of adding an item to the search array. If reaction time is independent of the number of items presented in the display, search is characterized as *parallel* (search rates < 10 ms/item). Subjectively, the target seems to 'pop-out' from the search array. If the search time increases linearly with the number of items in the display, then search is characterized as *serial* (search rates > 10 ms/item) suggesting that individual items are searched successively.

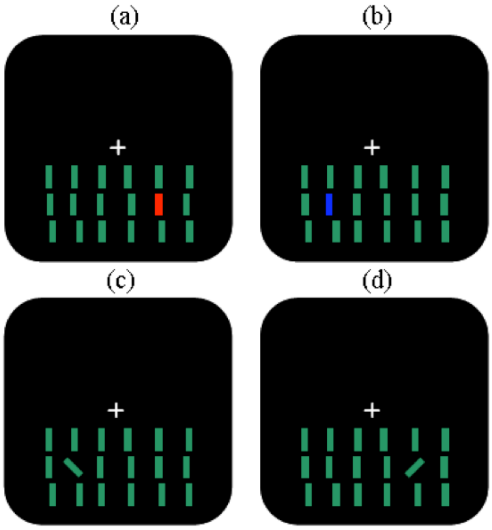

Figure 1. Examples of search arrays typically used in visual search tasks. On the upper panel (a & b), the target differs within the color dimension (red and green, vertical bars) from its neighbours (green, vertical bars). On the lower panel (c & d), the target is defined by a different orientation (45° left tilted and 45° right tilted, green bars) compared to its surrounding distractors (vertical, green bars).

This dichotomy of *parallel* and *serial* search modes seemed to be an attractive notion when it was suggested by the 'feature integration theory' (FIT) by Treisman and Gelade in 1980 (see below). Within this theory, Treisman and Gelade (see also Neisser, 1967) assume two successive stages of visual processing. When the target differs from the distractors in only one feature, search is assumed to function in parallel and preattentive. On the other hand, is the target is defined by a conjunction of features that are shared by the distracters, search is assumed to require a serial examination by some form of attentional spotlight (Treisman & Gelade, 1980; Wolfe, Cave, & Franzel, 1989). However, at variance with this strong classification of either parallel or serial search modes are various visual search studies reporting search

[2] In order to reduce the probability of eye movements, some ERP researcher prefer to present the search display for a fixed time period (e.g. 150 ms; Eimer, 1996).

slopes of the RT x display size function varying from flat to steep. Further, there are instances where feature searches produced 'serial' slopes (Nagy & Sanchez, 1990) whereas conjunction searches were found to produce 'shallow' slopes (Cohen & Ivry, 1991, Treisman & Sato, 1990). Thus, to incorporate these results, more recent theories of attention rejected this dualistic terminology and proposed the idea of a 'continuum' along a single dimension. According to this, Nakayama and colleagues (Nakayama & Joseph, 1998; Joseph, Chun, & Nakayama, 1997) suggested an 'easy versus difficult' continuum whereas Wolfe (Wolfe, 1988) proposed to describe searches within an 'efficient versus inefficient' continuum.

Following Wolfe's proposal, the question arises why some searches are performed efficient while others are not. To elaborate this issue, Wolfe and Horowitz (2004) reviewed several studies while characterizing different properties of visual stimuli in their ability to guide the deployment of visual attention. They suggested that visual attributes can be allocated to one of five possible categories ranging from 'undoubted attributes' to 'probable non-attributes'. For instance, color, size and orientation represent dimensions of the first ('undoubted attributes') category referring to their strong ability to control the deployment of attention. However, other attributes such as intersection, optic flow or faces ('probable non-attributes') have been shown as inappropriate when attention needs to be guided efficiently.

Models of visual search

Feature Integration Theory

Anne Treisman's seminal feature integration theory (Treisman & Gelade, 1980) has been the starting point for most current theories of visual attention. Within this theory, Treisman addresses the question of how different properties of the visual input, which are encoded in separate feature maps, can be combined into a coherent object representation. To solve this question, FIT proposes that visual processing could be dichotomized into two stages of visual processing: 'preattentive' and 'attentive'. The first 'preattentive' stage extracts basic visual features of the input signals (e.g., color or orientation) via dimension-specific input modules. These modules code signals across the whole visual field forming spatiotopically-organized feature maps that represent the location of each basic feature within the visual field. Treisman suggested that certain basic features such as color and orientation could be detected in parallel without the need of focused attention; however,

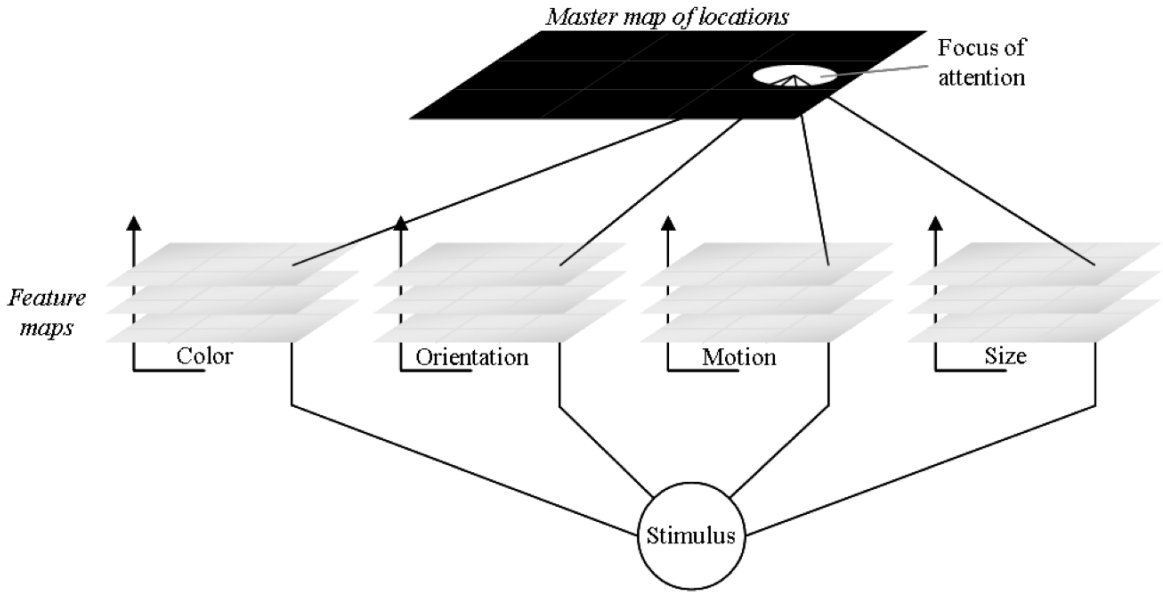

Figure 2. 'Feature Integration Theory' adapted from Treisman & Gelade (1980).

their conjunctions can only be recognized after attention had been focused on this particular location. According to FIT, this process is achieved by the second 'attentive' stage. In this stage, focused attention is assumed to operate on a *master map of locations* (figure 2) that receives input from all feature maps in the various modules. Directing focal attention to a specific location on the master map enables the gating of all features, being active at the corresponding feature map locations, into a temporary object representation - the 'object file'. Such an 'object file' represents an explicit and conscious representation of the object identities and is used to interface or match up with stored object representations. It is suggested (Luck & Vogel, 1997) that the total amount of 'object files' we are able to set up and maintain in working memory simultaneously is limited to the number of two to four bound objects.

Following the feature integration theory, several predictions can be derived and indeed, experimental data seemed to support this theory. First, the assumption of two successive (preattentive, attentive) stages of visual processing nicely explained the prolonged reaction times found for conjunction searches compared to feature searches. While the detection of singletons defined by a single feature can be performed preattentive and parallel across the whole visual field in a single step, the detection of targets defined by a conjunction of different features requires the deployment of focused attention in order to 'bind' features together, thus, resulting in a (time-consuming) serial scanning of the

visual scene (although, this generality was soon challenged as discussed above). Indirect evidence for FIT has been reported for spatial cueing paradigms, which found that the identification of conjunction targets benefited much more from spatial cueing than the identification of feature targets (Treisman, 1988). Also in line with FIT, participants often make binding errors if attention is diverted or overloaded. This 'illusory conjunctions' occur for instance in conditions when participants are flashed with displays of three colored letters while asked to attend primarily onto two flanking digits. Participants are very accurate in reporting the digits, but reported many 'illusory conjunctions' when asked to report the identity of the colored letters. Finally, FIT predicts that deficits in spatial attention would result in feature binding problems. To test this prediction, Robertson and colleagues (Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997) looked at search performances of a patient suffering from Balint's Syndrom[3], a condition which can dramatically affect the ability to attend to multiple objects in a scene. They found that the patient was unable to detect conjunction targets, however, no problems were observed for targets defined by a singleton feature.

In contrast, other experimental findings were not tenable by Treisman's original view. For instance the observation that some targets (letter Q) produced a pop-out from their surrounding distractors (letter O), while one such distractor did not pop-out among an array of targets ('search asymmetry'). More critically, the strong distinction between parallel and serial search modes has been challenged by findings that reported shallow or even flat search slopes for conjunction searches (Enns & Rensink, 1991; Wolfe, Cave, & Franzel, 1989; Kristjansson, Wang, &Nakayama, 2002) whereas feature searches could produce steep search functions (Mc Leod et al., 1988; Theeuwes & Kooi, 1994). To accommodate these contradictory findings, Treisman and colleagues reformulated the original feature integration theory (Treisman & Gormican, 1988; Treisman & Sato, 1990). To account for search asymmetries (as described above), Treisman and Gormican (1988) hypothesized that a deviating stimulus is distinguished from the standards by the additional activity the deviant generates in detectors for a positively coded dimension. This is, presenting the letter Q among O's produces a pop-out due to its additional feature (additional line segment). However, when presenting an O among Q's, additional activity originates from the distractors, thus, resulting in steeper search slopes. In other words, pop-

[3] Balint's Syndrom is a neuropsychological disorder typically resulting from bilateral damage to posterior parietal and lateral occipital areas.

out depends on the increased activity of the target against a low background. In contrast, when a target generates decreased activity against a high background, it fails to pop out.

Furthermore, to explain the flat search slopes some conjunction searches have revealed, Treisman and Sato (1990) suggested that search (attention) is controlled not only by spatial location but also by a form of feature-based inhibition. They implemented a top down component into FIT which uses prior knowledge about the relevant features. This is, when the target (e.g., green bar) and distractor (e.g., blue bars) features are known in advance, then master map locations that do not contain relevant target features are excluded from attentional scanning via inhibitory connections between master map locations and corresponding feature map locations. It is assumed that this feature inhibition could be generated in parallel within several feature maps coding distractor features, thus reducing the activity in all non-target locations. While this modification of the FIT is based on inhibition rather than activation, Treisman and Sato (1990) conceded that both might play a role.

Guided Search

One another influential model that *"… seeks to explain how humans find one visual stimulus in a world filled with other, distracting stimuli"* (Wolfe, 1996) is 'Guided Search' (GS) by Jeremy Wolfe and colleagues (Cave & Wolfe, 1990; Wolfe, 1994, 1998; Wolfe & Gancarz, 1996). Similar to earlier psychological theories (James, 1890; Neisser, 1967; Treisman & Gelade, 1980), GS assumes a two-stage model of visual selection. In the first (preattentive), massively parallel stage, large portions of the visual field are initially decomposed according to basic visual features (color, orientation, motion, etc.) into retinotopic maps. The second (attentive) limited-capacity stage is able to perform more complex operations (e.g., combinations of features, face recognition) over a limited portion of the visual field. In order to cover the entire visual scene, these limited-capacity processes have to be deployed in a serial manner. The idea behind GS is that the output of the earlier parallel processes guides the attentional deployment of limited resources of the second stage.

To achieve this guidance, GS assumes that each dimension-specific module encodes the presence of a particular feature across the visual field. In addition, this activation is modulated by similarity and spatial distance between surrounding items. For instance, if a red item is surrounded by green items, then its activation (saliency signal) at

the target location is higher than if the red item was surrounded by red items. That is, the more the target differs from its neighbours the higher its saliency signal. However, this activation decreases the further apart the items are. Saliency signals of all modules are then passed to a master map of activations, which integrates (sums) the saliency signals separately for each stimulus location. The most active location on this master map determines the deployment of focal attention. However, if this location did not contain the target, attention shifts from peak to peak on the master map until the target is found or the search is terminated.

It is important to note that this bottom-up activation is based solely on the difference between the target and its surroundings within the dimensions-specific saliency maps. While this is done via similarity comparisons, the saliency map only knows that there is a difference at one location relative to the others, but not on what the difference is built-on (e.g., in which particular feature the items differ). Thus, target detection can be accomplished even without prior knowledge of the targets identity. While this bottom-up processes guide attention only to salient items in the display, they will not guide attention to desired items if their attributes are not dissimilar relative to their neighbours. To account for those situations, GS incorporated top-down processes, which are able to modify activations on the master map. In contrast to revised versions of the FIT (Treisman and Sato, 1990), GS 2.0 (Wolfe, 1994) proposes that these modifications are achieved via top-down excitation mechanisms. For instance, if the target features are known in advance (e.g., search for a “small”, “green” paprika in the supermarket) then locations that might contain these desired features will be activated. This way, an object, that possesses both these features, can still gain a higher activation on the master map than objects which possess only one of these critical features. This can explain why some conjunction searches have been reported to produce flat search slopes (Wolfe, Cave, & Franzel, 1989). However, there is a limitation in tuning certain feature channels in advance. As the study by Wolfe and colleagues (Wolfe, Friedman-Hill, Stewart, & O’Connell, 1992) had revealed, participants could discriminate roughly four to five categories of orientation: steep, shallow, left, right, and tilted but not the actual angle (e.g., 20°) or a combination of categories (e.g., steep and left). From this the authors concluded that top-down activation might be accomplished by selecting only a single, broadly tuned input channel (e.g., “green” for color and “small” for size).

With a fixed set of parameters, Guided Search (2.0) is able to explain most human search behaviour. In particular, it accounts reasonable well for singleton feature searches as well as conjunction feature searches. Nevertheless, there are shortcomings. For example, following GS, search is self-terminating in trials when no target is present. The model predicts the termination of serial searches either when the activation is below a certain threshold, or when a certain period has elapsed. According to GS 2.0 (Wolfe, 1994), the variability of reaction times in target absent trials should be smaller compared to target present trials. However, the results of human visual search tasks tend to show the opposite. Related to that, an activation threshold accounting for self-terminating searches is not able to explain the rise in error rates that can be observed as the set size increases (Cave & Wolfe, 1990).

Especially earlier versions of the GS model were incomplete in order to account for cross-dimensional search behaviour. That is, when the target defining dimension (e.g., color, orientation, etc.) is not known in advance (dimensional uncertainty), participants are slower in discerning the presence (versus the absence) of a target. This pattern is incompatible with the assumption that the integration of saliency signals, derived from dimension-specific input modules by the master map, is accomplished in an *un-weighted* fashion. Exactly this question of how dimensional uncertainty affects human search behaviour is addressed by the Dimension Weighting Account (DWA) account.

Dimension Weighting Account

Similar to other dimension-based theories of visual attention (e.g., Treisman, 1969; Allport, 1971), the 'dimension weighting account' (DWA, Found & Müller, 1996) proposes that visual selection is limited by the dimensional nature of the discrimination required to discern response-relevant (target) attributes. This account is essentially based on studies of cross-dimensional singleton feature search. In this task, observers have to discern the presence (versus the absence) of an odd-one-out feature target within a field of homogeneous distractors, with the target-defining dimension varying unpredictably across trials (e.g., target variably defined by color (red or blue), or by orientation (left-tilted or right-tilted bar), among green vertical distractor bars). Search performance in this task indicates that the target does not automatically 'pop out' of the field of homogeneous distractors based on the operation of some early, saliency-based detection mechanism. Rather, target detection is influenced by an 'attentional' mechanism that modulates the processing system by allocating limited 'attentional

weight' to the various basic visual dimensions that potentially define the target. Dimensions are assigned weight largely passively, in bottom-up manner: the particular dimension defining the target on the current trial is allocated a larger weight than alternative dimensions (that may define the target on other trials). However, this weight set may be modified, to some extent, in top-down manner, based on advance information as to the target-defining dimension on a given trial (Müller et al., 2003).

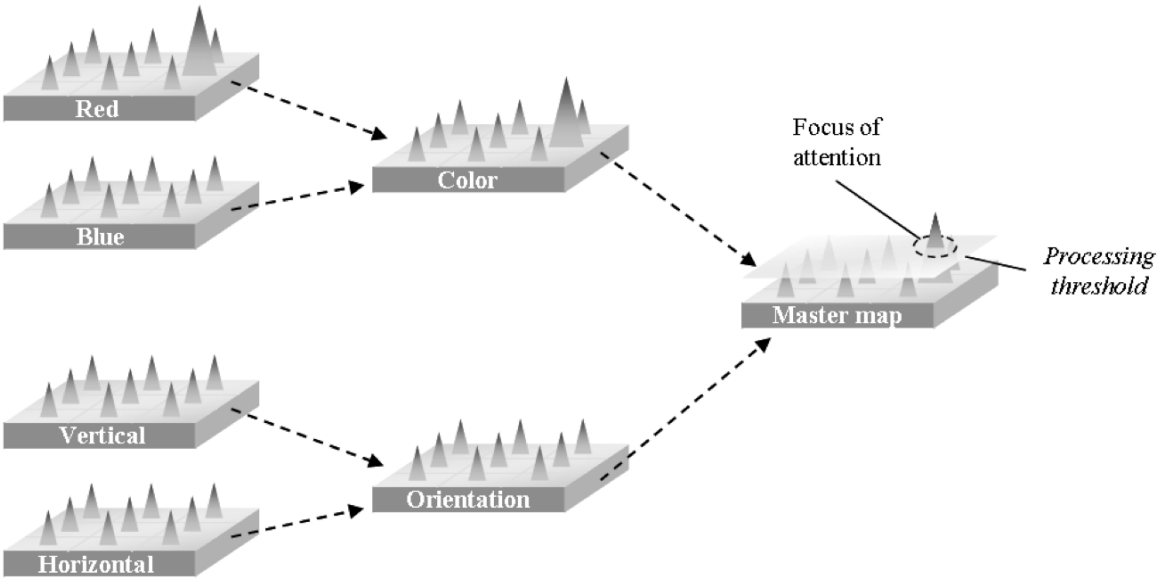

Figure 3. Functional architecture of the 'Dimension-Weighting' Account, adapted from Found & Müller (1996). The depicted situation shows essentially a bottom-up search for a color singleton while selective (focal) attention is assumed to operate at the master map unit of integrated (summed) saliency signals derived separately from dimension-specific modules. Following this example, attentional resources will be (implicitly) allocated to the color module, thus, facilitating the processing of any color target (e.g., red or blue) in the next trial.

Two important pieces of evidence for this account can be summarized: (i) the observation of cross-dimensional search costs, that is, slowed search performance when the target-defining dimension varies across trials (e.g., color, orientation) compared to when the target-defining feature varies within a fixed dimension (for color, e.g., red, blue); (ii) the observation of a dimension-specific inter-trial effect in cross-dimensional search, that is: slowed RTs when the target-defining dimension changes on consecutive trials (e.g., orientation-defined target on trial *n-1* followed by a color-defined target on trial *n*), compared to when it is repeated. Found and Müller (1996; see also Müller, Krummenacher, & Heller, 2004) showed that this

inter-trial effect is indeed dimension-specific, rather than feature-specific, in nature: there is a RT cost only when the target-defining dimension is changed, but not when the critical feature is changed within a constant dimension.

Müller and his colleagues (Müller et al., 1995, 2003; Found & Müller, 1996) took these cross-dimensional cost and dimension-specific intertrial effects as evidence for what they refer to as 'dimension weighting account' (Figure 3), which is essentially an extension of the Guided Search model proposed by Wolfe and colleagues (e.g., Wolfe, 1994). The DWA assumes that focal attention operates on a master map of integrated saliency signals derived separately in dimension-specific input modules. In contrast to earlier versions of GS, intra-dimensional saliency processing is 'weighted' prior to signal integration by the master map units. The greater the weight assigned to the target-defining dimension, the faster the rate at which evidence for a feature difference within this dimension accumulates at the master map level. When the target-defining dimension on a given trial is the same as that on the previous trial, the weight is already set to the correct dimension, permitting rapid search. By contrast, when the target-defining dimension is changed, a time-consuming 're-*weighting*' process is involved, possibly in order to determine the dimension defining the target and render it salient at the master map level. This assumes that the target dimension must be weighted to permit target detection (as originally proposed by Müller et al., 1995). Alternatively, the target is processed and eventually selected based on the relatively low weight allocated to its defining dimension, and the weight shift follows target detection. In either case, there is a weight shift to the new target-defining dimension, which influences the processing of any subsequent target. Importantly, the DWA interprets weighting effects to be pre-attentive ('perceptual') in nature, modulating signal strength prior to the selective-attention stage, which operates based on the overall-saliency map (Müller & Krummenacher, 2006; see also Folk & Remington, 1998).

Brain mechanisms of dimension-based visual attention

Over the last decade, several researchers have investigated the neural substrates of dimension-based visual attention using event-related functional magnetic resonance imaging (fMRI; Pollmann, 2004; Pollmann, Weidner, Müller, & von Cramon, 2000, 2006; Weidner, Pollmann, Müller, & von Cramon, 2002). In several studies, Pollmann and colleagues (e.g., Pollmann et al., 2000; Weidner et al., 2002) replicated a fronto-posterior network to be sensitive to visual dimension changes. In particular, frontal dimension

change-related activations were found in the left frontopolar cortex (BA 10) and in the anterior wall along the pregenual portion of the cingulate sulcus (BA 24/32). Posterior dimension change-related activations were mainly present in the right superior parietal lobule and the intraparietal sulcus. In addition, there were also increased activations in dorsal occipital visual areas specific to repetitions in the target dimension. Pollmann et al. (2006) concluded that prefrontal regions are the site of executive processes associated with the *control* of dimensional weight shifting, while higher visual areas in superior parietal and temporal cortex mediate the weight shifts via feedback pathways to the dimension-specific input areas in occipital cortex.

Another study by Weidner and colleagues (2002) examined the functional anatomical correlates of singleton feature search versus conjunction feature search. Behaviourally, for conjunction feature searches, target detection was prolonged for changes of the secondary target dimension (e.g., color or motion), but not for feature changes (e.g., red or blue) within a dimension. Generally, the time demands for changing the target-defining dimension were more pronounced for conjunction features searches than for singleton feature searches. This points to an involvement of top-down processes in conjunction features searches when the target dimension needs to be changed. By contrast, target dimension changes in singleton feature searches seem to be accomplished mainly stimulus-driven. When contrasting singleton feature search versus conjunction features search, Weidner and colleagues (2002) observed a double dissociation in anterior prefrontal cortex. There was a dimension change-related increase of activation in frontopolar cortex in singleton feature, but not conjunction feature search. By contrast, there was a dimension change-related activation in pregenual frontomedian cortex in conjunction feature, but not singleton feature search. This pattern of effects has been interpreted as frontopolar involvement in exogenous (stimulus-driven) task switches while the anterior frontomedian cortex seems to play a crucial role in endogenous (top-down) switches.

Recently, a patient study by Pollmann and colleagues (Pollmann, Mahn, Reimann, Weidner, Tittgemeyer, Preul, Müller, & von Cramon, 2007) provided deeper insights into the functional contributions of the left frontopolar cortex (LFP) to attentional control. Using a singleton feature search task, search performance of patients with left lateral anterior prefrontal lesions was compared with patients with frontomedian lesions and controls without lesions. Recall that left frontopolar area was interpreted as to be involved

in the *control* of dimensional weight shifting (Pollmann et al., 2006). However, it remained unclear, whether this process represents a pre-requisite of target detection, needed to shift attentional weight from the old to the new target-defining dimension in order to sufficiently amplify its saliency signal on the master map, or whether activity in this brain region reflects the (implicit) re-allocation of attentional resources that follows target detection influencing the processing of any subsequent target. The results obtained in this study suggest the latter. LFP patients were still able to detect the singleton, however, this was accompanied with a specific increase in dimension change costs, compared both with patients with frontomedian lesions and controls without lesions. This finding supports the proposal of earlier studies (Pollmann, 2000, 2006) that the left frontopolar cortex plays a critical role in the *control* of visual dimension shifting. Based on the selective increase of dimension change costs in the LFP patients, the authors concluded that this structure facilitates the (re-)allocation of attentional resources from the old to the new target-defining dimension.

The question of how attention modulates neural processing in one feature dimension was investigated by a study of Martinez-Trujillo & Treue (2004). They recorded 135 direction-selective neurons in the middle temporal area (MT) of two macaques to an unattended moving random dot pattern (the distractor) positioned inside a neuron's receptive field while the animals attended to a second moving pattern in the opposite hemifield. Direction changes of the distractor dots modulated neural responses as long as the attended direction remained identical. However, when the direction of the attended dots were varied systematically from a neuron's preferred to its anti-preferred direction, a systematic change of attentional modulation ranging from enhancement to suppression was observed, even though these variations occurred outside the neuron's receptive field. These results show that attention modulates neuronal responses based on the similarity between the cell's preferred feature and the attended feature (see also 'feature-similarity gain model' of Treue & Martinez-Trujillo, 1999). That is, the firing rate of a neuron is determined by sensory responses interacting with a multiplicative attentional modulation[4]. Furthermore, the results indicate that selectivity for attended features is achieved by increasing responses of neurons preferring this feature while, on the other hand, decreasing responses of neurons tuned to the opposite feature value.

[4] Similar effects have been reported for the human visual cortex (Saenz, Buracas, & Boynton, 2002).

Taken together, work by Pollmann and colleagues as well as Martinez-Trujillo and Treue provides evidence that in extrastriate areas, such as MT, 'bottom-up' (sensory) processes are joined with 'top-down' (attentional) mechanisms that together create an integrated saliency map[5]. This topographic representation is competent to direct limited attentional resources (of higher processing stages, such as 'object identification') to highly salient as well as behaviourally relevant items in the visual world.

Shifts of crossmodal attention

Most research on selective attention has considered only a single sensory modality at a time. For instance, in visual attention laboratories, participants typically were required to detect (or discriminate) objects surrounded by distractors. However, in the real world, objects often generate features defined in more than one modality. Continuously confronted with this massive amount of information, we need to 'bind' these features originating from several modalities into coherent object representations. Imagine you work as a sommelier in a restaurant. In order to determine the quality of a vine, you probably analyze its color, its aroma as well as its taste before you make your judgment. This simple example shows that many real life situations require crossmodally coordinated attention in order to determine an adequate response.

Early work on crossmodal attention

Almost a half century ago, Sperling (1960) was among the first scientists when he used crossmodal location cueing in order to study the storage capacity of very short-term (iconic) visual memory. He presented subjects briefly with visual stimulus displays (e.g., three rows of four letters) followed by a variable blank visual field. After the blank display, an auditory tone (location cue) was presented indicating which row of letters the subjects had to report. The top row was indicated by a high pitched tone, the middle row by a medium-pitched tone, and the bottom row by a low-pitched tone. Importantly, the auditory information always appeared after the visual information had physically disappeared. Thus, no prior knowledge about the relevant letter row (top, middle, or bottom) could be used. Sperling found that the auditory cue enabled subjects to direct their attention to the

[5] Other researchers (Zhaoping & Snowden, 2006) assume bottom-up saliency coding to occur even earlier (V1).

respective display location stored in (iconic) visual memory before this information decayed. In other words, this study had revealed evidence for crossmodal attention shifts.

In the seventies, Posner and colleagues (e.g., Posner, 1978; Posner, Nissen, & Ogden, 1978; Posner, Davidson, & Nissen, 1976) conducted pioneering work on attention research. In one study, they (Posner, Davidson, & Nissen) used - similar to the Sperling study (1960) - crossmodal location cueing, however this time, in order to explore the processes underlying stimulus detection. Surprisingly, there was no effect on the time required to simply detect sounds or touches when they were preceded by visual cues. However, when the task involved discrimination rather than detection, subjects benefited from the same (visual) cues resulting in expedited response times for sounds and touches. To explain these results, Posner et al. hypothesized that detection tasks differ from discrimination tasks in the way attentional mechanisms are activated in the different sensory modalities.

Stimulus-driven versus goal-driven shifts of crossmodal attention

Nowadays, it is well established that focusing on the same perceptual modality in successive trial episodes (e.g., tactile target on both the current trial *n* and the preceding trial *n-1*) facilitates performance, relative to when the modality changes across consecutive trials (e.g., tactile target on trial *n* preceded by visual target on trial *n-1*). A large number of studies have investigated these modality repetition/change effects in normal subjects (e.g., Cohen & Rist, 1992; Spence, Nicholls, & Driver, 2001; Gondan, Lange, Rösler, & Röder, 2004; Rodway, 2005) as well as patients (e.g., Verleger & Cohen, 1978; Manuzza, 1980, Hanewinkel & Ferstl, 1996) using different experimental paradigms. For example, Rodway (2005) used a cueing paradigm to investigate the efficiency of warning signals. He found that, for brief foreperiods, the warning signal (cue) was most efficient when it was presented within the same, rather than a different, modality to the subsequent target. Rodway concluded that the warning signal exogenously recruits attention to its modality, thereby facilitating responses to subsequent targets defined within the same modality as the warning signal. Thus, in this study, (crossmodal) attention was shifted in a *stimulus-driven* manner.

A similar pattern was observed by Spence et al. (2001) who examined the effect of modality expectancy in a task that required participants to judge the azimuth (left vs. right) of the target location in an unpredictable sequence of auditory, visual, and tactile targets.

There were two types of trial blocks: biased blocks in which the majority of targets (75%) was presented in one modality (participants were instructed to attend to this modality), and unbiased blocks in which the targets were equally likely to be defined in each modality (33%; participants were instructed to divide attention among the three modalities). With the majority of targets presented in one modality, Spence et al. observed prolonged RTs for targets defined within the unexpected compared to the expected modality. In trial blocks in which each target modality was equally likely, RT costs were observed for trials on which the modality changed relative to the preceding trial. In fact, such modality change costs were also evident in the biased trial blocks, accounting for almost all the benefits and for a large part of the costs in the 'expectancy' relative to the divided-attention conditions. Spence et al. interpreted this pattern of effects in terms of a passive, *stimulus-driven* 'modality shift effect'.

These *stimulus-driven* crossmodal attention shifts can be contrasted with *goal-driven* crossmodal attention shifts. A popular approach to studying this type of (voluntary) crossmodal attention shifting has been the deployment of symbolic cues on a trial-by-trial basis. In one event-related brain potential (ERP) study, participants had to detect peripheral tactile or, respectively, visual targets on the attended side, while ignoring any stimuli on the unattended side and in the currently irrelevant modality (Eimer & van Velzen (2002). The to-be-attended side and the relevant modality were indexed on a trial-by-trial basis by one of four different auditory symbolic pre-cues. The sound of one of two instruments (flute; marimba) indicated the stimulus modality relevant for a given trial (e.g., flute – vision; marimba - touch), the relevant location (left or right) was indicated by the pitch of the sound (low: 500 Hz; high: 1500 Hz). Spatial orienting in the cue-target interval affected two components of the ERP: the "anterior-directing attention negativity" (ADAN) and the "late-directing attention positivity" (LDAP) contralateral to the cued side reflecting spatial orienting, irrespectively of whether touch or vision was cued as relevant. While these components have been reported in previous studies investigating shifts of visual attention, the experimenters concluded that these two components are associated with the voluntary deployment of attention in space. More specifically, the ADAN and the LDAP seem to reflect supramodal control processes that operate independently from the cue modality.

However, this view has been challenged by a recent study of Green & Mc Donald (2006). They used symbolic visual cues to direct attention prior to auditory targets and vice versa, symbolic auditory cues were used to direct attention prior to visual targets. If both

components the ADAN and the LDAP reflect the deployment of spatial attention across sensory modalities (Eimer & van Velzen, 2002), they should be present for visual as well as auditory pre-cues. However, the results of the Green and Mc Donald study (2006) confirmed this hypothesis only partially. Here, the ADAN component was present for visual cues indicating the location of an auditory target, but absent for auditory cues indicating the location of a visual target[6]. These findings show that the processes underlying this component are not completely supramodal. Rather, this negativity seems to be the result of multiple processes involved in the analysis of the visual cue stimulus. Thus, the elicitation of the ADAN component is not a pre-requisite to shift attention from one location to the other. In contrast to the ADAN, the LDAP was observed not only when the visual cues were followed by auditory target, but also when the auditory cues were followed by visual target. Based on this observation and consistent with the Eimer and van Velzen study (2002), the authors interpreted the LDAP component as to reflect supramodal processes involved in spatial attention shifting.

To gain further insights into the brain areas involved in *goal-driven* crossmodal attention shifting, one study by Macaluso and colleagues (Macaluso, Frith, & Driver, 2002) employed event-related functional magnetic resonance imaging (fMRI). Similar to the above described ERP studies, a symbolic auditory cue (digitized male voice saying “left” or “right”; 80 % valid) indicated the most likely location (left or right) for the subsequent target, which was defined either within the visual or tactile modality appearing at the cued or uncued location. Both valid and invalid trials elicited a supramodal activation of a large superior parietal-frontal network consisiting of several frontal, intraparietal, and superior parietal regions. Interestingly, nearly the same brain regions have been associated with spatial attention in purely visual studies (Corbetta, Miezin, Shulman, & Peterson, 1993; Nobre, Sebestyen, Gitelman, Mesulam, Frackowiak, & Frith, 1997). When comparing invalid versus valid trials, selective activations were found in more inferior regions (temporo-parietal junction and inferior (premotor) cortices) in response to invalid (relative to valid) trials, regardless of the respective target modality. From this, Macaluso and colleagues (2002) concluded that brain mechanisms responsible for the reorienting of spatial attention to invalidly cued targets operate in a supramodal fashion.

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[6] It should be noted that in earlier studies by Eimer and colleagues (Eimer and van Velzen, 2002; Eimer, van Velzen, Forster, & Driver, 2003), auditory pre-cues have been reported to elicit the ADAN prior to visual and tactile targets.

Supramodal or modality-specific attentional control systems?

One question that recently has become a major focus in crossmodal attention research concerns the nature of attentional control mechanisms involved in shifts of crossmodal attention. As some studies have suggested (Eimer and van Velzen, 2002; Macaluso et al., 2002), such attentional shifts may be accomplished by a single supramodal system that mediates spatial attention in multiple sensory modalities. Alternatively, attentional reorienting may result from "separable-but-linked" modality-specific attentional control systems (Spence & Driver, 1996).

Over the last two decades, a large amount of studies (e.g., Farah, Wong, Monheit, & Morrow, 1989; Ward, 1994; Eimer & Driver, 2001; Macaluso, Frith, & Driver, 2002; Eimer & van Velzen, 2002; Eimer, van Velzen, Forster, & Driver, 2003; Green, Teder-Sälejärvi, & Mc Donald, 2005; Green & Mc Donald, 2006) accumulated evidence for the existence of a supramodal control system. One likely neuroanatomic candidate that might harbor these supramodal control processes is the parietal lobe. This has been suggested by many investigations, which showed that areas in the parietal cortex play a crucial role in spatial attention. For instance, Farah and co-workers (1989) investigated (right) parietal-lesioned patients in order to determine whether the parietal lobe houses a supramodal or modality-specific representation of space. To test this question, they presented the patients with either non-predictive lateralized visual cues or non-predictive lateralized auditory cues, followed by lateralized visual targets. A disproportionate slowing of the response times was observed for contralesional targets when they were preceded by ipsilesional invalid cues, suggesting an impaired attentional disengagement from the ipsi- to the contralesional side. The fact that this effect occurred independently from the cue's modality (visual or tactile) has been taken as evidence that parietal lobe mechanisms allocate attention based on a supramodal representation of space (Farah et al., 1989).

This is consistent with the pattern emerged from studies which have used neuro-physiological approaches (EEG/fMRI) to address this issue. Recall that ERP studies (e.g., Eimer & van Velzen, 2002, Green & Mc Donald, 2006) have revealed a relative positivity over posterior scalp sites contralateral to the to-be-attended location, termed as the LDAP component. Similarly, fMRI studies (e.g., Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Macaluso et al., 2002; Macaluso, Eimer, Frith, & Driver, 2003) revealed stronger activations of the temporo-parietal junction in invalidly (relative to validly) cued

trials, regardless of the target modality. All in all, these findings suggest that parietal lobe mechanisms seem to be associated with multimodal spatial coding.

However, at variance with this view are findings of a recent study by Chambers et al. (Chambers, Stokes, & Mattingley, 2004). This study used transcranial magnetic stimulation (TMS) in order to verify the supramodal attention hypothesis. Subjects performed a speeded orienting task in which a central presented visual cue (75 % valid) indicated the side (left or right) of a subsequent visual or somatosensory target. During the cue or target event, magnetic stimulation was delivered to subregions of the temporal and parietal cortex in the right hemisphere. Chambers et al. found that stimulations of the inferior parietal cortex during the cue period selectively reduced the cueing effect for visual, but not somatosensory, targets. Thus, this pattern of effects appears inconsistent with a single supramodal network and instead supports the idea that spatial attention is controlled by independent neural circuits that are modality specific.

This separable-but-linked view has also been advocated by Spence and Driver (1996). In one experiment (Experiment 7) of this audiovisual study, a verbal instruction at the beginning of each block specified (83 % valid) opposite sides as most likely for the two modalities (e.g., visual targets were more likely to appear at the left side and auditory targets on the right side, or vice versa). Nevertheless, participants still benefited from this blockwise cueing suggesting, that auditory attention can be endogenously directed to one side while, at the same time, visual attention is directed to the opposite side. This finding clearly shows that participants were able to “split” auditory and visual attention providing evidence that spatial attention is not purely supramodal.

Taken together, there is no clear-cut answer to the question whether attentional control mechanisms are supramodal or modality-specific in nature. But, experimental results emerged from a variety of studies suggesting that these two mechanisms don’t need to be considered as mutually exclusive. Rather, they both may exist, operating side by side. One account that tries to combine aspects of both supramodal and separable-but-linked approaches is the ‘hybrid’ account (Eimer, van Velzen, & Driver, 2002). According to this account, the *phasic* selection of locations relevant for a given task is accomplished by supramodal processes. This way, the processing of a specific location of a stimulus in one modality can influence spatial processing in other modalities. In addition, spatial selection of features defined in a particular modality also depends on the *tonic* state of activity in that modality. That is, each modality has a “baseline” activity which, depending on task

relevance, can be increased (for high relevance) or decreased (for low relevance). Thus, this hybrid account explains crossmodal attention shifting by assuming that spatial selection of a given stimulus depends on a dynamic interplay between phasic (supramodal) attentional shifts and tonic (modality-specific) baseline shifts.

As a closing remark (of this chapter), it should be noted that all crossmodal attention studies described so far have used stimuli defined either in the visual, auditory or somatosensory domain. But, apparently, every day life requires the coordination of information defined in much more (e.g., smell, taste) than these three modalities. Thus, it remains uncertain whether mechanisms of crossmodal attention can be generalized for all the existing senses[7].

Overview of the current thesis

It is well established that, besides top-down and bottom-up mechanisms, events of the immediate past (previous trial) can have a large influence on our current behaviour. This is especially evident in visual search tasks, where the outcome of each trial is shaped by the preceding events and/or motor actions. That is, facilitated processing can be observed for targets presented within the same (relative to different) visual dimension (e.g., color) as the previous trial. To explain this behavioural pattern, the DWA (Found & Müller, 1996) assumes that, as a consequence of the previous trial, early visual input modules (dimensions) are implicitly weighted, thus, facilitating the processing of all targets defined within the weighted dimension. By contrast, when the target appears in a different dimension as the previous trial, a time consuming *weight-shifting* processes is required to shift attentional weight from the old to the new target-defining dimension, as a pre-requisite for target detection (see page 16 for a more detailed description). Exactly this hypothesis of *weighting mechanisms* operating within the human processing system has been the starting point and main inspiration for the experiments, which will be outlined in the following.

The primary aim of the present thesis was to provide deeper insights into the underlying mechanisms responsible for the occurrence of intertrial facilitation. More specifically, the goal of the work summarized in Chapter II was to identify electro-cortical correlates of dimension changes in cross-dimensional singleton feature search. Chapter III

[7] A recent study by Ho & Spence (2005) had provided the first empirical demonstration that olfactory stimulation can facilitate tactile performance.

was designed to decompose perceptual from response-related components contributing to dimension-specific intertrial effects. The question, whether early visual processing can also be modulated by non-spatial (dimensional) stimulus attributes was addressed by Chapter IV. Finally, Chapter V describes experiments investigating whether findings and theoretical accounts postulated in the visual modality are extendable to a crossmodal level of processing.

To approach these issues, all experiments presented in Chapter II – V employed behavioural (error rates and reaction times, RT) as well as electrophysiological (Event-related Brain Potentials, ERP) methods. In addition, Chapter IV employed a spatio-temporal coupled current density reconstruction method (Electro-anatomical Source Inspection, EaSI) in order to identify neural sources associated with dimensional weighting.

Chapter II. The experimental part of the present thesis opens with the replication of two experiments performed in the study by Found & Müller (1996). Participants were required to detect (Experiment 1) or discriminate (Experiment 2) a feature singleton which was equiprobable defined in the colour (red or blue) or orientation dimension (45° left tilted or 45° right tilted). Simultaneous EEG recording was performed to gain further insights into the time course of information processing in cross-dimensional feature search. Both experiments replicated the behavioural pattern obtained in the Found & Müller study (1996): depending on the preceding trial, faster reactions were found for dimension repetitions relative to dimension changes. Further, this effect was largely unaffected by intra-dimensional feature changes. At the electrophysiological level, three components have been identified to reflect the behavioural dimension change effect: a frontal N2, largest over fronto-central electrode positions, in addition with the posterior P3 and Slow Wave (SW) showed stronger activations owing to dimension changes. Note, that the topographies of these three components are closely related to previous fMRI findings reported by Pollmann and colleagues (Pollmann, 2000; Pollmann et al., 2006) mirroring a fronto-posterior network. While earlier versions of the DWA (Found & Müller, 1996) assume that dimension change effects are based solely on early pre-attentive processes facilitating the early sensory coding of critical stimulus attributes, no such dimension change-related activation was present in early components of the ERP (e.g P1, N1). Nevertheless, the comparison between detection and discrimination tasks provided clear-cut evidence that all identified ERP components are based on perceptual, and not response-

related, information processing. This is indicated by the fact that all components (N2, P3, SW) were elicited in response to dimension changes, no matter whether this was automatically associated with a response change (Experiment 2) or not (Experiment 1). In this regard, the systematic modulation of the N2 component has been interpreted to reflect the detection of a dimension change and the initiation of the re-distribution of dimensional weights, whereas the P3 and SW were proposed to mediate the weight shifts via feedback pathways to dimension-specific input modules in higher-level visual areas.

Chapter III. One highly debated issue in the visual search literature concerns the origin of intertrial facilitation. '*Perceptually* based' accounts (Found & Müller, 1996; Wolfe, Butcher, Lee, & Hyle, 2003) assume that intertrial facilitation originates from pre-attentive processes, prior to focal-attentional selection of the target. In contrast, '*response*-based' accounts (Cohen & Magen, 1999; Mortier et al., 2005) claim that intertrial facilitation effects are generated at later stages, after visual encoding mechanisms have been completed. To resolve this issue, Experiment 3 was designed to dissociate perceptual from response-related stages in visual search. Using a compound search task, participants first had to search for a singleton (defined by a unique colour or form), before the appropriate response (defined by the orientation of the singleton) could be selected. This way, a dimension change could occur independently from a response change and vice versa. Furthermore, two components of the ERP were focused on which are directly linkable to either perceptual (N2pc) or response-related (Lateralized Readiness Potential; LRP) processes.

Analyses of the ERPs revealed that changes of the visual dimension were, independently from response changes, mirrored by faster latencies and enhanced amplitudes of the N2pc component. This suggests that (at least parts of) the behavioural intertrial effect originates from perceptual processing stages, thus providing evidence in favour of the DWA. Response changes were, independently from dimension changes, reflected in enhanced amplitudes of the response-locked LRP amplitude. This indicates that unchanged responses benefit from residual activations of the previous trial biasing the correct response. So far, electrophysiological findings provided evidence that effects of dimension and response changes are generated at separable perceptual and response-related stages of processing. However, the RT data did not show an additive pattern of dimension change and response change effects. Reaction times were found to be fastest when both dimension and response stayed identical across consecutive trials. When one or both

factors changed, reaction times slowed down to a similar level. To explain this interactive RT pattern with regard to the ERP data, an account is proposed which assumes that the interaction arises at a processing stage intermediate between focal-attentional selection and response production: that is 'response selection'. Further analyses of the stimulus-locked LRP onset latencies provided evidence in favour of this account suggesting that dimension-specific intertrial facilitation in visual search originates from both perceptual and response selection-related stages of processing. In addition, the observed response-locked LRP indicates that a correct (repeated) response experienced facilitated processing due to pre-existing activations ("*weighting*") by the motor system.

Chapter IV. One possibility why Experiment 1 and 2 failed to find dimension change effects in early ERP components might be the temporal decay of attentional weights allocated to early visual input modules. In other words, to catch early dimension change effects using the ERP method, the time interval between two sensory events may not exceed a certain temporal limit (intertrial interval in addition with response times in Chapter II were about 2000 ms). One likely candidate for dimension-based attention effects in early visual areas is the visual evoked P1 component. However, over the last two decades of ERP research, this component has been demonstrated to mirror early attentional processes based solely on spatial stimulus attributes. This view originates from studies showing enhanced P1 amplitudes when the target location was indexed by a valid, relative to an invalid, cue and has been interpreted as a 'sensory gain' or 'amplification' mechanism improving perceptual accuracy at an indexed target location (Eimer, 1994; Hillyard, Vogel & Luck, 1998). The goals of Chapter V was to determine (i) whether early visual processing can also be modulated by dimensional stimulus attributes, and (ii) whether these effects are dependent on the number of possible target locations in visual search. To test this, visual search for pop-out targets was used with non-predictive dimensional but locational predictive trial-by-trial cueing (Experiment 4), or non-predictive dimensional and non-predictive locational identity of the upcoming target (Experiment 5). The results demonstrated systematic dimension-based variations of the early visual evoked P1 component and the frontal N2 component in both experiments, while these effects occurred independently from the featural identity within the cued dimension. This non-spatial variation of early visual processing is in line with dimension-based theories on visual attention, such as the DWA, and provides evidence for a dimension-specific top-down influence. According to the DWA, early visual input modules

(dimensions) are attentionally *weighted* facilitating the sensory coding of critical non-spatial target attributes. Thus, the attentional spotlight metaphor for early spatial attention effects has to be broadened to include dimension-based effects as early as 110 ms post-stimulus. The later N2 effect replicates the findings observed in Experiment 1 and 2 suggesting frontal executive control processes being involved in visual dimension weighting.

To gain further information regarding the neural regions associated with dimensional weighting, Chapter IV employed a spatio-temporal coupled current density reconstruction method (EaSI). More specifically, this reconstruction method was based on high-density EEG (recording of 128 channels in Experiment 5) to guarantee a reasonable spatial resolution. Electro-anatomical source inspection was performed for the visual P1 and frontal N2 component, which showed reliable increased activation for dimension changes (relative to dimension repetitions) and was interpreted as to be associated with visual dimension weighting. Consistent with earlier fMRI findings of a fronto-posterior network involved in dimension switching (Pollmann, 2000, Pollmann et al., 2006); this method revealed sources located within the left frontopolar cortex (BA 10) as well as inferior (BA 18) and superior occipital areas (BA 19). Thus, these electro-anatomical observations strengthen the assumption that these brain region harbour processes critical for dimensional weight-setting, based on electro-cortical brain responses,

Chapter V. So far, all presented experiments were performed to explore intertrial facilitation within the visual modality. The current chapter closes the experimental part of the present thesis investigating whether findings and theoretical accounts, postulated in the visual modality, can be transferred to a cross-modal level of processing. Previous studies (e.g., Spence, Nicholls, & Driver, 2001) have indicated that the processing of a given target is facilitated when it appeared in the same (e.g., visual - visual), compared to a different (e.g., tactile - visual), modality as on the previous trial, termed as ‘modality shift effect’. Thus, the aim of the present chapter was (i) to replicate earlier findings of prolonged RTs for changes, relative to repetitions, of the target-defining modality and (ii) to identify the electro-cortical correlates underlying this modality change effect. More specifically, the examined question was whether *weighing mechanisms* responsible for the frontal N2 in visual dimension weighting (see Chapter II and IV) might also control the re-setting of attentional weights across sensory modalities. This was tested using a discrimination task in which participants indicated the target modality (visual or tactile) of a single stimulus

via foot pedal responses (Experiment 6). As expected, a change (relative to repetition) of the target-defining modality resulted in prolonged response times. Independently from the target's modality, this behavioral effect was mirrored by enhanced amplitudes of the anterior N1 component, which were strongest over fronto-central electrode positions. To rule out the theoretical possibility that this N1 effect was simply attributable to repetitions/changes in the motor response (since a modality change was invariably associated with a response change), Experiment 7 employed two features per modality, with one feature in each modality mapped to the same motor response. This way, a modality change could occur independently of repetitions/changes in the motor response. Although the RT data of Experiment 7 revealed an interactive pattern between both factors, the ERP analyses assured that, independently from the target's modality, spatial stimulus qualities, and motor requirements, the anterior N1 effect was purely 'modality change-driven'. Based on these findings, a 'modality-weighting' account (MWA) is introduced which is essentially a generalization of the DWA. That is, the MWA assumes similar *weighting mechanisms* for perceptual modalities as assumed for dimensions within the visual modality. The fact that the N1 effect was found to be largest at the same electrode position as the N2 effect of Chapter II and IV suggests similar brain regions being engaged in both components. Hence, processes represented by the anterior N1 effect might be associated with the control of modality-specific weight-shifting.

Conclusions

It is widely accepted that our current behaviour is shaped by the preceding sensory events as well as motor actions. Experiments summarized in the present thesis were designed to gain deeper insights into the mechanisms that implicitly carry information of the past in order to modulate future actions. This issue was approached by starting to explore dimension-specific intertrial effects in the visual modality. Based on electro-cortical brain responses, these studies revealed additional information regarding the time course in which weight shifting is accomplished across successive trial episodes. In agreement with previous findings based on hemodynamic brain responses (Pollmann, 2000, 2006), several subcomponents were identified contributing to visual dimension weighting. Here, a (pre-) frontal subcomponent (as reflected by the anterior N2 in Chapter II and IV) seems to be associated with the control of weight-shifting, reflecting the detection of a change and the initiation of a re-setting/re-distribution of weights according

to the currently processed sensory event for an optimized stimulus processing in the subsequent trial episode. This is followed by processes (as reflected by the P3 and slow wave in Chapter II) harboured within higher-level visual areas in superior parietal and temporal cortex mediating these weight shifts via feedback pathways to the dimension-specific input modules in early visual areas. Thus, modulations of early pre-attentive processing (as reflected by the N2pc in Chapter III and the visual P1 in Chapter IV) represent the facilitated sensory coding of the relevant visual dimension as a consequence of the previous trial.

Additionally, the present thesis revealed converging evidence that *weighting mechanisms* as postulated for visual dimensions (DWA; Found & Müller, 1996) might be operating at several stages of human information processing. That is, similar sequential effects were observable at a cross-modal level of processing and even for response activation processes. Regarding perceptually-related processing stages, this would have important implications concerning the functional architecture of the DWA. As suggested in Chapter V, there might be an additional saliency-based modality map involved capable to shift attentional resources across modalities. On the other hand, Chapter III has demonstrated that motor responses experience facilitated processing if they remain identical across consecutive trials. As for perceptual processing, this facilitation might originate from pre-existing (weighted) response activations within the motor system.

The picture emerging from these studies is that different weighting mechanisms might be engaged in, and thereby modulate the time course of, distinct sub-stages (e.g., perceptual versus motor) within the information processing stream. Thus, albeit experimental conditions are measured as identical in terms of their behavioural performance (RT's), they might remarkably differ with respect to their underlying sub-stages of processing (as demonstrated by Chapter III: sDdR=dDsR=dDdR). This view is further supported by a recent study (Rangelov, 2007) which identified similar weighting mechanisms possibly influencing the extraction of rule requirements. More specifically, behavioural performance was markedly impaired, when participants had to switch (relative to maintain) a given task set. Taking all these different aspects of information processing into consideration, it seems that that weighting represents a general (neuro-)biological principle implemented in order to optimize the processing of proximal future events. The underlying natural relevance of this mechanism might be based on the simplified assumption: "*What is relevant now will possibly be relevant subsequently*".

Taken together, results accumulated in the present thesis provide evidence that, besides bottom-up and top-down mechanisms, events of the immediate past (previous trial episode) have a significant impact on our current behaviour. Thus, traditional theories modelling visual as well as cross-modal attention must be updated to account for these intertrial facilitation effects.

CHAPTER II

Brain electrical correlates of visual dimension weighting

Abstract

In visual search, there is a RT cost for targets on a given trial if the previous target was defined in a different (e.g., orientation - color), compared to the same (e.g., color - color), visual dimension. According to the 'dimension-weighting' account (Müller et al., 1995), limited attentional weight needs to be shifted from the old to the new target-defining dimension, resulting in prolonged behavioral response times. The present study aimed at identifying brain electrical correlates associated with this weight shifting process. Analyses of ERPs revealed several components to reflect dimension changes whether the task was to detect the target or to identify its defining dimension. N2 amplitudes were more negative whenever the dimension changed. The P3 exhibited latency differences that mirrored RTs in both tasks; but the amplitudes showed no direct relation to stimulus- or response-related processing. Finally, slow-wave amplitudes were enhanced for dimension changes. Taken together, the results provide support for relatively early, perceptual-related processes involved in the generation of behavioral dimension change costs.

Introduction

One prime function of visual attention is to select relevant information from the huge variety of structures present in the visual field at any one time. Selective attention may be guided bottom-up by salient features in the field, or top-down by the intention to seek particular information relevant to the task at hand. Selective-attention mechanisms can also be differentiated according to the type of information that forms the basis for selection: space-based, object-based, and dimension- (or feature-) based. Space-based theories of attention (e.g., Posner, 1980; Eriksen, & St. James, 1986) propose that observers direct (a 'spotlight' of) attention to particular locations in space. However, observers can also attend to a particular task-relevant object even if this object shares the same location with another, irrelevant object – which has led to the notion of attentional selection being object-based (e.g., Duncan, 1984; Baylis & Driver, 1993). Finally, dimension-based theories of attention (e.g., Allport, 1971; Müller, Heller, & Ziegler, 1995) propose that selection is based on dimensional properties of the objects in the visual field. The latter notion is of special relevance to visual search tasks in which observers have to find a target embedded in an array of irrelevant distractors, with the target being singled out by a unique feature in one dimension or a conjunction of features in separable dimensions. Since dimension-based selection is of special interest for the present investigation, it is considered in more detail below.

Dimension-based Visual Selection

Dimension-based theories of visual selection assume that selection is limited by the dimensional nature of the discrimination required to discern response-relevant (target) attributes. A well-supported account has recently been developed by Müller and colleagues (e.g., Found & Müller, 1996; Müller, Heller, & Ziegler, 1995; Müller, Reimann, & Krummenacher, 2003), based on a set of findings observed in visual search tasks. First, search times are remarkably slowed for cross-dimensional compared to intra-dimensional search. That is, the target-defining dimension (e.g., color, orientation) can vary across consecutive trial in the former (e.g., orientation, color), but remains constant in the latter (e.g., color), search condition, in which the critical feature is variable within a fixed dimension (for orientation, e.g., horizontal, vertical). In addition to this general cross-dimensional search cost, search performance is further modulated by the history of successive trial episodes. More specifically, behavioral response times are further slowed when the current target appears in a different (e.g., motion → color), relative to the same (e.g., color → color), visual dimension as on the previous trial, irrespective

of whether or not the target-defining feature had intra-dimensionally changed (e.g., blue → red) across trials.

Based on the dimension-specific, rather than feature-specific, nature of this *intertrial facilitation* effect, Müller and his colleagues (Müller et al., 1995; Found & Müller, 1996) have advocated a 'dimension-weighting' account (DWA). In line with other theories modeling visual search performance (e.g., Guided Search; Cave & Wolfe, 1990; Wolfe, 1994, 1998), the DWA assumes focal attention to operate on a master map of integrated saliency signals derived separately in dimension-specific analyzer units. Importantly, Müller and his colleagues implemented a (implicit) weighting mechanism into this processing architecture which assigns limited attentional weight to the various dimension-specific input modules depending on the previous sensory event. That is, if a visual dimension (e.g., motion) has been revealed to be relevant (e.g., defining the target) for a given trial then this dimension is assigned with larger weight compared to other visual dimensions (e.g., orientation, color, …) thereby modulating the integration process of dimension-specific saliency signals onto to the master map unit. Thus, targets presented within the same dimension as on the previous trial are processed faster based on the weighted saliency signal of this dimension (compared to others) at the sensory input level. However, the presentation of a target defined within a different visual dimension as on previous trial requires a time-consuming *'(re-)weighting'* process, which is needed to transfer attentional weight from the old to the new target-defining dimension, possibly in order to optimize target detection. While Müller and colleagues originally proposed that this weight shift process represents a pre-requisite for target detection, the target might also be detected, albeit slower, in a non-weighted dimension and the re-weighting follows target detection as an implicit update/adjustment for the subsequent event. Ultimately, the dimension-weighting account is neutral with respect to this issue. Dimensions are assigned weight largely passively, in bottom-up manner; however, this weight set may be modified, to some extent, in top-down manner, based on advance information as to the target-defining dimension on a given trial (Müller et al., 2003).

Neural signatures of dimensional weighting

The neural correlates of dimension weight-setting have been investigated in a set of studies by Pollmann and his colleagues, using event-related functional magnetic resonance imaging (fMRI) (Pollmann, 2004; Pollmann, Weidner, Müller, & von Cramon, 2000, 2006; Weidner, Pollmann, Müller, & von Cramon, 2002). Pollmann and his colleagues

identified a fronto-posterior network consisting of a variety of areas that have been reported to be involved in visual search and shifts of visuo-spatial attention. They interpreted the specific activation pattern revealed in prefrontal cortex, increased activation on dimension change relative to no-change trials, as reflecting processes critical for dimensional weight shifting (Pollmann et al., 2000, Pollmann, 2004). Extending the search task from singleton feature to singleton conjunction search, Weidner et al. (2002) found a double dissociation. There was a dimension change-related increase of activation in frontopolar cortex in singleton feature, but not singleton conjunction search. By contrast, there was a dimension change-related activation in pregenual frontomedian cortex in singleton conjunction, but not singleton feature search. This pattern of activations gave rise to the assumption that frontal areas are involved in the control of dimensional weight shifting – 'automatic' in singleton feature search, 'voluntary' in singleton conjunction search – while higher-level visual areas in superior parietal and temporal cortex mediate the weight shifts via feedback to the dimension-specific input areas in occipital gyrus (Pollmann et al., 2006).

Rationale of the present study

The present investigation was designed to identify electro-cortical correlates of dimension weighting in cross-dimensional singleton feature search by means of ERP analysis. The fMRI studies reported above provided evidence that anterior brain structures are involved in the attentional weighting of target defining dimensions. These findings make it likely that ERP correlates of dimensional weighting can be discovered as well, providing insight into the time course of the weighting processes. This was the aim of the present study, which examined ERP components time-locked to the onset of a search display on a given trial n containing a target defined in a particular dimension, contingent on the target-defining dimension on the preceding trial n-1. That is, the present study looked for ERP components that systematically vary with changes versus repetitions, across trials, in the target-defining dimension and thus presumably reflect the (re-)allocation of attentional weight to relevant dimensions.

According to the dimension-weighting account, a change of the target-defining dimension on consecutive trials would lead to a shifting of attentional weight from the old to the new dimension. Thus, before a weight shift is initiated, a change in the target-defining dimension has to be detected. This process may be associated with systematic variations in the anterior N2 component, which has been shown to reflect the detection of pop-out targets in

visual search (Luck & Hillyard, 1994). In a series of experiments, Luck and Hillyard demonstrated that this component was elicited by task-relevant singleton feature 'targets' as well as non-relevant singletons, which they took to *"suggest[s] that it may be related to the auditory mismatch negativity"* (Näätänen, Simpson, & Loveless, 1982; p. 305), although it appeared to be modulated by top-down task set. However, Luck and Hillyard did not directly examine repetitions versus changes in the target-defining dimension on consecutive trials, making it difficult to compare their findings with the inter-trial effects that were the focus of the present study. A more direct comparison can be made with other investigations that have revealed the N2 to reflect perceptual mismatch or cognitive conflict (Pritchard, Shappell, & Brandt, 1991; Wang, Cui, Wang, Tian, & Zhang, 2004) and the inhibition of overt or covert responses (Kiefer, Marzinzik, Weisbrod, Scherg, & Spitzer, 1998; Pfefferbaum, Ford, Weller, & Koppel, 1985). Thus, the anterior N2 might be a possible indicator of dimension changes in visual search for pop-out targets. Following detection of a change in the target-defining dimension, weight is shifted to the new dimension. This process may be associated with variations in later ERP components such as the P3 or Slow Wave (SW), though the weight shifting may not have to be completed prior to response execution. In contrast, repetition of the target-defining dimension on consecutive trials might be linked to ERP components preceding the N2, such as the P1-N1 complex which is thought to reflect early attentional processes (e.g., Luck, Woodman, & Vogel, 2000).

According to Müller and colleagues, the weight shifting should be reflected in an ERP component prior to the initiation of the response. Failure to identify such a component prior to response would support theories that account for dimension change costs in terms of response-related processes (e.g., Cohen & Magen, 1999; Mortier, Theeuwes, & Starreveld, 2005). Thus, in addition to identifying ERP components associated with attentional weight shifting, the time course of the ERP can provide new insights into the controversial issue of the point in time, and stage of processing, at which the weight adjustment occurs.

These questions were examined in two experiments which adapted the two singleton feature search tasks used by Found and Müller (1996) for EEG recording. In both experiments, the target on a given trial differed from the distractors in either color or orientation. In Experiment 1 (with 30% target-absent trials), observers were required to simply respond 'target-present' or 'absent' (target-present/absent discrimination); in Experiment 2 (with target-present trials only), observers had to explicitly indicate the target-defining dimension (color/orientation-target discrimination). These tasks were compared to examine the relation of

dimensional-weight shifting to target detection and (dimensional) identification, respectively. Müller et al. (1995; see also Müller et al., 2004) argued that target detection requires at least implicit knowledge, that is, attentional weighting, of its defining dimension, while explicit identification of this dimension involves an extra, time-consuming process, that is, focal-attentional analysis of the type of feature contrast generated by the target (according to Müller et al., simple detection responses can be initiated prior to target analysis). If this is correct, then no differences in ERP components reflecting weight shifting should be observed between the simple target detection (Experiment 1) and the explicit identification task (Experiment 2). In contrast, if processing differed fundamentally between the two tasks, systematic differences in ERP effects should be observed.

EXPERIMENT 1

Method

Participants. Eleven observers (7 female) took part in Experiment 1. One observer had to be excluded from the analyses of ERPs, due to excessive artifacts. The ages of the resulting 10 observers ranged from 20 to 28 years (X = 25.7, SD = 2.5 years). Observers were either paid or received course credit for participating. All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological disorder.

Stimuli and procedure. The experiment was conducted in a dimly illuminated, sound-attenuated, and electrically shielded chamber. A 21" display monitor was placed 110 cm in front of the observer, with the central fixation cross aligned with the observer's horizontal straight-ahead line of sight. Each trial started with a central asterisk presented for 500 ms. This was followed by the search display, which consisted of 18 elements presented below the fixation marker and remained in view until the observer reacted. Distractor elements in the search display were green vertical bars, the singleton target element was either a red or a blue vertical bar (color-defined targets) or a 45° left- or right-tilted green bar (orientation-defined targets). Targets could appear, unpredictably on a trial, at one of four possible locations (two to the left and two to the right) of the fixation marker. Search displays contained a target on 70% (and no target on 30%) of the trials, with targets positioned equally likely to the left and right of the fixation. Observers were instructed to press a button with the index finger of one hand to respond 'target present',

and with the index finger of the other hand to respond 'target absent'. Responses were to be made as fast and accurately as possible. After an inter-trial-interval of 1000 ms, the next trial was initiated. After half of the experiment, the response assignment was reversed.

The order of target-defining dimensions (and features) on consecutive trials was pseudo-randomized, to ensure comparable numbers of trials with dimension (and feature) repetitions and changes across trials. There was a total of 360 trials with repeated color targets (Color same Dimension, CsD), 178 trials with a repetition of target's color feature (e.g., red–red; Color: same Dimension same Feature, CsF) and 182 trials with a color feature change (e.g., red–blue; Color: same Dimension different Feature, CdF). Similarly, there was a total of 358 trials with repeated orientation targets (Orientation same Dimension, OsD), 182 trials with a repetition of the target's orientation feature (e.g., left-tilted–left-tilted; Orientation: same Dimension same Feature, OsF) and 176 trials with an orientation feature change (e.g., left-tilted–right-tilted; Orientation: same Dimension different Feature, OdF). Further, on 194 trials, the dimension changed from orientation to color on consecutive trials (Color: different Dimension, CdD); and on 194 trials, it changed from color to orientation (Orientation: different Dimension, OdD).

Component	Mean time window	Latency Window	Recording site (left, midline, right)
P1	50 ms – 90 ms	40 ms – 100 ms	frontal, central, parietal, occipital
N1	115 ms – 155 ms	100 ms – 170 ms	frontal, central, parietal, occipital
N2	250 ms – 300 ms	220 ms – 330 ms	frontal, central, parietal, occipital
P3	340 ms – 380 ms	320 ms – 420 ms	frontal, central, parietal, occipital
Slow Wave	420 ms – 600 ms	-	frontal, central, parietal, occipital

Table 1. Detection task: Time windows for calculating mean amplitudes of ERP components at various recording sites, and latency windows for determining peak latency of ERP components at the corresponding sites.

EEG Recordings. The electroencephalogram (EEG) was recorded continuously, at a sampling rate of 500 Hz, using 64 Ag/AgCl electrodes including those corresponding to the 10-10 system (American Electroencephalographic Society, 1994). The electrodes were mounted on an elastic cap (Easy Cap, Falk Minow Services). Vertical and horizontal

eye-movements were monitored by means of electrodes placed at the outer canthi of the eyes and the superior and inferior orbits. Electrophysiological signals were amplified using a 0.1–100-Hz bandpass filter via BrainAmps (BrainProducts, Munich). All electrodes were referenced to Cz and re-referenced off-line to linked mastoids. ERPs were averaged off-line over a 1000-ms epoch relative to a 200-ms pre-stimulus baseline. Eye movements were corrected by means of independent component analyses (ICA) implemented in the Brain Vision Analyzer software (Brain Products, Munich). Epochs with artifacts, that is: excessive peak-to-peak deflections (>100 μV or <-100 μV), bursts of electromyographic activity (permitted maximal voltage step / sampling points 50 μV), and activity lower than 0.5 μV within intervals of 500 ms (indicating 'dead channels' in the montage), were excluded from averaging on an individual-channel basis.

Following the elimination of artifacts, latencies of the P1, N1, N2, and P3 components were determined as the maximum deflection within the time windows derived by visual inspection of the grand average potentials (see Table 1). After identification of component latencies, mean amplitudes were calculated using the time windows specified in Table 1. Note that only trials n with a correct response, following trials n-1 with a correct response, were included in the analyses. Amplitudes and latencies were analyzed by repeated-measures ANOVAS with the factors 'Dimension' (color vs. orientation), 'Transition' (same feature, different feature, different dimension), 'Electrode site' (frontal, central, parietal, and occipital), and 'Electrode position' (left, midline, and right). Whenever required, significant main effects and interactions were further examined using Tukey HSD post-hoc contrasts.

Results

Behavioral Data

Overall, 1.2% of all trials resulted in misses and 1.8% in false alarms indicative of no speed accuracy trade off. Figure 4 presents the correct detection (target-present) RTs dependent on the cross-trial transition (same Dimension same Feature sF, same Dimension different feature dF, different Dimension dD), separately for color- and orientation-defined targets. A repeated-measures ANOVA with the factors Dimension (color vs. orientation) and Transition (sF, dF, dD) revealed both main effects to be significant [$F(1,9)=42.06$, $p<.0001$, and, respectively $F(2,18)=65.89$, $p<.0001$]. The interaction was not significant [$F(2,18)=.832$, $p<.45$]. Color-defined targets were responded to overall faster than

orientation targets (382.5 vs. 414.2 ms). More importantly, the pattern of inter-trial transition effects replicated the pattern observed by Found and Müller (1996): There was a significant RT cost for changes, relative to repetitions, of the target-defining dimension across trials (39.6-ms cost for dD vs. sF; $p<.0002$), while there was no significant cost for feature changes, relative to repetitions, within a repeated dimension (6.5-ms cost for dF vs. sF; $p<.22$).

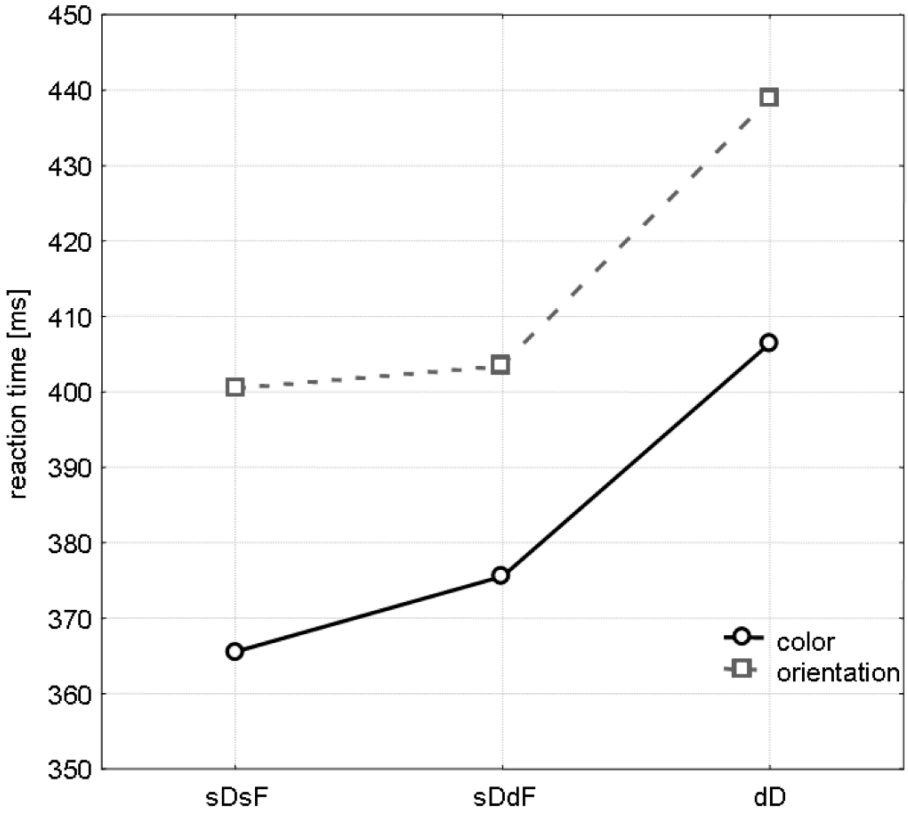

Figure 4. Detection task: Mean reaction times to color and, respectively, orientation targets on trial n dependent on the identity of the target on trial n-1: same-dimension same-feature (sF), same-dimension different-feature (dF), and different-dimension (dD). The black solid line indicates reaction times to color targets, the grey dashed line reaction times to orientation targets.

Electrophysiology

Figure 5 displays the grand average waveforms (collapsed over color and orientation targets) with the onset of same- and different-dimension targets on trial n, dependent on the target-defining dimension on trial n-1, for selected electrode locations. As indicated by this, target display onset was associated with a pronounced negative shift in the time range of the N2 at frontal and, less marked, central leads.

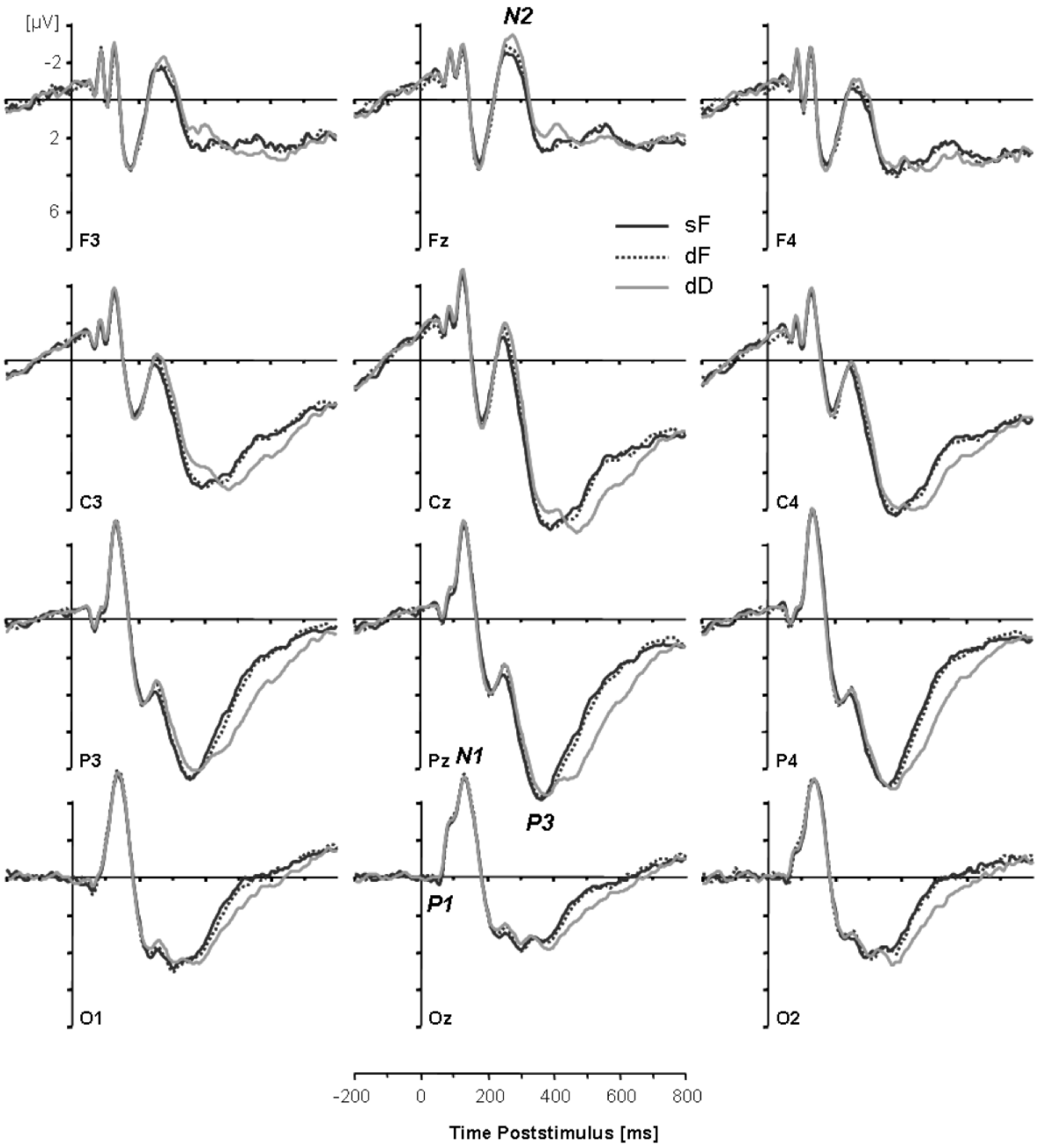

Figure 5. Detection task: Grand average waveforms elicited with onset of the target display on trial n dependent on the identity of the target on trial n-1, for selected electrode positions. Dark grey solid lines indicate same-dimension same-feature trials (sF), dark grey dotted lines same-dimension different-feature trials (dF), and light grey solid lines different-dimension trials (dD). Averages were collapsed across color and orientation targets, as the Dimension x Transition interaction was non- significant. Negativity is plotted upwards, and the data is presented relative to a 200-ms pre-stimulus baseline. Components labelled in italics are the N2 at Fz, the P3 at Pz, and the P1 and N1 at Oz.

In addition, a late positive complex revealed differences between same- and different-dimension targets dependent on the target-defining dimension on the previous (n-1) trial at posterior electrodes. Analyses of the various components showed the factor 'Transition' to have a significant effect on the N2, P3, and SW components. Since the present study was primarily designed to investigate neural mechanisms underlying the behavioral dimension change cost, only main effects and/or significant interactions involving the factor 'Transition' will be reported for the electrophysiological data.

P1 and N1. No significant main effects/interactions involving the factor Transition were obtained for the amplitudes and peak latencies of the P1 and N1 component.

N2. The ANOVA examining the N2 amplitudes revealed the main effect of Transition to be significant [$F(2,18) = 6.96$, $p<0.021$], with changes in the target-defining dimension giving rise to a more negative-going deflection of the N2 (with 2.2μV, 1.9μV, and 1.5μV for same feature, different feature, and different dimension trials averaged over all electrode sites, respectively). This main effects was qualified by significant interactions of Transition x Electrode position [$F(4,36) = 2.73$, $p<0.044$] and Transition x Electrode position x Electrode site [$F(12,108) = 3.15$, $p<0.021$]. The strongest negative deflections were observed at frontal electrodes, with a maximum over the frontal midline (Fz) recording site (-2.69 μV). The difference between same- and different-dimension trials was still pronounced at central midline electrodes and decreased towards posterior sites. The three-way interaction was due to decreasing differences between same- and different-dimension trials from left-occipital leads to midline- and right-occipital recording sites.

An analogous ANOVA of the N2-latencies revealed a marginally significant Dimension x Transition x Electrode site interaction [$F(6,54) = 3.03$, $p<0.052$], with increasing latency differences between color and orientation targets from frontal towards occipital leads. Orientation targets elicited an earlier N2 onset than color targets, irrespective of whether or not there was a dimension change, at all electrode locations – except for frontal sites. Here, at the maximum of the N2, earlier onset latencies for color compared to orientation targets were exhibited for same feature trials but the inverse amplitude pattern was found for different feature and dimension change trials.

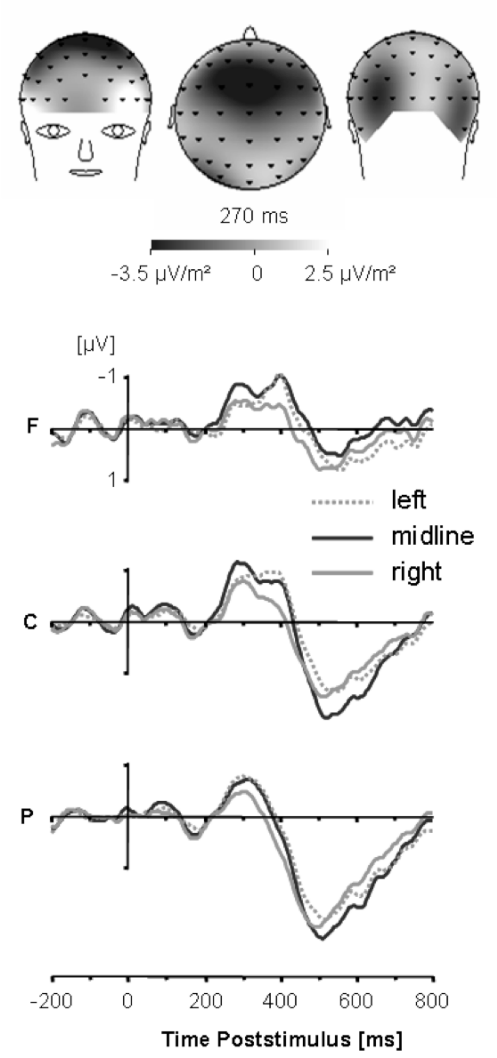

Figure 6. Detection task - Top panel: Current density distribution of the dimension change effect computed for the difference wave forms at 270 ms. Bottom panel: Difference waveform (different-dimension minus same-dimension) for frontal (F), central (C), and parietal (P) electrode positions. Light grey lines depict lateral (dottet = left; solid = right) and dark grey lines midline electrode positions.

Topography of N2 effect

To further explore the topography of the dimension change effect, difference waves were computed by subtracting same-dimension from different-dimension trial waveforms.[1] Figure 6 presents the resulting difference waves and the current source density map for the difference wave at 270 ms post target display onset. To examine whether the change effect was lateralized, difference wave amplitudes (mean amplitudes for the time range 270±30 ms) were examined by a repeated-measures ANOVA with the factors Dimension, Electrode position (left, midline, right), and Electrode site (frontal, central, parietal, occipital). The results revealed the main effect of Electrode position to be significant [$F(2,18) = 5.35$, $p<0.033$], with the strongest effect of dimensional repetition versus change at midline electrodes. Furthermore, the Electrode position x Electrode site interaction was significant [$F(6,54) = 3.30$, $p<0.008$]. At frontal and central sites, left- and right-lateral amplitudes did not differ (post-hoc contrasts, all $p>0.99$). Difference wave amplitudes at frontal midline electrodes were significantly more negative than left- and right-lateral amplitudes ($p<0.01$), but amplitudes at central midline sites did not differ significantly from central left- and right-lateral recording sites ($p >0.92$). There were

[1] Note that, since there were no significant differences in N2 amplitudes between color- and orientation-defined targets, the time course of activity was aggregated across the two dimensions; similarly, since there were no differences between same- and different-feature trials in the absence of a dimension change, both types of trial were aggregated in the condition ‘same dimension’.

no differences among any electrode positions at parietal and occipital electrode locations (all $p>0.36$). This pattern is consistent with a frontal maximum, without lateralization of the N2 component in the detection task.

P300 and Slow Wave. For the P300 amplitudes, the analyses revealed significant interactions of Dimension x Transition [$F(2,18) = 5.593$, $p<0.013$], Transition x Electrode position [$F(4,36) = 4.109$, $p<0.006$], and Dimension x Transition x Electrode site [$F(6,54) = 3.328$, $p<0.051$]. Maximum amplitudes of the P3 were located over parietal midline electrodes and revealed more positive-going deflections over the right as compared to the left hemisphere.

The influence of the factors Dimension and Transition at the parietal maximum of the P3-deflection was examined further by an ANOVA with the factors Dimension, Transition, and Electrode position (left, midline, right). This ANOVA revealed the interaction of Transition x Electrode position to be significant [$F(4,36) = 4.927$, $p<0.014$]. Post-hoc contrasts revealed a significant difference between feature repetitions and changes of the target-defining dimension ($p<.017$) with more positive going P3 amplitudes for dimension change trials (8.94 μV) as compared to feature repetition trials (8.58 μV). No difference between feature repetitions and changes ($p<.37$) or feature repetitions and dimension changes ($p<.88$) were observed at right-parietal electrode sites. While the strongest positive deflections were observed over parietal midline electrodes, no significant effects of dimension repetitions versus changes were present for left- and midline-parietal sites (all $p>.56$).

An analogous ANOVA of the P3-latencies revealed the main effect of Transition [$F(2,18) = 25.79$, $p<0.001$] to be significant. The P3 had an earlier onset for same-dimension (i.e., same- and different-feature) trials (365 and 369 ms, respectively) compared to different-dimension trials (393ms). Repetition of the target-defining dimension led to comparable onset latencies of the P3, whether or not the target feature was repeated ($p<.56$). In contrast, changes of the target-defining dimension were associated with significantly longer P3 latencies (all $p<.001$).

For the slow wave amplitudes, the ANOVA revealed the main effect of Transition [$F(2,18) = 12.398$, $p<0.004$] as well as the interaction of Transition x Electrode site [$F(6,54) = 9.37$, $p<0.001$] (see Figure 7) as significant. Slow-wave amplitudes were enhanced for different-dimension as compared to same-dimension (i.e., same- and

different-feature) trials. Post-hoc contrasts revealed significant differences between same-dimension trials (irrespective of a repetition/change of the target feature) and different-dimension trials at central, parietal, and occipital sites (all $p<.003$). For same-dimension trials, there were no significant differences between feature changes and repetitions at these locations ($p<.78$). In contrast to the central, parietal, and occipital sites, there were no differences between same- and different-dimension trials at frontal electrodes (all $p>.34$). The maximum absolute slow-wave deflection was located over central sites, with a non-significant decrease towards parietal locations ($p<.55$) and significantly less pronounced deflections over frontal and occipital leads (all $p<.03$). However, the largest amplitude difference between same- and different-dimension trials was observed over parietal leads.

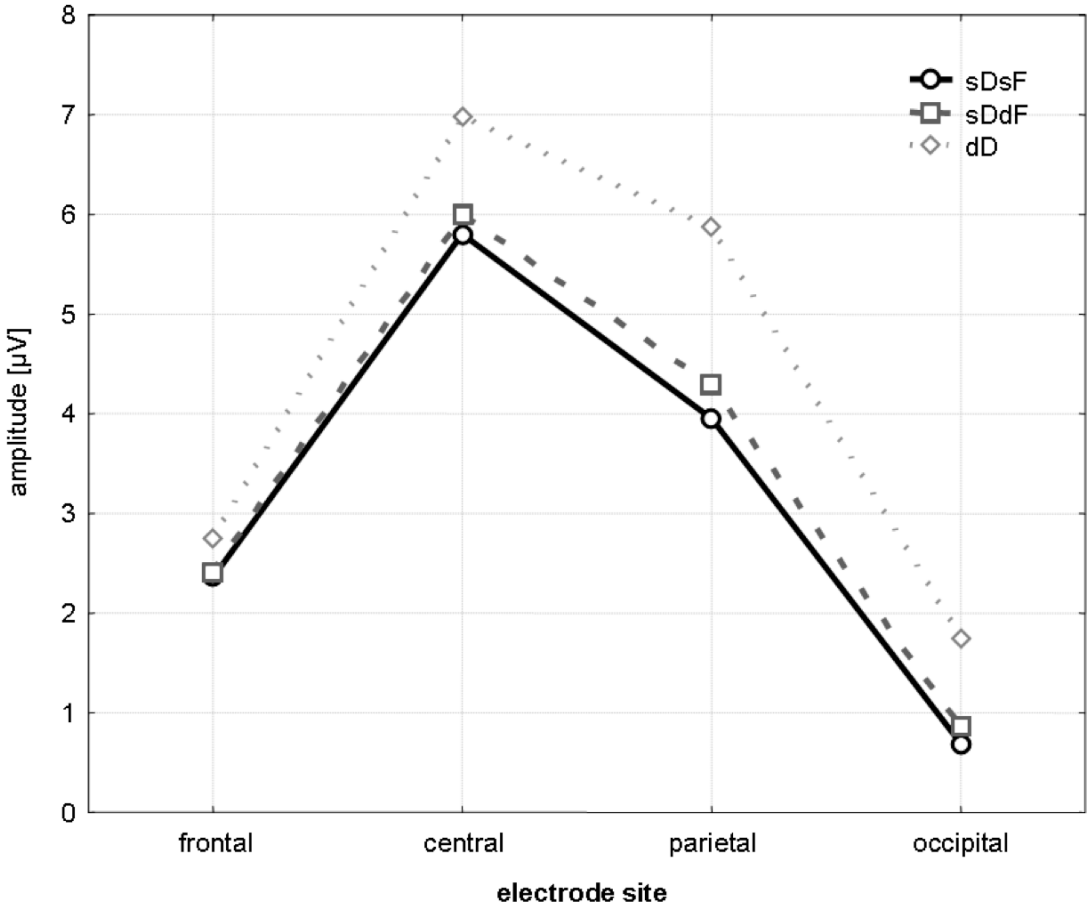

Figure 7. Detection task: Mean slow wave amplitudes from 420 to 600 ms post display onset as a function of (midline) electrode site positions (frontal, central, parietal, occipital), separately for the three intertrial transition conditions: same-dimension same-feature (sF), same-dimension different-feature (dF), and different-dimension (dD).

The largest transition effect at parietal electrodes was examined further by an ANOVA with the factors Dimension, Transition, and Electrode position (left, midline, right). This ANOVA revealed all three factors to have a significant impact on slow-wave amplitudes (all $p<.032$), including a significant interaction of Transition x Electrode position [$F(4,36) = 2.908$, $p<0.035$]. There were more positive-going deflections for orientation targets, with the strongest amplitude overall recorded at the parietal midline. Same- and different-feature trials did not differ significantly in slow-wave amplitude ($p<.59$), while both differed compared to different-dimension trials ($p<.001$). There were no differences in slow-wave amplitude for same- and different-feature trials at left- and right-parietal electrode locations (all $p<.97$), but significant differences between both lateral recording sites and the midline position (all $p<.001$). The interaction was due to a decreasing effect of dimension changes from left- to right-parietal recording sites for different-dimension trials.

Discussion

The RT data replicated the findings of Found and Müller (1996). There were general RT advantages for targets defined in the color dimension. However, for both color and orientation targets, RTs were markedly slower when the target-defining dimension changed across trials, while there were no RT differences between same-dimension trials with and without a change in the target feature. This pattern of effects is consistent with the notion that attentional weights are assigned to target dimensions rather than features, and that a dimension change requires (or is associated with) the shifting of attentional weight from the old to the new target-defining dimension.

The missing influence of dimension repetition versus change on event-related P1 and N1 is consistent with the assumption (e.g., Hillyard & Anllo-Vento, 1998) that these early components are associated with perceptual processing within the focus of attention, in particular, when focal attention is allocated in advance to a circumscribed display region where a target appears later. In contrast, these components are not significantly modulated when the display is processed in parallel to discern the presence of a feature contrast, that is, prior to the allocation of focal attention to a selected location.

The systematic pattern of RT effects was mirrored by effects in the fronto-centrally distributed N2 component of the visually evoked potential. Changes in the target-defining dimension were associated with stronger negative-going deflections in the time range 250

to 300 ms. Conversely, the negativities were less pronounced with repetitions of the target-defining dimension, whether or not the target feature changed (while there appeared to be some differences for feature changes within dimensions, these failed to reach significance – as with the RT data). The systematic pattern of N2 amplitude effects might be taken as evidence of an additional process that comes into play only when the target-defining dimension changes on consecutive trials. This pattern is consistent with the dimension-weighting account, which assumes that, when the target-defining dimension changes from trial n-1 to trial n, limited attentional weight has to be shifted to the new dimension. Increased negativities of the N2 therefore might be interpreted as being associated with the detection of a change in the relevant dimension, which signals that a new dimensional weight set (assigning greater weight to the new dimension for upcoming trials) is required. The change effect, as reflected in the difference waves (same-dimensions trials subtracted from different-dimension trials), revealed a frontal distribution. This is in line with several studies that have reported a frontally distributed effect of 'difference detection' (e.g., Näätänen, 1990; Wang, Cui, Wang, Tian, & Zhang, 2004), or a prefrontal effect reflecting response-independent inhibition-related executive functions (Kiefer et al., 1998).

The latency of another component of the ERP, the P3, showed a systematic relation to the RT pattern of effects. However, the P3 falls within a time window that involves several processes some of which are associated with response requirements. Thus, any interpretation of the P3 effects must consider several underlying processes. One tentative interpretation might be that, after the detection of a change of the target-defining dimension, as reflected by increased negativities of the N2 component, attentional weights have to be shifted. The time-consuming re-distribution of the dimensional weights might contribute to the P3 pattern in the present investigation, in line with the observed latency pattern for the P3 over parietal recording sites: prolonged onset latencies for a change of the target-defining dimension compared to a repetition, irrespective of target feature changes/repetitions within the repeated dimension. Finally, the slow wave (SW) exhibited a systematic variation that mirrored the RT pattern. The strongest effect of dimension change was observed over parietal leads, with a midline maximum. However, dimension change significantly influenced slow-wave amplitude at all posterior recording sites. This pattern started over central sites and continued over parietal to occipital sites, revealing a wide-spread effect of changes in the target-defining dimension.

The topography of the N2 modulations on dimension change trials is consistent with the results of Pollmann et al. (2000), who used fMRI to study the neural correlates of dimension weighting. Pollmann et al. interpreted the specific activation pattern revealed in frontal cortex as reflecting a critical process in dimensional weight shifting: the detection of environmental change that requires the re-allocation of dimension-specific processing resources (see also Pollmann, 2004). In line with these findings, the topography of the N2 modulation revealed in the present study points to a generator in frontal cortex. This is also consistent with a study by Kiefer et al. (1998), reporting an enhanced N2 component in a go/no-go task that was largely independent of motor-related processes and taken to reflect higher-level executive functions. Dipole reconstruction pointed to bilateral generators within the inferior prefrontal area. However, without reconstructing the sources of the present data, the assumption of frontal generators underlying the observed N2 pattern remains tentative.

In addition to the study of Kiefer and colleagues reported above, the present N2 modulation occurred within the time range of other negative components that reflect perceptual mismatch or cognitive conflict (Error Related Negativity, ERN, e.g., Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Mismatch Negativity, MMN, e.g., Näätänen, 1990; Mismatch N2, e.g., Pritchard, Shappell, & Brandt, 1991; Wang et al., 2004). In the present task, this might be the detection of a change in the target-defining dimension, signalling the need to redistribute the attentional weight to the new dimension.

If this is correct, the same pattern of N2 and P3 amplitude effects should be observed in Experiment 2, in which observers were required to explicitly discriminate the target-defining dimension, giving a ‘color’ vs. an ‘orientation’ response. Experiment 2 was expected to confirm the pattern of N2 modulations, as an indicator for the detection of changes in the target-defining dimension. Furthermore, the pattern of N2, P3, and SW effects were expected to shed light on the question whether (implicit) knowledge of the dimensional identity of the target is required to detect its presence. If so, the patterns of ERP components were expected to be comparable in the two experiments.

EXPERIMENT 2

Method

Participants. Twelve subjects (7 female) took part in Experiment 2; three of the twelve observers had already taken part in Experiment 1. One observer had to be excluded

from the ERP analyses due to excessive artifacts. The resultant 12 observers ranged in age from 22 to 32 years (X = 27.08 years, SD = 2.54). All subjects were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological disorder.

Stimuli and procedure. The procedure was the same as that of Experiment 1, except that a target was present on all trials. Observers had to respond to color-defined targets (whether red or blue) with the index finger of one hand and to orientation targets (whether left- or right-tilted) with the index finger of the other hand, with hand counterbalanced across observers. After half the experiment, the response assignment was reversed.

The order of target dimensions on consecutive trials was pseudo-randomized to assure approximately comparable number of dimension repetition and change trials. There were 506 trials in total with repeated color-defined targets (Color same Dimension, CsD), with a feature repetition (e.g., red–red) on 248 trials and a feature change (e.g., red–blue) on 258 trials. And there were 500 trials with repeated orientation-defined targets (Orientation same Dimension, OsD), with a feature repetition (e.g., left-tilted–left-tilted) on 248 trials and a feature change (e.g., left-tilted–right-tilted) on 252 trials. On 488 and 486 trials, the target-defining dimension changed from orientation to color (Color different Dimension, CdD) and, respectively, from color to orientation (Orientation different Dimension, OdD).

Component	Mean time window	Latency Window	Recording site (left, midline, right)
P1	50 ms – 90 ms	40 ms – 100 ms	frontal, central, parietal, occipital
N1	115 ms – 155 ms	100 ms – 170 ms	frontal, central, parietal, occipital
N2	250 ms – 300 ms	220 ms – 330 ms	frontal, central, parietal, occipital
P3	340 ms – 380 ms	320 ms – 420 ms	frontal, central, parietal, occipital
Slow Wave	420 ms – 600 ms	-	frontal, central, parietal, occipital

Table 2 Discrimination task: Time windows for calculating mean amplitudes of ERP components at various recording sites, and latency windows for determining peak latency of ERP components at the corresponding sites.

Data Processing. Manual response, EEG data recording and EEG data analysis was identical as in Experiment 1. For Experiment 2, amplitudes and latencies of the P1, N1, N2, and P3 components were derived from visual inspection of the Grand Average waveforms as maximum deflection within the time windows specified in Table 2. The maximum deflection within the defined time ranges was defined as the component's latency. Only trials with correct reaction, following a trial with a correct reaction, were included in the analyses.

Results

Behavioral Data

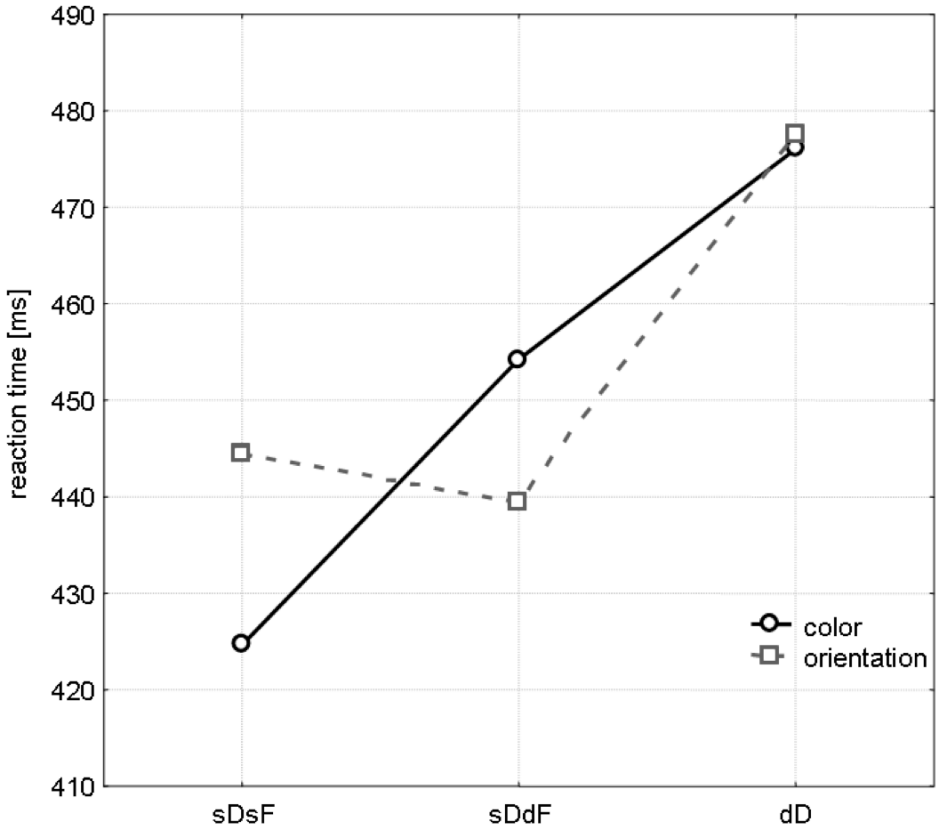

Figure 8. Discrimination task: Mean reaction times to color and, respectively, orientation targets on trial n dependent on the dimensional identity of the target on trial n-1: same-dimension same-feature (sF), same-dimension different-feature (dF), and different-dimension (dD). The black solid line indicates reaction times to color targets, the grey dashed line reaction times to orientation targets.

Overall, 3.9% incorrect reactions were recorded (4.1% and 3.5% for color and orientation targets, respectively). The RT results were again consistent with the general pattern of effects reported by Found and Müller (1996): costs for changes, relative to

repetitions, of the target-defining dimension, but little costs for changes, relative to repetitions, of the target-defining feature within a constant dimension. In contrast to Experiment 1 (detection task), a repeated-measures ANOVA with the factors Dimension (color, orientation) and Transition (same Feature, different Feature, different Dimension) failed to reveal a main effect of Dimension [$F(1,10)=.623$, $p<.448$]. However, as in Experiment 1, the main effect of Transition was significant [$F(2,20)=16.84$, $p<.0001$], though there was also a significant Dimension x Transition interaction [$F(2,20)=21.56$, $p<.0001$].

This interaction, which is illustrated in Figure 8, was due to orientation targets showing only a dimension-specific effect (i.e., increased RTs for different-dimension targets relative to different-feature targets), but no feature-specific change effect (i.e., no increased RTs for different-feature relative to same-feature targets; $p<.75$). In contrast, color targets showed both a dimension-specific (dD vs. dF, $p<.0001$) and a feature-specific change effect (dF vs. sF, $p<.0001$).

Electrophysiology

Figure 9 presents the ERPs with onset of the search display, collapsed over orientation and color targets. As in Experiment 1, there were no effects of the factor Transition for the early P1 and N1 components; however, the N2, P3 and SW components exhibited systematic variations with changes versus repetitions of the target-defining dimension across trials. For all analyses, only main effects and significant interactions involving the factor Transition are reported.

N2. The ANOVA examining the N2 amplitudes revealed a significant main effects of Transition [$F(2,20) = 3.88$, $p<0.038$], which was qualified by interactions of Dimension x Transition [$F(2,20) = 3.98$, $p<0.035$], Transition x Electrode position [$F(4,40) = 2.72$, $p<0.043$] and Transition x Electrode position x Electrode site [$F(12,120) = 3.32$, $p<0.023$]. Similar to Experiment 1, a change in the target-defining dimension resulted in a more negative-going deflection in the N2 range at frontal sites, compared to a repetition of the target dimension (main effect of Transition). This effect was strongest over frontal midline sites and decreased towards posterior sites. At frontal midline recordings, different-dimension trials exhibited significantly larger negative deflections compared to same-dimension trials, that is, relative to both same- and different feature trials (both $p<.001$), which did not differ between themselves ($p>.1$).

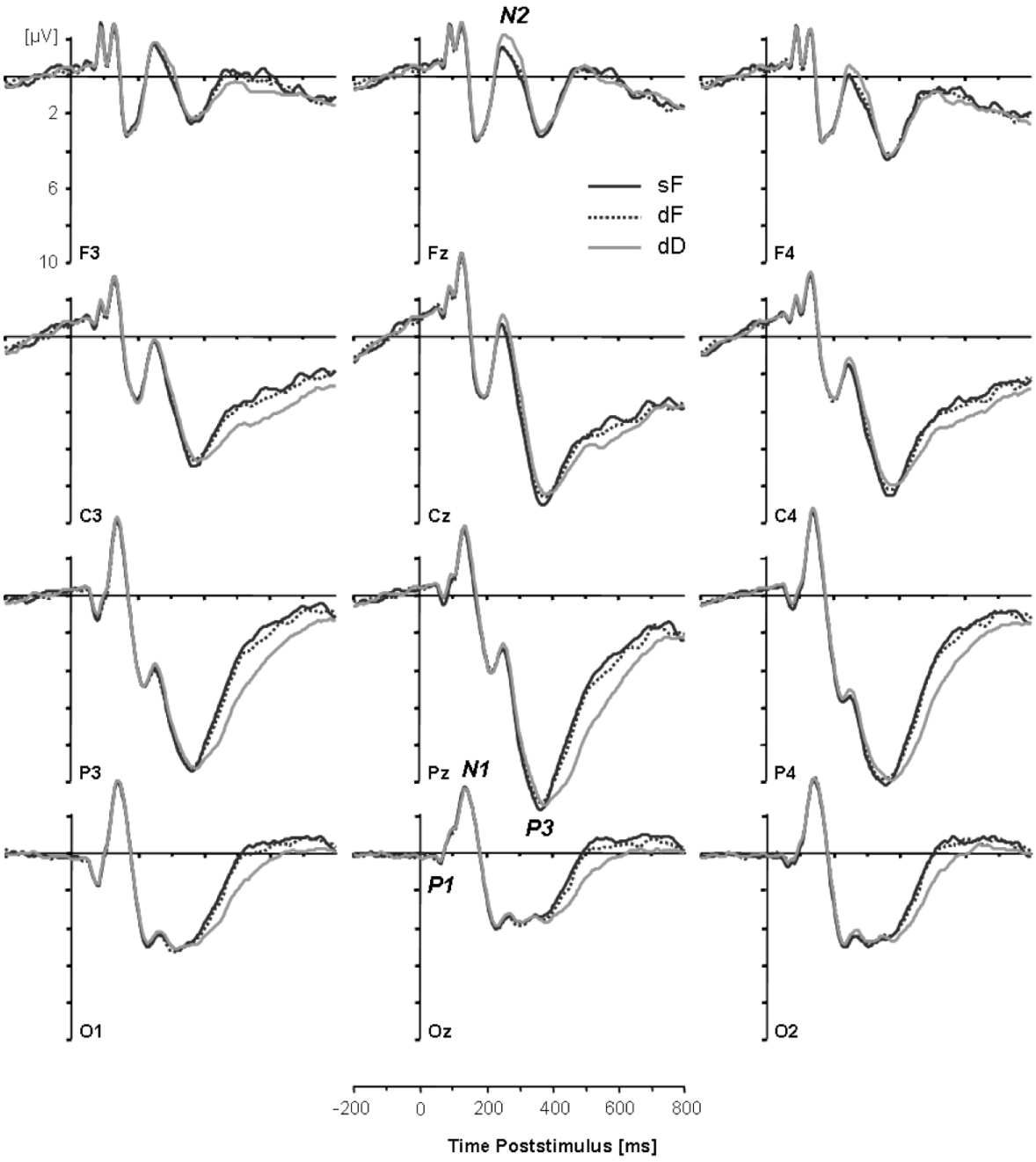

Figure 9. Discrimination task: Grand average waveforms elicited with onset of the target display on trial n dependent on the identity of the target on trial n-1, for selected electrode positions. Dark grey solid lines indicate same-dimension same-feature trials (sF), dark grey dotted lines same-dimension different-feature trials (dF), and light grey solid lines different-dimension trials (dD). Averages were collapsed across color and orientation targets, as the Dimension x Transition interaction was non-significant. Negativity is plotted upwards, and the data is presented relative to a 200-ms pre-stimulus baseline. Components labelled in italics are the N2 at Fz, the P3 at Pz, and the P1 and N1 at Oz.

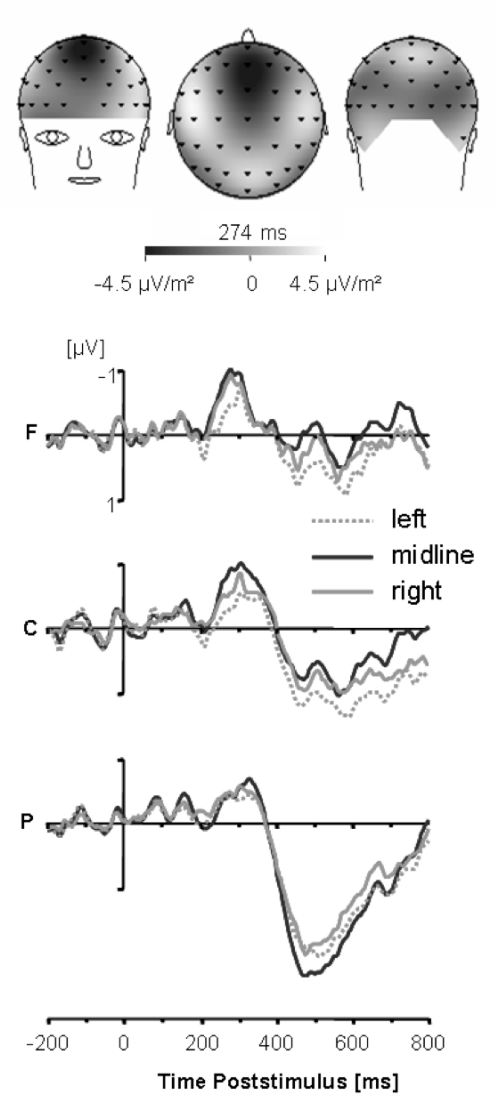

Figure 10. Discrimination task – Top panel: Current density distribution of the dimension change effect computed for the difference wave forms at 274 ms. Bottom panel: Difference waveform (different-dimension minus same-dimension) for frontal (F), central (C), and parietal (P) electrode positions. Light grey lines depict lateral (dottet = left, solid = right) and dark grey lines midline electrode positions.

The same pattern of effects was observed for right- and left-frontal electrode locations. Post-hoc contrasts revealed N2 amplitudes for different-dimension trials at frontal sites to be significantly different relative to same-dimension, that is, both same- and different-feature trials ($p<0.007$ and $p<0.026$, respectively), without the latter showing a difference ($p<.082$). An analysis of N2 latencies revealed no significant effects/interactions involving the factor Transition.

Topography of N2 effect. To map the N2 dimension change effect topographically, difference waves were computed by subtracting same-dimension trials (combined across same- and different-feature trials and both dimensions) from different-dimension trials (combined across color and orientation dimensions). Figure 10 presents the resulting difference wave forms and the current source density distribution at 274 ms post stimulus onset.

A repeated-measures ANOVA of the mean difference wave (274 +/- 30 ms) with the factors Dimension, Electrode position (left, midline, right), and Electrode site (frontal, central, parietal, occipital) revealed the main effect of Electrode position to be marginally significant [$F(2,20) = 3.29$, $p<0.058$], with the strongest activations at midline electrodes. In addition, the interaction Electrode position x Electrode site [$F(6,60) = 5.81$, $p<0.005$] and the three-way interaction reached significance [$F(6,60) = 2.37$, $p<0.041$]. As in Experiment 1, there were no significant differences between left-lateral, midline, and right-lateral electrodes at parietal and occipital recordings

(all p>0.99). In contrast to Experiment 1, frontal midline amplitudes did differ from left-, but not right-lateral electrodes (p<0.001 and p>0.95, respectively). This pattern suggests a slight right-lateralization of the frontal N2 component in the discrimination task.

P300 and Slow Wave. While the P3 amplitude ANOVA failed to reveal any significant transition effect/interaction, this factor was found to affect P3 peak latencies [F(2,20) = 4.84, p<0.040]. As in Experiment 1, P3 peak latencies did not differ between same- and different-feature trials (359 vs. 360 ms), but, for both types of trial, latencies were faster compared to different-dimension trials (371ms; both p<0.001).

In contrast to Experiment 1, the interaction Dimension x Transition was significant [F(2,20) = 8.00, p<0.003]. For orientation targets, the latencies of the P300 were comparable for same- and different-feature trials (p>0.23), but significantly longer for different-dimension trials (all p<0.001). Color targets, by contrast, were associated with monotonically increasing onset latencies: same-feature < different-feature < different dimension. Post-hoc contrasts revealed the P3 onset latency to be significantly shorter for same-feature as compared to both different-feature and different-dimension trials (p<0.043 and p<0.001, respectively); there was no difference between different-feature and different-dimension trials (p>0.35).

Amplitudes in the slow-wave window were found to depend on the transition factor as suggested by the main effects of Transition [F(2,20) = 16.31, p<0.001], with strongest positive amplitudes for dimension change trials. A post-hoc contrast revealed no significant differences between same- and different-feature trials (p>.43), while both types of trial differed significantly from different-dimension trials (all p<.001). Further, the Transition x Electrode site interaction reached significance, due to the strongest effect of dimension change being located over parietal sites. Although there was no dimension change effect at frontal electrodes (all p>.31), there were significant differences between same- and different-dimension trials at all posterior locations (sF and, respectively, dF vs. dD, all p<.007; sF vs. dF, all p>.68). Confirming the observation of Experiment 1, the dimension change effect was most prominent at parietal sites, followed by central and occipital electrode positions (see Figure 11).

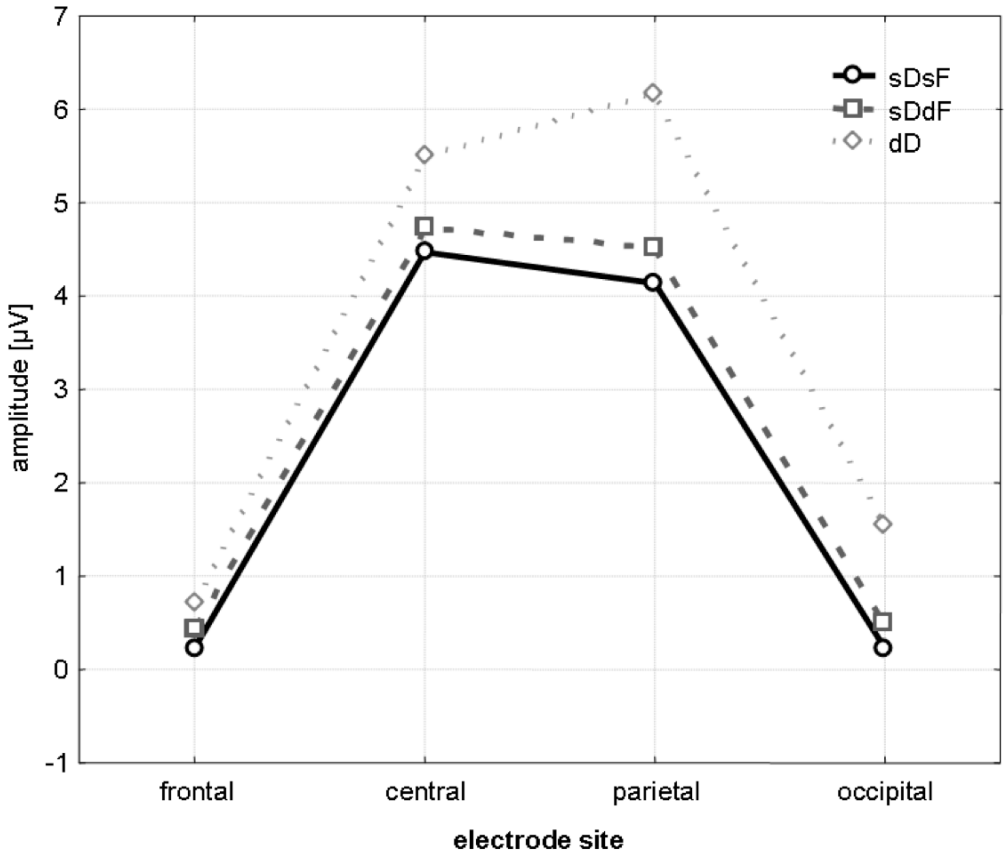

Figure 11. Discrimination task: Mean slow wave amplitudes from 420 to 600 ms post display onset as a function of (midline) electrode site positions (frontal, central, parietal, occipital), separately for the three intertrial transition conditions: same-dimension same-feature (sF), same-dimension different-feature (dF), and different-dimension (dD).

Discussion

In Experiment 2, observers had to explicitly identify the dimensional identity of the target in order to respond. As in Experiment 1, performance measures exhibited the general pattern of slowed RTs on trials with a change, compared to a repetition, of the target-defining dimension. However, in contrast to Experiment 1, for color-defined targets, there was a feature-specific as well as a dimension-specific change effect, whereas orientation-defined targets only showed the latter effect. The feature change effect (i.e., prolonged RTs for different- compared to same-feature targets in the absence of a dimensional change) replicates the findings of Found and Müller (1996), who reported such an effect only with color, but not with orientation targets (see also Müller et al., 2003). To explain this effect, Found and Müller suggested that, in the color dimension, feature contrast may be computed in a number of 'sub-dimensions' or channels coding the inputs from separable

populations of color analyzers (see also Wolfe, Chun, & Friedman-Hill, 1995). Thus, a change in the target-defining color across trials would lead to similar, albeit less marked, costs as a change in the target-defining dimension.

As in Experiment 1, there was no influence of dimension repetition versus change on early visual evoked components. This is consistent with the P1 and N1 reflecting the processing of non-spatial features within the (allocated) focus of attention, rather than parallel processes coding feature contrast prior to the allocation of focal attention.

Importantly in the present context, the differences in RT performance between the two dimensions were not associated with differential N2 amplitude effects at frontal sites. For both dimensions, identical patterns of enhanced N2 amplitudes were observed. As in Experiment 1, the strongest N2 enhancement was found at frontal sites with changes in the target-defining dimension, while there were no significant differences between same- and different-feature trials at frontal leads. Note that, while the change effect – reflected in the N2 enhancement – was located fronto-centrally without any lateralization in Experiment 1, a slight right-lateralization was evident in Experiment 2. Further work is necessary to replicate and account for this change in topography. This general pattern of N2 amplitude modulations is consistent with the dimension-weighting account of Müller and his colleagues (e.g., Müller et al., 1995; Found & Müller, 1996) arguing that these modulations reflect processes of detecting that a new dimensional weight set must be established. Importantly, the N2 enhancements (associated with changes in the target-defining dimension) were similar, both in terms of latency and topography, whether observers had to simply discern the presence of an odd-one-out target (Experiment 1) or explicitly identify its defining dimension (Experiment 2). The similar topography in the two tasks (experiments) supports the assumption of one-and-the-same generator being active during a cognitive process shared by the two tasks.

The P3 component exhibited a different pattern in the discrimination, compared to the detection, task: there was no effect of the factor Transition on P3 amplitudes. However, there were transition effects on P3 latencies: For orientation targets, there was an effect of dimension change (versus repetition), in the absence of an effect of feature change (versus repetition) when the dimension was repeated); in contrast, for color targets, there was both a dimension change effect (sF vs. dD) and a feature change effect (sF vs. dF). This differential pattern of P3 effects is in line with dimension change, but not feature change, effects in the RTs to orientation-defined targets and monotonically increasing RTs (sF < dF

< dD) for color-defined targets. Thus, the pattern of P3 latencies exactly matches that of the RTs in the discrimination task, further supporting the assumption that processes of attentional weight shifting might contribute to this component. By contrast, the pattern of slow-wave amplitudes observed in the discrimination task confirmed that in the detection task. In particular, there was a systematic SW variation that mirrored the RT pattern, with the strongest effect of dimension change (versus repetition) observed over parietal leads with a midline maximum. Again, all posterior recordings showed dimension changes to provoke significantly more positive-going deflections from central over parietal to occipital recordings, implicating a wide-spread effect of dimension changes on consecutive trials.

In summary, the N2, P3, and SW amplitude and latency effects in the 'discrimination' Experiment 2 were comparable to the effects in the 'detection' Experiment 1. Thus, the systematic and similar variations of both components support the assumption that the detection of an odd-one-out feature target requires (at least implicit) knowledge of its dimensional identity. If processing differed fundamentally between the two tasks, then systematic differences in ERP effects should have been observed. However, the N2 latencies were virtually equivalent (252 and 257 ms sD and, respectively, dD trials in the detection, as compared to 258 ms and 259 ms in the discrimination task), and, if anything, the P3 latencies were shorter for the discrimination than the detection task (367 and 393 ms for sD and, respectively, dD trials in the detection task, as compared to 360 and 374 ms the discrimination task). The latter difference may be taken to suggest that weight shifting is expedited when the task requires explicit knowledge of the target-defining dimension (Müller et al., 2004). However, since different observers participated in the two experiments, any direct comparison must be interpreted with caution.

General Discussion

Two experiments examining visual search for singleton feature targets across dimensions replicated the pattern of RT effects described by Found and Müller (1996): Repetitions of the target-defining dimension on consecutive trials led to faster RTs, whether or not the target-defining feature changed within the repeated dimension, compared to changes in the target-defining dimension. This pattern is consistent with the dimension-weighting account proposed by Müller and his colleagues (e.g., Müller et al., 1995, 2003; Found & Müller, 1996). The aim of the present study was to identify

parameters of the EEG associated with the pattern of RT effects described above – predicated on the idea (i) that components of the ERP that display the same systematic variation with changes versus repetitions of the target-defining dimension can help to trace the time course of the dimension-weighting process, and (ii) that the topography of possible indicators would provide tentatively information about the brain areas involved in the dimension-based modulation of visual search.

Analyses of ERPs with onset of the target display, dependent on the dimensional identity of the target on the previous trial, revealed three components to exhibit such a systematic variation: the N2, the P3 (with respect to its onset latency), and the SW. Whether the task required simple target detection (Experiment 1) or discrimination of the target-defining dimension (Experiment 2), the three components showed the same pattern: changes (versus repetitions) of the target-defining dimension led to an increased negativity of the N2, longer latencies of the P3, and an increased positive deflection within the SW time range. Besides minor differences between color- and orientation-defined targets, these amplitude and latency effects mirror the RT patterns typically observed in cross-dimension search for singleton feature targets. This also extends to the amplitude modulations for same-dimension trials, which were unaffected by whether or not the target-defining feature changed within the repeated dimension. This pattern of effects reinforces the proposal that the attentional weighting is dimension-, rather than feature-, specific in nature.

The identification of ERP parameters likely reflecting attentional (re-)weighting at the level of electrocortical activity pertains to an important issue controversially discussed in the literature: the question as to the point in time, and stage of processing, of the weight adjustment. The present findings favor an account which assumes that attentional weight is (re-)assigned at a relatively early point in time, and is associated with the generation of dimension-based (saliency) representations. That is, limited ‘weight’ resources need to be (re-)allocated to the mechanisms establishing the presence of a target or, respectively, its dimensional identity. Accordingly, the (re-)allocation of attentional weight is a prerequisite for the selection and execution of a manual response (Müller et al., 1995; Found et al., 1996). The dimension-based account, which associates weight shifting with perceptual processes, has recently been challenged by models in which the (re-)allocation of attentional resources is assumed to occur after visual encoding mechanisms have completed processing and the relevant response is selected. For example, Cohen and Magen (1999) argued that dimension-based inter-trial effects arise at a (dimensions-

specific) response selection stage. A similar, response-based, stance was advocated by Mortier, Theeuwes, and Starreveld (2005). They failed to find dimension-based inter-trial effects in a 'compound' search task, in which observers' responses are based not on the search-relevant feature of the target (e.g., its unique outline shape, such as a circle amongst squares), but on some additional attribute associated with the target (e.g., the orientation of a line presented within the circular target). In compound tasks, perceptual (search-related) and response-related effects of the task are assumed to be dissociable – so that inter-trial effects, if they were indeed perceptual in nature, should be observed in compound as well as detection tasks. It is important to note, however, that the above 'non-findings' are not unequivocal. For example, dimension-based inter-trial RT effects in a compound search tasks were reported by both Krummenacher, Müller, and Heller (2002) and Wolfe, Butcher, Lee, and Hyle (2003), and doubt has been cast on the simple dissociability of search- and response-related processes in compound tasks (e.g., Müller & Krummenacher, 2006; Pollmann, Weidner, Müller, & von Cramon, 2006).

Frontal effects of dimension change

The results of the present study support the assumption that the requirement for a (re-)allocation of attentional resources is detected before visual encoding mechanisms have completed processing and the relevant response is selected. In Experiment 1, observers were required to respond to a target with the index finger of one-and-the-same hand irrespective of its defining dimension. Despite this, there was an amplitude modulation of the N2, arguing that this modulation is unrelated to changes in manual response processes (selection, preparation, or execution). In Experiment 2, changes in the target-defining dimension were coupled to changes in response selection and execution. Yet, the N2 showed a similar pattern of effects to that in Experiment 1. Thus, the N2 modulation is selectively associated with (perceptual) changes in the target-defining dimension, while being unrelated with response times. Thus, a re-distribution of attentional weight is initiated prior to response selection taking place. Taken together, the present results argue that the detection of dimensional change and the initiation of weight shifting are independent of and occur prior to response selection.

The topography of the N2 effect indicates that frontal brain areas are likely involved in the dimension weighting process. A frontally distributed negativity was also found in several studies that have used EEG to identify change-related activity in matching

tasks, revealing enhanced N270 amplitudes for changes between the S1 and S2 stimuli (Wang, Tang, Kong, Zhuang, & Li, 1998; Wang, Tian, Wang, Cui, Zhang, & Zhang, 2003; Tian, Wang, Wang, & Cui, 2001; Zhang, Wang, Wang, Cui, Tian, & Wang, 2001; Cui, Wang, Wang, Tian, & Kong, 2000). Such enhanced negativities have been taken to reflect the detection of change or the processing of conflict. Further analyses aimed at reconstructing the source of the measured surface potentials are needed to identify the neural generators underlying the N2. However, the results are in line with the work of Pollmann and his colleagues (Pollmann, 2004; Pollmann et al., 2000, 2006; Weidner et al., 2002), who used fMRI to identify a fronto-posterior network of brain areas playing a critical role in dimensional weight shifting. The pattern of frontal activations was interpreted as reflecting the control of dimensional weight shifting, while higher-level visual areas in superior parietal and temporal cortex were assumed to mediate the weight shifts via feedback pathways to the dimension-specific input areas in occipital cortex (Pollmann et al., 2006).

In the present experiments, the N2 modulation occurred about 250 ms after search display onset with a frontal distribution. The systematic variation of the N2 with changes in the target-defining dimension is a novel finding, likely reflecting the detection of dimension change and the initiation of the re-setting of dimensional weights. The redistribution of the attentional weights might contribute to the subsequent P3 and SW-effects revealing systematic variations with changes in the target-defining dimension (but not feature changes within a repeated dimension). Since the N2 modulation in the present study was revealed by analyses of ERP components dependent on the intertrial history of target ‘events’, it is proposed to term this modulation ‘transition N2’ (tN2) in visual search. Further work is required to investigate these findings in more detail and to examine whether early indicators of dimensional change may be found dependent on dimensional intertrial transitions in singleton feature search.

Posterior effects of dimension change

Further support for the assumption of weight shifting processes being initiated and carried out before response selection is initiated stems from the observed P3 modulations. In Experiment 1, observers had to respond to odd-one-out targets with the index finger of one-and-the-same hand. Therefore, dimension changes were not associated with changes in response selection. Thus, purely response-driven effects cannot explain the differential P3

effects found in the present study. To further examine whether P3 latency modulations induced by dimension change across trials were primarily associated with stimulus- or response-related processing, additional analyses were carried out on stimulus- and response-locked P3s. These revealed no systematic differences in P3 amplitudes dependent on the reference event (stimulus-locked vs. response-locked) in the detection or the discrimination task – arguing against the P3 modulations observed in the present tasks being driven by response processes, and instead supporting the assumption that the P3 is mediating between perceptual (search-related) and response-related processes (Verleger et al., 2005). In particular, dimensional weight-shifting processes might contribute to the P3 'complex' observed in both the detection and the discrimination experiment of the present study.

Finally, the pattern of SW amplitudes mirrored that of the RTs in both experiments, with increased positive deflections for dimension change, compared to repetition (i.e., both same- and different feature), trials. These effects cannot simply be attributed to response-related processes, since the required (target-present) response in Experiment 1 was the same for all targets, irrespective of the target-defining dimension. In Experiment 2, the two dimensions were associated with different responses – nevertheless, the pattern of SW amplitudes was comparable to that in the detection task. This implies that the weight shifting process, initiated with the N2 component, influences the ERP beyond the P3.

CHAPTER III

Electrophysiological markers of visual dimension changes and response changes

Abstract

In cross-dimensional visual search tasks, target discrimination is faster when the previous trial contained a target defined in the same visual dimension as the current trial. The 'dimension-weighting' account (DWA; Found & Müller, 1996) explains this intertrial facilitation by assuming that visual dimensions are weighted at an early perceptual stage of processing. Recently, this view has been challenged by models claiming that intertrial facilitation effects are generated at later stages that follow attentional target selection (Mortier et al., 2005). To determine whether intertrial facilitation is generated at a perceptual stage, at the response selection stage, or both, we focused on specific ERP components (directly linkable to perceptual and response-related processing) during a compound search task. Visual dimension repetitions were mirrored by shorter latencies and enhanced amplitudes of the N2pc suggesting a facilitated allocation of attentional resources to the target. Response repetitions and changes systematically modulated the LRP amplitude suggesting a benefit from residual activations of the previous trial biasing the correct response. Overall, the present findings strengthen the DWA indicating a perceptual origin of dimension change costs in visual search.

Introduction

Over the last decade, there have been a growing number of reports of intertrial facilitation effects on the performance in visual search tasks. Such effects are found even in 'pop-out' search tasks, in which the target is a singleton element defined by a simple feature difference relative to the distractor elements in the search display: responses to a singleton target on a given trial *n* are faster when target-defining attributes are the same as on the preceding trial *n-1* (or, more generally, *n-i*, where i>1 – though the strongest effect is typically found for i=1).[1] These attributes include, besides target position (e.g., Maljkovic & Nakayama, 1996), the target-defining *feature* (e.g., when, variably across trials, the target was either red amongst green distractors or green amongst red distractors; Maljkovic & Nakayama, 1994), and the target-defining *dimension* (e.g., when the target was variably different in color or different in orientation from the distractors; Müller, Heller, & Ziegler, 1995). Intertrial facilitation effects have been found both in standard visual search tasks, in which observers had to make a 'target-present/absent' decision (e.g., Müller et al., 1995), and in so-called 'compound' search tasks (Duncan, 1985), in which the target-defining feature differs from the feature that determines response selection (e.g., when the target is singled out by being the only red element in the display, while the response is determined by a shape aspect of the target; e.g., Maljkovic & Nakayama, 1994). Müller and colleagues have argued in favor of a primary role for the target-defining *dimension* in generating such effects: under comparable conditions (target-present/absent task, constant distractor definition), intertrial facilitation was larger for a dimension repetition versus a change, compared to a feature repetition versus change within the same dimension (e.g., Found & Müller, 1996; Müller, Krummenacher, & Heller, 2004; Müller, Reimann, & Krummenacher, 2003; see also Olivers & Meeter, 2006, for a systematic comparison). Note that Müller and colleagues also found feature repetition effects – though, generally, these were robust only for the color dimension. Despite this primacy of dimensions, dimension-specific intertrial facilitation has tended to be weak, if at all present, in compound tasks, at least under conditions in which the target was highly salient (e.g., Chan & Hayword, 2007; Cohen & Magen, 1999; Krummenacher, Müller, & Heller, 2002; Kumada, 2001; Mortier, Theeuwes, & Starreveld, 2005; Theeuwes, Reimann, &

[1] More recently, such effects have also been found in singleton conjunction search tasks (e.g., Geyer, Müller, & Krummenacher, 2006; Hillstrom, 2000; Kristjánsson, Wang, & Nakayama, 2002; Weidner, Pollmann, Müller, & von Cramon, 2002).

Mortier, 2006).[2] Based on this and other dissociations with visual search tasks requiring a simple target-present/absent decision, several authors have recently proposed that target detection relies on different mechanisms in compound, relative to simple, visual search tasks (Chan & Hayword, 2007; Mortier, van Zoest, Meeter, & Theeuwes, 2007). On this background, the present study was designed to investigate (i) why RT intertrial facilitation is overall reduced under compound-task conditions in efficient visual search and (ii) whether any effects observable arise at an early perceptual and/or a later response-related stage of processing.

Perceptual and response-based accounts of intertrial facilitation

Several accounts of the origin of intertrial facilitation effects have been proposed, which may be classified as either '*perceptually* based' or '*response*-based' (see Meeter & Olivers, 2006, and Olivers & Meeter, 2006, for a systematic discussion). Perceptual accounts (e.g., Müller et al., 1995; Müller et al., 2003; Wolfe, Butcher, Lee, & Hyle, 2003) assume that repetition of target-defining attributes on successive trials facilitates the early sensory coding of critical attributes – which, in efficient visual search, is assumed to occur pre-attentively and in parallel across the search display. In contrast, response-based accounts assume that intertrial facilitation originates at a processing stage after focal-attentional selection of the target, at which the target is attentionally analyzed and translated into an appropriate response (e.g., Cohen & Magen, 1999; Mortier et al., 2005; Theeuwes et al., 2006).

There have been other attempts to explain intertrial effects in terms of the retrieval of task-relevant episodic memories. On one such account, proposed by Huang, Holcombe, and Pashler (2004), the translation from stimulus to response involves a process in which memories of previous episodes with similar stimuli and associated responses are automatically retrieved. If retrieved and currently required responses match, the current response is expedited; if they do not match, the current response is delayed (e.g., see Logan, 1990, 2002; Neill, 1997; Waszak, Hommel, & Allport, 2003). Thus, this hypothesis

[2] Olivers and Meeter (2006) have recently shown that intertrial effects in compound tasks are larger when the target is less salient – i.e., ambiguously defined in terms of their 'ambiguity resolution account' (though see Lamy, Carmel, Egeth, & Leber, 2006). When taken together with the feature-specific effect observed by Müller and Found (1996) for the color dimension, this could explain why Maljkovic and Nakayama (1994) found relatively large intertrial effects in a compound search task for color-defined targets: the target was ambiguously defined by being a uniquely colored element amongst only two distractors, and the target and distractors could exchange color across trials.

is essentially a variant of the response-based account. An alternative episodic-retrieval account proposed by Hillstrom (2000) assumes that retrieval of earlier trial episodes re-establishes the attentional priorization settings that had led to the detection of the previous targets. However, as noted by Meeter and Olivers (2006), "this idea is very difficult to distinguish from a [perceptually-based] view, in which the priorization settings are more directly altered by the preceding trial" (p. 218). Overall, the relevant episodic-memory retrieval notions can be subsumed under either perceptually- or response-based accounts.

Although some theorists (e.g., Cohen & Magen, 1999; Mortier et al., 2005; Theeuwes et al., 2006) have tended to treat perceptually- or response-based accounts as mutually exclusive, they are at least logically compatible with each other. Intertrial facilitation may operate at both pre-attentive perceptual and post-selective response-related stages of processing, as has been explicitly acknowledged by Müller et al. (2003) as well as by Meeter and Olivers (2006). Nevertheless, it remains an open issue whether, in a particular task, intertrial facilitation arises at perceptual, at response-related, or at both stages of processing. The present study was designed to address this issue in relation to dimension-based intertrial facilitation in compound-search tasks under conditions of high target saliency (i.e., low target ambiguity).

Dimension-specific intertrial facilitation in compound search tasks

As noted above, the detection of search targets defined by a singleton feature in dimensions such as color and orientation (with the critical dimension varying randomly across trials) is faster when the target-defining dimension remains the same across consecutive trials, and this effect is largely unaffected by whether or not the target feature is also repeated. To explain this reaction time (RT) pattern, Müller and colleagues proposed a 'dimension-weighting' account (DWA; e.g., Found & Müller, 1996; Müller et al., 1995), which is essentially an extension of the Guided Search model proposed by Wolfe and colleagues (e.g., Wolfe, 1994). The DWA assumes that attentional weight can be allocated to various basic visual dimensions (such as orientation, color, motion), with the total weight being limited. Preferential weighting of one dimension leads to faster detection of singleton feature targets defined in this dimension, relative to targets defined in other dimensions. This facilitation results from enhanced coding of feature contrast (saliency) signals within the weighted dimension and/or amplified transmission of dimension-specific feature contrast signals onto an overall-saliency map of the visual

display, which determines the allocation of focal selective attention. The delay in target detection observed when the target dimension changes across trials may have two causes. It is possible that sufficient attentional weight must be shifted from the old to the new target-defining dimension as a pre-condition for target detection (i.e., to sufficiently amplify the feature contrast signal at the overall-saliency map level). Alternatively, the target is processed and eventually selected based on the relatively low weight allocated to its defining dimension, and the weight shift follows target detection (e.g., see Chapter II). In either case, there is a weight shift to the new target-defining dimension, which influences the processing of any subsequent target. While this weight shift is largely bottom-up controlled by the presence of a feature contrast signal in a given dimension, it can to some extent be top-down modulated when a target is expected to be defined in another dimension (see Müller et al., 2003). Importantly, the DWA interprets weighting effects to be pre-attentive ('perceptual') in nature, modulating signal strength prior to the selective-attention stage, which operates based on the overall-saliency map (Müller & Krummenacher, 2006; see also Folk & Remington, 1998).

Recently, this view has been challenged by models which assume that the 'weighting' effects described by Müller and his colleagues are post-selective in nature, arising at a stage following focal-attentional selection (which is itself top-down impenetrable), at which detected targets are translated into responses (e.g., Cohen & Magen, 1999; Mortier et al., 2005; Theeuwes et al., 2006). This challenge has been based in part on findings in compound search tasks in which the detection-relevant target attribute is independent of the response-relevant attribute. One example is illustrated in Figure 12: The target is defined by a unique shape, while the response is determined by the vertical or horizontal orientation of a grating within the target object. In such compound tasks, dimension-specific intertrial effects are greatly reduced, if at all present, relative to simple detection tasks in which observers are instructed to make a target-present/absent response (e.g., intertrial effects of 9 vs. 34 ms in the study of Theeuwes et al., 2006; see also Krummenacher et al., 2002, and Kumada, 2001), which is not easily explained in terms of the DWA. Instead, the fact that such effects are scarcely evident in compound tasks has been taken as evidence that dimension repetition/change "modulates the speed with which one can give a response *after the target has been detected*"; for example, on a dimension repetition trial, "after entering the second [attentional] stage of processing, less sensory evidence is required to decide whether an item is a target or a distractor"

(paraphrase of Theeuwes, personal communication, 30 October, 2001, and Theeuwes, 1992, p. 605)[3].

However, Müller and Krummenacher (2006) have recently proposed that the central assumption underlying this argument – that the processes of target selection (assumed to be pre-attentive) and response selection (assumed to be post-selective) are independent in compound tasks – may not be tenable. They reanalyzed various sets of compound-task data (Krummenacher et al., 2002; Müller & Krummenacher, 2006; Pollmann, Weidner, Müller, Maertens, & von Cramon, 2006) to examine whether and how the effect of a change in the target-defining dimension was contingent on a change in the response, that is, in the target attribute that determined the response hand (change vs. no-change). For all data sets, an identical pattern of results was observed: An intertrial dimension change effect was present only when the response (attribute) was repeated, in which case RTs were significantly faster with a dimension repetition as compared to a change. In contrast, no such effect was evident when the response (attribute) changed. Essentially, with any change, whether in dimension and/or response, RTs were equally slow. A similar, albeit non-significant, interactive pattern can also be seen in Figure 7 of Olivers and Meeter (2006; see also Figure 5 of Chan & Hayword, 2007). Müller and Krummenacher took this pattern to suggest that, although, statistically, there was no correlation between the two types of change (target-defining dimension, response attribute), the system 'assumes' there is one (see also, e.g., Kingstone, 1992[4]). If the target dimension (the task attribute that becomes available fastest) remains unchanged, the system implicitly assumes that the attribute on which the response will be based will also be unchanged; that is, the unchanged response is facilitated, and there is a cost if the response attribute actually changes. In contrast, if the dimension changes, the system may cancel any prior assumptions as to the response attribute to be expected and start processing from scratch. Whatever the explanation, dimension-specific RT intertrial effects are overall reduced in compound tasks because they are evident only in the absence of a response change. Therefore, behavioral effects observed in such compound tasks may not

[3] Theeuwes et al. (2006) do acknowledge that some part of the intertrial effects observed in visual search tasks arise at a pre-selective stage of processing, based on their finding of a significant compound task effect of 9 ms. However, logically, they must then attribute the larger part of the effect, that is, the difference between the simple-detection and the compound task (25 = 34 – 9 ms), to response-related processes.

[4] Note that the 'combining of expectancies' revealed by Kingstone (1992) involved non-spatial with non-spatial (e.g., color and form) as well as spatial with non-spatial stimulus attributes (e.g., position and form).

permit the dissociation of perceptual and response-related processes associated with dimension changes/repetitions in a simple and straightforward manner.

Rationale of the present study

The present EEG study was designed to overcome this limitation by examining not only response times in a compound-search task, but also event-related brain potentials (ERPs) associated with dimension and response repetitions versus changes. In the present task, participants had to first search for a singleton target uniquely defined in either the color or the shape dimension, before they could select the appropriate response, which was determined by the orientation of a grating within the target object (horizontal vs. vertical). In this way, a target defined in a changed dimension could be associated with either the same (e.g., a horizontal color target preceded by a horizontal shape target) or a different response (e.g., a horizontal color target preceded by a vertical shape target) as the preceding target, as could be a target defined in a dimension that was repeated across successive trials. This resulted in four experimental conditions: same dimension – same response (sDsR), same dimension – different response (sDdR), different dimension – same response (dDsR), and different dimension – different response (dDdR). A similar paradigm was employed in an event-related fMRI study by Pollmann et al. (2006). The behavioral results revealed the interactive pattern of dimension and response change effects described above. At the neuronal level, dimension changes were associated with activations primarily in posterior visual areas, whereas response changes elicited activations primarily in motor-related areas of the parietal and frontal cortices.

To gain further insights into the time course of pre-attentive perceptual and post-selective response-related processes in cross-dimensional search, the present study focused on two specific components of the ERP, which can be directly linked to perceptual-related and response-related stages of information processing, respectively. The first component, the N2pc, is a negative-going deflection with a maximum over visual areas of the hemisphere contralateral to the location of an attended stimulus. The N2pc has been observed in numerous previous visual search experiments, typically between 175 and 300 ms after the onset of the search array. It is interpreted as reflecting the attentional selection of target among non-target stimuli, based on target-defining perceptual attributes (e.g., Eimer, 1996; Woodman & Luck, 1999; Hopf, Boelmans, Schoenfeld, Heinze, & Luck, 2002). Thus, the onset of the N2pc can be interpreted as a marker of the transition from the

pre-attentive perceptual coding of the whole search array to the focal-attentional processing of selected – target – stimuli. Factors that facilitate the perceptual analysis of visual features should also facilitate subsequent feature-based attentional target selection processes, and this should result in an earlier onset and possibly also enhanced amplitude of the N2pc component. In the present study, we measured the N2pc in order to examine whether the intertrial facilitation effect in cross-dimensional visual search tasks is linked to the focal-attentional selection of targets. If this effect arises from enhanced perceptual processing within the target dimension on dimension repetition trials, resulting in more efficient attentional target selection (as assumed by the DWA), the N2pc elicited on such trials should be triggered earlier and/or be more pronounced than that on dimension change trials. In contrast to the RT effects, where intertrial facilitation effects are also dependent on response repetition (see above), this N2pc modulation should be observed irrespective of whether the response is repeated or changed. Alternatively, if the intertrial facilitation effect arises exclusively at a post-selective response selection stage, the N2pc should not differ between dimension repetition and dimension change trials.

The second component examined in the present study was the lateralized readiness potential (LRP). This component, typically observed over the motor area contralateral to the side of a unimanual response, is linked to the activation and execution of motor responses (e.g., Hackley & Valle-Inclán, 2003). To extract this component from the ERP, waveforms recorded from electrodes ipsilateral to the side of a response are subtracted from contralateral ERPs (Hackley & Valle-Inclán, 2003; see also Eimer, 1998, and Eimer & Coles, 2003, for methodological details about the derivation and interpretation of the LRP). LRP onset marks the start of effector-specific response activation and execution processes that occur after response selection has been completed. When measured relative to stimulus onset (stimulus-locked LRP), LRP onset differences across task conditions therefore reflect differences in the time demands of processing stages that occur prior to response activation. When measured relative to response onset (response-locked LRP), LRP differences across task conditions indicate differences in response activation and execution processes.

In the present study, both stimulus-locked and response-locked LRPs were measured to investigate whether and how changes versus repetitions of target dimensions and responses across successive trials affect response-related processing stages. Response-locked LRP waveforms were computed to assess any effects on response activation and

execution stages. Response-locked LRPs were expected to be differentially affected by response repetitions versus alternations; the critical question was whether these LRPs would also be modulated by dimension changes. This should not be the case if dimension-specific intertrial effects in visual search only affect perceptual-attentional stages prior to response-related stages, as postulated by the DWA. In addition, stimulus-locked LRPs were computed to further investigate how dimension and response changes versus repetitions affect processing stages that precede response activation and execution. Because stimulus-locked LRP latencies are determined both by the time it takes to attentionally select and analyze the target and by the time required to select an appropriate response, these latencies may allow insights into the time demands of response selection processes that are intermediate between attentional target selection (indexed by the N2pc) and response production (indexed by the response-locked LRP).[5] More specifically, we investigated whether processes at this stage might be responsible for the interaction between dimension and response changes previously observed for behavioral intertrial facilitation effects in compound tasks (Müller & Krummenacher, 2006). In contrast, the hypothesis that dimension-specific intertrial effects are based solely on response selection processes, as suggested by Mortier and colleagues (e.g., Mortier et al., 2005), would be consistent with systematic stimulus-locked LRP differences between dimension repetition and dimension change trials.

EXPERIMENT 3

Method

Participants. Thirteen observers (8 female) took part in the Experiment. Their ages ranged from 21 to 36 years (mean age 28.5 years; SD = 6.5 years). Observers were either paid or received course credit for participating. All observers were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological disorder. One observer had to be excluded from the analyses due to excessive eye-blink artifacts.

Stimuli and task. As illustrated in Figure12, the visual search display consisted of eight colored shape stimuli presented in a circular array against a black background, each presented equidistant (3.0° of visual angle) from a white central fixation cross. Each stimulus array contained one singleton which was equally likely defined in the color

[5] We thank Jan Theeuwes and Clayton Hickey for suggesting this additional analysis.

dimension (red circle, 1.2° radius) or the shape dimension (square, 2.4° x 2.4°) among seven distracters (blue circles, 1.2° radius). The position of the singleton was selected randomly from one of the six lateral positions. Each single stimulus contained a grating that was oriented either vertically or horizontally. The gratings consisted of three black bars (0.4° x 2.4°) separated by two gaps (0.3° x 2.4°). Observers were instructed to maintain central fixation throughout the experiment and to give a speeded forced-choice response indicating the grating orientation of the singleton target, using their left index finger or right index finger, respectively.

Figure 12. Example for the visual search array with a vertically oriented target defined in the shape dimension. Search arrays consisted of 8 stimuli in a circular array against a black background, each presented equidistant from a white central fixation cross. Distractors were blue circles and targets were defined in the color dimension (red) or shape dimension (square). Each stimulus was either horizontally or vertically oriented. Participants were asked to discriminate the orientation of the singleton target as fast and accurately as possible.

Procedure. Observers were seated in a dimly lit experimental chamber, with response buttons under their left and right index fingers. The positions of the response buttons were vertically aligned to avoid spatial stimulus-response compatibility effects. Stimuli were presented on a 17” computer screen placed at a viewing distance of approximately 55 cm. Twenty experimental blocks of 72 trials were run. Each trial started with a white fixation cross for 500 ms, followed by the search array for 200 ms. The trial was terminated by the observer’s response or after a maximum duration of 1000 ms. During the intertrial interval, a central white fixation cross was shown for a variable duration of 950, 1000, or 1050 ms. Trials on which singletons were defined in terms of either color or shape, and trials on which target gratings were horizontal or vertical in orientation were presented in random order and with equal probability, thus resulting in an equal proportion of each of the four experimental trial conditions: same dimension – same response (sDsR), same dimension – different response (sDdR), different dimension – same

response (dDsR), different dimension – different response (dDdR). Observers with odd participant numbers started with their left index finger on the upper button and their right index finger on the lower button, and vice versa for observers with even participant numbers. These response button assignments were changed in the second experimental half after ten experimental blocks. Prior to the start of each experimental half, observers performed at least one block of practice trials.

EEG recording and data analysis. EEG was recorded with Ag-AgCl electrodes mounted in an elastic cap (Falk Minow Service, Munich) referenced to linked earlobes. Electrode positions were a subset of the international 10/10 system sites (FPz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3 Pz, P4, P8, PO7, PO3, PO4, PO8, O1, Oz, and O2). The horizontal electrooculogram (HEOG) was recorded from the outer canthi of both eyes. Data was recorded with a BrainAmp amplifier (Brain Products, Munich) using an analog bandpass from 0.1 to 40 Hz and a digitization rate of 500 Hz. All electrode impedances were kept below 5 kΩ. Prior to epoching the EEG, Independent Component Analysis (ICA), as implemented in the software package Brain Vision Analyzer (Brain Products, Munich), was performed to eliminate blinks and horizontal eye movements from the EEG. Only trials with correct responses during the current and the preceding trial were selected for further analyses. Trials with signals exceeding +/- 60 μV on any recording channel were excluded from further analysis before the ERPs were averaged.

For the N2pc analysis, EEG data were epoched off-line into 1200 ms periods with a 200-ms pre-stimulus baseline that was used for the baseline correction. The N2pc was computed by subtracting ERPs obtained at lateral posterior electrodes PO7/PO8 ipsilateral to the side of the singleton stimulus in the visual search display from contralateral ERPs. Statistical analyses were conducted for N2pc peak latencies (latency of maximal negative amplitude in N2pc waveform between 190 and 270 ms post-stimulus) and mean amplitudes (obtained in the 190-270 ms post-stimulus latency window where the N2pc is maximal).

For the LRP analysis, response- and stimulus-locked waveforms were extracted from the EEG data. To obtain the response-locked LRP, EEG was epoched into 1200-ms periods that ranged from 800 ms before to 400 ms after response onset. No baseline correction was applied prior to artifact rejection and averaging. The stimulus-locked LRP

was measured within a 1000 ms period after the onset of the search display, relative to a 200 ms pre-stimulus baseline. Both LRP waveforms were computed separately for all four trial conditions. This was done by subtracting the waveforms at electrodes C3/C4 ipsilateral to the side of the manual response from contralateral ERPs (used formula: (C4(*left*)-C3(*left*) + C3(*right*)-C4(*right*)) / 2). To determine the onset latencies of stimulus- and response-locked LRPs, we used the jackknife-based scoring method proposed by Ulrich and Miller (2001; see also Miller et al., 1998), which defines the LRP onset as the point in time where LRP amplitudes reach a specific criterion value relative to the pre-stimulus baseline. According to Miller et al. (1998) we used 50% and 90% of maximum LRP amplitude as an optimal criterion for determining stimulus-locked and response-locked LRP onset latencies, respectively. Statistical analyses were performed on stimulus- and response-locked LRP latencies, as well as on mean response-locked LRP amplitudes (obtained in the 100–20 ms interval prior to response onset).

Results

Behavioral data

Trials on which observers made an incorrect response (7.53% of all trials), trials on which the reaction time was excessively slow (> 1000 ms; 0.89%), and trials for which the response on the previous trial was incorrect (6.65%) were excluded from analysis (15.07% of all trials). Figure 13 displays the error rates and reaction times obtained in the remaining trials separately for each of the four experimental conditions. Reaction times were analyzed by a repeated-measure ANOVA with the factors Dimension change (same dimension, different dimension) and Response change (same response, different response). Both factors (Dimension change: $F(1,11) = 41.486$, $p<.001$; $\eta^2 = .790$); Response change: $F(1,11) = 8.909$, $p<.012$; $\eta^2 = .447$), as well as their interaction ($F(1,11) = 57.73$, $p<.001$; $\eta^2 = .840$) were significant. Further analysis (post-hoc contrasts, Tukey HSD) confirmed that RTs were significantly faster ($p<.001$) on trials on which neither the dimension nor the response changed relative to each of the other three trial conditions. There were no significant RT differences among trials on which either the dimension, or the response, or both factors changed (see Figure 13). This interactive pattern of effects mirror that observed in previous studies (Krummenacher et al., 2002; Müller & Krummenacher, 2006; Pollmann et al., 2006).

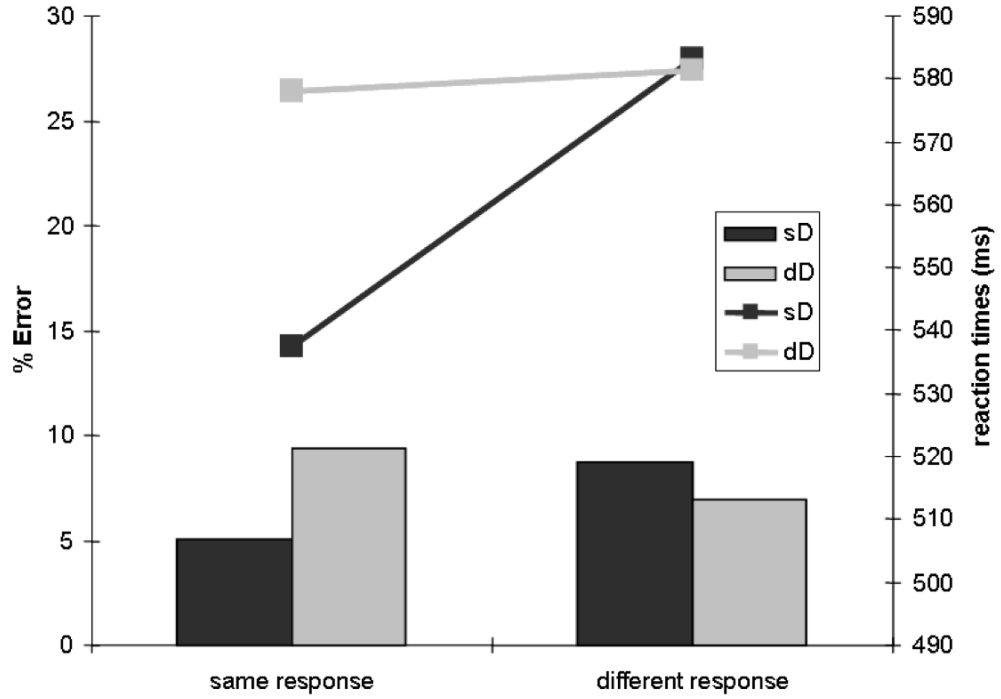

Figure 13. Reaction times (lines) and errors rates (bars) as a function of dimension and response changes (sD = same dimension; dD = different dimension).

Error rates were examined by an analogous ANOVA, which revealed a main effect of Dimension change ($F(1,11) = 6.102$, $p<.031$; $\eta^2 = .357$) as well as a significant Dimension change x Response change interaction ($F(1,11) = 19.306$, $p<.001$; $\eta^2 = .637$). Further analyses (post-hoc contrasts, Tukey HSD) revealed that, when the target-defining dimension stayed the same, more errors ($p<.01$) were made when the response changed than when it was repeated (i.e., observers tended to respond 'same'). In contrast, when the dimension changed, slightly more errors ($p<.11$) were made when the response was repeated rather than changed (i.e, there was tendency to respond 'different').

Electrophysiological data

N2pc. Figure 14A shows the ERPs obtained at PO7/PO8 contralateral and ipsilateral to the side of a singleton target, collapsed across all four experimental conditions. As expected, an N2pc component was clearly visible. As can be seen from Figure 14B, search arrays that were preceded by same target-defining dimension elicited enhanced N2pc amplitudes as compared to arrays preceded by a different dimension (-2.25 μV (± 1.47) vs. -1.95 μV (± 1.29)). This effect was observed independently of repetitions or changes in the manual response.

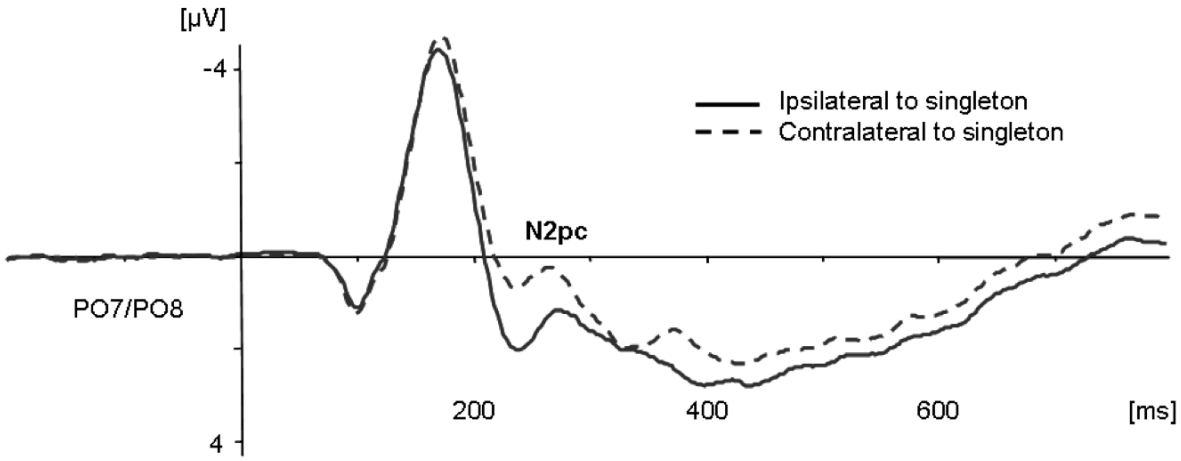

Figure 14A. Grand-averaged ERPs collapsed across all for experimental conditions at electrodes PO7/PO8. The solid line indicates ipsilateral activity and the dashed line contralateral activity in response to the singleton target.

To formally assess the effects of dimension changes and response changes on this component, the N2pc was quantified by computing difference waves (contralateral activity minus ipsilateral activity) for each of the four experimental conditions, and repeated-measures ANOVAs were conducted for the mean N2pc amplitude obtained between 190 and 270 ms post stimulus. To test whether the N2pc was reliably elicited, we initially compared ERP mean amplitudes obtained during the baseline period and during the N2pc time window in a repeated-measure ANOVA for the factor Period (baseline versus N2pc time window). A highly significant main effect of Period ($F(1,11) = 32.161$, $p<.001$; $\eta^2 = .745$) confirmed the presence of the N2pc. Next, we conducted an ANOVA on mean N2pc amplitudes for the factors Dimension change and Response change that revealed a significant main effect of Dimension change ($F(1,11) = 5.984$, $p<.032$; $\eta^2 = .352$). In contrast, there was no effect of Response change ($F(1,11) = 0.471$, $p<.507$; $\eta^2 = .041$), and no interaction between the two factors ($F(1,11) = 0.001$, $p<.977$; $\eta^2 = .000$). An analogous repeated-measures ANOVA was used to examine N2pc peak latencies. As for the mean amplitude analysis, only the dimension change effect was significant ($F(1,11) = 17.498$, $p<.002$; $\eta^2 = .614$), with earlier peak latencies for trials on which the target-defining dimension was repeated relative to dimension change trials (243 ms (± 16) vs. 251 ms (± 17)). Again, no significant effect for Response change ($F(1,11) = 1.479$, $p<.249$; $\eta^2 = .119$) and no significant interaction ($F(1,11) = 0.364$, $p<.558$; $\eta^2 = .032$) were obtained,

indicating that the dimension change effect was manifest independently of the required response.[6]

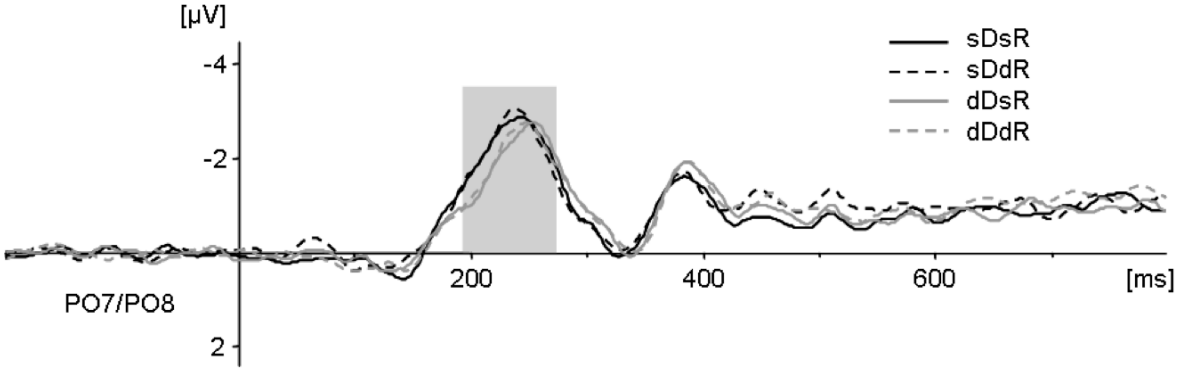

Figure 14B. N2pc. Averaged difference waves (contralateral activity minus ipsilateral activity) of the N2pc component for each of the four experimental conditions at electrodes PO7/PO8. Dark grey lines indicate dimension repetitions, light grey lines indicate dimension changes in consecutive trials. Solid lines indicate response repetitions and dashed lines response changes. The analyzed time window ranged from 190 to 270 ms poststimulus.

LRP. Figure 15 presents the *response-locked LRP waveforms* for all four experimental conditions at C3/C4. There were no systematic onset latency differences between conditions. A dimension change x response change repeated-measures ANOVA of the response-locked LRP onset latencies (determined by the jackknife method of Ulrich & Miller, 2001) revealed no significant effects (Dimension change, $F(1,11) = 1.533$; Response change, $F(1,11) = 1.913$; interaction, $F(1,11) = 0.014$)[7]. However, there were systematic response-locked LRP amplitude differences: conditions in which the response on the current trial differed from that on the preceding trial exhibited more negative-going deflections prior to response onset (see Figure 15). For statistical examination, the LRP mean amplitudes obtained in the 100-20-ms window preceding response onset were subjected to a repeated-measures ANOVA with the factors Dimension change and Response change. In marked contrast to the N2pc, only the response change effect ($F(1,11) = 7.115$, $p<.022$; $\eta^2 = .393$) was significant, reflecting enhanced response-locked LRP

[6] Essentially the same pattern of statistically significant effects was observed when these N2pc analyses were conducted for ERP waveforms that were averaged after trials with eye movements were rejected (using a rejection criterion of HEOG amplitude values exceeding +/-30µV), thereby demonstrating that these effects were not affected by systematic eye movements artefacts.

[7] F-values of all LRP onset latencies are corrected according to the formula: $F = F/(n-1)^2$ (see also Ulrich & Miller, 2001).

amplitudes for response change trials (-1.76 μV (± 1.19) vs. -1.31 μV (± 1.13)). In contrast, the dimension change effect ($F(1,11) = 0.464$, $p<.51$; $\eta^2 = .040$) and the interaction between the two factors ($F(1,11) = 2.142$, $p<.171$; $\eta^2 = .163$) were non-significant. Hence, response-locked LRP amplitude was affected by Response change only, independently of repetitions or changes in the target-defining dimension.

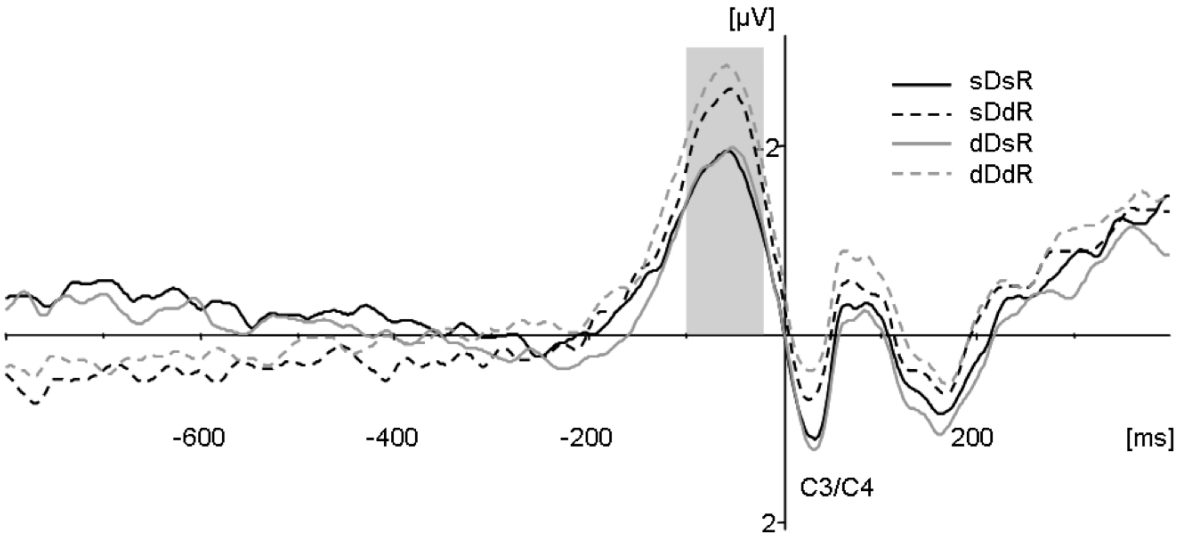

Figure 15. Lateralized readiness potential. Response-locked averages for each of the four experimental conditions at electrodes C3/C4. Solid lines indicate response repetitions and dashed lines indicate response changes. Dark grey lines indicate dimension repetitions and light grey lines indicate dimension changes in consecutive trials. The analyzed time window ranged from -100 to -20 ms pre-response.

Figure 16 presents the stimulus-locked LRP waveforms obtained at C3/4, for all four experimental conditions. A dimension change x response change repeated-measures ANOVA was performed on the *stimulus-locked LRP onset latencies* (determined by the jackknife method of Miller et al., 1998). The fastest onset latencies were found for sDsR trials (341 ms (± 8)), followed by the latencies for dDdR (357 ms (± 4)) and sDdR trials (372 ms (± 5)). Stimulus-locked LRP onsets were most delayed for dDsR trials (407 ms (± 6)). The ANOVA revealed the main effect for Dimension change ($F(1,11) = 10.513$, $p>.008$) as well as the interaction between Dimension change and Response change to be significant ($F(1,11) = 14.232$, $p>.003$), while the main effects for Response change ($F(1,11) = 0.262$, $p>.62$) was not significant. The interaction was further examined by a series of pairwise comparisons using a Bonferroni *p*-level correction (as suggested by

Miller et al., 1998). These comparisons revealed significant stimulus-locked LRP onset latency differences between all experimental conditions ($p<.001$).

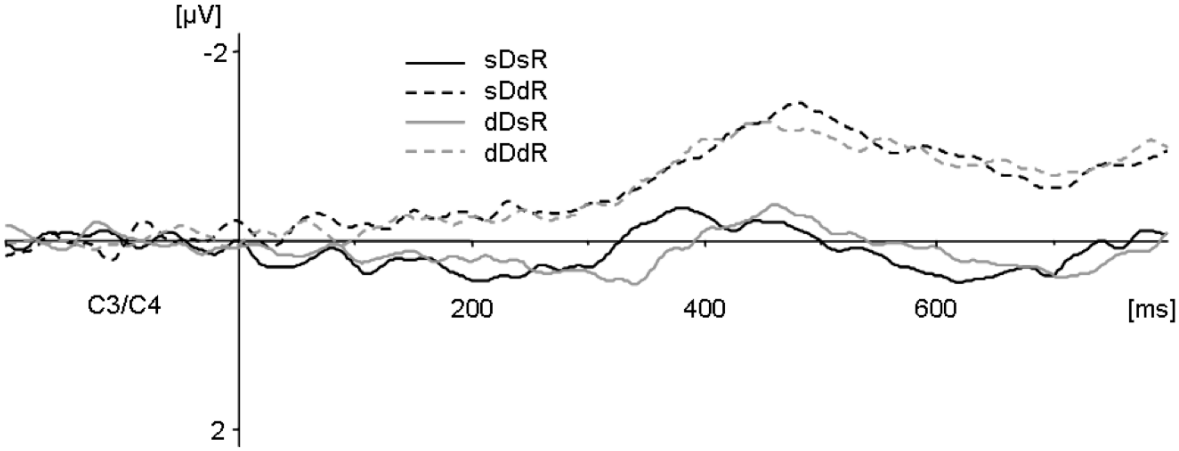

Figure 16. Lateralized readiness potential. Stimulus-locked averages for each of the four experimental conditions at electrodes C3/C4 for the 800-ms post-stimulus time interval relative to a 200-ms pre-stimulus baseline. Solid lines indicate response repetitions and dashed lines indicate response changes. Dark grey lines indicate dimension repetitions and light grey lines indicate dimension changes in consecutive trials.

Discussion

The present study was designed to investigate the mechanisms underlying dimension-specific intertrial effects in cross-dimensional visual search tasks. Specifically, the aim was to resolve the question whether the intertrial effects can be attributed to a single information processing stage, either a pre-attentive 'perceptual' or a post-selective 'response selection' stage, or whether both stages are responsible for some aspect of these effects. To address this issue, different ERP components which can be directly linked to different stages of information processing were examined: the N2pc, which reflects the allocation of focal attention to task-relevant stimuli based on perceptual attributes (Eimer, 1996; Woodman & Luck, 1999), and the LRP, which reflects the activation and execution of uni-manual motor responses (Hackley & Valle-Inclán, 2003; Eimer & Coles, 2003). These components were measured in a 'compound' task in which a dimension change across consecutive trials could occur independently of a response change, and vice versa. This task required observers to detect a color- or, alternatively, a shape-defined singleton target and then to select the appropriate left- or right-hand response which was determined by the horizontal or vertical orientation of a grating within the target object.

Effects of dimension change

Repetitions of the target-defining dimension on consecutive trials were associated with both shorter peak latencies and enhanced amplitudes of the N2pc component. In line with previous work on the N2pc (Eimer, 1996; Woodman & Luck, 1999), this pattern of effects can be interpreted in terms of a more efficient and faster allocation of focal attention to the current (repeated) target. Importantly, this effect was independent of repetitions or changes in the manual response, indicating that the efficiency of focal-attentional selection is solely determined by repetitions versus changes of the target-defining dimension across trials, and is not affected by concurrent repetitions versus changes in response-related attributes.

This systematic effect of visual dimension change on N2pc peak latencies is in line with the predictions of the DWA. According to this account, repeating the target-defining dimension on consecutive trials implies that the critical dimension is attentionally weighted on the current trial, thereby facilitating the emergence of the target's saliency signal at the level of the overall-saliency map which guides the allocation of focal attention. By contrast, changes of the target dimension on consecutive trials lead to the engagement of a time-consuming 'weight-shifting' process. This process transfers attentional weight from the old to the new target-defining dimension, so as to amplify the target's saliency signal above the detection threshold at the overall-saliency map level. The delayed peak latencies of the N2pc component for dimension change versus repetition trials may be interpreted as reflecting this weight-shifting process. It should be noted that the size of this N2pc latency shift (8 ms) was substantially smaller than the RT difference observed between sDsR trials and the other three trial types. This suggests that weight-shifting processes alone cannot account for this RT effect, but that other post-selective processing stages are also involved (see below). In addition, due to inter-individual and inter-trial variability of N2pc onsets, which will inevitably result in some 'temporal smearing' of this component, the observed onset latency differences are likely to underestimate the real contribution of dimension changes to the onset of the N2pc. Nevertheless, the fact that a significant delay of N2pc latencies on dimension change versus repetition trials was obtained demonstrates unequivocally that this factor did affect the timing of processes involved in attentional target selection.

In addition, target dimension changes also affected the amplitudes of the N2pc component. However, since the paradigm used in the present study does not provide a baseline measure, it is not clear whether the observed N2pc modulation represents an

amplitude enhancement on dimension repetition trials, an amplitude reduction on dimension change trials, or both. From the DWA perspective, the N2pc modulation may be interpreted as reflecting both. That is, if the pre-attentive perceptual processing of task-relevant dimensions is facilitated on dimension repetition trials, preferential weighting of a given visual dimension is assumed to give rise to increased activation, or synchronized firing, of groups of neurons processing feature contrast signals defined in this dimension, thus resulting in more efficient allocation of focal attention compared to dimension change trials, and in increased N2pc amplitudes.

Taken together, the present N2pc results provide clear evidence in favor of visual-dimension weighting as conceived by the DWA, and against alternative accounts which assume that dimension-specific intertrial effects in visual search are exclusively generated at post-selective processing stages, such as response selection (Cohen et al., 1999; Mortier et al. 2005; Theeuwes et al., 2006). The N2pc differences between dimension change and repetition trials started to emerge as early as around 180 ms post-stimulus. This makes it extremely unlikely that this effect is in any way related to the motor response, especially when considering that the average response latency was around 570 ms. Furthermore, the present findings are in agreement with the study of Pollmann et al. (2006), who identified activations primarily in posterior visual areas in response to dimension changes. The spatial overlap between the areas described by Pollmann et al. and the lateral parieto-occipital electrode positions analyzed in the present study suggests common neural generators involved in processes of visual-dimension weighting (see also Hopf et al., 2002, for an MEG analysis of the cortical generators underlying the N2pc component).

Effects of response change

While changes versus repetitions of the required response across trials had no impact on the N2pc amplitudes and latencies, this factor affected the amplitudes (but not the onset latencies) of response-locked LRP waveforms. LRP amplitudes measured immediately prior to response onset were enhanced on trials on which the response hand changed relative to trials on which it remained the same as on the preceding trial. These response-locked LRP amplitude modulations related to response change were completely independent of repetitions and changes in the visual dimension of the target (see Figure 15).

Experimental manipulations of factors affecting response-locked LRPs usually result in onset latency differences, with earlier response-locked LRP onsets for conditions where the duration of response activation and execution processes is prolonged (see Eimer & Coles, 2003, for more details). However, no such latency shifts were observed in the present study, where the difference between response alternation and repetition trials was reflected instead by response-locked LRP amplitude differences. Several previous experiments have already found modulations of response-locked LRP amplitudes under conditions where the demands on response-related processing stages were varied. For example, Miller and Low (2001) measured LRPs in a simple RT task where the response to a target stimulus was specified in advance by a cue, and in a choice RT task where the response remained uncertain until the target was presented. In the simple RT task, where the cued response could be fully prepared during the cue-target interval, reaction times were almost 100 ms faster and response-locked LRP amplitudes were significantly reduced relative to the choice RT task. Similar response-locked LRP amplitude modulations have also been reported in a recent task switching study (Karayanidis, Nicholson, Schall, Meem, Fulham, & Michie, 2006).

These earlier findings, and the response-locked LRP amplitude modulations observed in the present experiment, suggest that these amplitude measures might reflect weight-shifting processes in response activation and execution that could be analogous to the process postulated for dimension changes. When the response (e.g., left index finger) remains the same on consecutive trials, some partial activation of the required response is carried over from the preceding trial and can thus facilitate the accrual of activation initiated by the new response signal, leading to faster reactions. As a result of the pre-existing response activation in the motor system, less additional activation is required to reach the motor threshold on response repetition trials, and this is reflected by reduced response-locked LRP amplitudes relative to trials on which the response hand had to be changed. On the latter trials, activation of the correct response involves an additional time-consuming shift of motor activation across hemispheres, prolonging the time required for the response activation process to be completed. It should be noted that, although response repetition and response change trials may have differed with respect to pre-existing response activation levels, response-locked LRP onset latencies were not modulated by response change (see Figure 15), suggesting that this factor did not systematically affect the time demands of response execution processes.

Interactions between dimension change and response change

The electrophysiological results discussed so far (N2pc and response-locked LRP) provide evidence that effects of dimension changes and response changes in visual search are generated at separate perceptual-attentional and response-related processing stages. However, the observation that the RT data did not show an additive pattern of dimension change and response change effects appears to be at variance with this conclusion. Recall that the observed RT pattern revealed fastest reactions when both the target-defining dimension and the required response remained the same on consecutive trials. Changes of the dimension, the response, or both, all slowed down RTs to a similar level. This interactive pattern of RT effects resembles that observed in previous studies (Krummenacher & Müller, 2002; Müller & Krummenacher, 2006; Pollmann et al., 2006; see also Olivers & Meeter, 2006, Figure 7; though some of the earlier studies had revealed marginal RT differences between conditions with at least one change, and, in Olivers and Meeter's meta-analysis of five compound-task experiments, the interaction was not statistically reliable[8]). Thus, the present RT findings may be taken as supporting an interpretation along the lines suggested by Pollmann et al. (2006), namely, that repetitions of the target-defining dimension facilitate unchanged responses, whereas a dimension change disrupts any pre-set stimulus-response links, so that response selection and programming must start from scratch.

However, the present electrophysiological findings suggest a somewhat different account of the interactive pattern of RT effects. On this account, a heuristic version of which is illustrated in Figure 17, the interaction arises at a processing stage intermediate between focal-attentional selection and the response production, that is: stimulus-to-response translation or 'response selection'. This account assumes that the observed effects on the N2pc and the response-locked LRP can be interpreted in terms of facilitated processing (resulting in faster processing times) at perceptual and response production stages, respectively, and takes into consideration the latencies and topographies of the N2pc (around 250 ms; extrastriate cortex) and the response-locked LRP (around 460 ms post-stimulus, i.e., 100 ms prior to response; primary motor cortex). Thus, as is illustrated in Figure 17, the early stage of focal-attentional selection is facilitated when the target-

[8] One reason for this may be that Olivers and Meeter examined this interaction on data combined across rather heterogeneous stimulus and task conditions. In some conditions, a singleton distractor could be present in either the same or a different dimension to the target. Since the distractor could be associated with either a same of or a different response, it potentially caused conflict in stimulus-response translation if it summoned focal attention prior to the target.

defining dimension remains unchanged, reflected in the present study by the effect of dimension change on N2pc amplitudes and latencies. The late stage of response production is facilitated when the response remains unchanged, and this was reflected (albeit indirectly) by the effect of response change on response-locked LRP amplitudes.

Given this pattern of electrophysiological results, and the overall RTs in the four (dimension change x response change) conditions, it is possible to make inferences about the processing time required by the intermediate response selection stage. As illustrated in Figure 17, the assumption is that the duration of this intermediate stage is shorter when either both the dimension and the response remain the same or when both change; in contrast, it is prolonged when either the dimension or the response changes. This may be explained by postulating that the response selection stage assumes a correlation between the two types of change, even though dimension and response changes occurred independently of each other in the event statistics. That is, if focal-attentional analysis confirms the target dimension to be the same as on the preceding trial, the response selection system implicitly assumes that the response (and/or the attribute on which the response is based) will also remain the same, thus facilitating the selection of an unchanged response. By contrast, if the target dimension changes, the system assumes that the response (attribute) will change, too, thus facilitating the selection of a changed response. Note that the error pattern is consistent with such a linking of dimension and response 'expectancies'. This linking may occur because it is easier for the system to change both expectancies than to change just one (see also Kingstone, 1992, who showed that such linkages may operate even when the relevant attributes are negatively correlated, rather than just uncorrelated). Note that, although phrased in terms of 'response selection', this account is neutral with respect to whether the linked expectancies exist between search-critical stimulus attributes and motor responses as such, or between search-critical and response-critical stimulus attributes (i.e., target-defining dimension and grating orientation).

Evidence in favor of the account illustrated in Figure 17 is provided by the pattern of stimulus-locked LRP onset latencies, which mark the transition between response selection and response production stages. The onset of response production is determined both by the duration of perceptual-attentional processes as well as by the duration of response selection. As demonstrated by the current N2pc results, perception and subsequent attentional selection are fast on trials on which the target-defining dimension is

repeated (sDsR, sDdR), and slow on dimension change trials (dDsR, dDdR). Response selection is assumed to be fast on trials on which target dimension and response are both repeated or both changed (sDsR, dDdR), and slow when only one of them is changed (sDdR, dDsR). Thus, stimulus-locked LRP onset latencies should be fastest on sDsR trials, slowest on dDsR trials, and intermediate on dDdR and sDdR trials (see Figure 17).

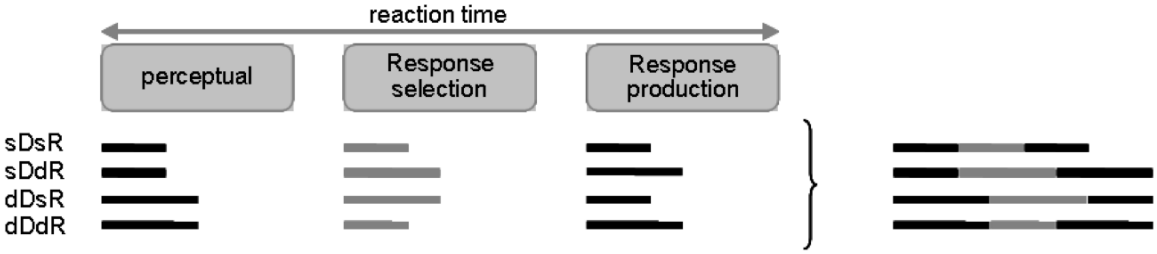

Figure 17. Schematic illustration of the inferred processing times (black and grey lines) required by successive processing stages involved in performing a compound search task, for each experimental (dimension change x response change) condition. The summed processing times of the three stages yield the overall reaction time for a given condition. Black lines indicate processing times derived from interpreting the ERP results (N2pc: prolonged processing times for dimension changes; response-locked LRP: prolonged processing times for response changes). Grey lines represent inferred processing times derived by subtracting black lines from the overall reaction times.

This predicted pattern of stimulus-locked LRP onset latencies (sDsR < dDdR = sDdR < dDsR) was almost exactly matched by the observed data (sDsR < dDdR < sDdR < dDsR). The only exception was that onset latencies were 15 ms faster for dDdR trials relative to sDdR trials, whereas the model shown in Figure 17 predicts no latency difference between these two conditions. However, this prediction is based on the simplifying assumption that the effects of dimension change on the duration of perceptual-attentional stages, and of linked expectancies regarding stimulus and response changes on the duration of response selection stages are of exactly the same magnitude, which need not be the case. The earlier stimulus-locked LRP onset for dDdR relative to sDdR trials can easily be explained by assuming that the impact of linked expectancies on the time demands of response selection is more pronounced than the impact of dimension change on perceptual-attentional processing. In addition, it is conceivable that any delay in detecting the target in the changed dimension may make the response selection system tend towards a changed response – similar to a target-present/absent search task, where a delay

in detecting the target makes the response system tend towards an ‘absent’ decision (see, e.g., Chun & Wolfe, 1996). This could have further shortened the duration of response selection on dDdR trials, resulting in an earlier stimulus-locked LRP onset. Whatever the exact explanation for the earlier LRP onset on dDdR trials, the more general and more important conclusion is that the observed stimulus-locked LRP onset latencies support the pattern derived from the proposed account.

Considering the pattern of stimulus-locked LRP effects together with the N2pc effects provides answers to the two questions addressed in the present study: (i) why is RT intertrial facilitation overall reduced in compound-search tasks and (ii) do these intertrial facilitation effects arise at an early perceptual and/or a later response-related stage of processing? The answer to the first question is that the overall RT intertrial facilitation effects are reduced because they are masked under response-change conditions by system-immanent linkages between stimulus and response. The answer to the second question is that RT intertrial facilitation effects originate at both (pre-attentive) perceptual and (post-selective) response selection-related stages of processing. Recall that the only effect evident in the RT data was the advantage for sDsR relative to dDsR trials (see Figure 13). According to our model, this advantage arises because of both faster perceptual processing and faster response selection on sD relative to dD trials. In contrast, there was no advantage for sDdR versus dDdR trials. According to our model, the lack on an effect is due to faster perceptual processing being counteracted by slower response selection on sD trials, with the reverse pattern on dD trials. In any case, where RT intertrial facilitation is observed, the N2pc latency advantage for dimension repetition trials (around 10 ms) is unlikely to account for the whole RT intertrial facilitation (of some 50 ms); rather, the effect is due to both expedited perceptual processing and expedited response selection.

In summary, the present study provides new insights into the mechanisms underlying dimension-specific intertrial effects in visual search tasks under conditions of high target saliency (low target ambiguity). Visual dimension changes and response changes elicited differential activation patterns affecting distinct ERP components. Dimension repetitions versus changes were reflected in the N2pc, indicating facilitated allocation of focal attention to targets defined in a repeated dimension. That is, at least part of the RT intertrial facilitation effect arises at a perceptual processing stage prior to focal-attentional selection. The observed response-locked LRP effects indicate that, with response repetitions on consecutive trials, the required response was pre-activated

('weighted') by the motor system. Concerning processes between focal-attentional selection and motor-response generation, the stimulus-locked LRP effects taken together with the N2pc effects suggest that another part of the RT intertrial facilitation effect arises at the response selection stage. This pattern of effects provides strong support for the dimension-weighting account, and appears inconsistent with views that dimension-specific intertrial effects are generated *exclusively* at post-selective response-related stages of processing.

CHAPTER IV

Dimension-based attention modulates early visual processing

Abstract

The selection of targets in a visual scene can be based on positional information or non-spatial features operating in a location-independent manner. In the present study we investigated whether dimension-based attention effects (i) can be observed for early visual information processing and (ii) whether the number of possible target locations in visual search influences dimension based processes. To test this, a visual search task for singletons with non-predictive featural but predictive locational trial-by-trial cueing (Experiment 4), or non-predictive dimensional and non-predictive locational identity of the upcoming target (Experiment 5) was conducted. The results revealed systematic dimension-based variations of the early visual evoked P1 in both experiments. This effect was independent of the featural identity within the cued dimension. In addition, the anterior transition N2 (tN2) was increased for dimension changes relative to repetitions. Based on these components, source reconstructions demonstrated dimension change-related activations in left frontopolar and dorsal occipital cortex. The dimension-based non-spatial influence on early visual processing is in line with dimension-based theories on visual attention (e.g., DWA) and provides evidence for the processing of dimensional information as early as 110 ms post-stimulus.

Introduction

It is well established that visual attention can be oriented to spatial locations without overt gaze shifts (e.g., Posner, 1980). Electrophysiologically, the covert orientation of spatial attention is reflected by early sensory evoked potentials (ERPs) (e.g., Eimer, 1994; Hillyard & Mangun, 1987; Hillyard & Munte, 1984; Mangun & Hillyard, 1988; Rugg, Milner, Lines, & Phalp, 1987), with the earliest marker being the visual P1 component. Typically, this component peaks around 100 ms post-stimulus, with a maximum over occipital and/or parieto-occipital electrode positions. When subjects are provided with prior knowledge about the upcoming target location (e.g., by spatial pre-cueing), the amplitudes of the visual P1 component are enhanced for targets occurring at the attended (as compared to unattended) location(s). As demonstrated by Martinez, Anllo-Vento, Sereno, Frank, Buxton, and Dubowitz (1999), the early phase of this spatially selective P1 effect is likely to be generated within dorsal extrastriate cortex of the middle occipital gyrus, while the later phase originates from the ventral fusiform area. Traditionally, such P1 amplitude modulations have been interpreted in terms of a sensory 'gain control' mechanism which increases the signal gain at the attended location, thereby leading to substantially improved perceptual processing (Eimer, 1994; Hillyard, Vogel, & Luck, 1998; Luck, Woodman, & Vogel, 2000).

Visual selection based on non-spatial stimulus qualities

More recently, electrophysiological studies have provided evidence that attention can also be allocated to non-spatial visual features defining the target, in a location-independent manner (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). Moreover, feature-based attention has been found to influence early stages of processing, reflected in modulations of the visually evoked P1 (Han, Liu, Yund, & Woods, 2000; Mouchetant-Rostaing, Giard, Delpuech, Echallier, & Pernier, 2000; Taylor, 2002). The evidence for target detection based on selective attention to target-defining features is in agreement with single-cell studies (in macaque monkeys) that have demonstrated feature-dependent tuning of receptive fields (Treue & Martinez Trujillo, 1999), parallel feature-selective processing across the topographic map of V4 (Motter, 1994), and interactive (spatial and non-spatial) processes that influence early stages of cortical processing (Bullier, Hupe, James, & Girard, 2001).

Feature-based attention plays an important role in current theories of visual search, which assume that target-relevant feature information is encoded selectively in order to

guide the allocation of focal spatial attention to the target (Treisman & Sato, 1990; Wolfe, Cave, & Franzel, 1989). Once focal attention has been allocated to the target, suppression of information from surrounding positions improves the perceptual analysis at the attended location (Luck, Chelazzi, Hillyard, & Desimone, 1997).

Recently, the emphasis on the *feature*-specificity of attentional processes in the guidance of visual search has been challenged by Müller and his colleagues (e.g., Found & Müller, 1996; Müller, Heller, & Ziegler, 1995; Weidner, Pollmann, Müller, & von Cramon, 2002; see also Wei, Lü, Müller, & Zhou, 2007), who instead proposed a *dimension*-based, or 'dimension weighting', account (DWA) of search guidance. This account assumes that, besides space- and object-based limits of visual selection, selection is also limited by the dimensional nature of the discrimination required to discern search-relevant target attributes. In more detail, target detection is influenced by an 'attentional' mechanism that modulates the processing system by allocating limited 'selection weight' to the various dimensions which potentially define the target. Dimensions are assigned weight largely automatically, in bottom-up manner – in particular, a larger weight is allocated to the dimension defining the target on the current trial (relative to current non-target dimensions), implicitly 'predicting' that the next target will also be defined (by any feature) in this dimension. Thus, when the next target is indeed defined in this dimension, target detection is expedited compared to a dimension change. However, the bottom-up established weight set may be modified, to some extent, in top-down manner, based on advance information as to the target-defining dimension on a given trial (Müller, Reimann, & Krummenacher, 2003). Importantly, under comparable conditions, dimension-based effects are always larger than feature-based effects (e.g., Found & Müller, 1995; Meeter & Olivers, 2007), supporting the primacy of dimension-based processes in the guidance of visual search.

One fundamental postulate of the DWA is the weighting of early, dimensionally organized modules of analyzers responsible for the sensory coding of target attributes. Recently, fMRI studies by Pollmann, Weidner, Müller, and von Cramon (2000, 2006) investigated cross-dimensional search for pop-out (singleton) targets unpredictably defined in either the color or the motion dimension. Besides the identification of a fronto-posterior network involved in dimension weighting, Pollmann et al. found increased activations in occipital areas depending on the dimensional identity of the target: repeated color-defined targets on successive trials were accompanied by increases of activation in extrastriate area V4 (more precisely, posterior fusiform gyrus, which contains V4), and repeated motion-defined targets by increases in area

V5 (more precisely, lateral occipital cortex, which contains the human MT+ complex). This pattern of hemodynamic activations is consistent with the hypothesis that early visual analyzer modules are modulated depending on the dimensional (rather than the featural) nature of the preceding target event, thus providing strong support in favor of the DWA. However, due to the sluggish nature of hemodynamic responses, imaging studies are inappropriate to further specify the time course of dimensional weighting mechanisms.

Rationale of the present study

The current study was designed to verify whether early visual processing on a given trial, as reflected by the visual P1 component, can indeed be modulated dependent on the dimensional identity of the sensory event on the preceding trial. Previous work (Chapter II and III) has revealed evidence of dimension-specific inter-trial effects on an electrophysiological level. Comparisons of event-related potentials elicited by the current target dependent on the inter-trial history (the definition of the previous target) revealed dimension-based effects starting around 240 ms (tN2) and 190 ms (N2pc) post-stimulus; these effects were evident only for dimension changes versus repetitions, but not for feature changes versus repetitions within the same dimension. Changes of the target-defining dimension were associated with pronounced negative shifts of the anterior 'transition N2' (tN2) and more positive-going deflections of the slow wave (SW) in a pop-out search task, and delayed latencies and enhanced amplitudes of the N2pc in a compound search task (where the search- and response-critical attributes of the target are different). Importantly, changes of the target-defining feature in a repeated dimension failed to yield any significant differences (see also Found & Müller, 1996), supporting a dimension-based account of attentional weighting. In summary, the N2pc was observed to be the earliest ERP marker of dimension-based effects; that is, to date, no dimension-specific modulations have been demonstrated for any earlier components, such as the visual P1.

The latter is at odds with the DWA, which explicitly assumes that the beneficial effect of dimension repetition on search performance arises from enhanced coding of (intra-dimensional) feature contrast, due to the preferential weighting of the relevant pre-attentive coding stages prior to the allocation of focal attention to the target. On this hypothesis, modulations of P1 amplitudes would be expected, representing differential activations over early sensory areas depending on the preceding sensory event. To systematically assess this prediction, a pop-out visual search task was introduced in the present study in which the search display that contained the response-relevant target singleton was preceded by a

response-irrelevant cue display. The cue display consisted of a similar array as the subsequent target display, containing a singleton element, the cue, amongst homogeneous non-singleton elements. In Experiment 4, the cue was non-predictive as to the defining dimension/feature of the upcoming target, but predictive as to its location; and in Experiment 5, the cue was neither dimensionally/featurally nor locationally predictive. Thus, Experiment 4 was designed to examine the nature of non-spatial cueing effects (that is, the dimension and/or feature specificity of such effects) on the early P1 component. And, by additionally creating uncertainty about the upcoming target location, Experiment 5 was designed to examine how non-spatial and spatial attentional processes would interact in this paradigm. In addition to the primary focus on the early P1 component, the anterior N2 component was expected to be modulated by the dimensional identity of the previous sensory event (the cue), similar to the (tN2) pattern observed in earlier experiments (Chapter II). That is, a stronger negativity due to dimension changes was expected over fronto-central electrode positions, reflecting the *control* of (implicit) dimensional weight setting (see also Pollmann, Mahn, Reimann, Weidner, Tittgemeyer, Preul, Müller, & von Cramon, 2007).

EXPERIMENT 4

Method

Participants. Twelve subjects (2 female) took part in Experiment 4. One participant had to be excluded from the analyses, due to excessive artifacts. The ages of the remaining eleven subjects ranged from 21 to 25 years (X = 23.1 SD = 2.2 years); all were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological disorder. Subjects were either paid or received course credit for participating.

Stimuli and procedure. Subjects were seated in a dimly lit experimental chamber. Stimuli were projected by a beamer (Sanyo PLC-XU47), situated approximately 60 cm above the subject's head, on a 150 cm x 150 cm white screen. The subject viewed the screen from a distance of 130 cm, with the centre of the display adjusted to the individual straight-ahead line of view.

Successively presented cue and target displays consisted of a circular array of eight colored stimuli on a black background (see Figure 18). The stimuli were equidistant (3.9° of visual angle) from a white fixation cross in the centre. Each stimulus array contained one singleton, which was equally likely defined in either the color or the shape dimension

(*red* or *green* circle, of radius 1.2°; blue *diamond* or *triangle*, 2.1° x 2.1° or, respectively 2.8° x 3.2° in size among seven identical distracters (blue circles, of diameter 2.4°). All stimuli were matched in size. The singleton could appear randomly at one of the six lateral array positions; however, its location was always the same in the cue and the (subsequent) target display. Observers were instructed to maintain central fixation throughout a trial (the sequence of cue and target display), and to indicate the dimension of the singleton *target*, using their left- or right-hand index finger to respond 'color' or 'shape', respectively. The response buttons were positioned vertically aligned to avoid spatial stimulus-response compatibility effects. Half the subjects started with the left index finger on the upper button and the right index finger on the lower button, and vice versa for the other half. For all subjects, the response button assignment was reversed in the second half of the experiment. Note that a speeded dimension discrimination task was used in order to avoid (theoretically uninteresting) target-absent trials; Found and Müller (1996) had shown that dimension-specific inter-trial effects are comparable between simple search (target-present/absent response) and dimension discrimination tasks (e.g., color/shape response).

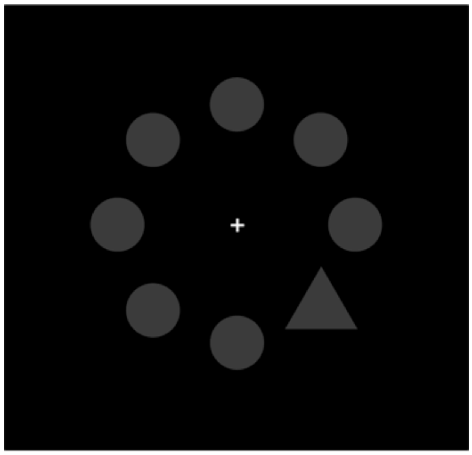

Figure 18. Example of the (preceding) cue as well as (subsequent) target displays, with the singleton being defined in the shape dimension. The arrays consisted of a circular arrangement of eight stimuli presented against a black background, with a white fixation cross in the center. Distractors were blue circles, and targets were defined in either the color dimension (*red* or *green* circle) or the shape dimension (blue *triangle* or *diamond*). Participants were asked to discriminate the dimension of the singleton target as fast and accurately as possible.

One experimental session consisted of eighteen experimental blocks of 72 trials each. A trial started with a white fixation cross for 500 ms, followed by the cue display for 200 ms. After a constant cue-target interval of 700 ms during which only the fixation cross was visible, the target display was presented for 200 ms. The trial was terminated by the subject's response or after a maximum duration of 1000 ms. During the inter-trial interval, a black screen was shown for 1000 ms. The feature defining the singleton in the cue

display (red, green, diamond, or triangle) was selected in pseudo-random order. With respect to the singleton feature in the cue display, the target display could contain (at the same position) a singleton defined by the same feature (same Dimension same Feature, sF), by a different feature in the same dimension (same Dimension different Feature, dF), or by a feature in a different dimension (different Dimension, dD), each with a probability of one-third. On trials with targets defined in a different dimension, each of the two alternative features was equally likely.

EEG recording and data analysis. The electroencephalogram (EEG) was recorded continuously, at a sampling rate of 500 Hz, using 64 Ag/AgCl electrodes including those corresponding to the 10-10 system (American Electroencephalographic Society Guidelines in Electroencephalography, Evoked Potentials, and Polysomnography, 1994). The electrodes were mounted on an elastic cap (Easy Cap, Falk Minow Services). Horizontal and vertical eye movements were monitored by means of electrodes placed at the outer canthi of the eyes and, respectively, the superior and inferior orbits. Electrophysiological signals were amplified using a 0.1–100-Hz bandpass filter via BrainAmps (BrainProducts, Munich) and filtered offline with a 1–40-Hz bandpass (Butterworth zero phase, 24 dB/Oct). All electrodes were referenced to Cz and re-referenced off-line to linked mastoids. ERPs were averaged off-line over an 800-ms epoch relative to a 200-ms pre-stimulus baseline. Eye movements were corrected by means of independent component analyses (ICA) implemented in the Brain Vision Analyzer software (Brain Products, Munich). Epochs with artifacts, that is: excessive peak-to-peak deflections (>60 μV or <-60 μV), bursts of electromyographic activity (permitted maximal voltage step / sampling points 50 μV), and activity lower than 0.5 μV within intervals of 500 ms (indicating 'dead channels' in the montage), were excluded from averaging on an individual-channel basis.

Following the elimination of artifacts, latencies of the P1 and N2 components were determined individually as the maximum deflection within the respective time windows (P1: 80–140 ms; N2: 230–300 ms) derived by visual inspection of the grand average potentials. The mean amplitudes were calculated using five sample points before and after the maximum peak deflection. Note that only trials with a correct response were included in the analyses. Amplitudes and latencies of the P1 component were analyzed by repeated-measures analyses of variance (ANOVAs) with the factors (cue-target) Transition (sF, dF, dD), Hemifield of the target (left, right) and Electrode Position (left, right recording

position) at PO7 and PO8. Amplitudes and latencies of the anterior N2 component were analyzed using a repeated-measures ANOVA with the factors (cue-target) Transition (sF, dF, dD), Electrode Site (frontal, fronto-central, central), and Electrode Position (left, midline, right).

Since the present study was primarily designed to provide insight into the neural mechanisms underlying dimensional cueing effects, only main effects and interactions involving the factor (cue-target) Transition will be reported for the electrophysiological data. Whenever required, significant main effects and interactions were further examined using Tukey HSD post-hoc contrasts.

Results

Behavioral data

On 2.7% of all trials, subjects reacted faster than 100 ms or slower than 1000 ms (sF 2.7%, dF 2.4%, and dD 2.9%). In addition, subjects reacted incorrectly on 4.0% of all trials. The distribution of errors was slightly shifted towards dD trials, with 6.6% incorrect reactions as compared to 2.7% for sF and 2.7% dF trials. A repeated-measures ANOVA with the factors 'Dimension' (color vs. shape) and (cue-target) 'Transition' (sF, dF, dD) revealed this difference in response errors to be significant [main effect of Transition, $F(2,20)=7.09$, $p<.019$; $\eta 2 = 0.415$]. The two-way interaction was also significant [$(2,20)=4.41$, $p<.026$; $\eta 2 = 0.306$]: for validly cued dimensions (i.e., when the target was defined within the same dimension as the cue), the percentages of errors were comparable between trials with and without a change in the target-defining feature (color: 2.7% and 2.6% for dF and sF; form: 2.7% and 2.8% for dF and sF). However, invalid dimensions cues were associated with significantly more errors when the target was defined within the shape as compared to the color dimension (5.4% vs. 7.8%).

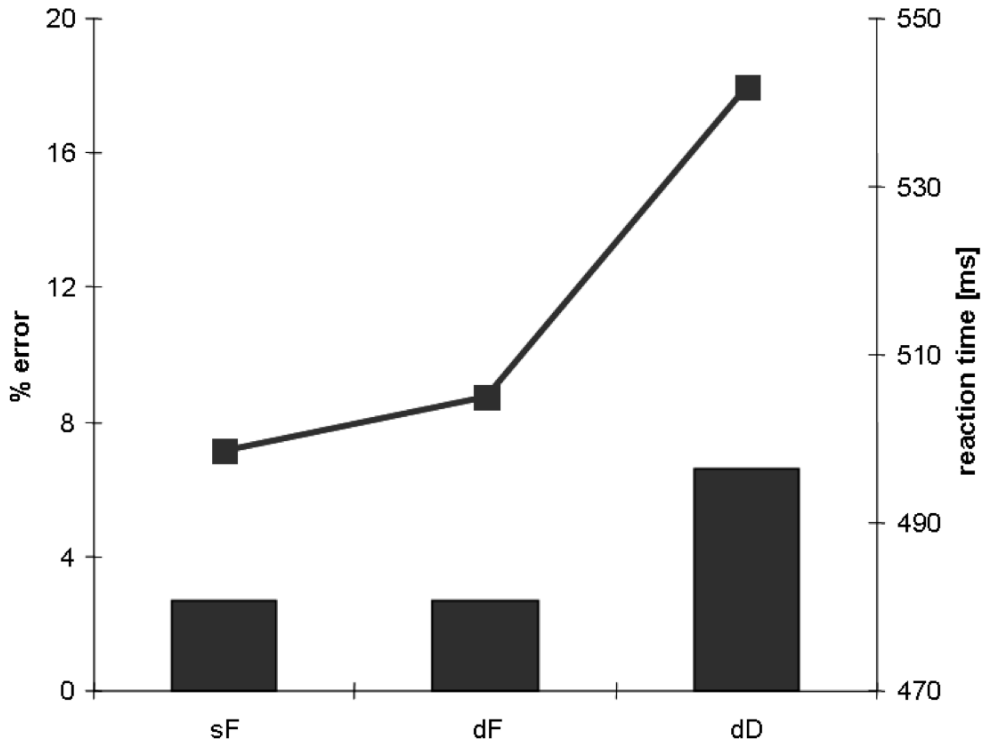

Figure 19. Mean reaction times (in milliseconds), and associated error rates (in percent), for the target singleton, dependent on the identity of the singleton in the cue display: same dimension same feature (sF), same dimension different feature (dF), and different dimension (dD).

Reaction times (RTs) on correct trials were analyzed using the same ANOVA, which revealed only the main effect of Transition [$F(2,20) = 13.79$, $p<.001$; $\eta 2 = 0.580$] to be significant [main effect of Dimension: $F(2,20) = 2.91$, $p>.119$; $\eta 2 = 0.225$; interaction: $F(2,20) = 1.25$, $p>.31$; $\eta 2 = 0.111$]. Figure 19 presents the correct RTs dependent on the cue-target transition aggregated over color- and shape-defined targets. The pattern of cue-target transition effects replicates the pattern of inter-trial effects described by Found and Müller (1996): there was a significant RT cost for invalidly cued, relative to validly cued, dimensions (43.3-ms cost for dD vs. sF, $p<.001$, and 37.1-ms cost for dD vs. dF, $p<.003$), while there was no significant cost for invalidly cued features, relative to validly cued features, within a dimension (6.3-ms cost for dF vs. sF, $p<.76$).

Electrophysiology

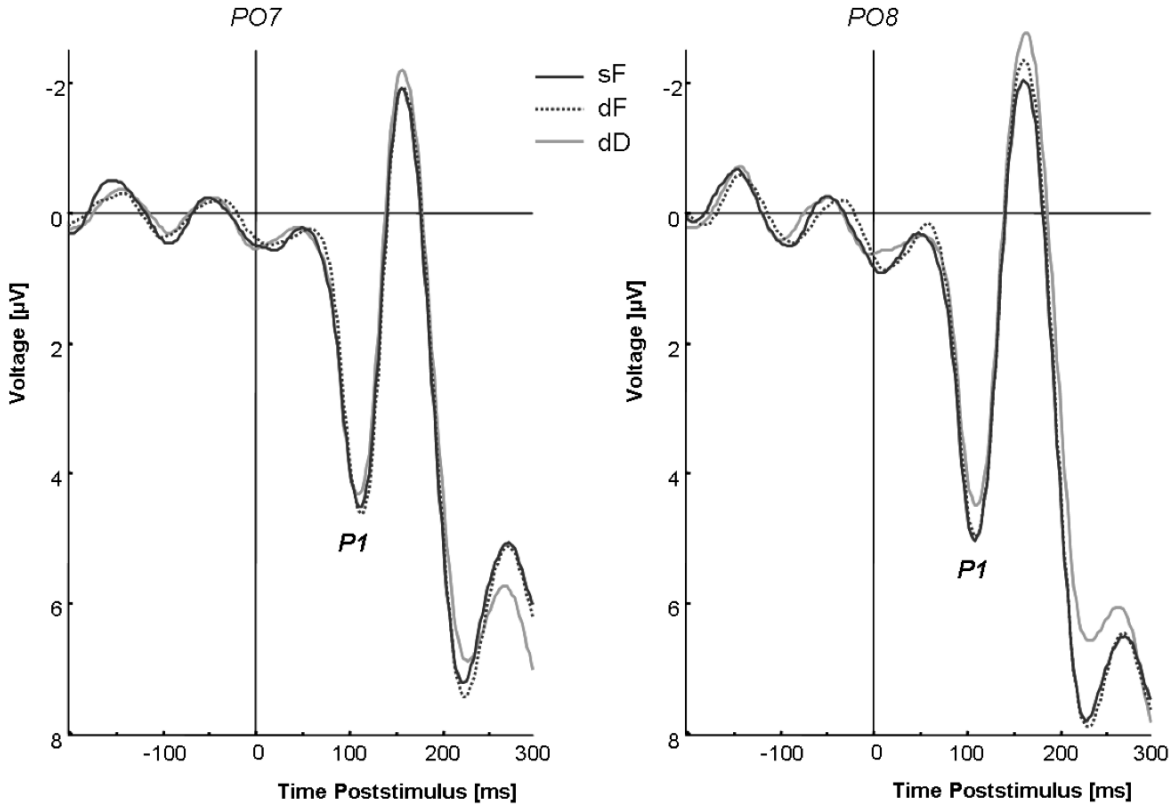

Figure 20. Grand-averaged ERP waveforms elicited over early visual areas at electrode positions PO7/PO8 in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Dark grey lines indicate feature repetitions, light grey lines dimension changes. Dotted lines indicate intra-dimensional feature changes.

P1. Analyses of P1 amplitudes revealed a significant main effect of Transition ($F(2,20) = 8.94$, $p>0.002$; $\eta^2 = 0.472$), with the strongest P1 deflections when the target-defining dimension was validly cued (4.30µV for sF and 4.23 µV for dF), as compared to invalidly cued dimensions (3.97 µV for dD) (Figure 20). Post-hoc contrasts revealed no difference between dimensionally validly cued targets dependent on whether or not there was a feature change between the cue and the target ($p<0.70$ for dF vs. sF). However, as depicted in Figure 21, invalid dimension cues led to less positive amplitude deflections with onset of the target display compared to valid cues ($p<0.002$ for dD vs. sF and $p<0.012$ for dD vs. dF). No effects were revealed for the P1 latencies.

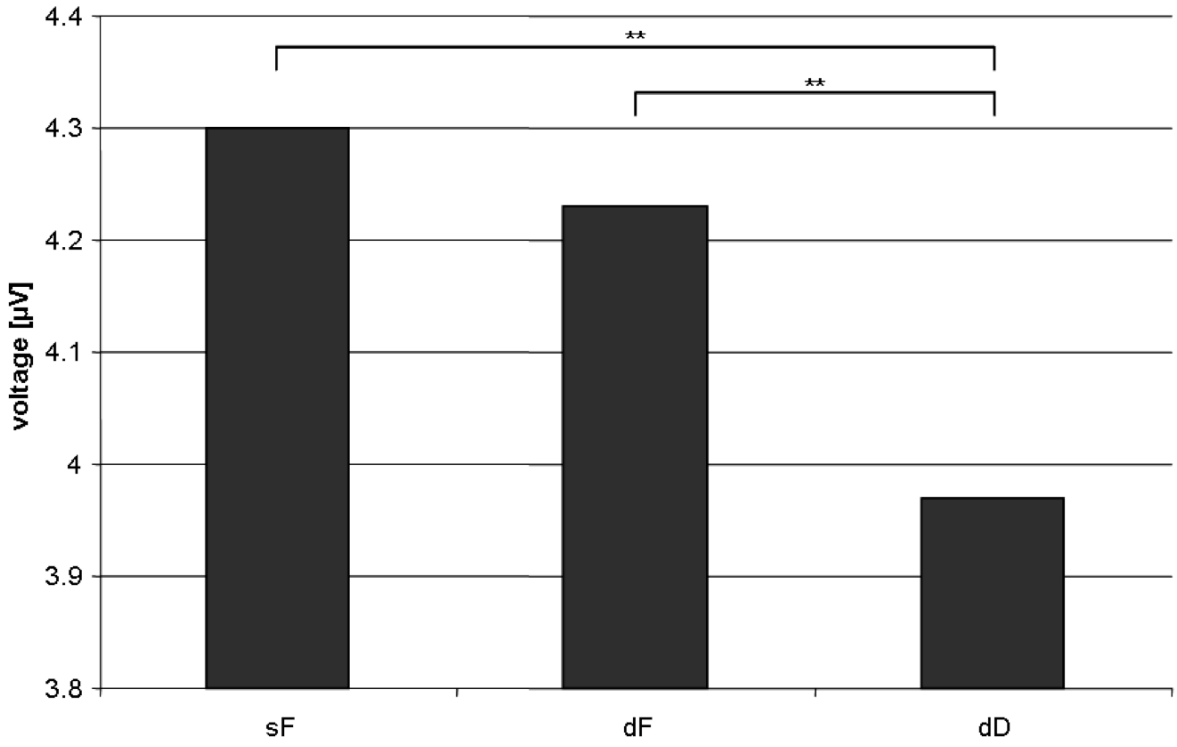

Figure 21: Mean P1 peak amplitudes elicited at PO7/PO8 in response to the target display dependent on the identity of the singleton in the cueing display: same-dimension same feature (sF), same-dimension different feature (dF), and different-dimension (dD).

N2. The ANOVA of the N2 amplitudes (see Figure 22) revealed the factor Transition to interact with both Electrode Site [$F(4,40) = 5.09$, $p>0.002$; $\eta^2 = 0.337$] and Electrode Position [$F(4,40) = 3.87$, $p>0.009$; $\eta^2 = 0.279$]. Furthermore, the three-way interaction was significant [$F(8,80) = 2.14$, $p>0.042$; $\eta^2 = 0.176$]. Post-hoc contrasts revealed reliable Transition effects at right frontal, midline, right fronto-central, and central electrodes. Importantly, these effects were purely dimension-specific ($p<.001$), with no difference between sF and dF conditions ($p>.531$). In summary, a change of the singleton-defining dimension was associated with enlarged N2 amplitudes, with a slight right-lateralisation largest over fronto-central electrode positions. An identical ANOVA performed on the N2 latencies revealed a significant Transition x Electrode Site interaction [$F(4,40) = 4.47$, $p>0.004$; $\eta^2 = 0.309$], due to prolonged latencies for dD conditions at frontal compared to fronto-central and central electrodes ($p< 0.038$).

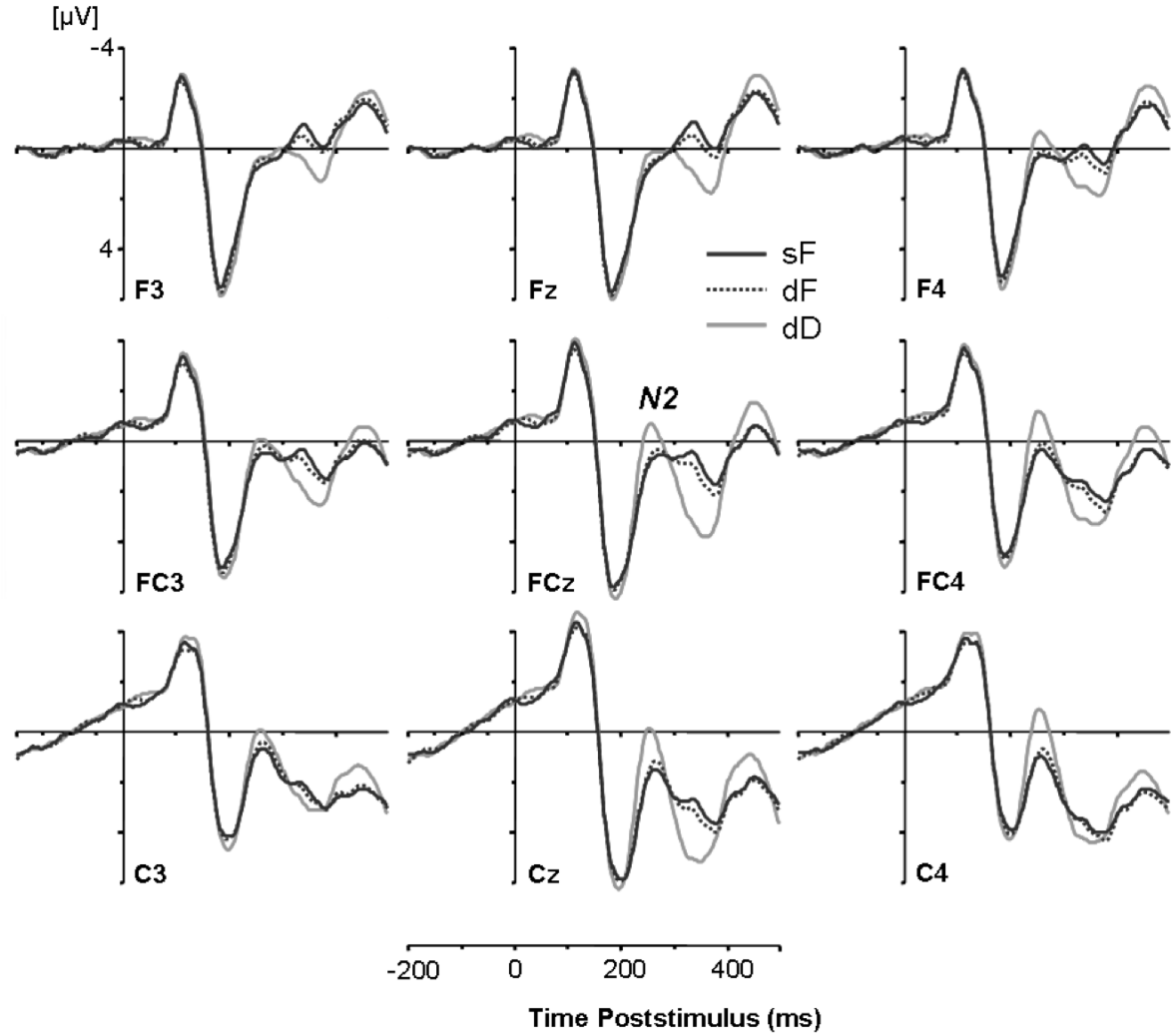

Figure 22. Grand-averaged ERP waveforms elicited over fronto-central electrode positions in the 500-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Dark grey lines indicate feature repetitions, light grey lines dimension changes. Dotted lines indicate intra-dimensional feature changes.

Discussion

In Experiment 4, the pattern of RT effects was exactly as predicted by the DWA: when the target singleton was defined in the same visual dimension as the cue singleton (e.g., shape→shape), RTs were faster compared to when the singleton dimension changed from the cue to the target display (e.g., color→shape). Importantly, this RT advantage was independent of intra-dimensional feature changes between the cue and the target display (e.g., red → green), pointing to a 'special' role of visual dimensions in search guidance.

At the electrophysiological level, both ERP components examined were affected by visual dimension changes. Theoretically of most importance, repetitions of the singleton-

defining dimension resulted in enhanced peak amplitudes of the visual evoked P1 component. Similar to the RT data, this effect was independent of featural repetition/change within the cued dimension. This finding is as predicted by the DWA. According to this account, dimensionally organized modules of visual analyzer units are weighted on a given (cue) trial, thus expediting the emergence of the target's saliency signal at the level of the (attention-guiding) overall-saliency map on the next (target) trial. In line with a sensory 'gain control' interpretation of the P1 component (Luck et al., 2000), enhanced amplitudes reflect facilitated perceptual coding within the attended dimension. Thus, the notion of an 'attentional spotlight' to account for early spatial-attention effects would have to be broadened to include dimension-based effects as early as 110 ms post-stimulus. However, because the paradigm used in Experiment 4 does not provide a baseline measure, it is not clear whether the observed P1 modulation represents an amplitude enhancement on dimension repetition trials, an amplitude reduction on dimension change trials, or both.

In addition to the new finding of a P1 modulation, Experiment 4 replicated the tN2 modulation observed for dimension changes in Chapter II, demonstrating an identical pattern for dimensional cueing as for cross-dimensional search tasks. That is, irrespective of the featural identity of the cue, a change of the singleton-defining dimension was reflected in enhanced amplitudes, with a slight right-lateralisation largest over fronto-central electrode positions. This systematic pattern of N2 amplitude effects provides further evidence for the involvement of frontal control processes engaged in the shifting of limited attentional resources (weight) from the old (cue-defining) to the new (target-defining) dimension.

EXPERIMENT 5

Experiment 4 demonstrated that the visual evoked P1 component can be modulated by non-spatial (dimensional) stimulus attributes, provided that prior knowledge about the position of the upcoming target is available. Given the broad ERP literature that has traditionally linked this brain potential to processes based solely on *spatial* stimulus attributes, the question immediately arises as to how spatial and non-spatial processes would interact in the present search paradigm. To address this question, Experiment 5 presented non-predictive dimensional and non-predictive locational cues about the upcoming target. Combining previous findings of enhanced P1 amplitudes for validly cued locations (Eimer, 1994; Hillyard et al., 1998) with the present findings (in Experiment 4) of enhanced P1 amplitudes for validly cued dimensions, one might expect an additive effect of both factors. This seems reasonable, since both effects can be interpreted as reflecting 'sensory gain' or 'amplification' mechanisms. On this assumption, in Experiment 5, the most enhanced P1 amplitudes were expected for targets validly cued with respect to both location and dimension. Conversely, the smallest P1 amplitudes were expected for targets invalidly cued with respect to both location and dimension. And intermediate P1 amplitudes were expected to be elicited in response to targets following cues that correctly predicted only one of the two stimulus attributes (spatial or non-spatial).

In addition, to gain deeper insights into the origins of dimension-based ERP effects, a spatio-temporal current density reconstruction was performed based on brain regions that have previously been associated with dimensional weighting. More specifically, it was examined whether the activation strengths in these regions would co-vary with the dimensional nature of the previous sensory event – and, thus, contribute to dimension-based ERP effects. Based on several reports by Pollmann and colleagues (Pollmann et al., 2000, 2006a, 2006b, 2007; Weidner, Pollmann, Müller, & von Cramon, 2002), sources within the left frontopolar cortex were expected to be involved in the *control* of dimensional weight setting, in turn modulating signal processing in early visual areas within extrastriate occipital regions.

Method

Participants. Eleven subjects (all male) took part in Experiment 5. Their ages ranged from 21 to 26 years (X = 23.1, SD = 1.8 years); all were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological disorder. Subjects were either paid or received course credit for participating.

Stimuli and Procedure. The general experimental set-up and procedure were the same as in Experiment 4, except that the position of the cue did not predict the position of the subsequent target, and that the singletons presented in the cue and target displays were either a *red* circle (color singleton) or a blue *diamond* (shape singleton; i.e., there was no variability of the singleton-defining feature in the color and the shape dimension).

The singleton feature and the position of the cue were selected in pseudo-random order, and the target display contained a singleton varying in the following way with respect to the cue display: same-dimension same-position (sDsP) singleton, same-dimension different-position (sDdP) singleton, different-dimension same-position (dDsP) singleton, and different-dimension different-position (dDdP) singleton, each with a probability of one-quarter. On different-position trials, target singletons were always located at one of the three possible contralateral hemifield positions relative to the cue position. Prior to the start of each experimental half, subjects performed at least one block of practice trials.

EEG Recording and data analysis. In contrast to Experiment 4, the EEG was recorded continuously using 128 Ag/AgCl electrodes, including those corresponding to the 10-10 system. A larger number of electrodes were used in order to ensure the high spatial resolution of the recorded signal required for distributed source reconstructions (Michel et al., 2004).

Behavioral data were analyzed by repeated-measures ANOVAs with the factors ‘Dimension change’ (same vs. different dimension compared to the cue) and ‘Position change’ (same vs. different position compared to the cue). To examine the electrophysiological data, an ANOVA with the factors Dimension change (same vs. different dimension), Position change (same vs. different position), Hemifield (left vs. right), and Electrode Position (left vs. right recording position) at electrodes PO7/PO8 was performed for the P1 component, and an ANOVA with the factors Dimension change, Position change, ‘Electrode Site (frontal, fronto-central, central), and Electrode Position (left, midline, right) for the tN2 component. Since Experiment 5 was primarily conducted to investigate whether and how spatial and non-spatial processes might interact in the present cueing paradigm, only main effects and interactions involving the factor ‘Dimension change’ and/or ‘Position change’ will be reported for the electrophysiological data. Whenever required, significant main effects and interactions were further examined

by means of Tukey HSD post-hoc contrasts. In all other respects (procedure, EEG recording, and data analysis), Experiment 5 was identical to Experiment 4.

Spatiotemporal Current Density Reconstruction (stCDR). A spatio-temporal coupled reconstruction algorithm as implemented in the EaSI software package (Electro-anatomical Source Imaging, Brain Products Munich, Germany) was used for source reconstruction. Within this software, the representation of a normal brain is implemented according to the T1-weighted structural MR provided by the Montreal Neurological Institute. A finite-element model was used with the gray matter serving as source space. The model is based on a regular grid, normalized to the AC-PC line, providing 1.650 possible source locations. The exact positions of all electrodes were measured for each subject individually (Zebris ultrasound system) and then mapped onto the surface of the T1 image based on three land marks (nasion, pre-auricular left, and pre-auricular right) and nineteen electrode positions. To identify neural sources underlying dimension-specific P1 and tN2 effects, individual CDRs were computed combined for the averaged data sets of all four experimental conditions (sDsR, sDdR, dDsR, and dDdR), for the time window of 0–400 ms relative to a -100 to 0-ms baseline. Source reconstructions were based on the LORETA algorithm (Pascual-Marqui & Biscay-Lirio, 1993) using the L2-Norm with temporal coupling (Darvas et al., 2001). By computing source activity for the four different experimental conditions in one combined computational step, activation strength of all data sets was standardized by the maximum source activation in one of the four conditions. In the second step, clusters of sources were computed using the implemented clustering algorithm. Here, the strength of each source was computed and local maxima for each point in the respective time range were determined. This was followed by the computation of a matrix representing the distances between all maxima separately for each subject and data set. Finally, all sources located within a distance of 30 mm were combined into one cluster. The time windows for clustering were based on the individual peak latencies of the respective ERP components (P1, tN2) in each condition (individual peaks ±10 ms), resulting in a mean location for the various clusters and mean source magnitude within a cluster.

Next, separate regions of interests (ROIs) were specified with regard to the respective ERP components. For the visual P1, ROIs were based on the perceptual target dimensions used in the present study: *visual area V4* (BA 19) for color processing and

visual area V2 (BA 18) for form processing. Evidence for the involvement of such early visual areas in visual dimension changes is provided by an fMRI study of Pollmann et al. (2000), who reported differential activation levels in dorsal occipital brain regions (BA 19) dependent on the previous target dimension. More specifically, dimension change-related effects were observed in visual areas V4 and V5, dependent on whether the target was defined in the color or the motion dimension. Moreover, an involvement of extrastriate areas within occipital cortex contributing to the P1 component is in strong agreement with the study of Martinez et al. (1999), who investigated neural sources underlying the P1 based on hemodynamic brain responses. This study revealed two phases associated with two separate brain regions underlying the visual evoked P1 component: one early phase of the P1 due to activations within dorsal extrastriate areas, and one slightly later phase originating from activations in ventral occipital regions. Thus, taking these previous findings into consideration, two ROIs were identified for the present P1 investigation: (1) ventral extrastriate areas (V2; BA 18) and (2) dorsal occipital regions (V4; BA 19). For the N2 component, one further ROI was specified based on a series of fMRI (Pollmann et al., 2000, 2006a, 2007) demonstrating increased activations within the left frontopolar cortex (BA 10) accompanying changes of the target-defining dimension (see also Pollmann et al., 2007).

All clusters were anatomically specified by means of Talairach and Tournoux coordinates using the Talairach demon software (http://ric.uthscsa.edu/projects/registration). For clusters in left frontopolar cortex, the mean activation strengths for each of the four experimental conditions were subjected to a repeated-measures ANOVA with the factors Dimension change (same vs. different dimension) and Position change (same vs. different position). This ANOVA was extended by the factor Hemisphere (left vs. right) for clusters in occipital cortex.

Results

Behavioral data

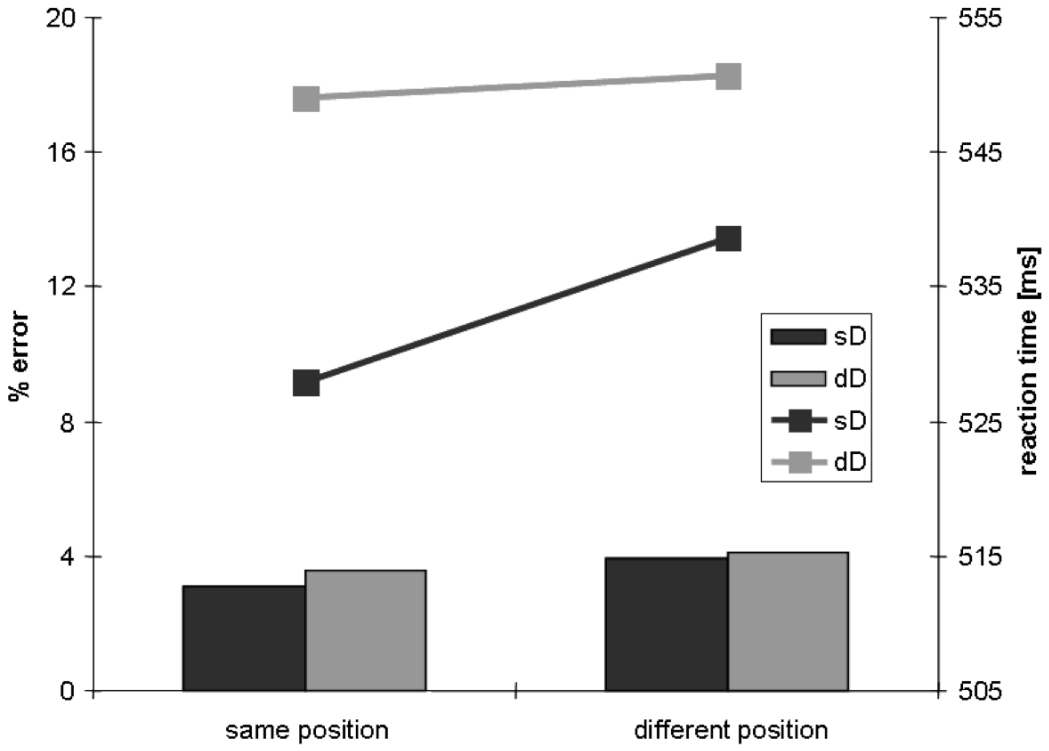

Figure 23. Reaction times as a function of dimension change and position change. Dark grey lines indicate dimension repetitions, light grey lines dimension changes.

Overall, subjects reacted incorrect on 3.7 % of all trials (sDsP 3.1%, sDdP 3.9%, dDsP 3.6%, and dDdP 4.1%), and on 3.2% of all trials subjects reacted faster than 100 ms or slower than 1000 ms (sDsP 2.7%, sDdP 3.2%, dDsP 3.1%, and dDdP 3.6%). A repeated-measures ANOVA of the error trials with the factors Dimension change and Position change failed to reveal any significant effects. RTs on correct trials were also analyzed by a Dimension change x Position change ANOVA, which revealed all effects to be significant [dimension change: $F(1,10)= 7.48$, $p<0.021$; $\eta 2 = 0.428$; position change: $F(1,10)= 6.22$, $p<0.032$; $\eta 2 = 0.383$; interaction: $F(1,10)= 5.40$, $p<0.042$; $\eta 2 = 0.351$]. As can be seen from Figure 23, subjects reacted fastest to targets defined in the same dimension and appearing at the same position as the preceding cue. The second fastest RTs were made to targets defined in the same dimension as the cue, but occurring at a different position. And the slowest RTs were found for targets defined in a different dimension to

the cue, regardless of whether they occurred at the same or at a different position ($p>0.933$).

Electrophysiology

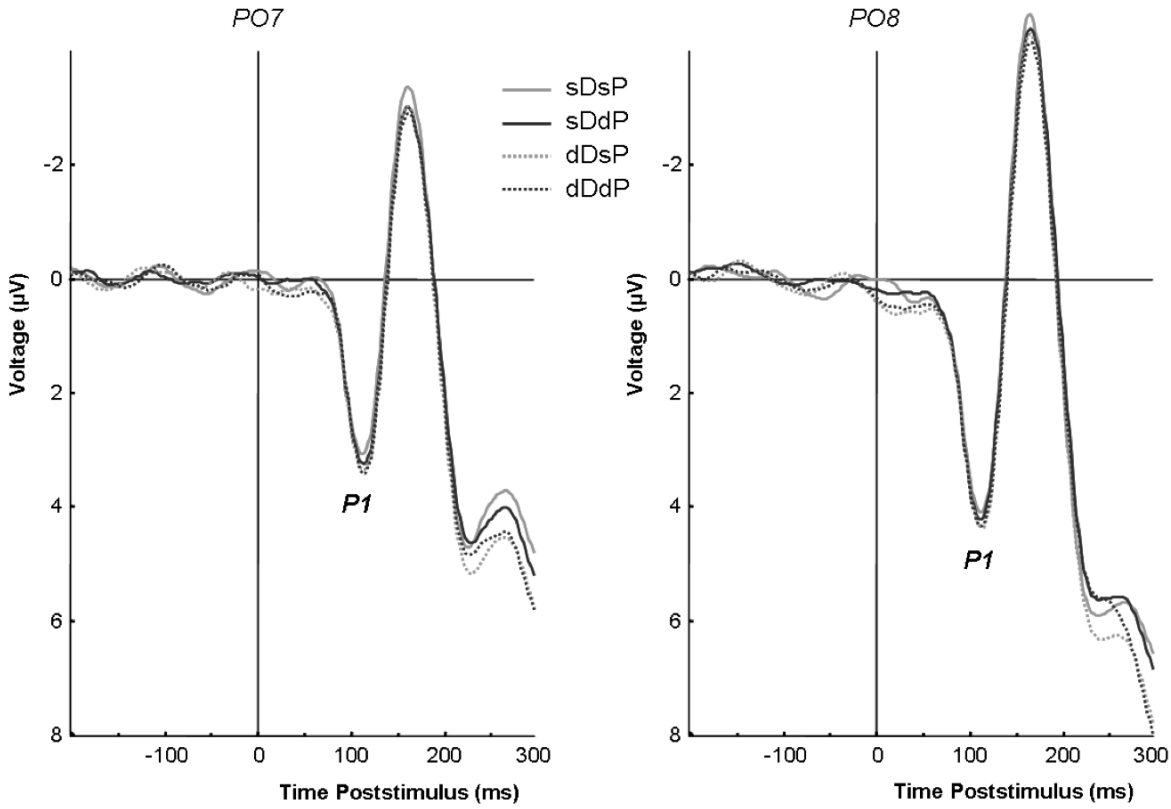

Figure 24. Grand-averaged ERP waveforms elicited over early visual areas at electrode positions PO7/PO8 in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate dimension repetitions, dotted lines dimension changes. Light grey lines indicate position repetitions, dark grey lines position changes.

P1. P1 amplitudes (see Figure 24) were significantly larger [$F(1,10)= 8.63$, $p<0.015$; $\eta2 = 0.463$] for dimension changes compared to repetitions (4.34 μV vs. 4.16 μV) – that is, the effect is reversed relative to Experiment 4. Furthermore, the two-way interaction between Position change and Hemifield [$F(1,10)= 14.06$, $p<0.004$; $\eta2 = 0.584$] as well as the three-way interaction between Position change, Hemifield, and Electrode Position [$F(1,10)= 24.91$, $p<0.001$; $\eta2 = 0.714$] were significant. The latter interaction was due to enhanced amplitudes for invalidly cued positions for left (but not right) hemifield targets, evident at left (but not right) electrode positions ($p<0.019$). Note that there was no

statistical validation of an interactive behavior between dimension changes and position changes (see Figure 25): the interaction between the two factors was not significant [$F(1,10)= 2.69$, $p<0.132$; $\eta 2 = 0.212$]. No effects were obtained for the P1 latencies.

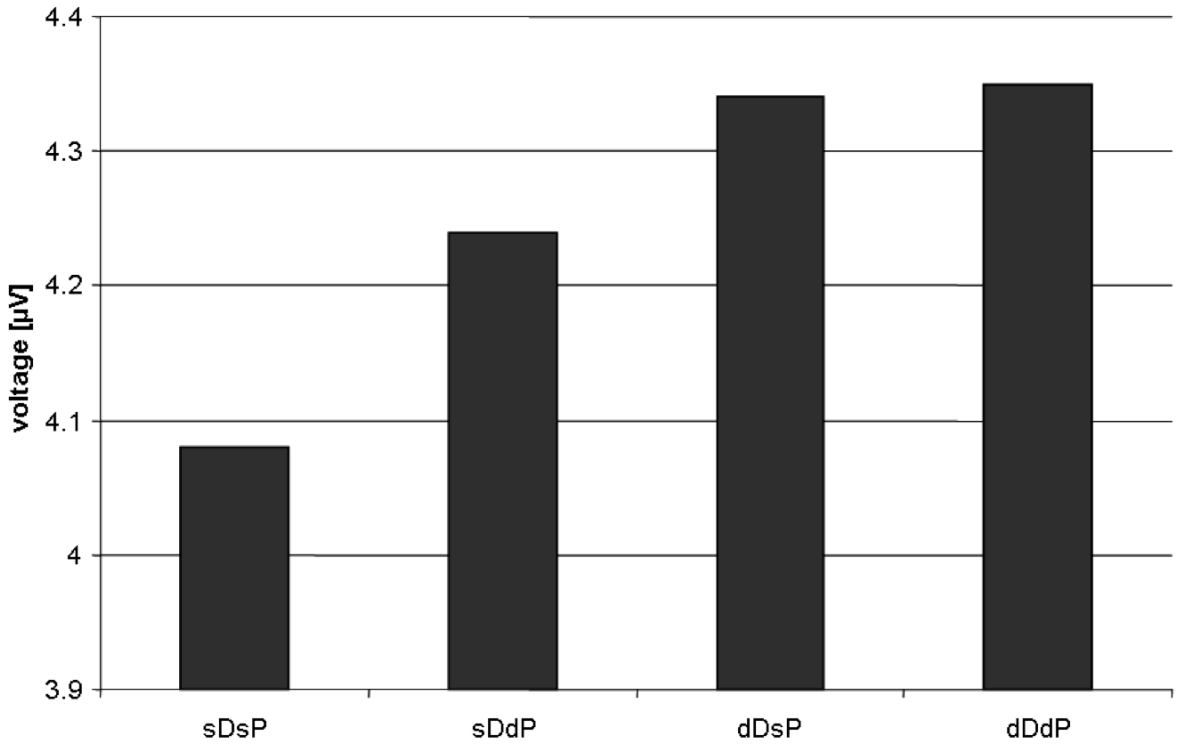

Figure 25. Mean P1 peak amplitudes elicited at PO7/PO8 in response to the target display dependent on the identity of the singleton in the cueing display: same-dimension same-position (sF), same-dimension different-position (dF), different-dimension same-position (dD), and different-dimension different-position.

N2. For the N2 amplitudes (see Figure 26), a significant interaction between Dimension change and Electrode Position was revealed [$F(2,20)= 6.25$, $p<0.008$; $\eta 2 = 0.385$]. This interaction was due to enhanced amplitudes associated with dimension change compared to repetition trials, while dD-trial amplitudes were further increased at midline compared to lateral electrode positions ($p<.004$). N2 latencies were affected by Position change interacting with Electrode Site [$F(2,20)= 4.62$, $p<0.022$; $\eta 2 = 0.316$] as well as with Electrode Position and Electrode Site [$F(4,40)= 2.82$, $p<0.037$; $\eta 2 = 0.220$]. As revealed by further analyses, N2 latencies peaked earlier at midline and right frontal electrodes (Fz and F4; $p<.004$) when the position of the target singleton was the same (rather than different) compared to the cue display.

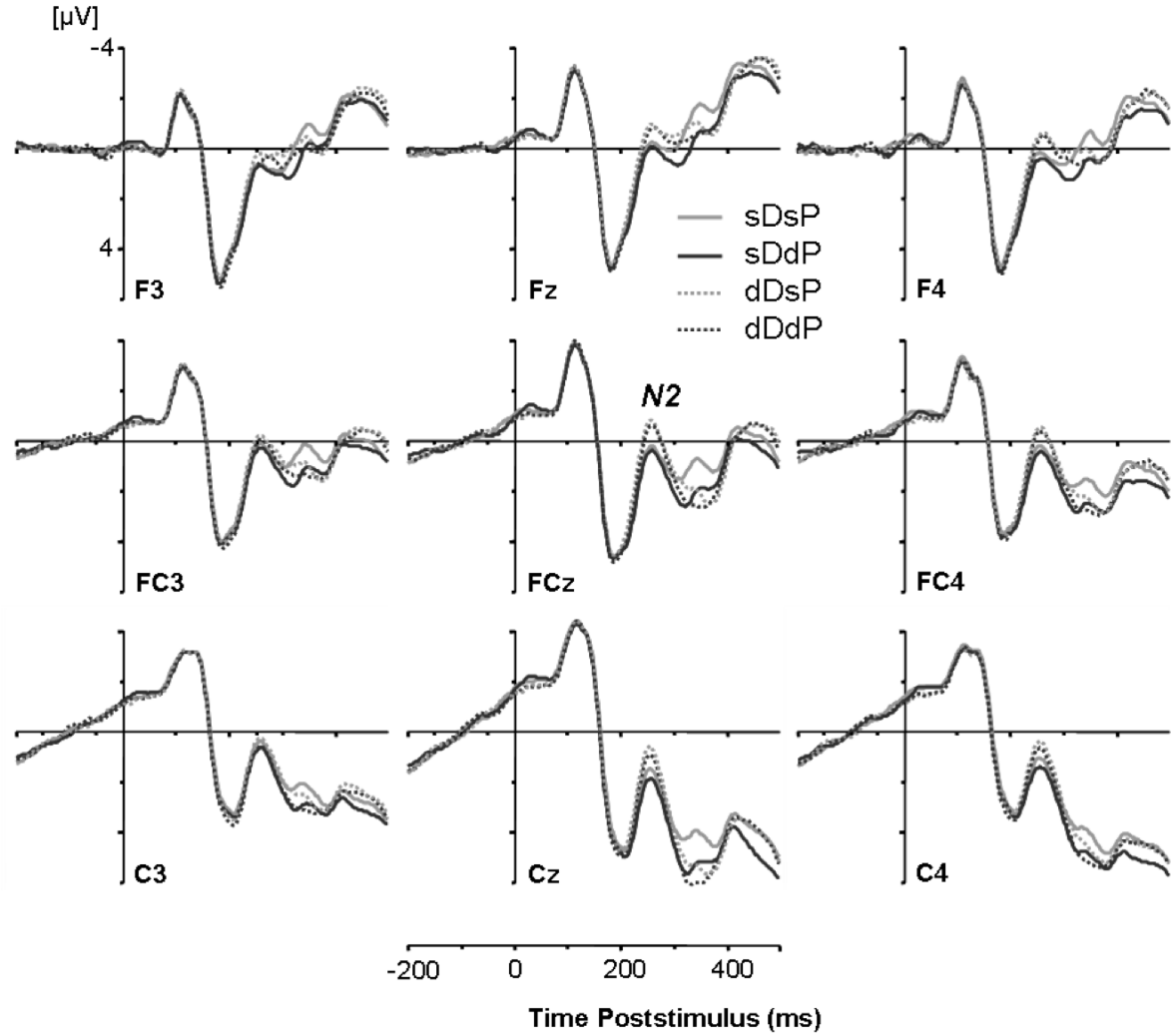

Figure 26. Grand-averaged ERP waveforms elicited over fronto-central electrode positions in the 500-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate dimension repetitions, dotted lines dimension changes. Light grey lines indicate position repetitions, dark grey lines position changes.

Current Density Reconstruction

In accordance with the pre-specified regions of interests, the reconstruction of current density revealed clusters within brain areas roughly corresponding to the left medial frontal gyrus (BA 10), the left and right inferior occipital gyrus (BA 18), and the left and right superior occipital gyrus (BA 19). The respective Talairach-coordinates (averaged across subjects) are displayed in Table 3.

Regions	x	y	z	Brodman Area	Mean Strength	Participants
Left inferior occipital gyrus	-37	-92	-1	BA 18	2.68	11/11
Right inferior occipital gyrus	37	-92	-4	BA 18	1.93	11/11
Left superior occipital gyrus	-30	-89	34	BA 19	2.60	11/11
Right superior occipital gyrus	32	-92	31	BA 19	3.17	11/11
Left medial frontal gyrus	-21	47	12	BA 10	1.28	10/11

Table 3: Brain areas associated with visual dimension changes, based on stCDR. Displayed coordinates (x,y,z) represent mean values averaged across subjects. Cluster mean strengths are represented in $\mu A/m^2$.

Posterior activations. Clusters (Figure 27) identified bilaterally in superior occipital gyrus (BA 19) were activated more strongly following cue-to-target dimension changes compared to repetitions. This was statistically validated by the significant main effect of Dimension change [$F(1,10)= 5.32$, $p<0.044$; $\eta 2 = 0.347$]. The absence of further effects/interactions indicates that the dimension change effect occurred independently of spatial stimulus characteristics.

Nearly an identical activation pattern was observed for the clusters identified bilaterally in inferior occipital gyrus (BA 18). However, the ANOVA failed to reveal significant effects/interactions and, thus, to statistically validate the numerical tendency for stronger activations caused by cue-to-target dimension changes in this area [$F(1,10)= 2.88$, $p>0.12$; $\eta 2 = 0.224$].

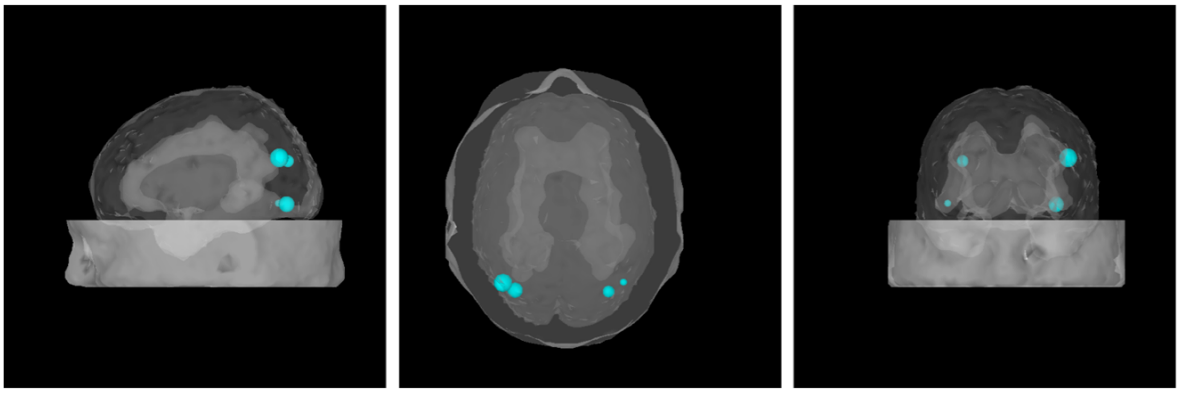

Figure 27. Grand-averaged source activity bilateral within inferior occipital gyrus (BA 18) and superior occipital gyrus (BA 19), based on the time range of the visual evoked P1 component.

Frontal activations. Activation within a left frontopolar cluster (see Figure 28) accompanying dimension changes was identified for all but one subject. Thus, statistical analyses of source activations were based on the remaining subjects using a repeated-measure ANOVA with the factors Dimension change and Position change. This ANOVA revealed a main effect of Dimension change [$F(1,9)= 7.16$, $p<0.025$; $\eta 2 = 0.443$], with stronger source activations for changes, relative to repetitions, of the singleton-defining dimension between the cue and the target display. No significant differences were revealed involving the factor Position change [main effect: $F(1,9)= 1.05$, $p>0.333$; $\eta 2 = 0.104$; interaction: $F(1,9)= 1.18$, $p>0306$; $\eta 2 = 0.116$], confirming that this effect was based solely on changes of the visual dimension.

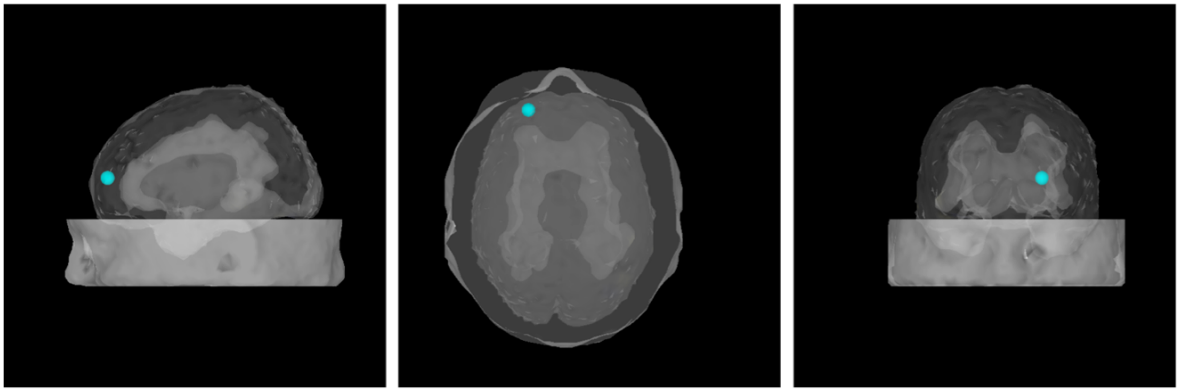

Figure 28. Grand-averaged source activity within left frontopolar cortex (BA 10), based on the time range of the N2 component.

Discussion

In Experiment 5, the cue provided no information as to the dimension or location of the upcoming target. Using this experimental design, it was possible to determine whether and how processes concerned with spatial and non-spatial stimulus attributes might interact in order to detect the target and explicitly discriminate its defining dimension. Moreover, the results were expected to provide insight into the hierarchy of dimensional and positional influences on visual selection. The behavioral data clearly suggest an interactive behavior of both factors: subjects responded fastest when the target singleton was validly pre-cued with respect to its defining dimension, with additional benefits when it was validly cued with respect to its position. By contrast, RTs were prolonged for invalidly cued target dimensions, irrespective of whether or not the target position was validly pre-cued.

At variance with this behavioral finding and with the initial predictions is the pattern observed for the visual evoked P1 component. In Experiment 4, systematic enhancements of P1 amplitudes were based solely on the dimensional identity of the preceding cue – suggesting that, if the upcoming target position is known in advance, early visual processing is affected by the dimensional nature of the target. Systematic dimension-based P1 modulations were also evident in Experiment 5 – however, the direction of the effect was reversed compared to Experiment 4, with reduced amplitudes elicited in response to validly cued target dimensions.

A reduction of P1-amplitudes to validly cued target locations can be observed in studies investigating inhibition of return (IOR). In these studies a facilitation of manual responses and more positive going P1-amplitudes are demonstrated when the interval between cue and target (i.e., stimulus onset asynchrony, SAO) is short (below 200 ms), whereas this effect is reversed to prolonged RTs and a suppression of P1-amplitudes with longer SOAs. A suppression of P1-amplitudes with long SOAs is assumed to reflect a suppression of sensory-perceptual processing at cued locations improving search performance by keeping attention from returning to already scanned irrelevant information (McDonald, Ward & Kiehl, 1999). The SOA used in the present Experiments lies in the range that is typically associated with IOR for discrimination tasks (Klein, 2000; Van der Lubbe et al., 2005). Thus, reduced P1-amplitues for validly cued targets observed in the present study might indicate inhibitory sensory-perceptual processes. Importantly, the strongest suppression of P1-amplitudes was associated with dimensional attributes but not the position of the cue. Thus, P1 suppression for validly cued targets in the present study would indicate that the inhibition of sensory-perceptual processes would be primarily related to the dimensional identity of the cue, rather than to it's location. However, this interpretation of the electrophysiological results is not substantiated by performance measures, i.e., there was no inhibition observed for RTs.

However, several investigations draw a complex picture regarding IOR effects revealing several factors like the nature of the task (detection vs. discrimination, e.g., Klein, 2000; Lupianez, Milan, Tornay, Madrid & Tuleda, 1997; Van der Lubbe, Vogel & Postma, 2005), the duration of the cue (transient vs. sustained, e.g., Eimer, 1994a; Wascher & Tipper, 2004), and the kind of cue (onset vs. offset, e.g., Hopfinger & Mangun, 1998) to have an impact on P1 amplitudes. More important, some studies reported significant P1 suppression when no behavioural evidence for inhibition was observed (Eimer, 1994a,

1994b; Wascher & Tipper, 2004). Thus, the observed suppression of P1-amplitudes in Experiment 5 might be related to inhibitory processes even in the absence of inhibition of return on the level of performance measures.

As compared to the standard IOR paradigm, the present Experiment used a discrimination task with two target dimensions and six possible target locations. Therefore, visual search was conducted under high uncertainty regarding the dimensional and positional nature of the upcoming target. One tentative (post-hoc) explanation for the observed P1-amplitude patterns might be that dimensional weighting of the cued dimension with exogenous cues leads to an inhibition of sensory-perceptual processing when the SOA is sufficiently long (in the case of discrimination tasks, see Van der Lubbe et al., 2005).

Amplitudes of the tN2 exactly replicated the pattern observed in Experiment 4. Enhanced peak amplitudes were evident when the cue and target displays contained singletons defined within different (rather than the same) dimension. This tN2 effect occurred irrespective of position changes/repetitions of the singleton, that is, it is based solely on dimensional, and not spatial, stimulus attributes.

Spatiotemporal Current Density Reconstructions revealed an influence of dimensional, but not spatial, stimulus attributes on source activations in the pre-specified areas. Enhanced N2 amplitudes were accompanied by increased activations within left frontopolar cortex (BA 10), while enlarged P1 amplitudes were accompanied by increased source activations in dorsal occipital regions (BA 19). In addition, the stCDR confirmed a second (pre-specified) source within inferior occipital regions (BA 18) as contributing to the P1 component. Note that, although the activation strength of this source only tended to depend on dimensional stimulus characteristics, the reconstruction of these two brain areas contributing to the visual P1 component is consistent with the pattern described by Martinez et al. (1999), who observed similar regions to be involved in the generation of P1 activation based on hemodynamic brain responses. However, the present stCDR selectively focused on pre-specified ROIs to gain further insights into the sources of brain activity accompanying dimension-based attention. Thus, it is likely that additional sources that were not analyzed in the present investigation are contributing to the P1 and N2.

General Discussion

The aim of the present study was to identify electro-cortical parameters associated with dimensional cueing effects. Behaviorally, such effects are manifested in faster RTs to targets defined in the same, as compared to a different, visual dimension as the cue (Müller et al., 2003). Experiment 4 showed that, when the upcoming target location is known in advance, dimensional information has a significant influence on early visual evoked potentials. The fact that this effect was independent of intra-dimensional feature changes is in accordance with dimension-based theories of visual attention, such as the DWA. Experiment 5 showed that, if the dimension *and* location of the upcoming target are unpredictable, RTs are further modulated by spatial stimulus attributes: RTs were fastest when the singleton's dimension *and* position remained constant from the cue to the target display; this was followed by RTs to targets defined in the same dimension as the cue, but occurring at a different position; and the slowest RTs were observed when the singleton's dimension changed from the cue to the target display (and this was independent of whether or not its position changed). These predominantly dimension-based RT effects, demonstrated by both experiments, were accompanied by systematic dimension-based modulations of P1 and N2 amplitudes as well as activation strengths of neural sources involved in the generation of the P1 and N2 components.

Electro-cortical activations of dimensional cueing

The main question examined in the present study was whether early visual processing stages can be modulated by non-spatial, in particular: dimensional stimulus attributes. To address this question, the visual evoked P1 component was analyzed. In line with the finding of enhanced visual P1 amplitudes for validly, as compared to invalidly, cued target positions, the P1 has traditionally been regarded as reflecting attentional modulation of early visual processing based solely on spatial stimulus attributes. Specifically, the spatial-attentional P1 modulation has been interpreted in terms of a 'sensory gain' mechanism which enhances early perceptual coding, in extrastriate ventral and dorsal occipital brain regions, for an attended stimulus location (Eimer, 1994; Luck et al., 2000; Martinez et al., 1999).

The present results have important implications for the interpretation of the early visual evoked P1 component, since both experiments revealed systematic dimension-based (cueing) modulations of this component. However, the pattern of dimension-based effects

varied across experiments. With matching positions of the cue and target singletons (Experiment 4), peak P1 amplitudes were enhanced for targets defined in the *same* dimension as the cue, and this enhancement was independent of whether or not the target-defining feature was the same as that of the cue. In contrast, when the positions of the cue and the target were varied independently (Experiment 5), peak P1 amplitudes were enhanced for targets defined in a *different* dimension to the cue, and this enhancement was independent of whether the target position was the same or different relative to the cue position. The only difference between the two experiments was the predictability of the upcoming target location.

The results of Experiment 4 may be interpreted along the lines of the DWA. Enhanced amplitudes might reflect the *weighting* of early visual input modules, facilitating the sensory coding of attributes singling out the target amongst the nontargets. That is, when the cue appears in one dimension, say color, attentional weight resources are allocated to this dimension, thus enhancing the saliency of all kinds of singleton defined in the same dimension (whether or not they featurally match the cue). Note that there was no obvious strategic reason to weight color over the shape dimension, since the cue predicted the upcoming target dimension only at chance level. This points to the largely implicit nature of the processes determining the allocation of attentional weight resources in Experiment 4.

The reversed direction of the dimension-based P1-amplitude effect in Experiment 5 suggests that, with both positional and dimensional uncertainty, the early visual processing system might suppress the processing of already scanned information (i.e., dimension and position) to improve search performance (Klein & McInnes, 1999). Thus, inhibition of the cued dimension would lead to the suppression of P1-amplitudes for validly cued dimensions as observed in Experiment 5. The absence of P1-amplitude suppression in Experiment 4 can be explained by the absence of any changes for cue and target positions. Since the target position was always validly cued, attention could dwell continuously on the exogenous cued location leading to maintained excitation and thus, enhanced P1-amplitudes for validly cued dimensions. Thus, if there is no need to re-orient to improve target detection at other possible target positions no IOR is observed.

Whatever the exact explanation of this reversed pattern of P1 amplitude effects, the general observation in two separate experiments is that the early visual P1 component is dependent on the dimensional nature of the previous sensory event. Furthermore,

Experiment 5 showed that, when the position of the target is unpredictable as well as its defining dimension, P1 amplitudes are modulated primarily by the dimensional identity of the previous sensory event. This suggests that the early visual system, although both factors were entirely non-predictive, uses dimensional information in order to optimize target detection, which further underscores the implicit nature of dimensional weighting processes. Taken together, the present results have implications for traditional interpretations of the early visual P1 component: they do demonstrate that this component is influenced by non-spatial, in particular: dimension-based coding processes – as well as by space-based processes.

In addition, dimensional cueing was found to influence the amplitude of the N2 component, with the strongest modulation observed over fronto-central electrode positions. This tN2 effect occurred irrespective of intra-dimensional feature changes/repetitions (Experiment 4) and positional changes/repetitions (Experiment 5) of the target relative to the cue – demonstrating that the enlarged amplitudes of the tN2 originate from processes purely related with the (change in the) dimensional identity of the target relative to that of the cue, similar to visual P1 component. The tN2 pattern observed in the present study exactly matches that observed in Chapter II – suggesting that similar *control* processes are associated with visual dimension weighting in cross-dimensional cueing and in cross-dimensional search tasks.

Neural sources of dimensional cueing

To gain further information about the brain regions involved in the generation of the dimension-specific cueing effects on the P1 and N2 components, source reconstruction was applied based on the high-density recordings in Experiment 5. In line with previous fMRI studies of dimension weighting (Pollmann et al., 2006; Pollmann et al., 2000), the source reconstruction confirmed that a region within left medial frontal gyrus (BA 10) contributed to the surface N2 component, whereas sources contributing to the visual P1 component were localized within inferior occipital gyrus (BA 18) and superior occipital gyrus (BA 19). The reconstruction of two different sources within the inferior and superior occipital cortex associated with the visual evoked P1 component is in line with Martinez et al. (1999), providing further support for an involvement of these brain regions in generating the visual P1. Furthermore, the activation strengths of left frontopolar and dorsal occipital sources were revealed to depend on the dimension, but not position, of the

previous sensory (cue) event, suggesting that non-spatial, rather than spatial, processes are involved in the elicitation of the P1 and N2 components. Stronger source activations were evident for conditions in which the critical visual dimension was changed (vs. repeated), a pattern which exactly mirrors the amplitude variations observed for the P1 and N2 components. This indicates a prominent role of these brain regions for eliciting dimension-specific ERP cueing effects in the present paradigm.

Taken together, the present findings provide further evidence for the dimension-specific nature of weighting mechanisms as proposed by the DWA, based on ERP and source reconstruction analyses. The close resemblance of source locations in the present study with the results from imaging studies (Pollmann et al., 2000, 2006b) further underlines the notion of left frontopolar regions being engaged in the control of attentional weight setting (see also Pollmann et al., 2007), which modulate sensory coding of relevant (non-spatial) stimulus attributes in dorsal occipital regions.

CHAPTER V

The anterior N1 component as an index of modality shifting

Abstract

Processing of a given target is facilitated when it is defined within the same (e.g., visual-visual), compared to a different (e.g., tactile-visual), perceptual modality as on the previous trial (Spence et al., 2001). The present study was designed to identify electro-cortical (EEG) correlates underlying this 'modality shift effect'. Participants had to discriminate (via foot pedal responses) the modality of the target stimulus, visual versus tactile (Experiment 6), or respond based on the target-defining features (Experiment 7). Thus, modality changes were associated with response changes in Experiment 6, but dissociated in Experiment 7. Both experiments confirmed previous behavioral findings with slower discrimination times for modality change, relative to repetition, trials. Independently of the target-defining modality, spatial stimulus characteristics, and the motor response, this effect was mirrored by enhanced amplitudes of the anterior N1 component. These findings are explained in terms of a generalized 'modality-weighting' account, which extends the 'dimension-weighting' account proposed by Müller et al. (1995) for the visual modality. On this account, the anterior N1 enhancement is assumed to reflect the detection of a modality change and initiation of the re-adjustment of attentional weight-setting from the old to the new target-defining modality in order to optimize target detection.

Introduction

In everyday life, we encounter numerous situations in which we have to direct attention selectively to a particular perceptual modality (e.g., visual, auditory, tactile) in order to acquire information necessary for achieving our current action goals. Whether we are *looking* for a book in the library, *listen* to a conversation at a cocktail party, or evaluate the surface texture of an object via *tactile* sensing, our brain employs some top-down perceptual set, or 'template' of the objects of interest, to guide the extraction of the relevant information. Interestingly, the guidance becomes even more efficient when we attend to the same modality (e.g., *touch*; Spence, Nicholls, & Driver, 2001) or to the same dimension (e.g., *color*; Found & Müller, 1996) within one modality on successive perceptual episodes. That is, how efficiently we select relevant information is also determined by what (e.g., which modality) was selected just before.[1]

Modality changes

It is well established that focusing on the same perceptual modality in successive trial episodes (e.g., tactile target on both the current trial *n* and the preceding trial *n-1*) facilitates performance, relative to when the modality changes across consecutive trials (e.g., tactile target on trial *n* preceded by visual target on trial *n-1*). A large number of studies have used different experimental paradigms to investigate these modality repetition/change effects in normal subjects (e.g., Spence, Nicholls, & Driver, 2001; Gondan, Lange, Rösler, & Röder, 2007; Rodway, 2005) as well as patients (e.g., Cohen & Rist, 1992; Verleger & Cohen, 1978; Manuzza, 1980, Hanewinkel & Ferstl, 1996). For example, Rodway (2005) used a cueing paradigm to investigate the efficiency of warning signals. He found that, for brief foreperiods, the warning signal (cue) was most efficient when it was presented within the same, rather than a different, modality to the subsequent target. Rodway concluded that the warning signal exogenously attracts attention to its modality, thereby facilitating responses to subsequent targets defined within the same modality. A similar pattern was observed by Spence and colleagues (2001) who examined the effect of modality expectancy in a task that required participants to judge the azimuth (left vs. right) of the target location in an unpredictable sequence of auditory, visual, and tactile targets. There were two types of trial blocks: biased blocks in which the majority of

[1] As Maljkovic and Nakayama (1994) have demonstrated, this influence is strongest immediately after a given trial and decreases gradually over the following five to eight trials.

targets (75%) was presented in one modality (participants were instructed to attend to this modality), and unbiased blocks in which the targets were equally likely to be defined in each modality (33%; participants were instructed to divide attention among the three modalities). With the majority of targets presented in one modality, Spence et al. observed prolonged RTs for targets defined within the unexpected compared to the expected modality. In trial blocks in which each target modality was equally likely, RT costs were observed for trials on which the modality changed relative to the preceding trial. In fact, such modality change costs were also evident in the biased trial blocks, accounting for almost all the benefits and for a large part of the costs in the 'expectancy' relative to the 'divided-attention' conditions.[2] Spence et al. interpreted this pattern of results in terms of a stimulus-driven 'modality shift effect'.

At the electrophysiological level, the effects accompanying modalities changes have been linked to processes that operate in a modality-unspecific fashion, as well as to modality-specific processes within sensory brain areas. As indicated by several studies examining the performance difference between (schizophrenia) patients and normal controls, the modality shift effect (MSE) seems to modulate the amplitudes of the P3 component. However, the direction of this P3 amplitude effect varied across experimental studies. While Levit et al. (1973) and Verleger and Cohen (1978) observed larger P3 amplitudes following modality changes relative to repetitions (in normal controls, but not in schizophrenics), the reversed effect has been reported by Rist and Cohen (1987). On the other hand, a recent study by Gondan and colleagues (2004) reported N1 amplitude modulations owing to modality shifts over modality-specific sensory areas. However, these MSE modulations varied depending on the respective modality. Specifically, when the stimulus modality changed across trials, auditory N1 amplitudes were found to be enlarged while the amplitudes of the visual N1 component were decreased.

While such modality repetition/change effects have been noted in the literature, there has been little systematic attempt to integrate these findings into a coherent theoretical framework. We propose that a model originally developed to account for dimension repetition/change effects within the visual (as well as the auditory) modality can be extended to account for the mechanisms underlying modality switch cost.

[2] This pattern is similar to the dimension cueing effects revealed for the visual modality (see Müller, Heller, & Ziegler, 1995, and Müller, Reimann, & Krummenacher, 2003).

'Dimension Weighting' as a Model of 'Modality Weighting'?

Similar to such modality change effects, sequential effects have also been reported in visual search for singleton feature targets, both when the target and distractor features were repeated or changed roles (e.g., Maljkovic & Nakayama, 1994) and when the target-defining dimension was repeated or changed across trials (e.g., Müller, Heller, & Ziegler, 1995; Found & Müller, 1996). In the latter case, the target could be defined by an odd-one-out feature within one of several possible dimensions (e.g., color, orientation), and participants were required to simply discern the presence (vs. the absence) of any target. Participants were faster to detect a target when the target-defining dimension remained the same on consecutive trials (e.g., a color-defined target on trial *n* following a color-defined target on trial *n-1*), compared to when the target-defining dimension changed (e.g., color-defined target on trial *n* following an orientation-defined target on trial *n-1*). Importantly, this effect of dimension repetition was largely unaffected by changes of the target feature (e.g., red target on trial *n*, blue target on trial *n-1*) within the repeated dimension (Found & Müller, 1996)[3].

To explain this set of findings, Müller and colleagues proposed a 'dimension-weighting' account (DWA; e.g., Müller et al., 1995; Found & Müller, 1996). Similar to visual-search theories such as Guided Search (e.g., Wolfe, 1994), the DWA assumes that focal (selective) attention operates at a master map of integrated (summed) feature contrast signals derived separately in dimension-specific input modules. Detection of a singleton target requires that sufficient attentional weight is allocated to the corresponding dimension-specific input module, effectively amplifying its feature contrast signal and rendering it salient on the master map. The dimensional weight pattern established on a trial persists into the next trial, facilitating the processing of any subsequent target (whatever its feature description) defined within the same visual dimension. However, when the next target is defined in a different dimension, the wrong dimension is weighted initially, delaying target detection. In this case, a process is initiated in which attentional weight is shifted from the old to the new target-defining dimension – as a prerequisite for target detection and/or as a post-selective adjustment process.

Recently, several studies have investigated the neural substrates of dimensional weighting using event-related potentials (ERP; Chapter II, III and VI of the present thesis)

[3] Similar effects have also been described for *discriminations* of the visual target dimension (e.g., color vs. orientation; Found & Müller, 1996) as well as for the auditory modality (e.g., Dyson & Quinlan, 2002).

and event-related functional magnetic resonance imaging (fMRI; Pollmann, 2004; Pollmann, Weidner, Müller, & von Cramon, 2000, 2006; Weidner, Pollmann, Müller, & von Cramon, 2002). In Chapter II, three components of the ERP were found to be associated with changes in the target-defining dimension on consecutive trials: dimension changes were associated with an enhanced (anterior) transition N2 (tN2), delayed P3 latencies, and enhanced slow wave (SW) amplitudes. As suggested in Chapter II, the systematic modulation of the tN2 might reflect the detection of a dimension change and the initiation of the re-setting of dimensional weights, whereas the P3 and SW seem to mediate the weight shifts via feedback pathways to dimension-specific input modules in higher-level visual areas. This pattern of ERP effects is in line with results from fMRI studies of Pollmann and colleagues (e.g., Pollmann et al., 2000; Weidner et al., 2002) identifying a fronto-posterior network to be sensitive to visual-dimension changes. Pollmann et al. (2006) concluded that prefrontal regions are the site of executive processes associated with the *control* of dimensional weight shifting (see also Pollmann, Mahn, Reimann, Weidner, Tittgemeyer, Preul, Müller, & von Cramon, 2007), while higher visual areas in superior parietal and temporal cortex mediate the weight shifts via feedback pathways to the dimension-specific input areas in occipital cortex.

Rationale of the present study

By analyzing ERPs, the present study aimed at identifying electro-cortical correlates that accompany modality switches independently of the current target modality and, thus, to provide further insights regarding the time course of behavioral modality shift effects. More specifically, it was examined whether an ERP component analogous to the tN2 component of Chapter II would be elicited as a consequence of modality changes across successive trial episodes. Recall that the tN2 component was previously found to be sensitive to visual-dimension changes, and thus interpreted as reflecting a process of weight shifting that operates within sensory (e.g., visual, auditory) modalities. The presence of a similar ERP component that is sensitive to changes in the target modality might reflect a *supramodal* process that controls attentional weight shifting across sensory modalities (for previous research into supramodal attentional control processes in spatial attention, see Farah, Wong, Monheit, & Morrow, 1989; Eimer & van Velzen, 2002). This would have important implications with respect to the scope of the DWA. As noted above, the tN2 was interpreted (Chapter II) to reflect the detection of a dimension change and the

initiation of the re-setting of dimensional (attentional) weights based on visual information. If the present study reveals an analogous component to reflect weight shifting across modalities, then a generalized '*weighting account*', with an extended functional architecture, could be proposed to account for modality switching effects observed in earlier behavioral studies.

Taken together, the aim of the present study was (i) to confirm earlier findings of prolonged RTs for changes, relative to repetitions, of the target-defining modality and (ii) to identify an electro-cortical correlate of this behavioral modality shift effect that is elicited independently of the current target modality.

EXPERIMENT 6

Method

Participants

Twelve paid volunteers (3 males; all right-handed; age range 21–35 years, mean age 27.9 years) recruited from the Birkbeck College subject panel gave their written informed consent to participate in the experiment. They all had normal or corrected-to-normal vision and reported having normal touch sensitivity. All were naïve as to the purpose of the study.

Stimuli and Apparatus

Participants were seated in a dimly lit and sound-attenuated experimental chamber. A 17" computer screen was placed centrally in front of the participant at a viewing distance of 55 cm. Tactile stimuli were presented using 5 mV solenoids, driving a metal rod with a blunt conical tip to the fingertip of the left and right index fingers. The index fingers were placed palm side down to the solenoids and were fixed using a Velcro strip. The rods made contact with the fingers whenever a current was passed through the solenoids. White noise was presented from a central loudspeaker (hidden behind the computer screen) throughout the experimental blocks to mask any sounds produced by the operation of the tactile stimulators. Visual stimuli were presented by illuminating a circular ensemble of seven green LEDs (i.e., 6 LEDs arranged around 1 central LED). The angular size of each LED was 0.65°, and the circle diameter was 2.4° of visual angle. A white fixation cross against a black background was presented centrally at the bottom of the computer screen throughout the experimental blocks. Two tactile stimulators were

positioned together with two visual stimulators 15 cm apart, 7.5 cm to either side to the fixation cross, and 50 cm from the edge of the table (from the participant's perspective) directly in front of the computer screen. The LED ensembles were attached to the computer screen positioned 1 cm directly above the tactile stimulators. Tactile stimuli consisted of one rod contacting a finger for 200 ms, visual stimuli consisted of the illumination of one LED ensemble for 200 ms. To give a response, participants had to press either the left or the right foot pedal placed on the floor. The exact position of the footpedals was adjusted for each participant individually to ensure a comfortable seating position.

Procedure

The experiment comprised 20 experimental blocks of 72 trials each. Trials started with the presentation of the fixation cross for 500 ms, followed by either a visual or a tactile stimulus for 200 ms. The trial was terminated by the participant's response or after a maximum duration of 1000 ms. The intertrial interval was 1000 ± 50 ms. On each trial, a single stimulus, either visual or tactile, was presented at one of the two possible stimulus locations. Participants were instructed to maintain eye fixation throughout the experimental block and to give a speeded forced-choice response indicating the modality of the stimulus. Half the participants responded with their left foot to visual stimuli and with their right foot to tactile stimuli, with the stimulus-response mapping changed after the first half of the experiment. For the other participants, the stimulus-response assignment was reversed. No feedback was given as to the correctness of the response. Visual and tactile stimuli were equally likely, and they were equally likely presented to the left and the right. To further examine whether effects of modality changes might interact with the positional identity of the stimulus, all behavioral and electrophysiological data were analyzed with respect to the target modality and target position on the current trial *n* relative to preceding trial *n-1*, resulting in four intertrial transition conditions: same modality – same position (sMsP), same modality – different position (sMdP), different modality – same position (dMsP), different modality – different position (dMdP). Prior to the start of each experimental half, participants performed at least one practice block.

Note that the presentation of only a single (lateral) stimulus in the present paradigm differs from previous studies investigating the DWA, which used visual-search tasks with a singleton target presented amongst a set of distracter stimuli. However, dimensional

intertrial repetition/change effects are also found when the display contains only a single target defined in one of several visual dimensions (Mortier, Starrefeld, & Theeuwes, 2005; see also Müller & O'Grady, 2000). Consequently, it was reasonable to expect modality repetition/change effects under the stimulus conditions employed in the present study.

EEG recording and data analysis

The Electroencephalogram (EEG) was recorded using Ag-AgCl electrodes mounted on an elastic cap (Falk Minow Service, Munich), referenced to linked earlobes. Electrode positions were a subset of the international 10/10 system sites (FPz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3 Pz, P4, P8, PO7, PO3, PO4, PO8, O1, Oz, and O2). The horizontal electrooculogram (HEOG) was recorded from the outer canthi of both eyes. Data were recorded with BrainAmp amplifiers (Brain Products, Munich; Germany), using an analog bandpass from 0.1 to 40 Hz and a digitization rate of 500 Hz. All electrode impedances were kept below 5 kΩ.

Prior to epoching the EEG, an independent-component analysis, as implemented in the Brain Vision Analyzer (Brain Products) software, was performed to identify and eliminate blinks and horizontal eye movements. EEG data were epoched off-line into 1200-ms periods with a 200-ms pre-stimulus baseline. Note that only trials with correct responses on both the current and the preceding trial were selected for further analyses. The pre-stimulus period was used for baseline correction. Trials with signals exceeding ± 60 μV were excluded from further analysis before the ERPs were averaged.

According to the DWA, processes associated with the control of (dimensional) attentional weighting are characterized as pre-attentive in locus (e.g., Müller & Krummenacher, 2006). Therefore, we focused on early ERP components (*P1*, *N1*, *N2*) as potential markers for modality shifts irrespective of the target's modality. Mean amplitudes of these components were derived from visual inspection of the grand-average potentials (see Table 4) and examined using repeated-measures ANOVAs, with the factors Modality change (same vs. different modality), Position change (same vs. different position), Electrode site (frontal, central, parietal), and Electrode position (left, midline, right), separately for each modality. These analyses were conducted for electrodes F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4. Further analyses were conducted for early modality-specific ERP components (somatosensory *P50* [45-75ms] and *N90* [85-115ms] at electrodes C3/C4 contralateral to the stimulated hand; visual *P1* [100-130ms] and *N1* [150-180ms] at lateral

occipital sites PO7/PO8) in order to investigate modality-specific modulations over early sensory areas that might additionally contribute to behavioral modality switch costs. Mean amplitudes of the early modality-specific ERP components were analyzed using repeated-measures ANOVAs, with the factors Modality change, Position change, Stimulus side (left vs. right), and Electrode position (left vs. right). Since the experiment focused on the neural mechanisms underlying modality shifting, only main effects and interactions involving the factor 'Modality change' will be reported for the electrophysiological data. Whenever required, significant main effects and interactions were further examined using Tukey HSD post-hoc contrasts.

Component	Mean time window	Recording site (left, midline, right)
somatosensory P1	80 – 120 ms	frontal, central, parietal
somatosensory N1	140 – 180 ms	frontal, central, parietal
somatosensory N2	215 – 255 ms	frontal, central, parietal
visual P1	70 – 110 ms	frontal, central, parietal
visual N1	140 – 180 ms	frontal, central, parietal
visual N2	230 – 270 ms	frontal, central, parietal

Table 4. Time windows for calculating mean amplitudes for all modality-unspecific ERP component examined in Experiment 6.

Results

Behavioral data

Trials on which participants responded incorrectly (4.93% of all trials), on which the RT was excessively slow (>1000 ms; 1.36% of all trials), and for which the response on the preceding trial was incorrect (4.35% of all trials) were excluded from further RT analysis (10.65% of all trials in total). Figure 29 displays the error rates and RTs (for the remaining trials), for each of the four intertrial conditions. A repeated-measures ANOVA of the RT data, with the factors Modality (visual, tactile), Modality change (same vs. different modality), and Position change (same vs. different position), revealed a main effect of Modality change [$F(1,11) = 30.33$, $p<.001$, $\eta^2 = .734$], with markedly slower reactions for modality changes compared to repetitions (511 vs. 461 ms). Furthermore,

there was a main effect of Position change [$F(1,11) = 10.48$, $p<.008$, $\eta^2 = .488$], with slower reactions for position changes relative to repetitions (490 vs. 481 ms). The modality change x position change interaction was also significant [$F(1,11) = 75.97$, $p<.001$, $\eta^2 = .874$]. This interaction was due to an increased RT advantage for modality repetition (as compared to change) trials when the target position was also repeated (as compared to changing); in contrast, with modality changes, RTs were faster when the position was also changed. Post-hoc contrasts confirmed that RTs were significantly different between all four experimental conditions ($p<.001$).

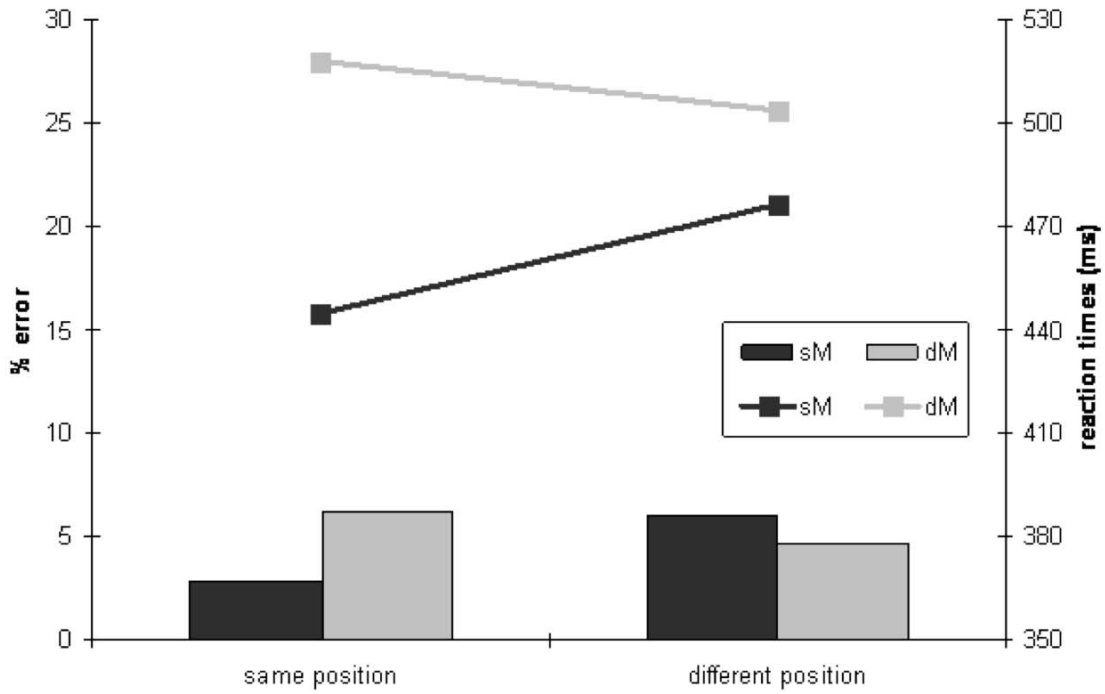

Figure 29. Reaction times (lines) and error rates (bars) as a function of Modality change and Position change (sM = same modality; dM = different modality)

An analogous ANOVA on the error rates revealed the main effects of modality [$F(1,11) = 11.12$, $p<.007$, $\eta^2 = .503$] and position change [$F(1,11) = 7.82$, $p<.017$, $\eta^2 = .416$] to be significant, with slightly fewer errors in response to visual as compared to tactile stimuli (4.2% vs. 5.6%) and for repetitions as compared changes in the stimulus position (4.5% vs. 5.4%). The interaction between modality change and position change

was also significant [$F(1,11) = 18.57$, $p<.001$, $\eta^2 = .658$]. As can be seen from Figure 29, this interaction was due to fewer errors being made for modality repetition (compared to change) trials when the position was repeated, relative to being changed. The reversed pattern was observed for modality change trials. This pattern of effects indicates that RT effects were not confounded by speed-accuracy trade-offs.

Effects on somatosensory ERPs

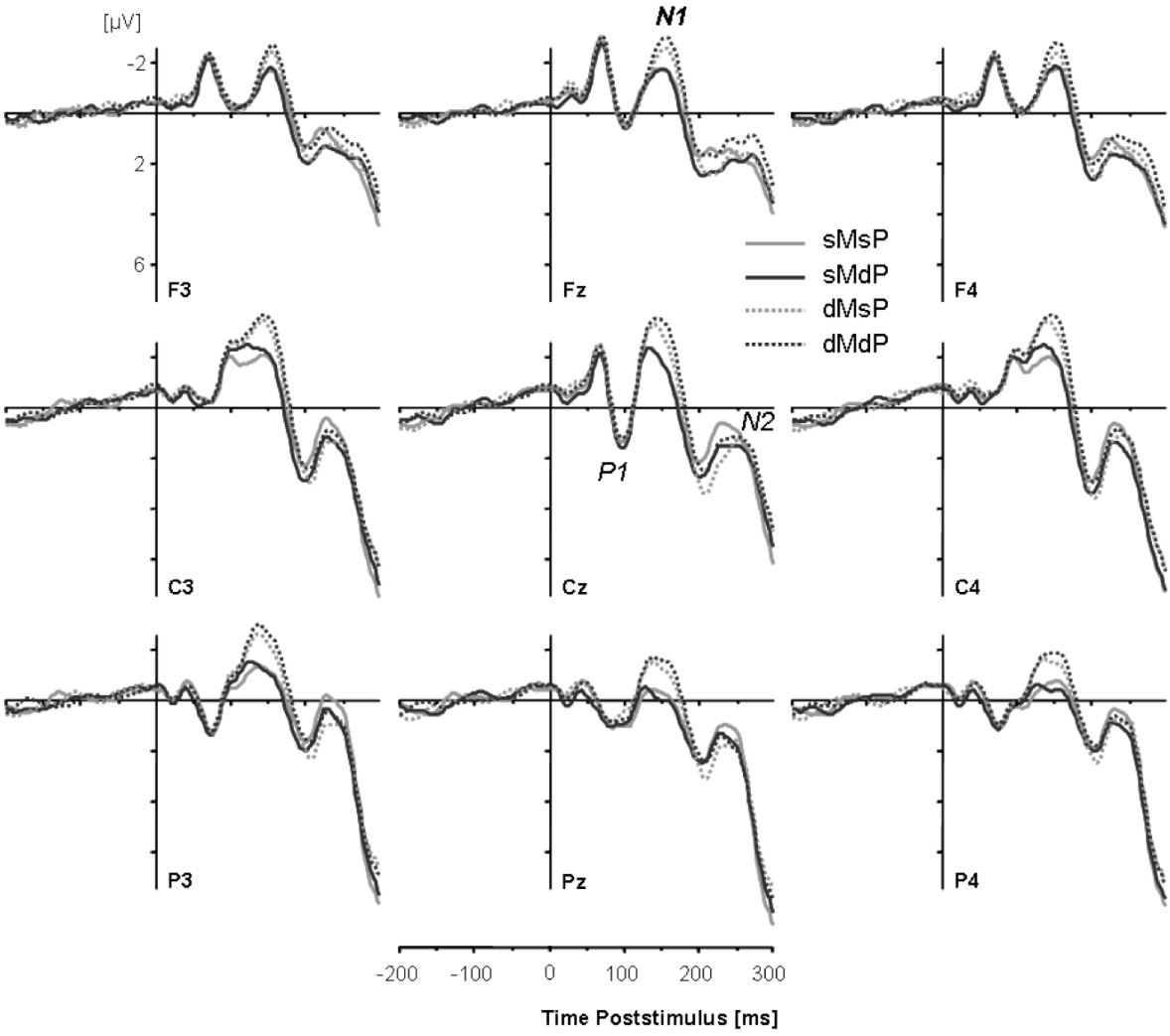

Figure 30A. Grand-averaged ERP waveforms elicited in response to somatosensory stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate position repetitions, dark grey lines position changes.

ERPs elicited in response to somatosensory stimuli are presented in Figure 30A, separately for each of the four experimental conditions. No main effects of any of the experimental variables were observed for the P1 amplitudes. Although a moderately significant three-way interaction between Modality change, Position change, and Electrode site [$F(2,22) = 3.85$, $p<.037$, $\eta^2 = .259$] was observed for P1 amplitudes, this was not further substantiated by reliable main effects or interactions in follow-up analyses conducted separately for different electrode sites.

As can be seen from Figure 30A, modality changes were associated with enhanced amplitudes of the N1 component in the 140–180-ms time window[4], validated by a significant main effect of Modality change [$F(1,11) = 10.82$, $p<.007$, $\eta^2 = .496$]. There was no significant main effect of Position change [$F(1,11) = 0.45$] and no modality change x position change interaction [$F(1,11) = 1.49$], demonstrating that this N1 modulation was solely linked to changes versus repetitions of the target modality. No effects involving Modality change were observed for N2 amplitudes.

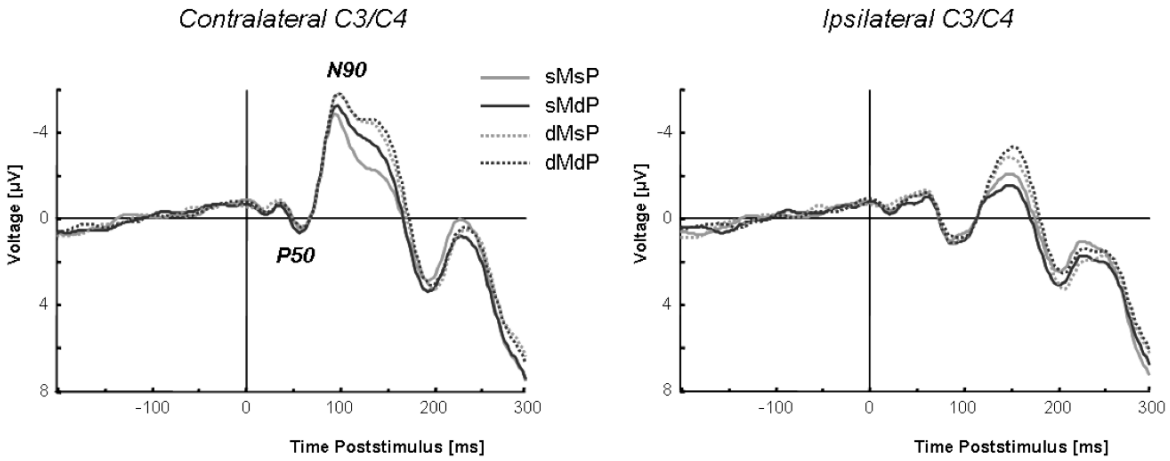

Figure 30B. Grand-averaged ERP waveforms elicited over modality-specific sensory areas at electrode positions C3/C4 by tactile stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate position repetitions, dark grey lines position changes.

Figure 30B shows somatosensory ERPs as a function of Modality change x Position change at electrodes C3/C4. As expected, the early somatosensory P50 and N90

[4] This component is often also referred to as N140 in the somatosensory ERP literature. We describe this component here as N1 in order to highlight the similarities of ERP modality shift effects across touch and vision.

components were only elicited contralaterally to the stimulated hand. While there was no significant effect of Modality change on P50 amplitudes, the subsequent N90 was enhanced for modality change trials, substantiated by a significant main effect of Modality change [$F(1,11) = 9.57$, $p<.010$, $\eta^2 = .465$]. Again, there was no interaction between Modality change and Position change [$F(1,11) = 1.22$], demonstrating that this early effect of Modality change is independent of changes versus repetitions of stimulus locations (see also Figure 30A).

Effects on visual ERPs

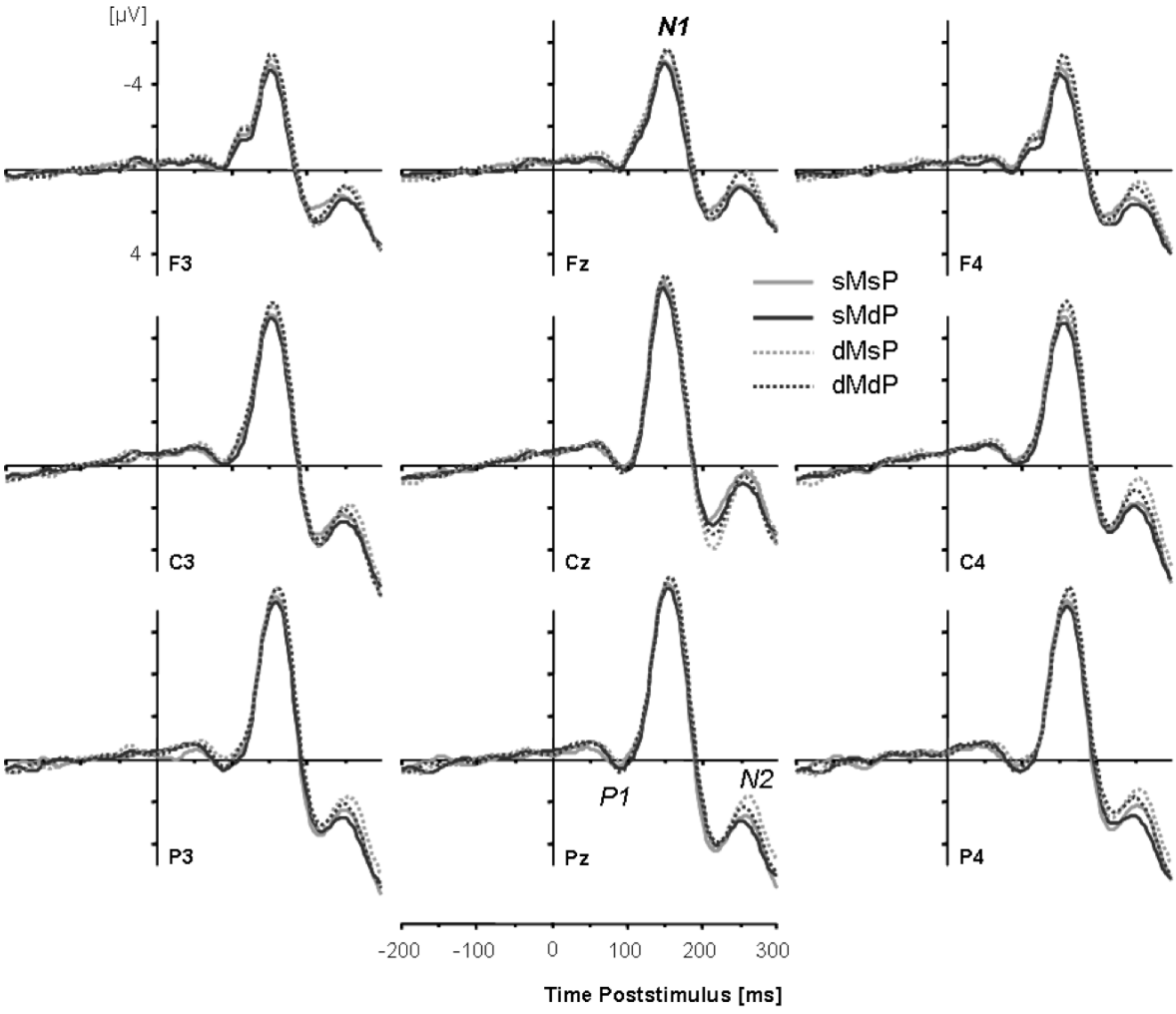

Figure 31A. Grand-averaged ERP waveforms elicited in response to visual stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate position repetitions, dark grey lines position changes.

Figure 31A displays ERPs elicited in response to visual stimuli, separately for each of the four experimental conditions. No significant effects or interactions involving the factor Modality change were found for the visual P1 component. In contrast, and analogous to the results found for somatosensory ERPs, the N1 component was strongly affected by Modality change, with significantly larger N1 amplitudes for trials on which the target modality was changed [main effect of Modality change, $F(1,11) = 7.94$, $p<.017$, $\eta^2 = .419$]. As was already observed for tactile ERPs, no significant main effect of Position change [$F(1,11) = 0.079$] and no modality change x position change interaction [$F(1,11) = 1.56$] were obtained for visual N1 amplitudes – thus confirming that N1 amplitude modulations were associated with modality change versus repetitions, irrespective of whether successive stimuli were presented at matching locations or in opposite hemifields.

For visual N2 amplitudes, the interaction between Modality change, Electrode site, and Electrode position reached significance [$F(1,11) = 3.73$, $p<.011$, $\eta^2 = .253$]. However, this was not substantiated by significant main effects or interactions in follow-up analyses conducted separately for different electrode sites.

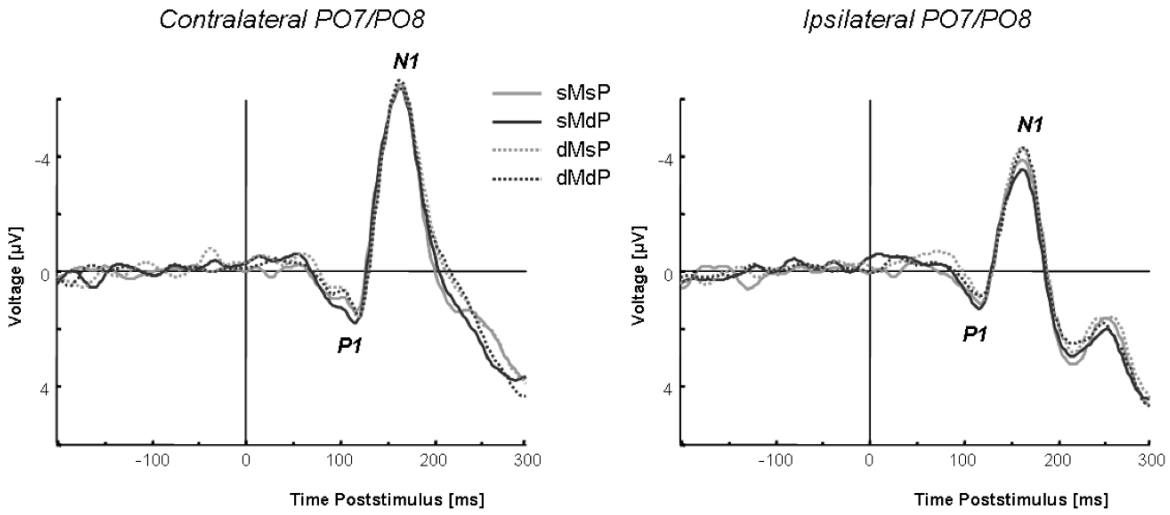

Figure 31B. Grand-averaged ERP waveforms elicited over modality-specific sensory areas at electrode positions PO7/PO8 by visual stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate position repetitions, dark grey lines position changes.

Figure 31B presents the early sensory evoked potentials specific for the vision modality over early visual areas at electrode positions PO7/PO8, separately for each of the

four experimental conditions. Statistical analyses revealed both components to be affected by shifts of the stimulus-defining modality across consecutive trials. Sensory evoked P1 amplitudes were modulated by modality changes interacting with Stimulus side [$F(1,11) = 6.96$, $p<.023$, $\eta^2 = .388$]. This interaction was based on significantly enhanced P1 amplitudes following modality changes if the stimulus appeared within the right (p<.015), but not the left (p<.403), hemifield.

Sensory evoked N1 amplitudes were modulated by modality changes interacting with Stimulus side and Electrode position [$F(1,11) = 4.94$, $p<.048$, $\eta^2 = .310$]. This three-way interaction was due to modality shift effects observable at ipsilateral, but not contralateral, electrode positions, that is: left hemifield stimuli produced enhanced amplitudes owing to modality shifts at PO7 (p<.043), but not PO8 (p>.455); conversely, right hemifield stimuli generated increased activations owing to modality shifts at PO8 (p<.011), but not PO7 (p<.109).

Comparison of N1 modality shift effect across modalities

Further analyses were conducted to verify whether the N1 modulation produced by a change in target modality across successive trials, which was observed for both visual and somatosensory ERPs within the same time range, represents a modality-unspecific process, or, alternatively, a process operating in a modality-specific fashion. This was examined by subjecting N1 mean amplitude values for both stimulus modalities to an omnibus ANOVA, with the additional factor Modality (touch, vision). As expected, this ANOVA revealed significant main effects of Modality [$F(1,11) = 37.08$, $p<.001$, $\eta^2 = .771$] and Modality change [$F(1,11) = 87.81$, $p<.001$, $\eta^2 = .889$] as well as an interaction between Modality x Electrode site [$F(1,11) = 21.31$, $p<.001$, $\eta^2 = .660$]. In contrast, and importantly, the interaction between Modality and Modality change was far from significant [$F(1,11) = 1.08$, $p>.320$, $\eta^2 = .090$], indicating that the N1 amplitude modulations resulting from modality change were triggered in an equivalent fashion regardless of whether visual or tactile target stimuli were presented.

Discussion

As expected, the RT data confirmed previous findings (e.g., Spence et al., 2001) of faster reactions when the current target was defined within the same, rather than a different, modality relative to the preceding target. However, performance was also

determined by the position of the stimulus. RTs were fastest when both the modality and the position of the target were repeated and slowest when the target modality was changed but the position repeated, with intermediate response latencies in the two remaining conditions. Thus, concurrent changes of modality and position did not produce additive effects – which indicate that, at some stage of processing, an interaction of modality-related and positional information processing must occur. However, since modality changes were associated with response changes in Experiment 6, it is not unequivocally clear at which stage of processing, *perceptual* versus *response-related*, this modality-specific intertrial facilitation arises.

At the electrophysiological level, modality changes affected the N1 component, *independently* of the target modality. For both somatosensory and visual stimuli, changes of the target modality on consecutive trials were associated with enhanced N1 amplitudes, relative to modality repetitions. Importantly, the modulation of the N1 was independent of the perceptual modality and repetitions/changes of the stimulus position, suggesting that the N1 effect originates from a purely 'modality change-driven' process. According to a generalized weighting account (along the lines of the DWA; Found & Müller, 1996), the enhanced amplitudes of the N1 component in response to modality changes might be interpreted as reflecting a control mechanism which is invoked to detect a (modality) change necessary to transfer attentional weight from the old to the new target-defining modality. Thus, optimized stimulus processing in the subsequent trial episode is accomplished by rendering the new target signal (more) salient at some supra-modal decision stage (see General Discussion for a more detailed discussion).

This hypothesized processing architecture is further supported by the results observed for the early sensory evoked potentials specific for somatosensory (*N90*) and visual (visual *P1* and *N1*) processing, which suggest that shifts of the target modality across consecutive trials led to differences already in the early sensory stages of information processing, possibly coding modality-specific information with differential efficiency. Importantly, there were no main effects of Position change, or interactions between Modality change and Position change, demonstrating that the amplitudes of these components (as well as the amplitudes of the modality-unspecific N1) were not affected by possible sensory refractoriness effects that might have been present when two tactile or two visual stimuli were presented on successive trials at identical locations.

EXPERIMENT 7

Experiment 7 was designed to rule out the possibility that the modulation of the N1 component as a result of modality changes versus repetitions observed in Experiment 6 was attributable to repetitions/changes in the motor response. Since a modality change was invariably associated with a response change in Experiment 6, it is not possible to decide whether the modality change effects are attributable to perceptually-related processes, response-related processes, or an interaction of both. To address this question, we introduced two features per modality in Experiment 7, with one feature in each modality mapped to the same motor response (e.g., 'green' & 'slow vibrating' → left foot; 'red' & 'fast vibrating' → right foot). Using this stimulus-response mapping, a modality change could occur independently of repetitions/changes in the motor response.

Methods

Participants

Twelve paid volunteers (3 males; all right handed; age range 21–35 years, mean age 27.3 years) were recruited from the Birkbeck College subject panel, after giving their written informed consent. One participant had to be excluded from data analysis due to excessive eye-blink artifacts.

Stimuli, Apparatus, and Procedure

The general experimental set-up and procedure were the same as in Experiment 6, except for the introduction of two features for each modality. Tactile stimuli were vibrations that differed in frequency. To present 'slow' vibrations, the contact time of the rod to the finger was set to 2 ms, followed by a 23-ms inter-pulse interval. This corresponded to a rectangular stimulation frequency of 40 Hz. 'Fast' vibrations were defined by a contact time of 2 ms and an inter-pulse interval of 8 ms, corresponding to a rectangular stimulation frequency of 100 Hz. These manipulations of the contact times and inter-pulse intervals resulted in two easily discriminable vibratory stimuli (40 Hz vs. 100 Hz). The duration of the stimuli (the interval between onset of the first pulse and the offset of the last pulse) was set to 200 ms. Visual stimuli consisted of illuminating an LED ensemble for 200 ms, as in Experiment 6. However, LEDs now differed in color (red or green). Prior to each experimental half, participants were informed about the required stimulus-response mapping. 50% of the participants responded with their left foot to red

and slow vibrating stimuli, and with their right food to green and fast vibrating stimuli, in the first half of the experiment, and vice versa in the second half. This was reversed for the other participants. Prior to the start of each experimental half, participants performed at least one trial block to practice the stimulus-response mapping. The defining features (red, green, slow vibrating, fast vibrating) and positions (left, right) of the target stimuli as well as the required motor responses were equally likely (and presented in random order across trials). All behavioral and electrophysiological data were analyzed with respect to the target modality, target position, and motor response on the current trial *n* relative to preceding trial *n-1*, thus adding to the four experimental conditions of Experiment 6 the factor response change (same vs. different response), which resulted in eight intertrial transition conditions (all with equal numbers of trials).

Statistical analyses of the electrophysiological data were focused primarily on the N1 component, which was found to be a modality-independent electro-cortical marker of modality shifting in Experiment 6. Mean amplitudes (identical time range as in Experiment 6) of the N1 were examined using a repeated-measures ANOVA with the factors Modality change (same modality, different modality), Response change (same response, different response), Position change (same position, different position), Electrode site (frontal, central, parietal), and Electrode position (left, midline, right), separately for each modality. Additionally, mean amplitudes of the early somatosensory contralateral P50 and N90 components were subjected to repeated-measure ANOVAs with the factors Modality change (same vs. different modality), Response change (same vs. different response), Position change (same vs. different position), and Stimulus side (left vs. right) at C3/C4. An ANOVA with the factors Modality change, Response change, Position change, Stimulus side, and Electrode position (left vs. right) was conducted to explore any effects on visual evoked *P1* and *N1* components at PO7/PO8. In all other respects (procedure, EEG recording, and data analysis), Experiment 7 was identical to Experiment 6.

Results

Behavioral data

Trials on which participants responded incorrectly (5.53% of all trials), on which the RT was excessively slow (>1000 ms; 1.37%), and with an incorrect response on the previous trial (5.06% of all trials) were excluded from further RT analyses (11.96% of the trials in total). RTs and error rates for the remaining trials are displayed as a function of

Modality change x Response change in Figure 32. A repeated-measures ANOVA of the RT data, with the factors Modality (visual, tactile), Modality change (same vs. different modality), Response change (same vs. different response), and Position change (same vs. different position) revealed significant main effects for Modality, Modality change, and Response change. The modality effect [$F(1,10) = 27.61$, $p<.001$, $\eta^2 = .734$] was caused by faster reactions for visual compared to tactile targets (546 vs. 595 ms). The modality change effect [$F(1,10) = 67.99$, $p<.001$, $\eta^2 = .872$] was due to slowed responses for modality changes relative to repetitions (596 vs. 545 ms). The response change effect [$F(1,10) = 33.82$, $p<.001$, $\eta^2 = .772$] was due to prolonged RTs for response changes compared to repetitions (584 vs. 557 ms). In addition, the interaction between Modality change and Response change was significant [$F(1,10) = 20.20$, $p<.001$, $\eta^2 = .669$].

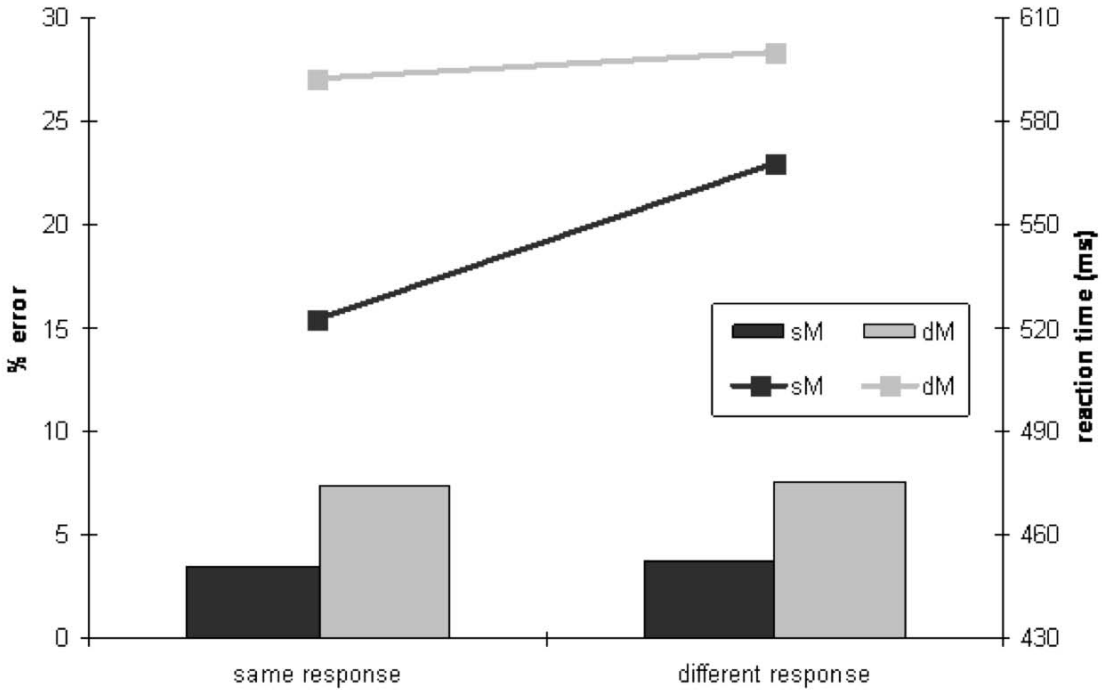

Figure 32. Reaction times (lines) and error rates (bars) as a function of Modality change and Response change (sM = same modality; dM = different modality)

Further analyses confirmed that participants reacted fastest when both the modality and the response stayed the same on consecutive trials, followed by trials on which the

modality was repeated and the response changed (p<.005). With modality changes, RTs did not differ between trials on which the response was repeated versus changed (p>.967). The factor Response change interacted further with Position change [F(1,10) = 8.44, p<.016, η^2 = .458]: a change of the required motor response resulted in slower RTs for position repetition than for position change trials. This observation was confirmed by further analyses. For position repetition trials, RTs were significantly slower for response changes relative to response repetitions (p<.001). For position change trials, the difference between same and different responses failed to reach significance (p>.06). Finally, the three-way interaction between Modality, Modality change, and Position change was significant [F(1,10) = 7.36, p<.022, η^2 = .424]. As revealed by further post-hoc contrasts, responses on tactile-modality repetition trials were faster when the target appeared at the same position as on the previous trial (p<.001). In contrast, there was no such influence of position repetitions/changes on visual modality repetition trials (p>.727).

An analogous ANOVA of the error rates revealed that participants made significantly fewer errors on modality repetition compared to change trials (3.6% vs. 7.5%) [main effect of Modality change, $F(1,10) = 14.53$, $p<.003$, η^2 = .592]. This indicates that the RT effects in Experiment 7 were not confounded by speed-accuracy trade-offs.

Effects on somatosensory ERPs

Similar to Experiment 6, the main effect of Modality change was significant for the somatosensory N1 amplitudes [$F(1,10) = 6.46$, $p<.029$, η^2 = .393]. As can be seen from Figure 33A, N1 amplitudes were enhanced for modality changes versus repetitions. There was no significant main effect of Response change [$F(1,10) = 0.52$], and no modality change x response change interaction [$F(1,10) = 1.86$], demonstrating that this N1 modulation was solely linked to changes versus repetitions of the target modality.

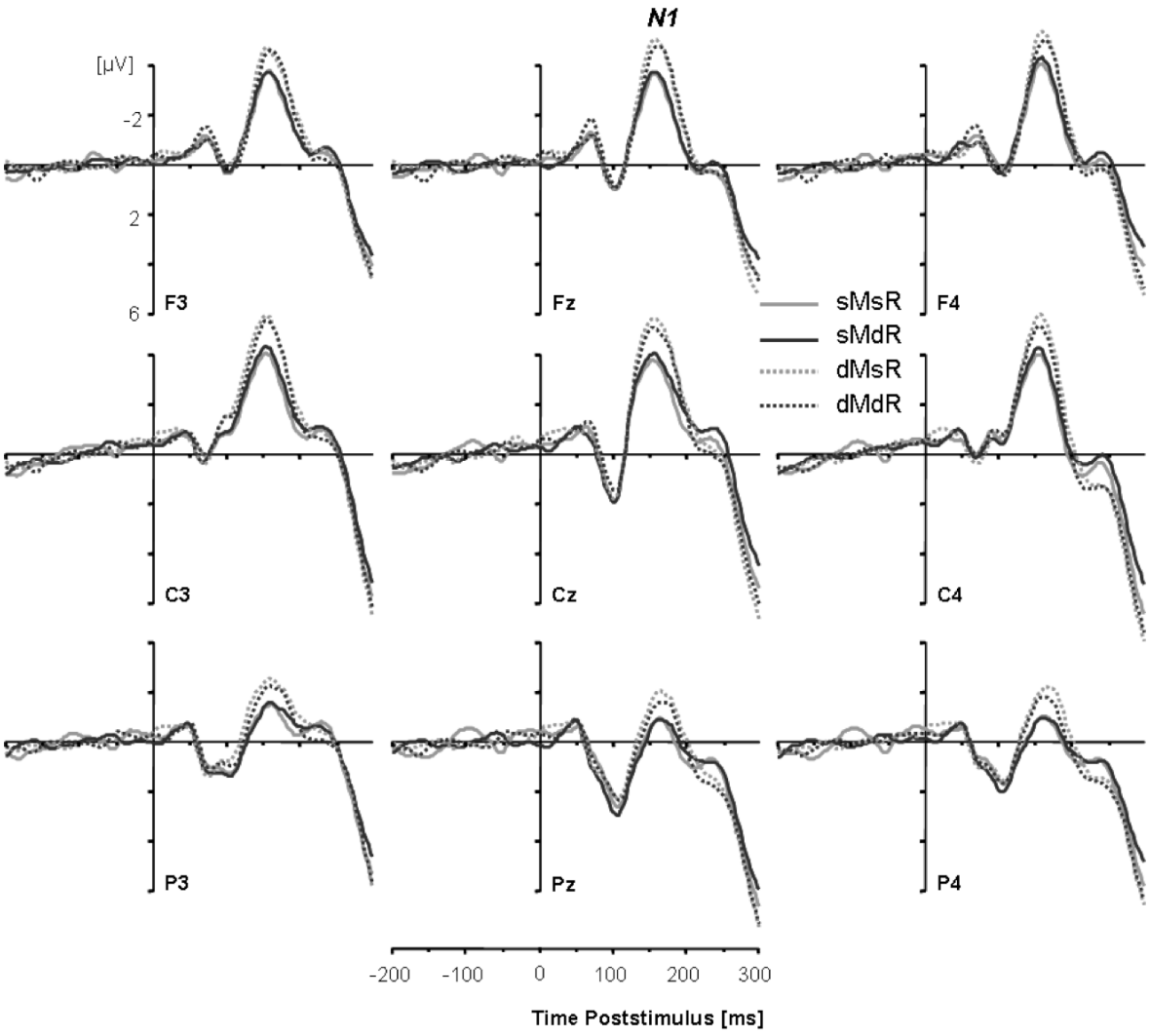

Figure 33A Grand-averaged ERP waveforms elicited in response to somatosensory stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate response repetitions, dark grey lines response changes.

Figure 33B shows somatosensory ERPs on modality change and modality repetition trials at electrodes C3/C4 contralateral to the stimulated hand. As for Experiment 6, amplitude modulations due to modality changes were evident for the N90, but not for the P50 component. For the N90 amplitudes, a significant main effect of Modality change [$F(1,10) = 6.13$, $p<.033$, $\eta^2 = .380$] was found, due to enhanced amplitudes on modality change trials. In addition, and in contrast to the results found for Experiment 6, there was now also an interaction between Modality change and Position change [$F(1,10) = 7.74$, $p<.019$, $\eta^2 = .436$]. This interaction was based on significantly enhanced amplitudes

following modality shifts occurring at the same location (p<.008), but not at the opposite location (p>.989), relative to the previous trial.

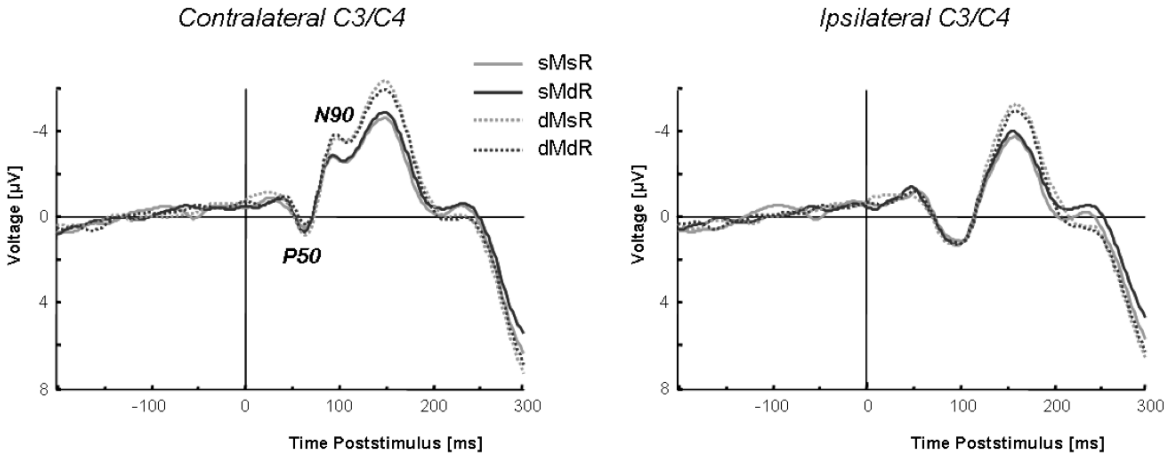

Figure 33B. Grand-averaged ERP waveforms elicited over modality-specific sensory areas at electrode positions C3/C4 by tactile stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate response repetitions, dark grey lines response changes.

Effects on visual ERPs

As can be seen from Figure 34A, changes of the target-defining modality were associated with more negative-going deflections of the N1 component, as compared to modality repetitions (main effect of Modality change [$F(1,10) = 5.87$, $p<.036$, $\eta^2 = .370$]). In addition, there was an (marginally significant) interaction between Modality change, Electrode site, and Electrode position revealed [$F(4,40) = 2.51$, $p<.057$, $\eta^2 = .201$]. This interaction reflects the fact that enhanced negativities owing to modality changes were most pronounced at frontal electrode positions, whereas this effect decreased towards midline and right central electrode positions, and was almost absent at midline and right parietal electrode positions. As with the tactile N1 amplitudes, there was no significant main effect of Response change [$F(1,10) = 0.44$], and no modality change x response change interaction [$F(1,10) = 0.02$] on visual N1 amplitudes, assuring that this N1 modulation was not affected by changes versus repetitions of the motor response.

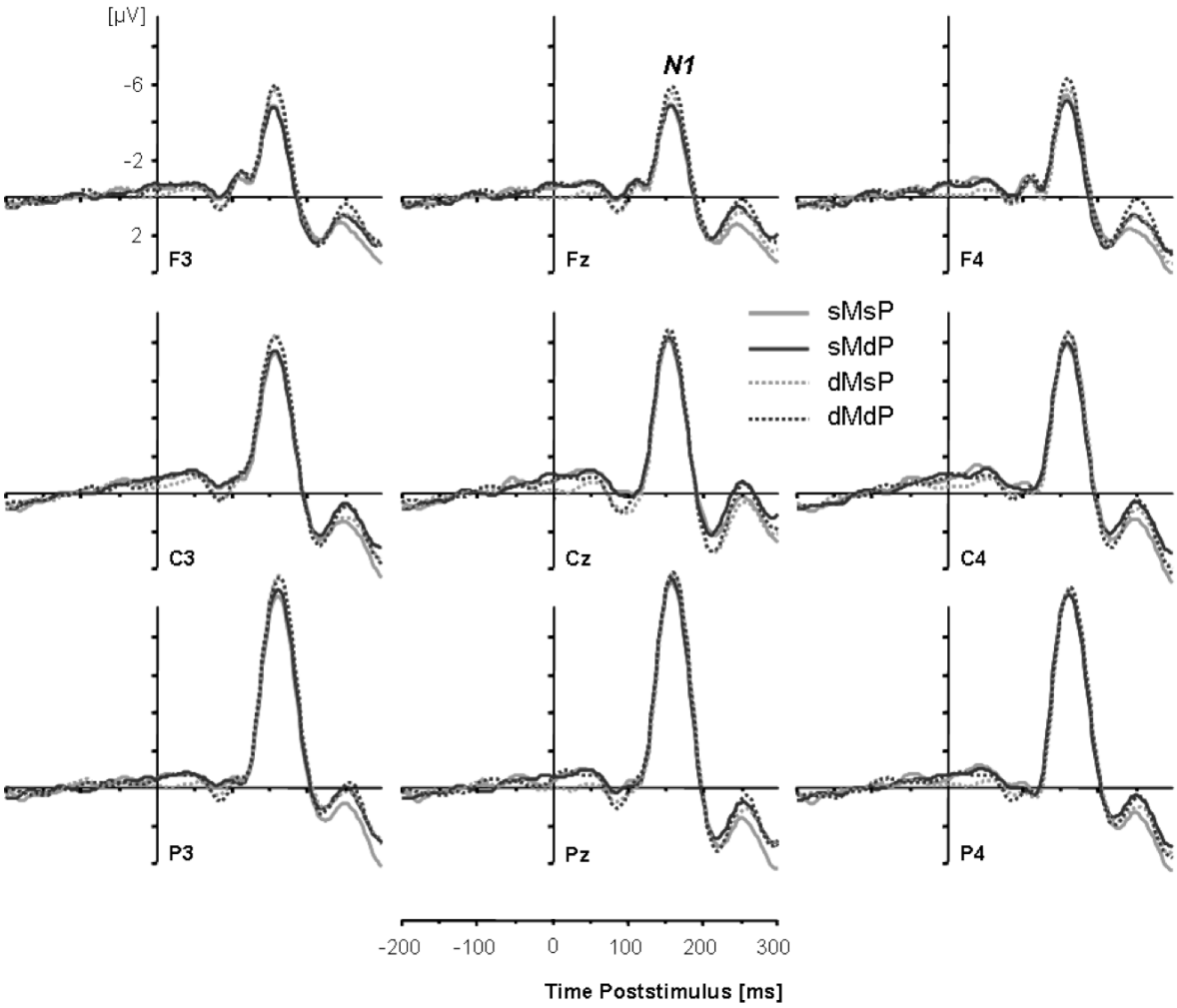

Figure 34A Grand-averaged ERP waveforms elicited in response to visual stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate response repetitions, dark grey lines response changes.

Figure 34B presents the early sensory evoked potentials specific for the visual modality, as a function of Modality change x Response change. Similar to Experiment 6, the early visual evoked P1 and N1 were influenced by the stimulus-defining modality of the preceding stimulus. However, this time, the modality change factor interacted with Electrode position (P1: [$F(1,10) = 7.89$, $p<.019$, $\eta^2 = .441$]; N1: [$F(1,10) = 8.98$, $p<.013$, $\eta^2 = .473$]). For both components, shifts of the stimulus-defining modality were accompanied by unilateral amplitude enhancement at either the left (N1) or the right (P1) electrode position.

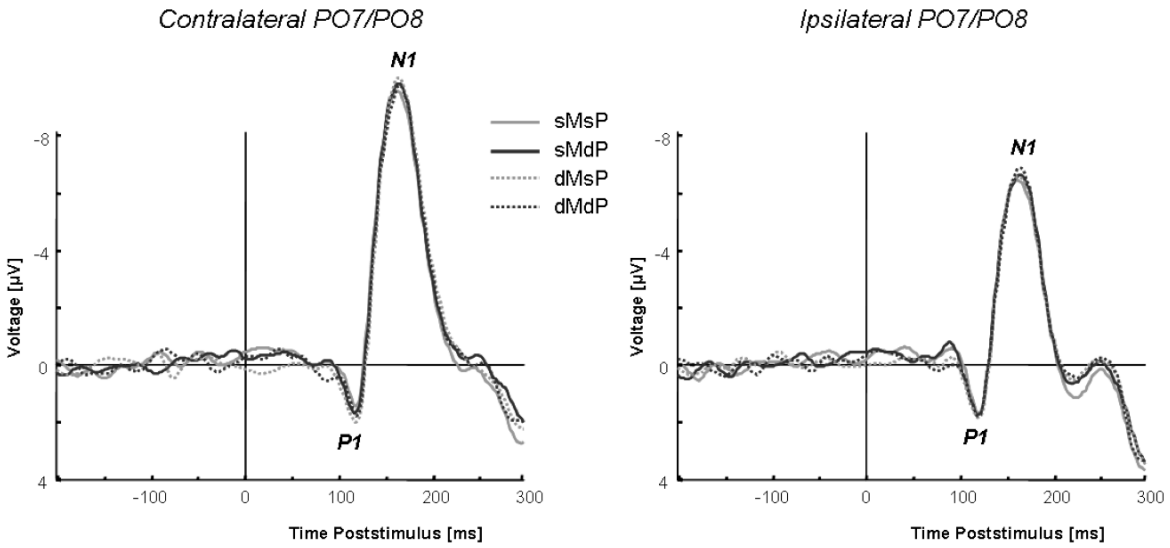

Figure 34B. Grand-averaged ERP waveforms elicited over modality-specific sensory areas at electrode positions PO7/PO8 by visual stimuli in the 300-ms interval following stimulus onset, relative to a 200-ms pre-stimulus baseline. Solid lines indicate modality repetitions, dotted lines modality changes. Light grey lines indicate response repetitions, dark grey lines response changes.

Comparison of N1 modality shift effect across modalities

As for Experiment 6, N1 mean amplitude values for both modalities were subjected to an omnibus ANOVA in order to investigate the modality-independence of the N1 modality shift effect. The results exactly replicated the pattern observed for Experiment 6. There were main effects of Modality [$F(1,10) = 25.47$, $p<.001$, $\eta^2 = .718$] and Modality change [$F(1,10) = 13.25$, $p<.005$, $\eta^2 = .570$], as well as an interaction between Modality and Electrode site [$F(1,10) = 21.28$, $p<.001$, $\eta^2 = .680$]. In contrast, there was no sign of differential activation patterns between trials with tactile and trials with visual stimuli, evidenced by the absence of a significant modality x modality change interaction [$F(1,10) = 1.00$, $p<.341$, $\eta^2 = .091$], in line with the assumption that the enhanced N1 amplitude following a change, versus a repetition, in the target modality is modality-unspecific in nature.

Discussion

The aim of Experiment 7 was to confirm the results of Experiment 6, while at the same time ruling out potential contributions of response repetitions versus alternations. This was done by using a stimulus-response mapping that allowed modality changes to

occur independently of response changes and vice versa. The RT data of Experiment 7 suggest an interactive behavior of the two factors. Repetitions/changes of the motor response influenced performance on modality repetition trials, with faster RTs when the response was repeated as well as the modality. However, no such influence was evident for modality change trials, on which RTs were generally slower compared to modality repetition trials. This interactive pattern of effects resembles that observed in previous studies (e.g., Müller & Krummenacher, 2006; Pollmann et al., 2006; Chapter III of the present thesis), which used a 'compound task' to dissociate perceptually-related from response-related processes in cross-dimensional singleton feature search. In these studies, participants produced the fastest responses when both the target-defining dimension and the response remained the same across consecutive trials. Changes of the visual dimension, the response, or both, all slowed the RTs to a similar level. As Chapter III of the present thesis had proposed, the interaction between the two factors might arise at the 'response selection' stage where perceptually analyzed information is translated into motor commands.

Confirming the observations of Experiment 6, the N1 component was modulated by modality changes in the same manner for somatosensory as for visual stimuli. Changes of the modality (from somatosensory to visual and vice versa) across consecutive trials were, irrespective of the perceptual modality and stimulus position (same vs. different as on the previous trial), associated with significantly enhanced N1 amplitudes. Importantly, this N1 effect occurred independently of repetitions/changes of the motor response, thereby ruling out any contribution of response-related factors. In Experiment 7, the visual modality shift effect of the N1 component was most pronounced at frontal leads and almost disappearing towards central and parietal leads, revealing a fronto-central process involved in modality shifting. This observation resembles the findings of Chapter II of the present thesis, suggesting that analogous brain regions are involved in the N1 modality shift effect observed in the present study as well as the tN2 visual-dimension shift effect in Chapter II.

Modulated processing owing to modality shifts was also obtained for the early sensory evoked components. Albeit interacting with other factors (tactile *N90*: Position change[5]; visual *P1* and *N1*: Electrode position), the results clearly demonstrated an influence of the previous perceptual modality on early tactile and visual processing. As for

[5] Note that tactile N90 amplitudes might have been further modulated by sensory refractoriness effects in the present experiment.

Experiment 6, these modulations might indicate differences in processing efficiency starting already in the modality-specific sensory brain regions.

General Discussion

In two ERP experiments investigating modality switch costs between vision and touch, we replicated the RT pattern described in previous studies (e.g., Spence et al., 2001): Changes in the target-defining modality across consecutive trials gave rise to prolonged RTs, compared to repetitions of the target modality. The purpose of the present study was to identify EEG parameters associated with this modality switch cost. A recent study of dimension change effects in the visual modality (Chapter II) had revealed the tN2 component as a marker of visual-dimension changes. This effect was strongest over fronto-central electrode positions, pointing to the involvement of a frontal executive process in the control of visual-dimension (re-)weighting. The present study was modeled after this earlier study, and examined whether visual dimension changes (as studied by Chapter II) and modality changes may be controlled by similar processes originating from similar brain regions. Specifically, a fronto-central ERP component analogous to the tN2 was expected to be sensitive to modality changes.

Brain electrical activity of modality changes

Analyses of ERPs revealed enhanced amplitudes of the N1 component for changes, relative to repetitions, of the target-defining modality. Importantly, the N1 modality shift effect was observed in response to both visual and tactile target changes in Experiment 6, suggesting a process that operates independently of and across sensory modalities. To examine whether the N1 component reflects change processes originating from *perceptual* versus *response-related* processing stages, Experiment 7 was conducted with modality changes occurring independently of response changes. Similar to Experiment 6, the N1 exhibited enhanced amplitudes for modality changes relative to repetitions, irrespective of the perceptual modality, spatial stimulus characteristics, and motor response requirements. This pattern strongly suggests that the N1 effect reflects a mechanism based solely on non-spatial perceptual stimulus attributes – consistent with theoretical accounts (such as DWA) that locate intertrial change/repetition effects at perceptual processing stages, and inconsistent with accounts that attribute such effects exclusively to response-related stages (e.g., Mortier et al., 2005).

In Experiment 7, the N1 modality shift effect was most pronounced in response to visual stimuli at frontal leads, with a significant decrease towards parietal leads. This finding is of special relevance with respect of the primary aim of the present study, namely to identify an ERP marker mirroring modality shifts irrespective of the perceptual modality. Note that only the anterior portion (possibly originating from fronto-centrally located sources) of the N1 component exhibited this characteristic behavior, for both modalities in both experiments. This accentuation of fronto-central electrode sites for the N1 modality shift effect revealed an analogous scalp distribution as observed in Chapter II for the tN2 in response to visual dimension changes. It is therefore possible that the anterior N1 modality shift effect observed in the present study and the tN2 reported in Chapter II originate from similar brain regions, in spite of the fact that their latency differed by some 100 ms. This latency difference might be due to the absence of a time-demanding search process in the present study. In Chapter II, participants had to search for a color- or orientation-defined singleton target among distracters. In contrast, in the present study, participants were always presented with a single stimulus, either visual or tactile, so that there was no need for a search process prior to target discrimination. Admittedly, the assumption of an identical neural generator for the anterior N1 and the tN2 remains speculative, and will require additional source reconstruction based on high-density EEG recording. Nonetheless, given its fronto-central focus, latency, and modulation independent of the target modality, stimulus location, and motor requirements, we interpret the anterior N1 as being associated with the control of modality-specific attentional weighting, that is: the detection of a modality change and initiation of the re-setting of weights to the new target-defining modality.

In agreement with this view, and with the study of Gondan et al. (2007), are the results for the early sensory evoked potentials obtained in the present study. In both experiments, early sensory modality-specific components were affected by shifts of the stimulus-defining modality across consecutive trials. This suggests that already early sensory stages of information processing are modulated by modality shifts, and, thus, might be contributing to behavioral modality switch costs. These modulations over modality-specific brain areas can be interpreted as reflecting the (implicit) *weighting* of one sensory stimulus modality over others, initiated via feedback pathways by frontal control mechanisms.

Introducing a 'Modality-Weighting' Account

The present findings revealed remarkable similarities between visual-dimension changes (Chapter II - IV) and modality changes (present Chapter). In both studies, the behavioral RTs were prolonged for changes, relative to repetitions, of the target-defining visual dimension and modality, respectively. Furthermore, the electrophysiological data suggest spatially overlapping neural sources contributing to both types of change effect. On this basis, we propose a '*modality-weighting*' account (MWA), which is essentially a generalization of the DWA. Specifically, the MWA assumes similar weighting mechanisms for perceptual modalities as assumed for dimensions within the visual (and the auditory, e.g., Dyson & Quinlan, 2002) modality. That is, to optimize task performance, attentional processing weight is allocated to task-relevant stimulus modalities (such as vision, audition, touch), with the total weight being limited. Weighting of one modality leads to facilitated processing of all targets defined in this modality, relative to targets defined in other modalities. This facilitation results from enhanced coding of target signals within the weighted modality and/or enhanced transmission of modality-specific target information to a cross-modal stage of processing (such as a supra-modal master map of locations), which determines the allocation of focal (selective) attention to the target event and mediates further perceptual analysis and response decisions (Figure 35).

In contrast, changes of the target-defining modality across consecutive trials involve a time-consuming *weight-shifting* process, in which attentional weight is transferred from the old to the new target-defining modality to amplify the target signal and render it salient at a supra-modal processing stage (master map). The modulation of the N1 component observed in the present study is assumed to reflect this *weight-shifting* process across modalities. Thus, regarding the time course of the processes involved in (implicit) attentional weight-setting, it is suggested that the anterior N1 effect is primarily generated on the current trial, keeping track of the prevailing stimulus modality in order to adjust/update the weight-setting for optimized stimulus processing in the next trial episode. By contrast, early sensory-specific ERP-effects of modality repetitions represent the facilitated sensory coding of the relevant stimulus modality as a consequence of the previous trial.

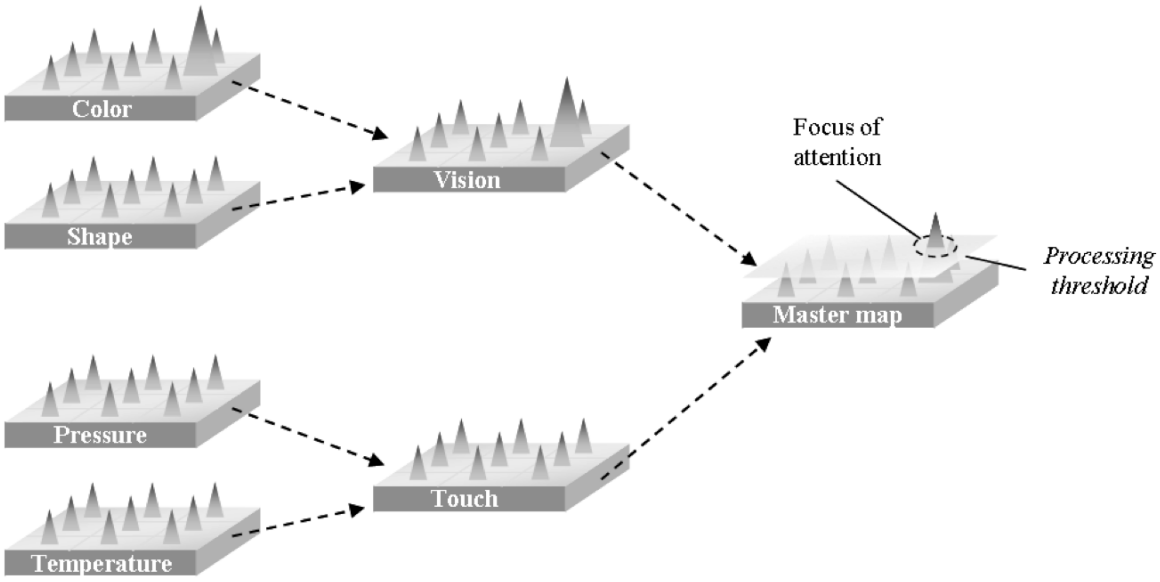

Figure 35. Functional architecture of the 'Modality-Weighting' Account, adapted from the DWA (Found & Müller, 1996), with additional saliency-based (modality) maps located between dimension maps and master map unit. Displayed is a schematic illustration of a feature search trial while the singleton is defined within the visual dimension 'color'. Selective (focal) attention operates at the master map unit of integrated (summed) saliency signals derived separately from modality-specific modules, which receive their (summed) saliency signals separately from dimension-specific input modules. It is assumed that dimension maps as well as modality maps are implicitly weighted depending on what was presented at the previous trial. The depicted situation shows essentially a bottom-up search. However, the MWA assumes interacting bottom-up and top-down mechanisms contributing to target detection.

Finally, it should be noted that modality weighting is theoretically consistent with (intra-modality) dimension weighting: the weighting mechanisms for modalities and (intra-modality) dimensions may be operating in tandem. That is, optimized intertrial facilitation for a given target depends on (at least) two factors: first, as a precondition, the target modality must stay the same; and second, the dimension must be repeated. However, the precise relationship between modality and dimension weighting must be worked out in future studies.

Deutsche Zusammenfassung

(German Summary)

Einleitung

Eine der wohl beeindruckendsten Leistungen unseres Gehirnes besteht darin, aus der gewaltigen Informationsmenge (bis zu 2 Gigabyte Datenvolumen/s allein für das visuelle System; Gegenfurtner, 2004), die kontinuierlich auf unsere sensorischen Sinnessysteme einströmt, saliente wie relevante Information herauszufiltern, um uns ein adäquates Verhalten in der Umwelt zu ermöglichen. Um diese enorme Datenreduktion zu erreichen, werden allgemein zwei (interagierende) attentionale Kontrollmechanismen angenommen (Corbetta & Shulman, 2002): das willkürliche Vorabselektieren bestimmter Information (z.B. Farbe des eigenen Autos) relevant für gegenwärtige Intentionen kann als *ziel-gesteuert* (top-down), die unwillkürliche Ausrichtung unserer Aufmerksamkeit bedingt durch saliente Information (z.B. Feueralarm) kann als *reiz-gesteuert* (bottom-up) bezeichnet werden. Diese funktionale Unterscheidung ist allgemein akzeptiert und Basis jüngerer (Wolfe, 1994; Itti & Koch, 2001) wie älterer (James, 1890) Modelle visueller Aufmerksamkeit.

Neuere Studien (z.B. Maljkovic & Nakayama, 1994; Found & Müller, 1996) konnten hingegen zeigen, dass die Zuwendung visueller Aufmerksamkeit nicht ausschließlich auf der Interaktion dieser zwei, top-down und bottom-up, Faktoren basiert, sondern deuten auf die Involvierung (zumindest) eines weiteren Faktors. So beobachteten Found & Müller (1996), dass die Reaktionszeit der Probanden für eine visuelle Suchaufgabe (nach pop-out Zielreizen) in großem Maße davon abhing, was im vorangegangen Suchdurchgang präsentiert wurde. War der Zielreiz in zwei aufeinander folgenden Durchgängen innerhalb der gleichen visuellen Dimension (z.B. Farbe in Durchgängen *n* und *n-1*) definiert, so ließen sich schnellere Reaktionszeiten im Vergleich

zu einem Dimensionswechsel (z.B. Farbe in Durchgang *n* und Orientierung in Durchgang *n-1*) beobachten. Dieses Effektmuster lieferte klare Evidenz, dass, neben top-down und bottom-up Faktoren, Ereignisse der unmittelbaren Vergangenheit (vorangegangene Durchgang) eine kritische Rolle für unser gegenwärtiges Verhalten spielen. Die Fragen wann und wo innerhalb des menschlichen Verarbeitungssystems Konsequenzen des vorangegangenen sensorischen Ereignisses (und/oder motorischen Aktion) auf die augenblickliche Performanz wirken, ist Thema der vorliegenden Dissertation.

Visuelle Suche

Das Paradigma der visuellen Suche hat sich aufgrund seiner vielseitigen Einsatzmöglichkeiten als eines der erfolgreichsten Paradigmen zur Erforschung selektiver visueller Aufmerksamkeit etabliert. In einer üblichen visuellen Suchaufgabe wird der Versuchsperson ein Display präsentiert, dass unter einer variablen Anzahl von Distraktoren einen Zielreiz enthalten kann. Die visuelle Suche nach „pop-out" Zielreizen (Singletons) ist dadurch gekennzeichnet, dass sich der zu entdeckende Zielreiz in einem einfachen Merkmal (z.B. Farbe) oder in einer Konjunktion dimensional verschiedener Merkmale von den Distraktoren unterscheidet, wodurch er dem Beobachter „ins Auge zu springen" scheint. Die Gesamtanzahl an Objekten präsentiert in einem Suchdisplay wird als Display-Größe bezeichnet. Üblicherweise erscheint in 50 % aller Suchdurchgänge ein Zielreiz wobei die Probanden aufgefordert sind, so schnell und akkurat wie möglich die Anwesenheit (versus Abwesenheit) eines Zielreiz innerhalb des Suchdisplays zu detektieren. Die hierfür benötigte Zeit (Reaktionszeit) sowie die Genauigkeit bilden in der Regel die kritischen Variablen. Stellt die Reaktionszeit die interessierende Variable dar, so verbleibt das Suchdisplay bis zur Reaktion der Probanden sichtbar. Analysiert man die Reaktionszeit nun in Abhängigkeit von der Display-Größe, so lassen sich Hinweise darüber gewinnen, wie viel Kosten durch ein zusätzlich präsentiertes Objekt verursacht werden. Verhält sich die RT unabhängig von der Objektanzahl im Suchdisplay (Suchrate < 10 ms/Objekt), wird die Suche als *parallel* charakterisiert. Steigt die RT mit zunehmender Objektanzahl des Suchdisplay (Suchrate > 10 ms/Objekt), so besitzt die Suche einen *seriellen* Charakter[1]. Während bei parallelen Suchen der Zielreiz regelrecht aus dem

[1] Aufgrund neuerer Befunde wurde hingegen vorgeschlagen, diese dualistische Terminologie (*parallel* vs. *seriell*) durch ein ‚*effizient* vs. *ineffizient*' Kontinuum zu ersetzen (Wolfe, 1988)

Suchdisplay herauszuspringen scheint, wird bei seriellen Suchen das Suchdisplay Objekt für Objekt abgescannt.

Modelle der visuellen Suche

Das wohl bekannteste Modell der visuellen Suche ist die *„Feature Integration Theory“* (FIT) von Anne Treisman (Treisman & Gelade, 1980; Treisman, 1988). Die FIT versucht zu erklären, wie aus den verschiedenen Merkmalen eines Objektes (z.B. Merkmale der Farbe, der Form etc.), die in separaten neuronalen Modulen enkodiert werden, eine kohärente Objektrepräsentation entsteht. Hierzu nimmt die FIT an, dass die Merkmalsintegration durch fokale Aufmerksamkeit, die auf der Basis einer „Hauptkarte der Positionen“ (*master map*) auf ausgewählte Reizorte ausgerichtet wird, vermittelt wird. Die Ausrichtung der Aufmerksamkeit auf einen bestimmten (Hauptkarten-) Ort ermöglicht die Übertragung (das „gating“) aller Merkmale, die an dem korrespondierenden Ort in den untergeordneten dimensionalen Merkmalskarten repräsentiert sind, in ein temporäres Objekterkennungssystem, wo sie zu einem integrierten „object file“ zusammengefasst und mit im Langzeitgedächtnis gespeicherten Objektbeschreibungen abgeglichen werden. In einer späteren Version der FIT (Treisman & Sato, 1990) wird zudem ein „top-down“ Kontrollmechanismus angenommen, mittels dessen die fokale Aufmerksamkeit nur auf solche (Hauptkarten-) Orte gelenkt wird, an denen sich Objekte mit zielreizdefinierenden Merkmalen befinden. Somit liefert die revidierte FIT eine Erklärung für einfache pop-out Suchen (sowie Konjunktionssuchen), bei denen Vorwissen über den zu entdeckenden Zielreiz gegeben ist. Sie hat aber Schwierigkeiten, die effiziente Entdeckung von Singleton-Zielreizen ohne etwaiges Vorwissen zu erklären.

Ein weiteres einflussreiches Modell der visuellen Suche ist das „*Guided Search*“ (GS) Modell von Jeremy Wolfe (Cave & Wolfe, 1990; Wolfe, 1994). Ähnlich wie die FIT geht dieses Modell von einer initialen prä-attentiven Verarbeitungsstufe aus, in der das visuelle Feld als Set basaler dimensionsspezifischer Merkmale (z.B. der Farbe, der Orientierung etc.) parallel enkodiert wird. Jedes Dimensionsmodul berechnet Salienzsignale für alle Stimulusorte, die den Merkmalskontrast zwischen jedem Item zu den anderen Items innerhalb desselben Moduls repräsentieren. Je unähnlicher dabei ein Item im Vergleich zu den anderen ist, umso größer ist seine Salienz. Anschließend werden die Salienzwerte aller Dimensionsmodule auf einer Gesamtsalienzkarte integriert (aufsummiert), und die Position mit dem höchsten Salienzwert bestimmt den Ort, auf den die fokale Aufmerksamkeit

ausgerichtet wird. Durch die Integration interaktiver „top-down“ und „bottom-up“ Mechanismen bietet das GS Modell einen guten Ansatz zum Problem der Entdeckung von Singleton-Zielreizen in visuellen Suchaufgaben. Zieht man jedoch die oben beschriebenen Befunde zur *crossdimensionalen* Suche in Betracht (Found & Müller, 1996), so bietet auch dieses Modell keine adäquate Erklärung dimensionsspezifischer Intertrial-Effekte. Gleichermaßen stehen die unterschiedlichen Verarbeitungszeiten zwischen intra- und crossdimensionaler Suche[2] im Widerspruch zu der Annahme, dass dimensionsspezifische Salienzsignale in *ungewichteter* Weise auf der Gesamtkarte integriert werden.

Einen möglichen Erklärungsansatz für dieses Effektmuster bietet der von Müller und Kollegen postulierte „*Dimension-Weighting Account*“ (DWA; z.B. Müller et al., 1995; Found & Müller, 1996). Dieser Ansatz basiert auf der Annahme einer attentionalen *Gewichtung* visueller Dimensionen, wobei der Gesamtbetrag an attentionalem Gewicht limitiert ist. Ähnlich wie im GS-Modell operiert die fokale Aufmerksamkeit auf einer topographischen „Gesamtsalienzkarte“ („*overall-saliency map*“) des visuellen Displays, die ihre Aktivierungen aus einer Reihe untergeordneter visueller Input-Module – dimensionsspezifische Merkmalskontrast- bzw. Salienzkarten – erhält. Dabei markiert die Einheit mit der höchsten (integrierten) Aktivität auf der Gesamtsalienzkarte den Ort, auf den fokale Aufmerksamkeit, die höhere Verarbeitungsprozesse wie Stimulusidentifikation und Reiz-Reaktions-Zuordnung vermittelt, verlagert wird. Im Rahmen dieses Ansatzes erfährt ein neu eintreffender Zielreiz immer dann eine effizientere Verarbeitung, wenn die ihn kennzeichnende visuelle Dimension bereits im vorausgegangenen Durchgang attentional gewichtet wurde. Durch die Gewichtung werden Salienzsignale in dieser Dimension entweder rascher berechnet oder ihre Übertragung auf die Gesamtkarte wird verstärkt. Ist der Singleton im aktuellen Durchgang *n* in einer anderen Dimension als im Durchgang *n-1* definiert, so muss ein zeitverbrauchender „*Weight-shifting*“ Prozess ins Spiel kommen, in dem Aufmerksamkeitsgewicht von der alten hin zur neuen zielreizdefinierenden Dimension transferiert wird. Unklar ist, ob diese Verschiebung attentionaler Ressourcen eine (Grund-) Voraussetzung zur Zielreizdetektion auf der Master Map bildet (Müller et al., 1995), oder alternativ, der Zielreizdetektion (im aktuellen Durchgang) folgt und die Reizverarbeitung im folgenden Durchgang beeinflusst.

Zusammengefasst entstammen die bei einem Dimensionswechsel entstehenden Verarbeitungskosten dem DWA folgend einer präattentiv-perzeptiven Verarbeitungsstufe.

[2] > 60 ms verzögerte RT’s für cross- relativ zu intradimensionalen Suchen (Müller et al., 1995)

Die in diesem Modell hervorgehobene Stellung visueller Dimensionen ist zudem dadurch indiziert, dass verlangsamte Suchleistungen für Dimensionswechsel (z.B. Orientierung →Farbe) aber nicht für intra-dimensionale Merkmalswechsel (z.B. rot→blau) zu beobachten sind, was darauf hindeutet, dass der *Intertrial-Bahnungseffekt* Prozesse dimensionsspezifischer und nicht merkmalsspezifischer Verarbeitung reflektiert.

Neuronale Korrelate dimensionaler Wechsel

Um ein tieferes Verständnis über behaviorale Dimensionswechsel-Effekte zu gewinnen, wurden in einer Reihe von Studien (Pollmann, 2004; Pollmann et al., 2000, 2006; Weidner et al., 2002) die neuronalen Substrate dimensionaler Gewichtungsprozesse untersucht. Basierend auf hemodynamischen Aktivitätsänderungen konnte ein fronto-posteriores Netzwerk identifiziert werden. Spezieller: erhöhte frontale Aktivierungen ließen sich im linken frontopolaren Kortex (BA 10) sowie in der anterioren Grenze des ACC (BA24/32), erhöhte posteriore Aktivierungen im rechten superioren parietalen Lobus sowie im intraparietalen Sulcus lokalisieren. Zusätzlich zeigten sich erhöhten Aktivierungen in dorsalen okzipitalen Arealen infolge dimensionaler Wiederholungen. Basierend auf diesen Befunden schrieben Pollmann et al. (2006) präfrontalen Arealen die Funktion der Kontrolle dimensionaler Gewichtungsprozesse zu. Die eigentliche Gewichtung wird dann durch höhere Areale des superioren Temporal- und des Parietalkortex via Feedbackverbindungen zu den dimensionsspezifischen Eingangsarealen des Okzipitalkortex vermittelt.

Crossmodale Aufmerksamkeit

Die oben beschriebenen Modelle beziehen sich allein auf Mechanismen der selektiven Aufmerksamkeit in der visuellen Modalität. In der realen Welt werden wir jedoch mit einer Menge von Informationen aus unterschiedlichen Modalitäten konfrontiert, die in eine kohärente Repräsentation der aktuellen Situation mit allen handlungsrelevanten Aspekten integriert werden müssen. Um dem Rechnung zu tragen, wurden in neuerer Zeit zunehmend experimentelle Paradigmen entwickelt, die Fragen der „*crossmodalen* Aufmerksamkeit“ ansprechen. Ein Großteil der entsprechenden Studien befasste sich damit, wie die Verarbeitung von Reizen in einer beachteten (z.B. der visuellen) Modalität durch zusätzlich dargebotene Stimuli in einer anderen (im Bsp. etwa der auditiven) Modalität beeinflusst wird. So z.B. konnten Eimer und Driver (2001) für eine räumliche

Aufmerksamkeitsaufgabe zeigen, dass crossmodale Verbindungen frühe sensorische Prozesse innerhalb modalitätsspezifischer kortikaler Regionen modulieren. Dies ist plausibel, da aus der Umwelt eintreffende Informationen unterschiedlicher Modalitäten nicht selten von einem gemeinsamen Objekt bzw. Ereignis stammen. Daneben untersuchte eine Reihe von Studien den Einfluss der Cue-Modalität auf die Verarbeitung eines nachfolgenden Reizes (Eimer & van Velzen, 2005; Rodway, 2005; Townsend et al., 2006). Wie Rodway (2005) zeigen konnte, wird ein Zielreiz erleichtert verarbeitet, wenn ihm ein Signal vorausgeht, das innerhalb der gleichen Modalität definiert ist. Ein Wechsel der Modalität zwischen Hinweis- und Zielreiz führte dagegen zu Verarbeitungskosten („*modality change effect*"). Rodway erklärte dieses Befund mit einer exogenen Rekrutierung der Aufmerksamkeit hin zur Cue-Modalität, wodurch die Verarbeitung aller Zielreize erleichtert wird, die innerhalb derselben Modalität definiert sind. Ähnliche Befunde und damit Hinweise auf eine mögliche Modalitätsgewichtung lieferte die Studie von Spence et al. (2001). Die Probanden waren in einer Diskriminationsaufgabe aufgefordert, auf die Seite (links/ rechts) hin zu reagieren, auf der ein Zielreiz präsentiert wurde, wobei der Zielreiz visuell, auditiv oder taktil definiert sein konnte. In einigen Versuchsblöcken wurde die gleiche Anzahl von Zielreizen pro Modalität präsentiert, in anderen war die Mehrheit der Zielreize (75 %) innerhalb einer „erwarteten" Modalität definiert. Spence et al. beobachteten Kosten, wenn der Zielreiz in einer unerwarteten Modalität, gegenüber einer erwarteten Modalität, erschien. In Blöcken mit gleich verteilter Auftretenswahrscheinlichkeit der Modalitäten ergaben sich zudem Verarbeitungskosten, wenn die Modalität der Zielreize in aufeinander folgenden Durchgängen wechselte. Mit anderen Worten war die Verarbeitung immer dann erleichtert, wenn der vorausgegangene Zielreiz innerhalb derselben Modalität wie der aktuelle Zielreiz definiert war. Zusammen genommen deuten diese Befunde darauf hin, dass crossmodale Informationsverarbeitung durch ähnliche (supra-modale) Gewichtungsprozesse beeinflusst werden, wie sie von Müller und Kollegen für die crossdimensionale Informationsverarbeitung innerhalb einer (nämlich der visuellen) Modalität beschrieben wurden.

Experimentelle Befunde der vorliegenden Dissertation

Die vorliegende Dissertation knüpft an die Befunde der (oben beschriebenen) Found & Müller Studie (1996) an, und war somit wesentlich durch den in dieser Studie postulierten *Dimensionsgewichtungsansatz* motiviert und inspiriert. Die im Folgenden

dargestellten experimentellen Untersuchungen wurden mit dem Ziel durchgeführt, tiefere Einblicke in die zeitliche (und räumliche) Genese dimensionsbasierter Aufmerksamkeitseffekte zu gewinnen. Zudem wurde untersucht, inwieweit sich Gewichtungsmechanismen, wie sie der DWA für die visuelle Modalität annimmt, auf eine crossmodale Ebene der Informationsverarbeitung transferieren lassen. Zur Beantwortung dieser Fragenkomplexe wurden in Kapitel II bis V behaviorale (Reaktionszeiten, Fehlerraten) mit elektrophysiologischen (ereigniskorrelierte Potentiale im Electroencephalogramm) Parametern kombiniert. Um weiterführende Information über beteiligte Hirnregionen zu generieren, wurden in Kapitel IV die neuronalen Ursprungsorte elektrophysiologischer Dimensionswechsel-Effekte mittels „räumlich-zeitlich gekoppelter Stromdichte Rekonstruktion“ (EaSI) analysiert.

Kapitel II. Eröffnet wurde der experimentelle Teil der vorliegenden Arbeit mit der Replikation von zwei Experimenten der Found & Müller Studie (1996). Die Aufgabe der Probanden bestand darin, innerhalb einer visuellen Suchaufgabe einen pop-out Zielreiz (roter, blauer, 45° links geneigter, oder 45° rechts geneigter Balken) in einer 3 x 6 Suchmatrix (Distraktoren: grüne, vertikale Balken) zu entdecken (Experiment 1) bzw. zu diskriminieren (Experiment 2). Beide Experimente replizierten exakt die Befunde der Found & Müller-Studie (1996): schnellere Reaktionen wurden für Dimensionswiederholungen relativ zu Dimensionswechseln, jedoch unabhängig von intradimensionalen Merkmalswiederholungen/-wechseln erzielt. Auf elektrophysiologischer Ebene zeigten sich drei Komponenten des ereigniskorrelierten Potentials sensitiv zu diesem dimensionsbasierten Aufmerksamkeitseffekt: eine frontale N2 (tN2), sowie die posterior lokalisierbaren P3 und Slow Wave (SW) Komponenten. Während die tN2 und die SW verstärkte Aktivierungen infolge dimensionaler Wechsel zeigten, führte dieser Effekt in der P3 Komponente zu systematischen Latenzunterschieden. Entgegen früheren Versionen des DWA (Found & Müller, 1996), die dimensionale Wechseleffekte einzig präattentiven-perzeptiven Stufen der Informationsverarbeitung zuordnen, konnte in den vorliegenden Experimenten keine Modulation früher sensorischer Komponenten (P1, N1) festgestellt werden. Dennoch zeigt der Vergleich beider Experimente (Detektion vs. Diskrimination), dass alle identifizierten EKP Komponenten auf perzeptiven, und nicht antwort-basierten, Prozessen beruhen. Alle Komponenten (tN2, P3, SW) zeigten das identische Muster für Dimensionswechsel, unabhängig ob dieser automatisch mit einem Antwortwechsel assoziiert war (Experiment 2) oder nicht (Experiment 1).

Dementsprechend, und in Anlehnung an die Pollmann et al. Befunde, scheint die frontale N2 die Detektion eines Dimensionswechsels sowie die Initiierung einer entsprechenden Verschiebung dimensionaler Gewichte zu reflektieren, welche daraufhin via Feedback Mechanismen über höhere Areale des superioren Temporal- und des Parietalkortex, repräsentiert durch die P3 und SW, zu den dimensionsspezifischen Eingangsmodulen gelangt.

Kapitel III. Eine aktuelle Debatte zur dimensionsbasierten Aufmerksamkeit betrifft die Herkunft dimensionaler Wechseleffekte. „*Perzeptiv-basierte*“ Modell-vorstellungen (Found & Müller, 1996; Wolfe, Butcher, Lee, & Hyle, 2003) ordnen dimensionsbasierte Intertrial-Effekte frühen prä-attentiven Stufen der Informations-verarbeitung zu, bevor der Zielreiz fokal-attentional selektiert wird. Demgegenüber stehen „*antwort-basierte*“ Modellvorstellungen (Cohen & Magen, 1999; Mortier et al., 2005), die spätere Stufen (Stufe der „Antwortauswahl“) als Ursprung dimensionaler Wechseleffekte favorisieren, nachdem visuelle Enkodierungsmechanismen abgeschlossen sind. Das Ziel des dritten Kapitels lag in der Dissoziierung perzeptiver von motorischen Prozessen (in einer visuellen Suchaufgabe). Innerhalb einer „Compound“-Aufgabe (Experiment 3) musste zunächst der Zielreiz (definiert durch eine andere Farbe oder Form) gesucht werden, bevor eine adäquate motorische Antwort (definiert durch die Orientierung des Zielreizes) selektiert werden konnte. Somit konnte sich ein Dimensionswechsel unabhängig von einem Antwortwechsel ereignen und vice versa. Weiterhin wurde auf zwei Komponenten des EKP’s fokussiert, die direkt entweder perzeptive (N2pc) oder antwort-basierte (lateralisiertes Bereitschaftspotential; LRP) Prozesse repräsentieren.

Die EKP-Analyse zeigte, dass dimensionale Wechsel, unabhängig von Antwort-wechseln, in schnelleren Latenzen sowie verstärkten Amplituden der N2pc Komponente reflektiert waren. Diese Befunde deuten daraufhin, dass zumindest Teile des behavioralen dimensionsspezifischen Intertrial-Effektes einer perzeptiven Verarbeitungsstufe entstammen. Antwortwechsel hingegen waren, unabhängig von Dimensions-wechseln, in verstärkten Amplituden des (antwortkorrelierten) LRPs reflektiert, was daraufhin deutet, dass Antwortwiederholungen von residuellen Aktivierungen des vorangegangenen Durchganges profitieren. Bewertet man diese elektrophysiologischen Ergebnisse unbeachet von den Verhaltensdaten, so scheinen Dimensions- und Antwortwechsel in separaten, perzeptiven und antwort-basierten, Verarbeitungsstufen generiert zu werden. Bezieht man jedoch die Verhaltensdaten mit ein, so zeigt sich kein additives, sondern ein

interaktives Verhalten beider Faktoren. Schnellste Reaktionszeiten erzielten Bedingen, in denen beide Faktoren (Dimension und Antwort) in zwei aufeinander folgenden Durchgängen konstant blieben. Der Wechsel eines oder beider Faktoren führte hingegen gleichermaßen zu einer Verlangsamung der Reaktionen. Um dieses Muster in Verbindung mit den EKP Resultaten zu erklären, wird ein Modell vorgeschlagen, welches eine Interaktion beider Faktoren auf einer Verarbeitungsstufe zwischen fokaler Aufmerksamkeitszuweisung und motorischer Antwortproduktion vorschlägt: die Stufe der *Antwortauswahl*. Weiterführende Analysen des (stimulus-korrelierten) lateralisierten Bereitschaftspotentials bekräftigten diese Annahme. Zusammengenommen weisen die in diesem Kapitel erhobenen Daten daraufhin, dass dimensions-basierte Intertrial-Effekte in visuellen Suchaufgaben sowohl *perzeptiven* als auch *antwort-basierten* Stufen der Informationsverarbeitung zuzuordnen sind und erscheinen inkonsistent mit der Annahme, dass dimensionsspezifische Intertrial-Effekte exklusiv in *antwort-basierten* Stufen generiert werden. Zusätzlich bilden die (antwortkorrelierten) LRP Daten in Verbindung mit den Verhaltensdaten Grund zur Annahme, dass *Gewichtungsmechanismen*, ähnlich wie sie der DWA für visuelle Dimensionen vorschlägt, auch innerhalb des motorischen Systems existieren, wodurch korrekte (wiederholte) motorische Antworten (Programme) von Voraktivierungen seitens des motorischen Systems profitieren könnten.

Kaptitel IV. Ein Grundpostulat des DWA betrifft die Gewichtung früher sensorischer Inputareale. Derartige Modulationen würden sich in frühen visuellen Komponenten des EKP (P1, N1) reflektieren, jedoch ließen sich keine P1 oder N1 Effekte in Kapitel II identifizieren. Zudem deuten zahlreiche Befunde aus zwei Dekaden elektrophysiologischer Forschung daraufhin, dass diese Komponenten einzig auf Prozesse assoziiert mit räumlicher Aufmerksamkeit basieren, wohingegen die Verarbeitung nicht-räumlicher Stimuluseigenschaften erst in späteren EKP Komponenten (z.B. „*selection negativity*“) reflektiert scheint. Diese Sichtweise resultiert aus Befunden, die verstärkte P1/N1 Amplituden infolge valide (relativ zu invalide) indizierter Stimuluspositionen zeigten und diesen Effekt als „*Amplifizierungs*“-Mechanismus, der die perzeptive Genauigkeit auf einer aufgemerkten Stimulusposition verbessert, interpretierten (Eimer, 1994; Hillyard, Vogel & Luck, 1998). Eine alternative Erklärung könnte hingegen in der *transienten* Natur dimensionaler Gewichtungsmechanismen liegen. Mit anderen Worten besteht möglicherweise ein zeitliches Limit für zwei aufeinander folgende sensorische

Ereignisse (2000 ms ITI in Kapitel II), damit Dimensionwechsel-Effekte durch frühe *EKP Komponenten* indizierbar sind.

Das Ziel des vorliegenden Kapitels war es zu überprüfen, (i) ob frühe visuelle Verarbeitung durch (nicht-räumliche) dimensionale Stimulusattribute modulierbar ist, und (ii) ob diese Effekte von der Anzahl möglicher Zielreizpositionen abhängen. Zur Beantwortung dieser Fragestellungen wurde eine visuelle Suchaufgabe verwendet, in der ein Hinweisreiz die Position aber nicht die visuelle Dimension des Zielreizes (Experiment 4) indizierte, bzw. weder die Dimension noch die Position des Zielreizes durch den Hinweisreiz vermittelt wurde (Experiment 5). In beiden Experimenten zeigte sich eine dimensions-basierte Variation der frühen visuell evozierten P1 Amplituden sowie der anterioren N2 Amplituden (tN2), wobei sich diese Effekte unabhängig von intra-dimensionalen Merkmalswechseln (Experiment 4) und räumlichen Stimulusattributen (Experiment 5) ereigneten. Weiterführende Analysen (räumlich-zeitlich gekoppelte Stromdichterekonstruktion) zu den neuronalen Ursprungsorten dieser ereigniskorrelierten Dimensionswechsel-Effekte identifizierten, basierend auf deren Zeitverläufen, Quellen im linken frontopolaren Kortex (tN2) und im dorsalen okzipitalen Kortex (P1). Dieser dimensionsbasierte, nicht-räumliche Einfluss auf die frühe visuelle Informations-verarbeitung unterstreicht die Annahmen dimensionsbasierter Theorien zur visuellen Aufmerksamkeit (z.B. DWA) und liefert Evidenz für eine Verarbeitung dimensionaler Information bereits 110 Millisekunden nach der Stimuluspräsentation. Folglich empfehlen diese Ergebnisse eine Erweiterung der (räumlich-basierten) attentionalen *Spotlight-Metapher* früher visueller Verarbeitung um Prozesse (nicht-räumlicher) dimensionaler Stimuluskodierung.

Kapitel V. Nachdem in den vorangegangenen experimentellen Kapiteln klare psychophysiologische Indikatoren für Gewichtungsprozesse innerhalb der visuellen Modalität identifiziert werden konnten, sollte innerhalb des fünften Kapitels überprüft werden, ob und wieweit sich derartige Ergebnisse und Erklärungsansätze auf eine cross-modale Ebene der Informationsverarbeitung transferieren lassen, um ähnliche sequentielle Effekte (z.B. Spence et al., 2001: *modality shift effect*) innerhalb eines theoretischen Rahmens zu integrieren. Zur Umsetzung dieser Fragestellung waren die Probanden aufgefordert, die Modalität eines präsentierten Stimulus (taktil versus visuell) zu diskriminieren (Experiment 6) bzw. ein stimulus-definierendes Merkmal einer motorischen Antwort (z.B. *‚grün'* und *‚langsam vibrierend'* → linker Fuß; *‚rot'* und *‚schnell*

vibrierend' → rechter Fuß) zuzuordnen (Experiment 7). Folglich waren Modalitätswechsel konfundiert mit Antwortwechseln in Experiment 6, jedoch dissoziiert in Experiment 7. Beide Experimente bestätigten frühere behaviourale Verhaltensmuster mit langsameren Reaktionszeiten für Wechsel (z.B. visuell → taktil), relativ zu Wiederholungen (z.B. taktil → taktil), in der Stimulusmodalität. Unabhängig von der jeweiligen Stimulusmodalität, räumlichen Stimulusattributen und motorischen Antworten war dieser Effekt in verstärkten Amplituden der anterioren N1 Komponente reflektiert. Es wird vorgeschlagen, diese Befunde innerhalb eines generalisierten Gewichtungsansatzes zu interpretieren, der den von Müller und Kollegen (1996) postulierten Dimensionsgewichtungansatz um salienz-basierte Modalitätskarten erweitert. Dabei steht der anteriore N1 Amplitudeneffekt des vorliegenden Kapitels in Verdacht, einen *supramodalen* Gewichtsverschiebungsprozess abzubilden, der möglicherweise im Stande ist, attentionale Ressourcen über verschiedene Modalitäten hinweg zu adjustieren. Wie bereits innerhalb der vorausgegangenen visuellen Studien diskutiert, scheint die Funktion dieses frontalen exekutiven Prozesses in einem impliziten Update-Mechanismus zu liegen, der, um im folgenden Durchgang eine optimierte Stimulusverarbeitung zu ermöglichen, attentionales Gewicht entsprechende der aktuell-verarbeiteten Stimulusmodalität verschiebt. Im Einklang mit dieser hypothetisierten Verarbeitungsarchitektur stehen die Befunde früher sensorischer Komponenten, die in beiden Experimenten sowie für beide Modalitäten durch die vorhergehende stimulus-definierende Modalität moduliert waren. Folglich repräsentieren diese frühen modalitätsspezifischen Effekte *Konsequenzen* vorangegangener Ereignisse.

Schlussfolgerungen

Es ist weitgehend akzeptiert, dass unser gegenwärtiges Verhalten von vorhergehenden sensorischen und motorischen Ereignissen geformt wird. Die in der vorliegenden Dissertation zusammengefassten Experimente wurden mit dem Ziel durchgeführt, ein tieferes Verständnis in diejenigen Mechanismen zu gewinnen, die (implizit) Information der Vergangenheit konservieren, um Aktionen der unmittelbaren Zukunft zu modulieren. Dieser Fragestellung wurde sich zunächst mit der Erforschung dimensions-basierter Intertrial-Effekte innerhalb der visuellen Modalität genähert. Basierend auf elektro-kortikalen Signalen konnten hierbei weiterführende Erkenntnisse zur zeitlichen Genese gewichtsverschiebender Prozesse in sukzessiven Durchgangsepisoden gewonnen werden. In Übereinstimmung mit vorangegangenen fMRI Studien (z.B.

Pollmann, 2000; 2006) wurden mehrere Sub-Komponenten visueller Dimensions-gewichtung identifiziert. Ein (prä-)frontaler Prozess (reflektiert in der anterioren N2 in Kapitel II) scheint hierbei in die Kontrolle der Gewichtsverschiebung involviert zu sein, dessen Funktion darin bestehen könnte, einen Wechsel (der visuellen Dimension von *n*-1 nach *n*) zu detektieren und/oder attentionales Gewicht entsprechend des aktuell-verarbeiteten sensorischen Ereignisses für eine optimierte Stimulusverarbeitung (im folgenden Durchgang) zu adjustieren. Ein sich anschließender zweiter (Sub-) Mechanismus, residierend im superioren parietalen sowie temporalen Kortex (reflektiert in der P3 und SW in Kapitel II), könnte diese Gewichtsverschiebungen via Feedback Pfade hin zu dimensions-spezifischen Eingangsmodulen in frühen visuellen Arealen vermitteln. Folglich repräsentieren Modulationen früher pre-attentiver Verarbeitungsstufen (reflektiert in der N2pc in Kapitel III und der visuellen P1 in Kapitel IV) eine erleichterte sensorische Kodierung relevanter visueller Dimensionen als Konsequenz vorausgegangener sensorischer Ereignisse.

Zusätzlich konnte innerhalb der vorliegenden Dissertation konvergierende Evidenz dafür gefunden werden, dass Gewichtungsmechanismen, wie sie der DWA für visuelle Dimensionen postuliert (Found & Müller, 1996), auch auf anderen Stufen der Informationsverarbeitung zu existieren scheinen. So waren gleichartige sequentielle Effekte auf einer cross-modalen Verarbeitungsebene sowie in der Stufe der motorischen Antwortaktivierung zu beobachten. Zumindest für perzeptuelle Verarbeitungsstufen besitzen diese Resultate wichtige Implikationen hinsichtlich der funktionalen Architektur des DWA. Wie bereits im Kapitel V diskutiert, könnten diese Befunde innerhalb einer zusätzlichen salienz-basierten Modalitätskarte, fähig zur Verschiebung attentionaler Ressourcen über verschiedene Modalitäten hinweg, interpretiert werden. Zum anderen demonstrierte Kapitel III, dass motorische Antworten immer dann eine erleichterte Verarbeitung erfahren, wenn sie identisch in aufeinander folgenden Durchgängen blieben. Ähnlich zu perzeptuellen Verarbeitungsmechanismen könnte diese Erleichterung eine prä-existente (gewichtete) Antwortaktivierung innerhalb des motorischen Systems repräsentieren.

Basierend auf diesen experimentellen Befunden bildet sich das Bild heraus, dass mehrere separate Gewichtungsmechanismen in unterschiedlichen Substufen der Informationsverarbeitung zu wirken scheinen, und somit deren individuellen Verarbeitungszeiten (pro Stufe) modulieren. Folglich können experimentelle Bedingungen,

obwohl identisch in ihren Verhaltensdaten (RT), sich wesentlich hinsichtlich ihrer zugrunde liegenden Verarbeitungs-(Sub-)Stufen unterscheiden (siehe Kapitel III: sDdR=dDsR=dDdR). Diese Sichtweise erfährt Unterstützung von einer kürzlich durchgeführten Studie (Rangelov, 2007), die ähnliche Gewichtungsmechanismen bei einer weiteren Verarbeitungsstufe, nämlich bei der Extraktion von Regelanforderungen, beobachtete. So war die Performanz der Probanden immer dann beeinträchtigt, wenn diese ein Aufgaben-Set wechseln (relativ zu beibehalten) mussten. All diese unterschiedlichen Aspekte der Informationsverarbeitung berücksichtigt, scheint es, als ob Gewichtung ein generelles (neuro-)biologisches Prinzip für optimierte Informationsverarbeitung repräsentiert. Dabei könnte die zugrunde liegende naturgemäße Ratio dieser Mechanismen auf der vereinfachten Annahme basieren: Was *jetzt* relevant ist, sollte mit hoher Wahrscheinlichkeit auch *anschließend* relevant sein.

Zusammengenommen liefern die Ergebnisse der vorliegenden Dissertation klare Evidenz, dass, neben bottom-up and top-down Mechanismen, Ereignisse der unmittelbaren Vergangenheit (vorhergehende Durchgangsepisode) einen erheblichen Einfluss auf unser gegenwärtiges Verhalten ausüben. Folglich müssen traditionelle Modelle zur Modellierung visueller und cross-modaler Aufmerksamkeit aktualisiert werden, um diese *Intertrial-Effekte* zu inkorporieren.

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