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Space-Based and Feature-Based Attentional Selection in Perception and Working Memory

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ABSTRACT

In order to manage the high amount of sensory input we experience, attention processes enable the selective prioritization of goal-relevant information over irrelevant distractions. Two fundamental ways in which this is accomplished is by focusing attention at particular locations in the environment (spatial attention) or by focusing on specific forms of information (feature-based attention). Despite many decades of research examining these mechanisms, however, they have been seldom directly compared particularly in relation to their underlying neural mechanisms. In this thesis, the neural correlates of spatial and feature-based attentional selection for perception and working memory maintenance processes are contrasted. Event-related potential (ERP) components from electroencephalography (EEG) recordings are used as markers of such processes. The N2pc component is used to measure lateralised attentional selection to targets defined by one or a combination of spatial locations and features in perceptual tasks, whilst the CDA component is used to measure the active maintenance of target objects/locations in working memory tasks. In total, this thesis contains three lines of investigation. The first line compares these ERP components for attentional selection to targets defined by spatial locations and features and reveals that in many contexts, spatial attention is processed similarly to featural attention with a few notable exceptions (Chapter 2). The second line of enquiry examines how spatial configural information affects feature-based attentional selection when it is a critical component for successful goal-directed search, revealing that such information can guide attentional selection for some feature dimensions (Chapter 3). Finally, the third line of enquiry compares how spatial and feature-based attention influences visual perceptual and post-perceptual working memory processes (Chapters 4 and 5). This investigation lead to the observations that spatial attentional templates are quicker to guide attention when there is no SOA between the cue and target display onset, and that the two types of attention have similar working

memory capacity limitations. These findings culminate to provide one of the first direct comparisons of the neural correlates of attention to spatially or featurally-defined information, thereby expanding the current understanding of how spatial/feature-based attention operates. By measuring real-time event-related responses during these task contexts, the present thesis highlights the independent nature of spatial and feature-based attention and their qualitative similarities, but also how they interact upon one another under some circumstances. The findings aid the literature by shedding light on the argument perceptual and post-perceptual processes involved in spatial attention are qualitatively different from featural attention processes.

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Chapter 1

General Introduction

1.1 Chapter Overview

The brain is tasked with processing sensory input in order to make sense of the environment. Due to the huge quantity of constant input across sensory modalities, not all of this information is interpreted equally. Research has consistently shown that the brain has limited resources with which to attend to the world around us. As a result, some representations are amplified through selective attention whilst others are rapidly degraded and suppressed. What processes are involved in categorizing such input as important or unimportant? Collectively, the cognitive mechanisms that perform this function have been referred to as processes of selective attention.

A huge number of psychological experiments have examined how selective attention operates. Previous research shows that both bottom-up saliency and top-down goals can direct the allocation of attention. Research has shown that an item unique in one feature dimension (e.g. shape, colour, orientation...etc.) appears to 'pop-out' of a scene in which it is presented amongst homogeneous distractors. For example, in a display consisting of several green circles and one red circle, attention is quickly drawn towards the red item, in a reflexive bottom-up fashion. Importantly, attention can also be directed according to goals set by the task demands. In displays with several differently coloured items, for example, this pop-out effect is not available as the target is not differentiated by its unique colour from the distractors. However, attention can still be directed when tasked with locating an item of a particular task-relevant colour. In the evolutionary sense, these two processes are both important as bottom-up salience can help direct attention towards a threat that might be signalled by a rapid movement of an object in the periphery whilst top-down attention can help one pick out safe red berries from poisonous black ones.

This thesis will focus on examining the nature of the top-down processes involved in selective attention towards target objects defined either by their spatial locations or by their features. As outlined in this chapter, these two types of attention (spatial and feature-based attention) have been differentiated in the literature but are very rarely contrasted directly, highlighting the need for an integrative approach. These two types of attentional control will be investigated both for attentional selectivity during the perceptual processing of visual objects, and during the subsequent maintenance of specific objects in visual working memory. These experiments rely primarily on event-related brain potential (ERP) markers of attention. In this introductory chapter, the utility of using ERP measures to investigate basic issues in attention research will be discussed, and the main focus of the research questions addressed in this thesis will then be summarized.

1.2 Spatial Attention

Classical attention research (e.g. Helmholtz, 1925) observed the phenomenon that attention can be directed to a peripheral area of visual space without requiring one's direct gaze. Posner (1980) reviewed modern research on covert spatial attention, and suggested that these attended regions in the visual field have amplified processing power relative to unattended locations, akin to the manner in which a spotlight illuminates a specific area of space. This spotlight account has been largely supported by behavioural studies, both for exogenous (bottom-up) and endogenous (voluntary) spatial attention. Jonides (1976), for example, reported a study in which participants were required to report whether a letter L or a letter R were present in a display consisting of four unique letters. Before each visual search display, participants received a salient peripheral onset cue which indicated either the location of the target (valid cues) or the location of a distractor (invalid cues). The researchers

reported that participants were significantly quicker and more accurate at reporting target presence in the valid relative to the invalid cue trials, even when the cues were spatially uninformative. In terms of Posner's (1980) spotlight metaphor of attention, the cues in Jonides' (1976) study exogenously triggered an attention shift to the cued location and consequently amplified the processing in this region such that when the cue was valid, the target was detected with greater efficiency than when the target appeared outside the focus of attention. Posner, Snyder, and Davidson (1980) found similar spatial cueing effects in experiments where the attended location was indicated by symbolic informative cues (arrows), and observers had to direct their attention endogenously to the cued location. A large number of behavioural studies have used variations of the spatial cueing paradigm introduced by Posner and colleagues to investigate the mechanisms of spatial attention, but fundamental questions about how spatial attention affects visual processing remain unresolved. This showed that behavioural measures alone cannot illuminate all aspects of spatial attention. The use of electroencephalography (EEG), a functional imaging technique in which neural electrical activity is recorded, allowed researchers to investigate questions relating to the neural correlates of spatial attention, and in particular, address the classical question whether spatial attention operates at an early or late level of visual processing.

1.2.1 ERPs in Attention Research

Despite the fact that EEG dates back as early as the 1920s (Tudor et al., 2005), its use in the study of visual attention is relatively new. The breakthrough which facilitated the use of EEG paradigms in attention research was the discovery of the Event Related Potential (ERP) in the 1960s. An ERP is measured by averaging the electrical cortical activity recorded during numerous trials locked to the onset of the task-relevant stimuli. The positive and negative local peaks within the averaged ERP waveforms constitute the ERP components.

These components allow researchers to measure and compare the time-course of cognitive processes related to perception, cognition and action with a high degree of temporal precision. Given the electrical properties of the anatomical structures between the brain and the surface recording electrodes (skull, meninges, intracerebral fluids), and the simultaneous activity of multiple neural generator processes at different locations, EEG recordings have low spatial precision and are therefore not ideal for investigating the localization of these processes. In the following sections, core principles and debates within the attention literature which have been addressed with ERP methodologies will be explored. These include the time-course of the attention shift, the processes responsible for resolving competition in multiple-stimulus arrays, the serial or parallel nature of attention, and the dissociation between top-down and bottom-up processes. The roles that ERP measures have played in investigating a fundamental question related to the operation of spatial attention will be discussed – does it have its effects at early or late stages of visual processing?

1.2.2 Early or Late Selection in Spatial Attention

The use of ERPs has helped to resolve disputes within attention research based on behavioural experiments which once dominated the field. One such debate is related to the time-course by which a task-relevant item is selectively attended relative to stimuli onset in tasks where it is selected based on its spatial location. Broadbent's (1958) Filter Theory of Attention suggested that spatial attention operates rapidly during early stages of visual processing. His model outlined that all objects in the visual field are initially processed in parallel during an early pre-attentive stage. Only items with target-defining elementary physical features (most notably items presented at currently task-relevant locations) are then selected and gain access to a limited-capacity object recognition system, which operates in a strictly serial manner. This early selection model has not gone unopposed. Deutsch and

Deutsch (1963), for example, argued that parallel pre-attentive processing encompasses both the perceptual and the semantic analysis of visual stimuli, and that selective spatial attention only operates at a late stage close to response selection, after all stimuli have been analysed semantically. In order to resolve this long-standing dispute in the literature, ERP markers of spatial selectivity have been particularly helpful.

Early ERP research discovered the first components related to the process of space-based attention selection. In their study, Van Voorhis and Hillyard et al. (1977) had participants attend to a location either to the left or the right of a central fixation cross. On each trial, a single item was presented either at the attended location or in the unattended location. The researchers found that when the stimulus appeared in the attended location, there was a greater positive local peak in the ERP waveform, starting at about 80-90ms post-stimulus onset. This component, labelled the P1, represented a rapid, early modulation of visual processing related to spatial attention. Further studies using similar paradigms revealed other early components such as an enhanced N1 for spatially attended auditory stimuli (Hillyard et al., 1973). In these early studies, participants were asked to maintain their attention at a fixed location throughout a block. Other studies in which the attended location was instead directed on a trial-by-trial basis by a central arrow cue presented before the target stimulus reported similar modulations (Mangun & Hillyard, 1991; Eimer, 1994). These components are in line with the temporal order described by Broadbent's model, as they show that spatial attention can affect visual processing early, occurring within the first 100ms of stimulus-onset.

After realising that selective attention processes can occur at such early latencies, research shifted to search for the temporal transition between pre-attentive and attentive activity. Martinez et al. (1999) found that the C1 component, which is related to the initial V1 activation by sensory input (Clark et al., 1995) and occurs from 60 ms post-stimulus onset,

was not modulated by spatial attention manipulations. As a result, researchers have concluded that the short 20 – 30 ms interval between the C1 and P1 components might represent the narrow transition between pre-attentive and attentive processes. However, these results cannot be said to provide a comprehensive and general confirmation of Broadbent's early selection model, as they only show that early visual responses can be modulated as a function of the current focus of spatial attention. They do not show that attentional selectivity occurs always or exclusively at this early stage, or that early selection marks the transition from parallel to serial processing.

Other ERP research has supported Deutsch and Deutsch's (1963) claim that attentional selectivity can also affect later stages. Eimer (1994; 1996a), for example, reported the existence of a sustained component characterised by a greater posterior negative amplitude for spatially attended vs unattended stimuli from 200 ms to 400 ms post-stimulus onset. This component shows that attention can modulate activity in the later post-perceptual stages. If this was correct, even semantic processes like stimulus identification might occur pre-attentively, in contrast to what was claimed in Broadbent's model. This was supported by ERP studies using the attentional blink paradigm. In these studies, distractor items are shown in quick succession among two items with target-matching features. The temporal proximity of these two targets, T_1 and T_2 , is manipulated. Using this paradigm with words, Luck et al. (1996) found that when T_2 was presented near to the presentation of T_1 , the P1 and N1 components for T_2 were not modulated compared to distractors. However, when T_1 and T_2 were temporally separated, T_2 had enhanced P1/N1 components compared to the distractors. The researchers concluded that the analysis of T_1 resulted in the suppression of spatial attention for T_2 when the two were temporally proximal. Despite being apparently excluded from focal attentional processing, an N400, a marker for the semantic processing of words, was present for T_2 even when it was presented close to T_1 . Together, the ERP results do not

support either early or late selection models. Instead, they suggest that these early and late processing accounts represent a false dichotomy and show that selective attention processes can be flexible depending on stimulus parameters and task demands.

1.3 Feature-Based Attention

While spatial attention refers to the selective processing of visual stimuli at task-relevant spatial locations, feature-based attention describes attentional selectivity for items with relevant non-spatial features. In feature-based attention studies, researchers define the target by a unique feature or conjunction of features which physically identifies it from distractors in a visual search display. This continuing body of work strives to uncover how visual targets are selected in a top-down, goal-oriented manner in multiple-stimulus displays where their location is not known in advance, and what factors affect the efficiency of such processes.

1.3.1 Visual Search and Feature Integration Theory

Treisman and Gelade (1980) asked participants to search for a target in a visual display with multiple coloured letter distractors. In separate blocks, the target was defined either by a single unique feature (e.g. a blue S) or a conjunction of features (e.g. a green T amongst brown Ts and green Xs). The researchers reported that in the former condition, the target would ‘pop-out’ amongst the distractors as it was both the only blue item and the only letter S. This facilitation effect resulted in greatly reduced reaction times in comparison to the conjunction target condition. Furthermore, they found that when the number of distractors increased, the reaction time for single feature trials remained constant whilst it linearly increased in the conjunction feature trials. On the basis of these differential search slopes for

feature and conjunction search, Treisman and Gelade (1980) formulated the influential Feature Integration Theory, which outlined a new framework for the perception and selection of features and of integrated objects. In this framework, each feature dimension (colour, orientation, shape...etc.) is coded by separate feature maps, where all objects are represented in parallel. When searching for a target defined by a single feature, search can run in parallel, simultaneously between all objects in the visual field, as only one feature map is required. In conjunction tasks, however, coordination between feature maps is necessary and requires the serial attentional processing of objects. When visual attention is shifted to an object location, its features are bound together to form an object file – a mental representation of the object. If this object file fits the target specifications defined by the current task set, the target is selected and the search is over. If not, new object files will be created serially until an object is identified as the target.

The critical assumption of FIT is that attention is allocated serially to each object in a search display until the target is found. This serial processing component of the theory helped to explain the finding by Treisman and Gelade (1980) that search slopes were steep for conjunction search but flat for feature search. Under the FIT framework, the serial process of comparing each object file with the target specifications stored in long term memory is random. Therefore, in some trials, the participant would immediately process the target and in others they would process the target last. When averaged together, the mean reaction time will therefore represent the time to search half of the objects in the visual field. In the absent condition, however, all items must be searched in order to conclude that the target is not present. Thus, the serial processes in FIT are well-suited to explaining the nature of Treisman and Gelade's results.

Further work by Treisman and colleagues supported the FIT model. In one study, Treisman (1986) presented participants with a spatial cue before the visual search display

which either cued the location of the target (valid cue) or a distractor (invalid cue). Reaction times for conjunction targets were speeded by the presence of valid cues compared to invalid or neutral cues. Treisman concluded that this was because the cue triggered a shift of attention towards the object in the cued location. Whichever item was presented in the cued location was the first to be processed by serial focal attentional mechanisms. Hence, trials with valid cues, in which the target was processed first rather than a distractor, had faster RTs than trials with invalid cues. For single feature targets, however, there was no facilitation effect of RT for trials with valid compared to neutral or invalid trials. Under the framework of FIT, Treisman explained that this was because search for such 'pop-out' targets uses a parallel rather than a serial search mode. Hence, as all object features are processed simultaneously, and target detection can be based on single feature maps, pre-emptive shifts of attention would not increase search efficiency.

FIT also predicts that conjunction search should be adversely affected when attention is allocated elsewhere. Treisman and Schmidt (1982) presented participants with a brief display consisting of large, uniquely coloured letters sandwiched between two small black numerical digits. Participants were tasked first with reporting the identity of the digits followed by the position, colour, and identity of the three middle letters. Importantly, the researchers stressed that the digit task was the most important. Given the brief duration of the display, the lateral distance between the black digits, and the many features required to report, the task was difficult to perform and participants committed a relatively high number of errors. The researchers reported that, in line with their hypothesis, participants were significantly more likely to make errors in which the colour of a particular object was mistakenly recalled to be another colour in the same display than a colour not in the display. They concluded that the former was an example of an 'illusory conjunction'; a representation of an object in a display which is erroneously mixed with features from a different object in

the same display. In terms of Treisman's Feature Integration Theory, this study reveals that coordination between different feature maps can be disrupted when attention is allocated to different locations in the visual field.

1.3.2 Other Frameworks for Feature-Based Attention and Visual Search

As an extension of Feature Integration Theory, Wolfe (2007) developed his Guided Search model of feature-based visual search tasks. The critical advance to Treisman's previous suggestions concerns the concept of attentional guidance. According to Wolfe, attention is not allocated randomly to possible target objects until the real target is found, as proposed by Treisman, but can instead be guided by information from the feature maps. Target-defining features obtain higher attentional priority, and are therefore weighted more strongly on a hypothetical salience or priority map, which determines the order in which attention is directed to different objects during conjunction search. One object is then selected at a time, but multiple selected objects can be identified in parallel. Wolfe (2007) describes this hybrid parallel/ serial architecture by using the metaphor of a car wash: cars enter one at a time but many cars can be inside at once.

Another framework developed to explain feature-based attentional selectivity in visual search is the Attentional Engagement Theory introduced by Duncan and Humphreys (1989). In behavioural tasks, these researchers tested how both the physical similarity between the target and distractors and within distractors affects search efficiency in a visual search paradigm. In this experiment, participants were required to search for either an L or a T rotated at 45 degrees amongst either a homogeneous (all upright or 90 degree rotated Ts) or heterogeneous (equal number upright and 90 degree rotated Ts) array. Across the 4 experiments in this study, the similarity relationship between items within the visual search displays strongly affected search efficiency in ways not explained by FIT. According to

Duncan and Humphreys (1989), search efficiency is jointly determined by the similarity between the target and distractors (where low similarity affords efficient search), and the degree to which distractors are similar to each other (with high similarity linked to efficient search, as similar distractors can be grouped and inhibited together).

1.3.3 *ERP Correlates of Attentional Selectivity in Multiple-Stimulus Visual Search Displays*

While the P1 and N1 have helped researchers to understand the time at which attentive processes occur within spatial attention tasks, there are many real-life situations where feature-based selective attention is required to attend to an object within a busy visual field and advance spatial information about the likely location of the target is not available. This context, where the visual system must contend with many objects competing for the limited resources of the attentional system, is studied with visual search tasks. As described previously, targets are displayed among distractors and participants are tasked with finding the target according to certain defining features, and search efficiency is inferred from search slopes for reaction times and/or accuracy. In addition to these behavioural measures, many recent studies have also used ERP markers of attentional selection processes in visual search, to examine how stimulus features and differences in task demands affect the allocation of attention to particular objects in visual search displays. The most prominent ERP marker used in these experiments is the N2pc, a robust lateralised component characterised by a posterior negativity contralateral to the hemifield of a target which occurs from around 200 ms – 300 ms post-stimulus onset (Luck, Fan & Hillyard, 1993). Visual search studies have revealed that the N2pc reflects a lateralised attentional bias in visual processing that is triggered by targets defined by one feature (Luck & Hillyard, 1994a), multiple conjunctive features (Luck et al., 1997), and even by non-target distractors with one target-matching feature in conjunction tasks (Luck & Hillyard, 1994b). However, no N2pc is triggered by a salient

distractor with a pop-out task-irrelevant feature (Luck & Hillyard, 1994b). These early studies have suggested that the N2pc reflects the attentional selection of objects with target-matching features in visual search tasks.

It is important to note that the P1 and the N2pc are sensitive to different kinds of task manipulations. The P1, for example, only occurs when the target's location is known and attended to in advance of its onset. Furthermore, as Mangun and Hillyard (1987) reported, the amplitude of the P1 is not affected by whether the item presented at the focally attended location is a target or a distractor. As a result, researchers suggest that the effects of spatial attention on the P1 represent an attentional modulation during the feed-forward sweep of visual processing. In contrast, the N2pc is assumed to be generated at a later stage where visual activity starts to be affected by top-down feedback about the presence of potentially task-relevant features at specific locations in the visual field.

One of the early debates within the N2pc literature is whether the component reflects the selection of the target item or the inhibition of the distractor items in the visual field. Supporting the inhibition account, Luck and Hillyard (1994b) found that there were only N2pcs to targets when they were surrounded by distractors and not when they were presented in isolation. Furthermore, the N2pc has been shown to increase in amplitude relative to the number of distractors present (Mazza et al., 2009). However, other studies (e.g., Eimer, 1996) suggested that the N2pc primarily affects target facilitation. For example, Mazza et al. (2009) reported that N2pc amplitudes were not affected by the spatial proximity of the target and the distractors, supporting the target selection account. Other research points to a more nuanced answer. Hickey et al., (2009) found a distractor positivity (Pd), a component with a similar time course and localisation to the N2pc but characterised by a contralateral positivity rather than a contralateral negativity, to colour distractors when asked to report the orientation of luminance targets presented on the vertical meridian. However, when participants were

simply asked if the target was present, there was no Pd observed. Given these results, it is possible that in many contexts, the N2pc reflects the joint contributions of both the inhibition of salient distractors and the feature-based attentional selection of targets.

In the next sections, the results of recent N2pc research investigating different aspects of feature-guided attentional selectivity in visual search will be reviewed. First, the question is addressed whether candidate target objects are selected serially, as suggested by FIT, or in parallel. Next, the bottom-up versus top-down nature of attentional biases in visual search are discussed. Finally, the question how attentional guidance operates for single features, feature configurations, and objects defined by feature conjunctions will be considered.

1.3.4 Serial or Parallel Feature-Based Selection?

Another central issue within the attention literature is whether attentional selectivity in multiple stimulus arrays acts in a serial or parallel manner. Treisman's (1988) Feature Integration Theory argues that in difficult search tasks with heterogeneous distractors and/or targets defined by a conjunction of features, attention shifts from one object to the next in a serial fashion (see also Wolfe, 2007, for similar suggestions). This is supported by their finding that reaction times increase relative to increases in set size at a rate of about 20 – 80 ms per object. However, Duncan et al. (1994) argued that these rates are not an accurate assessment of what they call attentional dwell times, which are typically in the range of several hundreds of milliseconds, and that multiple objects can be selected and processed in parallel in a single attentional episode.

EEG work based on N2pc components (Woodman & Luck, 1999; 2003) attempted to resolve this issue. In one study, the N2pc was measured in a task where participants were asked to respond, via button press, according to the location of the gap in an infrequently present square target in a display composed of four differently coloured items on a black

background. The target was described as being one colour (e.g. red) for 75% of the target-present trials and another colour (e.g. blue) for the remaining 25% of target-present trials. In the target-absent condition, the display contained items with both of the target colours on opposite sides. The researchers reported that in the target absent condition, an initial N2pc marked an attention shift towards the more frequent target colour (e.g. red) followed by a polarity reversal in the posterior electrodes marking another shift 100 ms after the first one towards the less frequent target colour (e.g. blue). In a second experiment, the authors showed a similar pattern of serial attention shifts to first, a target-matching item near fixation, followed by another shift to an item at a greater spatial eccentricity from fixation. Together, this study appears to support the serial account of attention selectivity.

However, it is also possible that both items were selected and processed simultaneously, as the N2pc is only a measure of the relative attentional priority of two items in opposite hemifields. To address this criticism, the same researchers (Woodman & Luck, 2003) conducted a new experiment in which one target was placed on the vertical meridian and the other target was placed on the horizontal meridian. Given that the N2pc is only sensitive to attentional biases triggered by lateralized objects in the left/right visual field, the target item on the vertical meridian would not trigger an N2pc. The researchers reported that when the item on the horizontal meridian was close to fixation, it resulted in an N2pc which was 150 ms earlier than conditions in which the horizontal meridian target was at a greater eccentricity relative to fixation. They concluded that attention shifts first towards the target-matching item with greatest spatial proximity to fixation and then shifts in a serial manner towards the next target-matching item. These results support a serial account of feature-guided attentional selection mechanisms, in line with the predictions of FIT and Guided Search.

Other more recent N2pc studies have shown that such serial shifts can occur very rapidly. In experiments reported by Jenkins, Grubert and Eimer (2018), participants were presented with visual search displays, each consisting of four alphanumeric symbols and each within a shape in cardinal positions equidistant to a central fixation cross. One of these objects was the benchmark that had to be selected first, before attention could be shifted to another object (the target). In one condition (feature-guided attentional shifts), participants were required to first identify the colour of the character within a singleton shape and then report whether the colour-matching item at another location was a digit or a letter. In another condition (purely voluntary shifts), participants were required to identify the benchmark by its singleton shape and then report the alphanumeric status of the item clockwise or counter-clockwise from the benchmark. The results revealed that both lateral benchmarks and lateral targets yielded significant N2pcs, but, critically, that the onsets of these components were significantly earlier for the benchmark compared to the target. This supports the serial account of attention as it shows participants first attended to the benchmark and then shifted to the target location. On average, this attention shift from the benchmark to the target object was extremely rapid for the feature-guided task (47 ms) and considerably longer for the purely voluntary task (128 ms). Together, these results reveal that the speed of serial shifts can be very quick and differs substantially for feature-guided versus fully endogenous (voluntary) attention shifts.

1.3.5 Top-down or Bottom-up Attentional Control in Visual Search

Another important debate in visual attention and visual search is whether feature-based attentional selection processes operate in an exogenous, bottom-up manner or in an endogenous, top-down manner. Treisman and Gelade (1980) showed that when targets are defined by one unique feature, they can ‘pop-out’ among the distractors, yielding a very

efficient search. When targets ‘pop-out’, searching times are not increased when adding additional distractor items. In these circumstances, the authors argued that attention shifts towards the target item as a result of its perceptual salience (e.g. a red target among green distractors) and regardless of the top-down intentions of the participant. Koch and Ullman (1985) suggested that stimulus salience (e.g. unique features, local contrast) is represented topographically and that attention is automatically directed towards the region of space with the highest combined salience.

Given this finding, the question remains to what degree such bottom-up signals can be modulated by top-down processes. In a behavioural study, Theeuwes (1991) had participants search for a unique shape among distractor shapes (e.g. a diamond among circles). Reaction times (RTs) were slower for displays which had an additional salient colour singleton distractor than for those which did not. This work showed that the process of attention selection can be impeded by salient items which do not fit the current task set. These items appear to capture attention automatically even though they are known to be task-irrelevant. Other studies, however, suggest that these salient bottom-up signals can be efficiently ignored. In their study, Folk et al. (1992) gave participants a spatially non-predictive cue in advance of a target search display. They found that RTs were quicker for targets at cued compared to non-cued locations, showing that the cues attract attention. These cueing effects only occurred, however, when the cue features matched the task-set (e.g. red cue for a red target) and not when the cue colour did not match the task-set or when the cue was a singleton in another feature dimension (e.g. shape, orientation, etc.). In response, Theeuwes et al. (2000) suggested that the lack of spatial cueing effects for task-irrelevant cues was due to an initial attention shift towards the cue location followed by a rapid disengagement.

Eventually, evidence from electroencephalography helped to clear up this debate. Hickey et al. (2006) measured the N2pc in a task with shape singleton targets amongst salient

task-irrelevant colour distractors on a portion of trials. When the shape target was on the vertical meridian, there was an N2pc to laterally presented colour distractors. Furthermore, when the shape target and colour singleton were presented in opposing visual fields, there was an initial N2pc in the direction of the colour singleton followed by a second N2pc signalling another shift to the target location. This shows that salient bottom-up stimuli can attract attentional shifts despite their irrelevance to, and even distraction from, the task demands.

In contrast, other research suggests that in some circumstances, bottom-up salient objects do not capture attention when they are task-irrelevant. Eimer and Kiss (2008) presented participants with spatially uninformative colour singleton cues before a visual search display. In different blocks, participants either searched for a red target object among grey distractors (Colour Task) or a small bar among large bars (Size Task). In the colour task, the colour singleton cue elicited large N2pc components, indicating an attentional shift. In the shape task, however, this same colour singleton cue did not elicit an N2pc. Instead of a contralateral negativity, in fact, these cues yielded a contralateral positivity indicative of the Pd component, which is associated with distractor suppression. The authors concluded that N2pcs to salient cues only occurred when the cues had task-relevant features. Furthermore, given the precise temporal resolution of ERP markers, these results also provided evidence against Theeuwes' (2010) explanation that salient task-irrelevant cues initially capture attention, which is then rapidly disengaged.

Together, Eimer and Kiss (2008) and Hickey et al. (2006) offer conflicting conclusions about how the visual system deals with salient and task-irrelevant distractors in visual search paradigms. It is possible that the ability of salient distractors to capture attention depends on the constraints of the task at hand. In Eimer and Kiss' (2008) study, the visual search display was very brief and ended before a response could be generated. In the Hickey

et al. (2006) task, however, the visual search display was available on-screen until the participant responded. It is possible that in the former task, the visual attention system was primed to be as efficient as possible, as any delay caused by an erroneous attention shift would likely result in missing the target completely. In the latter task, however, participants had less temporal pressure to make a quick decision and so delays associated with shifts towards task-irrelevant distractors were less costly to task performance.

In order to investigate this possibility, Kiss et al. (2012) performed a study in which search arrays contained a shape singleton target and a colour singleton distractor. Display duration was manipulated such that in one condition, the visual search displays remained on-screen until the participants' response, similar to the Hickey et al. (2006) task, while in another condition, the visual search display was presented for only 200 ms. The researchers found that there was only an N2pc to the colour singleton distractor in the long duration condition. In the short duration condition, they reported the presence of a Pd component. In context, these results suggest that while attention can be erroneously captured by task-irrelevant salient stimuli, this only occurs when these shifts do not compromise task performance. When temporal pressure is high, the visual system can counteract such shifts by actively suppressing such distractors. In summary, there is evidence that top-down task sets for target features can override bottom-up attentional capture, but only when this is required by the specific temporal demands of an attentional task.

It should be noted that there is another possible source for feature-based attention effects that are not completely under top-down control. For example, Theeuwes (2013) argued that what often appears to be top-down attention to features may just be an effect of exogenous inter-trial priming. In one study, participants were presented with a display consisting of two salient colour singleton circles (e.g. a green and a red circle) among grey distractor circles. Within each of the circles was a line either at vertical or horizontal

orientation. Participants were cued with an always-valid word cue directing participants to one of the singleton items (e.g. 'green' or 'red'), and then tasked to report the orientation of the line within the relevant target singleton. When the lines within the two singleton circles were of the same orientation (congruent), RTs were quicker compared to when the lines were of different orientations (incongruent). Theeuwes suggested that if the top-down target definition cue was effective, participants would immediately select the target item, without attending to and identifying the lines at the other unattended location. In this case, there should be no difference in RT between the congruent and incongruent trials. Given these results, however, it is clear that participants were influenced by the orientation of the line within the other task-irrelevant salient colour singleton, indicating that top-down feature cues were unable to prevent the attentional processing of this irrelevant stimulus.

Using identical stimuli, Theeuwes (2011; unpublished data reported in Theeuwes 2013) had participants either report the orientation of the bar within a specific singleton colour (e.g. red or green) or alternating singletons on each trial (e.g. red then green...etc.). Under these circumstances, RTs were reduced for congruent compared to incongruent trials in only the alternating singleton condition. According to Theeuwes, this difference reflects exogenous inter-trial priming. When participants were given a single target sustained throughout a block, the opposing colour singleton was not primed. Hence, in these trials, there was no congruency effect between the line orientations of the two colour singletons. These results suggest that many studies involving feature-based attention do not only reflect top-down, goal-oriented attentional selection processes but that unintentional inter-trial priming effects may also be in operation, resulting in additional attentional biases that are generated in a bottom-up exogenous manner.

1.3.6 Attentional Guidance by Features, Feature Dimensions, Feature Configurations, and Feature Conjunctions

The increasing use of ERP methodologies has also helped to provide more detailed insights into the mechanisms and time course of feature-guided attentional control processes in different types of visual search tasks. Kiss, Jolicœur, Dell'Acqua and Eimer (2008) investigated whether the current task set can bias attention towards particular feature dimensions. In this task, the visual search display was composed of homogeneous green circle distractors and either a colour singleton (e.g. red circle) or a shape singleton (e.g. green diamond). In separate blocks, participants were tasked with either reporting the location of a specific colour singleton (e.g. a red circle in the Colour Task) or a specific shape singleton (e.g. a green diamond in the Shape Task) relative to the central fixation cross. When the target was absent in the display, which occurred on 67% of trials, the relevant singleton was replaced with either a nontarget colour singleton (e.g. a blue circle) or a nontarget shape singleton (e.g. a green diamond) depending on the task. Relevant-dimension nontarget singletons triggered larger N2pc than irrelevant-dimension nontarget singletons, despite being physically identical between tasks. Furthermore, Kiss et al. (2009) showed that only relevant-dimension nontarget singletons elicited an N2pc when appearing in task-irrelevant locations (experiment 2) and that there was a significant N2pc towards the relevant-dimension nontarget singleton when displayed opposite an irrelevant-dimension nontarget singleton (experiment 3). Together, these experiments support the notion that feature-guided attention involves top-down processes that can bias visual processing in favour of specific currently task-relevant feature dimensions, such as colour or shape.

Other work by Kiss, Grubert and Eimer (2013) investigated the nature of the representation of conjunction targets. Do such “target templates” represent target objects in a fully integrated fashion, or do they represent each target feature separately and

independently? In their study, participants were tasked with reporting the orientation (vertical or horizontal) of specific target singleton bars per block defined by both a colour (e.g. red or blue) and a size (e.g. small or large) among grey medium-sized distractors. Before the presentation of the target display, a task-irrelevant and spatially uninformative cue display consisting of a singleton appeared which either matched both, one, or none of the target features. The researchers reported cueing effects for fully matching targets but not for partially matching or non-matching nontargets. These results suggest that only cues that fully match the target were able to capture attention, indicating that the representation of the target features is integrated rather than independent. However, Kiss et al. (2013) also found that N2pc components were triggered by the cues when they were both fully matching and partially matching the target, indicating that – in contrast to what was suggested by the behavioural spatial cueing effects – both types of cues were able to attract attention. This apparent contradiction was resolved by assuming that feature-based attention for items defined by a conjunction of target features works in two separable stages. Firstly, attention selects all objects in the visual field which match at least one of the target-defining features. Secondly, attention quickly disengages from objects which do not fully correspond to the target definition (i.e. partial nontargets). In a second experiment, Kiss et al. (2013) presented participants with displays composed of singletons which were, with equiprobability, small blue, large blue, small red, and large red. In this task, participants had to remember two target features (e.g. red and small) and asked to respond if the singleton had one or both of these features. Under these conditions, unlike in Experiment 1, there was an equal RT cueing effect for cues which matched either one or both of the target-defining features. Kiss et al. (2013) concluded that the task instructions marking singletons matching only one of the target features as response-relevant bypassed the disengagement stage of the 2-step process.

Another important question in visual search is whether attention can be guided simultaneously by two features from the same dimension (e.g., two colours). According to the Guided Search model (Wolfe, 2007), this is not possible: Only one feature per dimension can be involved in the guidance of attention to visual search targets, as reflected by substantial performance cost when targets are defined by a combination of features from the same dimension (e.g., two colours). However, not all researchers agree. For example, Carrasco, Ponte, Rechea, and Sampedro (1998) showed that homogeneously coloured distractors in a search for a conjunction colour target can be rapidly rejected, resulting in a highly efficient search. To further examine the relative efficiency of searching for colour-colour conjunction targets, Berggren and Eimer (2016a) employed N2pc components. Participants searched for a target object defined by a particular configuration of colours (e.g. red above blue). They were required to respond, via button press, whether the target item was present or absent in the displays. In non-competition trials, targets or partially matching distractors, which matched one of the two target colours, were displayed amongst three similar dual-colour distractors. In competition trials, both a target and partially matching distractor were presented such that one item was on the vertical meridian and the other on the horizontal meridian. These displays had two non-matching distractors.

Results showed that N2pc components were elicited by both target objects and partially matching objects at the same onset latency. Furthermore, the sum of the N2pcs to the two partially matching objects was of equal amplitude to N2pcs to targets up to 250ms post-display. From this point onwards, the target N2pc was enhanced relative to the sum of the partially matching distractors. This suggests that attention was initially allocated in parallel and independently to target-matching features, regardless of whether or not the other target features were present. However, at about 250 ms post-stimulus, the presence of both target colours in the same object is registered and starts to affect the allocation of attention.

These findings suggest that, at least for colour, same-dimension conjunction targets can be found remarkably efficiently, and thus challenges one of the central assumptions of Guided Search (Wolfe, 2007).

Finally, another question is whether feature-based attentional guidance processes can be restricted to particular locations, thus effectively combining feature-based and space-based attentional control. To test this, recent N2pc work has investigated whether attentional selection can be guided by representations of target features at particular locations. Berggren, Jenkins, McCants and Eimer (2017) presented participants with visual search displays consisting of four uniquely coloured bars located diagonally from the central fixation at either vertical or horizontal orientation. Different colour targets were defined for opposing lateral visual fields (e.g. red in the left field, blue in the right field), so that the task set contained two colour/location combinations. Each target display was preceded by a noninformative cue containing target-coloured objects at locations that were either task-relevant or irrelevant for this particular colour (target-matching versus mismatching locations). In two experiments, N2pc to location-matching and mismatching colour cues were identical. This suggests that feature-based attention cannot operate selectively for specific areas of the visual field, suggesting that feature-based and space-based attentional control operate largely independently and cannot be integrated. Feature-based attention appears to work in a spatially global manner, irrespective of whether particular locations are relevant or irrelevant for specific features. This hypothesis will be further tested in the experiments reported in Chapter 4 of this thesis.

1.4 Spatial and Feature-Based Representations in Visual Working Memory

1.4.1 Sensory Recruitment Theory

Whilst most of the introduction thus far has focused on attentional control processes involved in space-based and feature-based modulations of sensory-perceptual visual processing, it is also important to understand how perceptually attended features and objects are stored in working memory for future use. Classic ideas about working memory have suggested that sensory perception and working memory storage are anatomically and functionally distinct. Baddeley and Hitch (1974) proposed a cognitive model which distinguishes separate processes involved in the maintenance of visuo-spatial and verbal information within working memory, both of which are controlled in a top-down manner by a central executive. Classic imaging studies have pointed to the prefrontal cortex (PFC) as the site of visual working memory storage (Goldman-Rakic, 1990; Fuster & Alexander, 1971). However, more recent work suggests that the PFC is the likely location of the top-down control processes governed by the central executive. In contrast, working memory storage may be implemented within the same posterior regions that are also responsible for the on-line perception and recognition of visual stimuli (Postle, 2006). This sensory recruitment hypothesis of working memory storage suggests a close neural and functional relationship between attentional mechanisms in visual perception and working memory.

Behavioural evidence has supported the existence of such links. Although previous research has typically concluded that working memory capacity is relatively constant, with an upper limit of three to four items (e.g. Cowan, 2001), capacity has been shown to vary considerably across participants. In one study, Anderson, Vogel and Awh (2013) found that the individual working memory capacity limitations of participants, measured through the ratio of error rate to set size, correlated with the search slopes of a subsequent visual search

task. Individuals with higher working memory capacities were shown to have shallower search slopes for displays with heterogeneous distractors, indicative of more efficient search, compared to individuals with lower capacities. Kane, Bleckley, Conway, and Engle (2001) also demonstrated that capacity limitations of working memory correlate with attentional control processes in a cued saccade/anti-saccade task. There was no difference in performance between the high and low working memory capacity individuals in a pro-saccade task. However, in the anti-saccade condition, where eye movements were required when the cue was presented opposite the target location, individuals with low working memory capacities had greater error rates and longer reaction times relative to those with high capacities, suggesting that working memory capacity and attentional control in on-line perceptual tasks are linked. Together, these and many other behavioural studies have supported the idea that attentional mechanisms are closely involved in the maintenance of visual stimuli in working memory (see Awh, Vogel, & Oh, 2006, for a review). If sensory-perceptual regions are recruited during working memory storage (Postle, 2006), the principles and mechanisms of space-based and feature-based attention uncovered during perceptual processing (as discussed previously) may also apply during the storage of selected visual objects in working memory.

ERP studies of visual working memory have revealed a lateralized marker of working memory maintenance processes. Vogel and Machizawa (2004) employed lateralized change detection tasks where they presented participants with a bilateral memory sample array composed of coloured objects to the left and right of fixation. Participants were instructed to memorize the colours of the objects in one hemifield and, after a retention period, to decide whether the colours in a subsequent test display were identical to the memory display or whether one object was different. Electroencephalographic activity measured throughout the retention interval revealed a sustained contralateral negativity in posterior occipital electrodes

from 250 ms post sample display onset which spanned to the end of the retention period. This component, called the Contralateral Delay Activity (CDA), was found to be sensitive to the number of items held in working memory (Luria, Balaban, Awh & Vogel, 2016), and to individual working memory capacity limitations (Vogel & Machizawa, 2004), and has thus been linked with the process of the maintenance of working memory representations.

Importantly, the time-frame and contralateral nature of this component correspond to the Sustained Posterior Contralateral Negativity (SPCN) (Jolicœur, Sessa, Dell'Acqua & Robitaille, 2006), a component which is typically observed during visual search tasks after the N2pc. The CDA and SPCN are also both sensitive to the number of relevant items in memory sample or visual search displays. As a result, they are discussed by many researchers as functionally equivalent (e.g. Heuer & Schubo, 2016) – both reflect the maintenance of task-relevant objects in working memory. However, there remains one subtle distinction between these two components. In search tasks which do not require the active maintenance of target objects, the SPCN lasts for only a few hundred milliseconds. In contrast, the CDA component is sustained throughout the duration of a memory delay period in typical working memory tasks. Thus, the SPCN component is often assumed to mark the encoding process of information into visual working memory (Jolicœur et al., 2006), whilst the CDA component is believed to involve the more sustained maintenance of visual objects in working memory (Vogel & Machizawa, 2004).

The CDA component is similar in nature to the N2pc component in that both reflect a lateral bias in processing visual information, and both have similar scalp topographies (Grubert & Eimer, 2015). Drew and Vogel (2008) found that both components are also similar in terms of sensitivity to set size and capacity limitations. In their study, participants were asked to track multiple moving black objects throughout a 1500 ms interval. The to-be-tracked items were initially identified by briefly appearing in a target colour amongst black

distractors in a static cuing display at the beginning of every trial. The N2pc during the initial selection, and the CDA during the retention and tracking interval, were equally modulated by the set size of the targets in the display until they both reached an asymptote at three target objects. Additionally, Anderson, Vogel and Awh (2013) showed that individuals with higher WM capacity perform visual search tasks with greater efficiency than those with lower WM capacities, and that this was also reflected by N2pc and CDA components recorded during task performance. Importantly, this was only observed when the distractors in the visual search display were heterogeneous and thus could not be rejected as a group. Together, these data provide strong evidence that maintaining WM representations and attentional selection appear to involve similar top-down control processes.

1.4.2 Position-Dependence of WM Representations

One enduring controversy within the literature on visual working memory is whether the spatial location of an object held within working memory is an obligatory aspect of maintaining its representation. Given that lateralized CDA components are elicited during the storage of colours in working memory (Vogel et al., 2004), it is clear that location at least affects the hemispheric differences in the encoding process of working memory representations. If working memory was strongly position-dependent, presenting the memory and test displays in opposing hemifields should adversely affect performance and neural substrates of working memory. To test this, Woodman, Vogel and Luck (2012) used variations of the change detection paradigm. In one condition, the memory display and test items were presented in the same hemifield, similar to Vogel et al. (2004). In the other condition, however, the test display was presented in the opposite hemifield to the memory display. The researchers found that there was no difference in performance between these two conditions and concluded that either working memory representations are position-invariant

or can be flexibly shifted in preparation for known translations, similar to mental rotation strategies (Shepard & Metzler, 1971).

In a similar task, Grubert and Eimer (2015) measured the CDA during memory retention to examine whether the CDA shifts polarity in tasks where memory and test displays are known to be presented on opposite sides, thus reflecting a horizontal translation of stored representations. In their study, memory and test displays, separated by a 900ms retention period, were composed of three coloured objects in both the left and right visual field, with a central pre-cue arrow indicating the location of the to-be remembered objects. In half of the blocks, the memory and test displays were presented on the same sides (no-shift condition), whilst in the remaining half, the test was presented in the contralateral visual field to the memory display (shift condition). Both conditions yielded significant CDA components of equal size and polarity. The absence of any CDA polarity reversal in the shift condition suggests that despite the anticipated translation of the test display, the maintenance of the object representations, marked by the CDA, did not shift between hemispheres. Furthermore, given that there were no differences in performance between the two conditions, it can be concluded that the maintenance process remained localized in the hemisphere ipsilateral to the target display. One possibility is that subsequent comparison processes between working memory representations and test displays were flexible enough to overcome the challenges posed by the spatial translation in the shift condition.

Other studies have used the CDA component to explore other aspects of the attentional control of working memory representations, such as the selective access to information already stored. Eimer and Kiss (2010), for example, presented participants with a bilateral stimulus array composed of five red items in one visual field and five green items in the opposing visual field. On each side, targets were defined as shape singletons (e.g. diamonds) amongst homogenous distractors (e.g. circles). Participants were required to

remember the location of the cut (top or bottom) in the diamond of both lateral targets. A subsequent centralized retro-cue was then presented in a colour matching one of the singletons to define the target. Participants were then required to respond if the cut of the target singleton was at the top or the bottom of the object. Prior to the arrival of the retro-cue, participants did not know which singleton was the target and were therefore required to hold both representations in working memory. Both early cues with a retention interval of only 150 ms and late cues with 700 to 1000 ms retention yielded sustained contralateral negativity analogous to the CDA component. These results show that attentional processes do not only control the encoding of visual objects into working memory, but can also selectively modulate the activation states of working memory representations that are already stored, by producing a spatially selective bias for representations that are signalled as task-relevant by retro-cues.

In summary, according to the sensory recruitment account, working memory uses the same neural substrate that is involved in visual perception. Importantly, this may also include attentional control processes which can be either space-based or feature-based. However, and similar to the field of perceptual attention, the mechanisms involved in feature-based and space-based working memory maintenance processes have so far rarely been investigated together and contrasted directly. How similar are the processes of maintaining features and spatial locations in visual working memory? Are locations stored in an obligatory manner when maintaining object features? Are similar space-based and feature-based attentional processes involved in the control of perceptual attention and working memory maintenance? These and related questions were addressed in the experiments presented in this thesis.

1.5 Thesis Outline

Collectively, this overview of current research on space-based and feature-based attentional selection in perception and on the role of these attentional mechanisms during visual working memory maintenance highlights a number of avenues requiring further investigation. In this thesis, experiments are presented that were designed to answer two general questions about interactions between space-based and feature-based attentional mechanisms, separately for perceptual processes and for visual working memory. Firstly, with respect to feature-based attentional control, it is known that task sets for specific visual features (like particular colours) result in selective attentional modulations at early stages of visual processing. However, the question how feature-based attention operates when targets are defined by multiple features still remains largely unanswered. This part will investigate one particular variant of this question that also includes spatial aspects of attentional control. How does attentional selectivity unfold in real time when target objects are defined by a particular spatial configuration of elementary features? This question is addressed in the experiments reported in Chapter 2. If spatial configurations of elementary features can guide perceptual attention, it is reasonable to assume that these target attributes are also represented as task sets or attentional templates in working memory. But how are such spatial-configural search templates organized, and does the way in which these templates are represented in working memory depend on the specific demands of an upcoming attentional selection task? This is addressed in Chapter 3. The second issue addressed in this thesis concerns the interactions between space-based and feature-based attentional control. As described above, the feature-based and space-based guidance of attention have both been richly studied, but they have for the most part been treated relatively separately in the literature. It remains unclear whether guidance by spatial and feature-based factors is qualitatively similar across

individuals or form part of separate attentional systems. These questions are examined in Chapters 4 and 5 of this thesis, separately for perceptual attention (Chapter 4) and visual working memory (Chapter 5). In the parts of this thesis that focus on attentional selectivity during on-line visual perception (Chapters 2 and 4 of this thesis), the N2pc component will be used as a temporally precise marker of attentional selection to track the emergence of space-based and feature-based modulations of visual processing and their interactions in real time. In the parts that focus on visual working memory (Chapters 3 and 5 of this thesis), the CDA component will be employed as a marker of visual maintenance processes that is sensitive to factors such as the quantity, quality, and complexity of visual information being maintained.

As a result of combining these two general questions about feature- and space-based attentional control with the two cognitive domains to which they are applied (visual perception and working memory), this thesis contains four separate projects:

1. The control of feature-based attention in perceptual attention during visual search by shape features and shape spatial configurations (Chapter 2)
2. The control of WM maintenance for shape features and shape spatial configurations (Chapter 3)
3. Spatial and feature-based attentional selection in visual perception (Chapter 4)
4. The mechanisms involved in maintaining non-spatial features or spatial locations in visual WM (Chapter 5)

Chapter 2

The guidance of visual search by shape features and shape configurations

The experiments presented in this chapter have been published in a peer-reviewed journal.

Experiments 1 and 2:

McCants, C., Berggren, N., & Eimer, M. (2018). The guidance of visual search by shape features and shape configurations. *Journal of Experimental Psychology: Human Perception and Performance*, 44(7), 1072-1085.

2.1 Chapter 2 Introduction

As discussed in Chapter 1, knowledge about the properties of target objects guides the attentional selection of these objects during visual search. Currently task-relevant features are represented in top-down task sets (e.g., Folk, Remington, & Johnston, 1992) or attentional templates (e.g., Duncan & Humphreys, 1989). Such target templates are activated during the preparation for a search episode, and bias attentional selection towards objects with target-matching features (Desimone & Duncan, 1995; Eimer, 2014). The effects of feature-specific target templates on attentional selectivity have been well documented. For example, when targets are defined by a particular colour, nontarget objects that match this colour will capture attention even when they have to be ignored, whereas objects without target-matching features will not trigger any task-set contingent attentional capture (e.g., Folk et al., 1992).

In many search tasks, target objects are not defined by a single feature but by a feature combination. Search for such conjunctively defined targets is typically less efficient than search for a unique target feature (e.g., Treisman & Gelade, 1980; Duncan & Humphreys, 1989, 1992). How do attentional templates control object selection during search for feature conjunctions? According to the Guided Search model (Wolfe, 1994, 2007), top-down attentional biases operate simultaneously and independently for different target-matching features to guide attention towards likely target objects. However, only one feature per dimension can be involved in this type of attentional guidance (Wolfe, 2007). In other words, conjunction search can be guided by templates for a particular target colour and target shape, but it is not possible to concurrently activate templates for two features from the same dimension (e.g., two colours or two shapes). This hypothesis is based on the observation that search for targets defined by the conjunction of two features from the same dimension (colour) is much more difficult than search for targets defined by a combination of features from two different dimensions (Wolfe, Yu, Stewart, Shorter, Friedman-Hill, & Cave, 1990;

but see Wolfe, Friedman-Hill, & Bilsky, 1994; Carrasco, Ponte, Rechea, & Sampedro, 1998, for task contexts where colour/colour conjunction search can be relatively efficient).

The role of attentional templates in guiding attentional target selection in feature and conjunction search can be assessed with event-related potential (ERP) measures, which are able to track such template-guided selection mechanisms on a millisecond-by-millisecond basis. As already described in Chapter 1, the N2pc component is an electrophysiological marker of the allocation of attention to lateralised objects with template-matching features among distractor objects in visual search displays (e.g., Eimer, 1996; Luck & Hillyard, 1994a). This component is characterised by an enhanced negativity at occipito-temporal electrodes contralateral to the side where a template-matching object is presented, and typically emerges around 180-200 ms after stimulus onset. While most N2pc studies have used tasks where targets were defined by one specific constant feature (e.g., Eimer & Kiss, 2008; Leblanc, Prime, & Jolicœur, 2008; Lien, Ruthruff, Goodin, & Remington, 2008), N2pc components are also triggered during conjunction search (e.g., Luck, Girelli, McDermott, & Ford, 1997; Fuggetta, Pavone, Walsh, Kiss, & Eimer, 2006). When search targets are defined by a conjunction of features from different dimensions (colour and size, or colour and shape), N2pc components are elicited not only by target objects, but also by nontargets that match one of these features (Kiss, Grubert, & Eimer, 2013). Notably, this is the case even when a target object is present in the same display (Eimer & Grubert, 2014). These observations suggest that template-guided attentional selection processes operate in parallel and independently for different target features at different locations in the same search display.

Several recent studies have shown that target selection can be guided by search templates for multiple features from the same dimension (colour), thus challenging the assumption of the Guided Search model that only a single feature per dimension can be involved in attentional guidance. Using behavioural measures, Irons, Folk, & Remington

(2012) showed that during search for one of two possible target colours (e.g., red or green objects), task-irrelevant stimuli that matched either of these colours captured attention, whereas nonmatching colours did not (see also Grubert & Eimer, 2016, for corresponding N2pc results). To assess how such multiple-colour templates control attentional target selection in search tasks where targets are defined by a combination of two colours (e.g., red and green objects), Berggren & Eimer (2016a) measured N2pc components to target objects with both two target-defining colours and to distractors that matched one of these colours. Reliable N2pc components were elicited not only by targets but also by partially matching distractor objects, even when a target was simultaneously present in the same display. This suggests that, analogous to colour/shape search (Eimer & Grubert, 2014), colour/colour conjunction search can be guided simultaneously by separate target templates for two different colours.

If the guidance of attention during conjunction search operates in parallel and independently for each target-defining feature, both within and across dimensions, this has important implications for the guidance of attention in conjunction search tasks where targets are defined by having two features (e.g., two colours) in a specific spatial arrangement (e.g., red above green). The spatial relationship between two target features should be entirely invisible to strictly feature-specific attentional guidance processes, which are sensitive only to the presence of task-relevant features, but not to their configuration within a target object. A recent N2pc study (Berggren & Eimer, 2016b, Experiment 3) investigated the attentional guidance of target selection in such a colour/colour configuration search task. Targets were defined by the spatial arrangement of two colours (e.g., objects with a red top half and a green bottom half). In a subset of all search displays, these targets were accompanied by reverse-colour distractor objects composed of both target-defining colours in the opposite spatial configuration (e.g., green top and red bottom half). When targets and reverse-colour

distractors appeared in opposite hemifields, no N2pc component was elicited at all, demonstrating that colour-based attentional guidance processes were insensitive to colour configuration information, and thus unable to distinguish between these two types of objects. For displays where targets and reverse-colour distractors appeared on the same side, the N2pc was nearly twice as large as for target displays without a reverse-colour distractor, suggesting that attention was allocated in parallel and independently to both types of objects.

These findings are relevant for models of attentional guidance mechanisms in visual search and for understanding the nature of attentional templates. They suggest that search goals are not represented as integrated objects or “images in the mind” (James, 1890), which would include information about the spatial/configural relationships between individual features, but instead separately as independent features. The critical question is whether this applies generally to all search tasks, or only to relatively artificial tasks where target objects are defined in a way that is rarely relevant in the real world. Apart from situations where one looks for the national flag of a particular country among other flags, one does not normally search for targets characterized by a specific spatial arrangement of different colours. It is possible that search can be guided by the spatial-configural arrangement of target features in other more ecologically relevant task contexts. Colour/colour configuration search could also be a special case because individual colours are powerful guiding features (e.g., D’Zmura, 1991; Wolfe & Horowitz, 2004) and therefore may override any residual effects of relational properties on attentional guidance during colour-colour configuration search.

The goal of the two experiments reported in Chapter 2 was to re-assess the roles of feature-based and configurational information for the guidance of attention in search tasks where targets are defined by the spatial arrangement of two features from the same dimension. Instead of colour, shape will be used as the task-relevant feature dimension. Unlike colour/colour configuration search (Berggren & Eimer, 2016b), search for target

objects that are defined by the arrangement of two (or more) component shapes is very common. Most real-world visual objects are characterised by specific spatial configurations of basic shape attributes, and the two- and three-dimensional arrangement of geometric components is critical for object recognition (e.g., Biederman, 1987). For this reason, the guidance of attention during shape/shape configuration search should not be primarily or exclusively based on independent templates for individual shape parts, but may also be sensitive to the overall spatial configuration of these parts. This possibility has so far rarely been addressed. In one behavioural study, Wolfe, Klempen, and Shulman (1999) found that search for target objects defined by two component shapes in a particular spatial arrangement (e.g., “snowmen” composed of a smaller circle on top of a larger circle) among rotated distractors (e.g., upside-down snowmen) was inefficient, suggesting that object polarity is not an effective guiding attribute. The goal of Experiments 1 and 2 of this thesis was to investigate this issue with electrophysiological measures.

To study attentional guidance during shape/shape configuration search, the most basic version of a search task will be used where only two objects on opposite sides compete for attentional selection. In Experiment 1, all objects were composed of two vertically aligned shapes selected from a set of four possible shapes (hexagon, cross, hourglass and circle). For each participant, the target object was defined by one particular spatial configuration of two shapes (e.g., hourglass above circle). This target was present on 50% of all trials, and was accompanied by one of three possible distractor objects on the opposite side (nonmatching distractors, partially matching distractors, or reverse distractors; see Figure 1). Nonmatching distractors (NM) were composed of the two nontarget shapes (e.g., cross above hexagon). Partially matching (PM) distractors contained one of the two target shapes in a target-matching vertical position (e.g., cross above circle). Reverse (Rev) distractor objects were composed of both target-defining shapes in the opposite vertical arrangement (e.g., circle

above hourglass; analogous to the inverted snowmen distractors used by Wolfe et al., 1999). On target-absent trials, one nonmatching distractor appeared together with a reverse distractor, a partially matching distractor, or distractor with a target-defining shape in its non-assigned vertical position (e.g., cross above hourglass; partially matching shape in wrong location: PMw). Participants had to report the presence or absence of the target object on each trial. EEG was recorded during task performance, and N2pc components were computed for targets (separately for trials where the target was accompanied by each of the three different types of distractors), and for the three different partially matching distractors on target-absent trials.

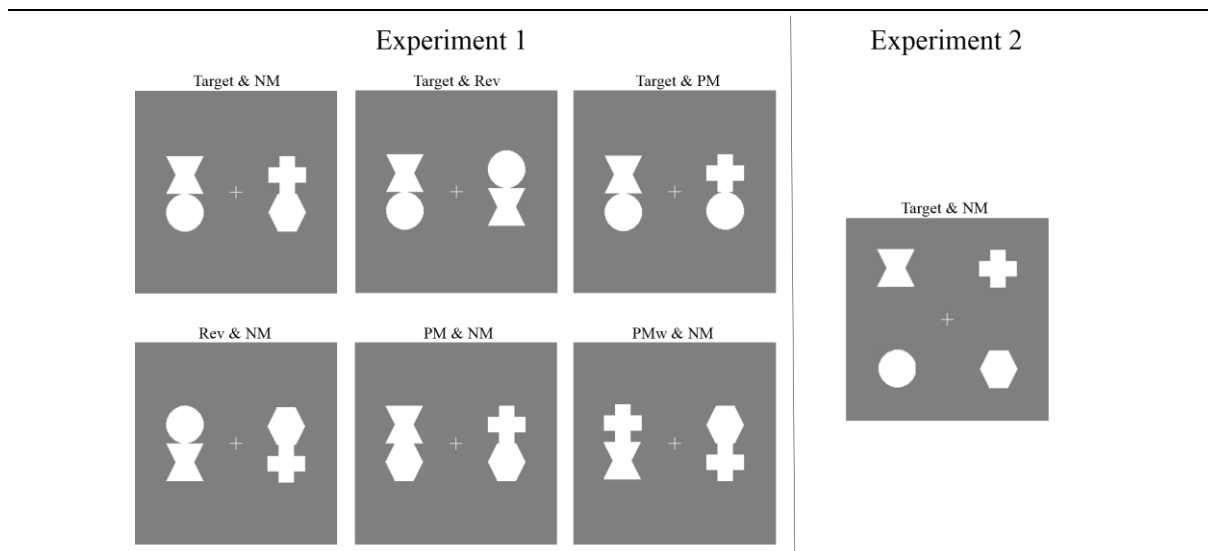


Figure 1. Left panel: Illustration of the six different stimulus display types in Experiment 1. In the example shown, targets were objects composed of an hourglass on top of a circle. On target-present trials, the target object was presented together with a distractor object with two nonmatching shapes (Target & NM), an object with both matching shapes in the reverse configuration (Target & Rev), or an object with one matching shape in its assigned vertical position (Target & PM). On target-absent trials, one nonmatching distractor was presented together with a reverse distractor (Rev & NM), a partially matching distractor (PM & NM), or an object with a matching shape in the wrong vertical position (PMw & NM). Right panel: Illustration of a Target & NM display in Experiment 2, where the two shapes on the left and right sides were spatially separated.

The pattern of N2pc components observed for these different displays will provide insights into the nature of the search templates that guide attention during shape/shape configuration search. One possibility is that these templates represent the overall shape of the target object in an integrated fashion, without any independent representation of its component parts. Because reverse or partially matching distractors do not match such an integrated object template, they should not be able to attract attention. On target-present trials, their presence

should therefore not have any effect on the amplitude or onset latency of the target N2pc. On target-absent trials, these distractor objects should not elicit an N2pc component. Another possibility is that target selection is guided exclusively by independent templates for each target-defining component shape. Because targets and reverse distractor objects contain the same two target-defining component shapes, they are not distinguishable by such strictly part-based attentional guidance mechanisms, and should therefore both attract attention to the same degree. As a result, these objects should trigger identical N2pc components when accompanied by a nonmatching distractor, and no N2pc should be observed at all when they appear on opposite sides of the same display (analogous to the N2pc pattern found for colour/colour configuration search; Berggren & Eimer, 2016b). Partially matching distractor objects should also trigger N2pc components, but they should be smaller because they only contain one template-matching shape. Whether this shape appears at its assigned or non-assigned vertical location should not affect the N2pc, reflecting the insensitivity of strictly feature-based attentional guidance to the spatial configuration of features. A third possibility is that both part-based and configuration-based guidance processes affect attentional object selection processes, but that part-based guidance emerges earlier (as suggested by previous N2pc evidence from colour/shape conjunction search; Eimer & Grubert, 2014). This hypothesis makes specific predictions about the time course of N2pc components elicited by targets and reverse distractors. Because these two types of objects will elicit the same early part-based attentional biases, they should initially trigger identical N2pc components. Once guidance starts to be affected by feature configurations, the target N2pc should become larger than the N2pc to reverse distractors in displays where these objects are accompanied by a nonmatching distractor. In displays where they appear together on opposite sides, no N2pc should be present initially (as both objects trigger the same part-based biases), and the point in time where a target

N2pc emerges should mark the moment where attentional processing starts to become sensitive to shape configurations.

2.2 EXPERIMENT 1

2.2.1 Methods

Participants

Fifteen participants with normal or corrected-to-normal vision were paid in exchange for their participation in Experiment 1. One participant was excluded from analysis due to excessive artifact rejection (over 50% of trials excluded), and another two due to faults in data recording. Of the remaining 12 participants, four were male and 3 were left-handed (M age = 31, $SD = 6$).

Sample size was set a priori at 12 participants, based on many previous N2pc studies in the Brain and Behaviour lab. To assess whether this sample size would be sufficient for the current feature configuration search task, the effect size was calculated from a previous N2pc study examining search for targets defined by the spatial configuration of two colours (Berggren & Eimer, 2016b, Experiment 3). In this experiment, the difference of target N2pc amplitudes in the presence versus absence of a reverse-colours distractor object showed a Cohen's d effect size of 1.79, suggesting a minimum required sample size as low as $N = 5$ when assuming standard power of 0.8 and an alpha level of 0.05. Furthermore, when determining effect size estimates on the higher order ANOVA interaction from this study, a partial eta squared effect size of .65 was obtained, suggesting a minimum sample size of $N = 7$. Cohen's d effect size was calculated using the classic method of dividing condition mean difference by the pooled standard deviation.

Stimuli and Procedure

The experiment was programmed and executed on-line using Matlab software (MathWorks, Natick, MA) and presented on a 24-inch BenQ widescreen monitor (60 Hz, 1920 x 1080 screen resolution) at a viewing distance of approximately 90 cm. Participants' behavioural responses and response times were recorded with a BlackBox Toolkit (The Black Box Toolkit Ltd, 2016) response box with a custom 4-button layout arranged in cardinal directions and equidistant from the centre of the box. In both experiments, only the top and bottom buttons were used.

All stimuli were presented on a black background. A grey fixation cross (subtending $0.31^\circ \times 0.31^\circ$ of visual angle) remained in the centre of the screen for the duration of each block. Each search display contained one object to the left and one to the right of fixation, at an eccentricity of 2.16° from the central fixation cross. Both objects were grey, and were composed of two vertically aligned geometric shapes (e.g., a hexagon above a cross). There were four possible shapes: hexagon, cross, hourglass, and circle. All shapes were vertically and horizontally symmetrical, and equal in size ($1.15^\circ \times 1.15^\circ$). Participants were instructed to maintain central fixation, and to detect a target object that was defined by a specific spatial arrangement of two shapes (e.g., hourglass above circle). Each participant was assigned a different target object, with the restriction that all four component shapes served as part of the target object for the same number of participants.

Search displays were presented for 150 ms, and the interval between two successive search displays was 1850 ms. Participants had to press the top response key when the target object item was present and the bottom key when it was absent. Target-present and target-absent displays were equiprobable and randomly intermixed in each block. There were three types of target-present trials that differed with respect to the distractor object that

accompanied the target on the opposite side. This distractor could be a nonmatching (NM) object composed of two nontarget shapes (Target & NM displays), a partially matching (PM) object that contained one target-defining shape in its correct vertical position and one nontarget shape (Target & PM displays), or an object that contained both target shapes but in the reverse (Rev) spatial arrangement (e.g., a circle above hourglass during search for hourglass above circle; Target & Rev displays). These three target-present trials were equiprobable, and targets were equally likely to appear on the left or right side. Target-absent trials always contained one nonmatching distractor object that was accompanied either by an object with both target shapes in the reverse configuration (Rev & NM displays), by an object with one target-matching shape in its correct vertical position (PM & NM displays), or by an object that also contained one target-matching shape but in the wrong vertical position (PMw & NM displays; see Figure 1 for an illustration of the different target-present and target-absent trials). These target-matching objects were equally likely to be presented on the left or right side on target-absent trials. Following practice, participants completed 20 blocks composed of 48 trials (960 trials in total).

EEG Recording and Data Analysis

EEG was DC-recorded at 27 scalp electrodes on an elastic cap at sites Fpz, F7, F8, F3, F4, Fz, FC5, FC6, T7, T8, C3, C4, Cz, CP5, CP6, P9, P10, P7, P8, P3, P4, Pz, PO7, PO8, PO9, PO10, and Oz. A sampling rate of 500 Hz was used, with a low-pass filter of 40 Hz. Channels were referenced online to an electrode on the left earlobe, and re-referenced to an average of both the left and right earlobes offline. No other filters were applied following EEG acquisition. Trials were rejected for incorrect responses, eye-blinks ($> \pm 60 \mu\text{V}$ at Fpz), eye-movements ($> \pm 30 \mu\text{V}$ in the HEOG channels), or muscle movement artefacts ($> \pm 80 \mu\text{V}$ at all other channels), and these trials were not included in any analysis. Remaining trials

were segmented into epochs from 100 ms before to 500 ms after the onset of each search display. Averaged ERP waveforms were then computed for each of the six types of search display, separately for trials where the target object (on target-present trials) or the distractor object with target-matching features (on target-absent trials) appeared in the left and right visual field. N2pc amplitudes were quantified as the difference between ERP mean amplitudes obtained between 200 and 300ms after search display onset at posterior electrode sites PO7 and PO8. N2pc onset latencies were calculated by assessing grand averaged difference waveforms (contralateral minus ipsilateral ERPs), using a jackknife-based analysis method (Miller, Patterson, & Ulrich, 1998). In this analysis, 12 subsamples of grand-averaged difference waves were computed, each excluding a different participant from the original grand-averaged sample. N2pc onset was defined as the time at which each of these subsamples reached an absolute threshold of $-1 \mu\text{V}$, except in the case of double-difference waves in which a relative threshold of 50% of N2pc peak amplitude was used. N2pc onset latency differences were assessed using repeated-measures ANOVAs and two-tailed t-tests, with F- and t-values corrected according to the formulas described by Ulrich and Miller (2001) and Miller et al. (1998). The corrected tests are indicated with F_c and t_c , respectively.

2.2.2 Results

Behavioural Analysis

Table 1 (left panel) shows mean reaction times (RTs) and error rates for the six different target-present and target-absent displays. RTs on target-present trials with correct responses were entered into a one-way repeated measures analysis of variance (ANOVA) with the factor Distractor Type (NM, Rev, PM). There was a main effect of Distractor Type ($F(2,22) = 7.91, p = .003, \eta_p^2 = .42$). Paired-sample t-tests revealed that the RTs were delayed

for displays where a target was accompanied by a reverse distractor ($M = 599$ ms) relative to trials with a nonmatching distractor ($M = 573$ ms; $t(11) = 3.69$, $p = .004$, $d = .28$), and with a partially matching distractor ($M = 579$ ms; $t(11) = 2.27$, $p = .044$, $d = .22$). RTs to targets with nonmatching and partially matching distractors did not differ reliably ($t(11) = 1.64$, $p = .129$). A separate ANOVA for target-absent displays with correct responses showed that RTs were reliably affected by the type of target-matching distractor in these displays (Rev, PM, PMw: $F(2,22) = 28.15$, $p < .001$, $\eta_p^2 = .719$). Target-absent RTs were slowest for displays that contained a reverse distractor ($M = 616$ ms) relative to displays with a partially matching distractor ($M = 580$ ms; $t(11) = 3.25$, $p = .008$, $d = .44$), and with a PMw distractor ($M = 552$ ms; $t(11) = 8.81$, $p < .001$, $d = .78$). Furthermore, a partially matching distractor with a target shape in its correct vertical position delayed target-absent RTs relative to PMw distractors ($t(11) = 4.27$, $p = .001$, $d = .35$).

	Exp. 1	Exp. 2
Targ vs NM	573 (94)	608 (109)
	3(2)	4 (6)
Targ vs Rev	599 (101)	639 (127)
	2 (2)	4 (6)
Targ vs PM	579 (95)	640 (117)
	3 (2)	6 (7)
NM vs Rev	616 (84)	660 (78)
	3 (4)	2 (2)
NM vs PM	580 (87)	607 (75)
	3 (2)	4 (3)
NM vs PMw	552 (76)	568 (70)
	1 (1)	1 (1)

Table 1: Mean reaction times (upper rows) and percentage error rates (lower rows) in Experiments 1 and 2 for the six different types of search displays (SD in parentheses).

Error rates were also entered into one-way ANOVAs, separately for target-present and target-absent trials. Incorrect target-absent responses occurred on 3% of all target-present trials, and there was no significant effect of Distractor Type ($F < 1$). The percentage of incorrect target-present responses on target-absent trials was affected by the type of target-matching object in these displays ($F(2,22) = 4.18, p = .029, \eta_p^2 = .275$). The presence of a

reverse distractor triggered more incorrect responses ($M = 3.49\%$) than a PMw distractor ($M = 0.89\%$; $t(11) = 2.44$, $p = .033$, $d = .86$). Additionally, incorrect target-present responses were more frequent for displays including a partially matching distractor ($M = 2.56\%$) than for displays with a PMw distractor ($t(11) = 3.03$, $p = .012$, $d = 1.09$). There was no difference in error rates between displays with reverse and partially matching distractors ($t < 1$).

ERP Analysis: N2pc Components

Target-present displays. Figure 2 shows ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to the target objects for the three different target-present display types, together with the corresponding contralateral-ipsilateral N2pc difference waveforms. Target N2pc components were present for all three display types, but appeared to be larger and emerge earlier when targets were accompanied by nonmatching distractors relative to displays with reverse or partially matching distractors. A 3 x 2 repeated-measures ANOVA of N2pc mean amplitudes measured on target-present trials in the 200-300 ms post-stimulus time window with the factors Distractor Type (NM, Rev, PM) and Laterality (electrode ipsilateral or contralateral to the target location) revealed a main effect of Laterality ($F(1,11) = 36.77$, $p < .001$, $\eta_p^2 = .77$), reflecting the presence of target N2pc components. Importantly, an interaction between Distractor Type and Laterality ($F(2,22) = 22.96$, $p < .001$, $\eta_p^2 = .67$) confirmed that target N2pc amplitudes were affected by the type of distractor object in the same display. Follow-up paired-samples t -test analyses comparing ipsilateral and contralateral mean amplitudes showed that significant target N2pc components were elicited for all three types of target-present displays (all t 's > 3.54 , p 's $< .01$, d 's $> .24$). When targets were accompanied by nonmatching distractors, they triggered larger N2pc components ($M = -3.42\ \mu\text{V}$) than when they were presented together with reverse distractors ($M = -1.15\ \mu\text{V}$; $t(11) = 5.32$, $p < .001$, $d = 1.61$), or with partially matching distractors ($M = -1.88\ \mu\text{V}$; $t(11)$

= 6.08, $p < .001$, $d = 1.05$). Furthermore, reverse distractors attenuated target N2pc amplitudes more strongly than partially matching distractors ($t(11) = 2.26$, $p = .045$, $d = .64$). N2pc onset latencies on target-present trials were also reliably affected by Distractor Type ($F_c(2,22) = 11.69$, $p < .001$, $\eta_{pc}^2 = .52$). When targets were presented together with nonmatching distractors, the N2pc emerged earlier ($M = 190$ ms) than when they appeared together with reverse distractors ($M = 238$ ms; $t_c(11) = 4.33$, $p = .001$, $\eta_{pc}^2 = .63$), or partially matching distractors ($M = 212$ ms; $t_c(11) = 2.57$, $p = .024$, $\eta_{pc}^2 = .38$). Reverse distractors delayed target N2pc onset latency more strongly than partially matching distractors ($t_c(11) = 2.61$, $p = .026$, $\eta_{pc}^2 = .37$).

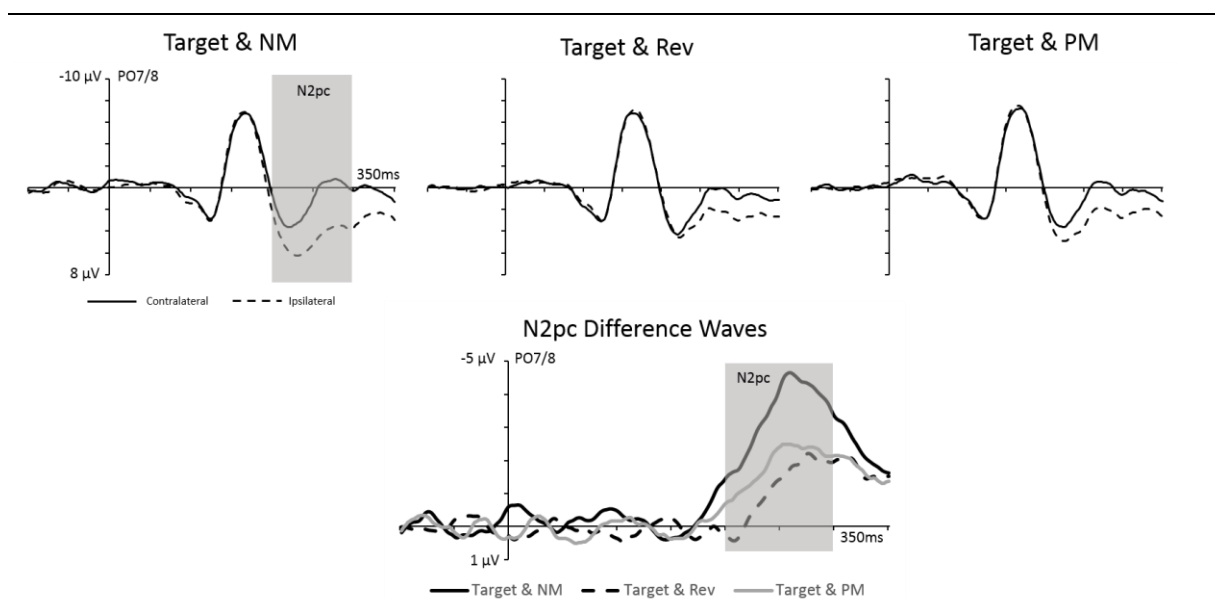


Figure 2. Top panel: Grand-average event-related brain potentials (ERPs) obtained in Experiment 1 on target-present trials at electrode sites PO7/8 contralateral and ipsilateral to the side of the target object during the 350 ms interval after display onset. ERPs are shown separately for the three different types of target-present displays. Bottom panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for the three target-present display types.

Target-absent displays. Figure 3 shows ERPs elicited contralateral and ipsilateral to target-matching distractors on target-absent trials, with the corresponding N2pc difference waveforms. Target-matching distractors triggered reliable N2pc components, as reflected by a main effect of Laterality ($F(1,11) = 20.76, p < .001, \eta_p^2 = .65$) for N2pc mean amplitudes. N2pcs were largest for displays with reverse distractors and smallest for displays with PMw distractors, confirmed by an interaction between Laterality and Distractor Type ($F(2,22) = 3.54, p = .046, \eta_p^2 = .24$). N2pc components elicited by PMw distractors were smaller ($M = -1.26 \mu\text{V}$) than N2pcs to partially matching distractors ($M = -1.78 \mu\text{V}; t(11) = 2.52, p = .028, d = .47$), and to reverse distractors ($M = -2.20 \mu\text{V}; t(11) = 2.59, p = .025, d = .60$). There was no significant N2pc amplitude difference between reverse and partially matching distractors ($t < 1$). Additional analyses confirmed that significant N2pc components were elicited for all three types of target-matching distractors displays (all t 's $> 3.78, p$'s $< .01, d$'s $> .29$). Although there were small numerical differences in N2pc onset latency between distractor types (see Figure 3), there was no overall reliable effect of Distractor Type on N2pc latencies on target-absent trials ($F_c(2,22) = 1.39, p = .271, \eta_{pc}^2 = .11$).

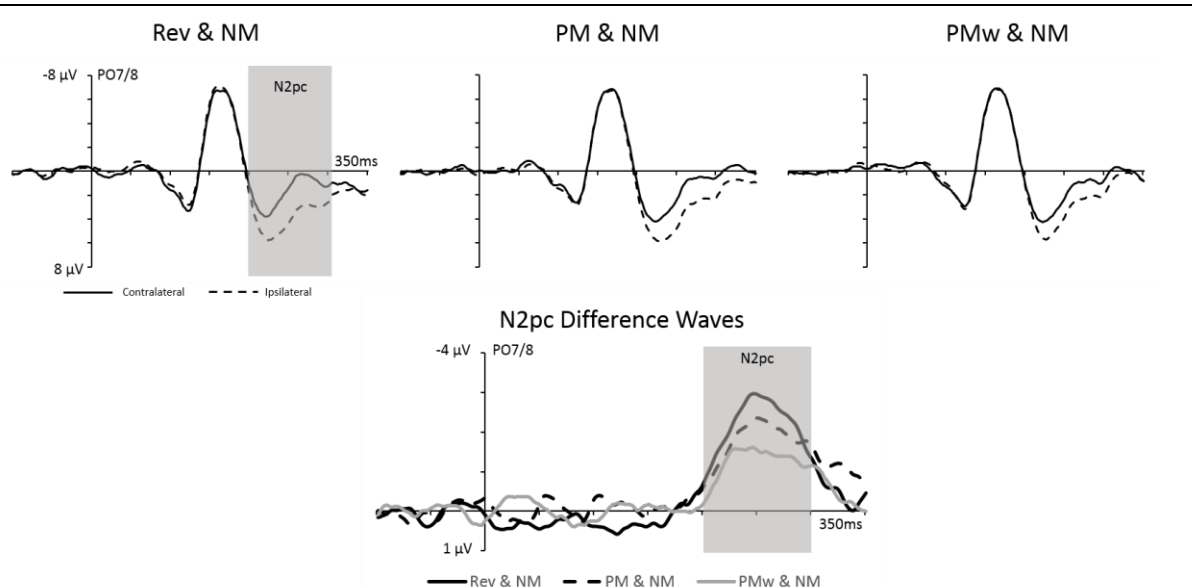


Figure 3. Top panel: Grand-average event-related brain potentials (ERPs) obtained in Experiment 1 on target-absent trials at electrode sites PO7/8 contralateral and ipsilateral to the side of the target object during the 350 ms interval after display onset. ERPs are shown separately for the three different types of target-absent displays. Bottom panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for the three target-absent display types.

N2pc analyses across target-present and target-absent trials. To investigate how the spatial configuration of target-matching shapes affected N2pc components in Experiment 1, N2pc components to targets objects and reverse distractors were compared on trials where they were accompanied by a nonmatching distractor. Across the whole N2pc measurement window, target N2pcs were larger than N2pcs to reverse distractor objects ($t(11) = 3.62$, $p = .004$, $d = .67$). To determine when this N2pcs amplitude difference started to emerge, two different methods were employed (see Jenkins, Grubert, & Eimer, in press, for analogous procedures). First, individual N2pc difference waves for targets and reverse distractors were compared with successive one-tailed paired t-tests for each sampling point after display onset. A significant amplitude difference between N2pcs to targets and reverse distractors

had to remain present for at least ten consecutive subsequent sampling points (corresponding to 20 ms) in order to be interpreted as marking the point in time where target N2pcs start to become larger than reverse distractor N2pcs. This procedure yielded an onset estimate of 226 ms after search display onset. In a second independent analysis, N2pc difference waveforms for reverse distractors was subtracted from N2pc difference waves for targets, separately for each participant, followed by a jackknife-based analysis of these double subtraction waveforms with a relative onset criterion of 50% of the peak N2pc amplitude. This analysis suggested a slightly later onset of N2pc amplitude differences between targets and reverse distractors (248 ms post-stimulus). The same two analyses were also employed to compare N2pc amplitudes to PM and PMw distractors. These analyses showed that the N2pc to PM distractors started to become larger than the N2pc to PMw distractors from 236 ms (t-test analysis) or 234 ms (jackknife analysis) post-stimulus.

The attenuation and delay of target N2pcs in displays where targets and reverse distractors appeared on opposite sides relative to Tar & NM displays could be due to the concurrent presence of a smaller N2pc of opposite polarity triggered in parallel by reverse distractors. If this was the case, the difference between N2pc components for Target & NM versus Target & Rev displays should match the N2pc elicited by reverse distractors on target-absent trials. As can be seen from the N2pc difference waveforms shown in Figure 4 (left panel), the N2pc to reverse distractors (solid line) was indeed equal in size to the difference between N2pcs to targets in the absence versus presence of a reverse distractor (dashed line; $t < 1$). The same result was obtained when the attenuation of target N2pcs by the presence of partially matching distractors was assessed in the same way (Figure 4, right panel). The N2pc to partially matching distractors was identical in size to the difference of target N2pcs between displays with and without a partially matching distractor ($t < 1$).

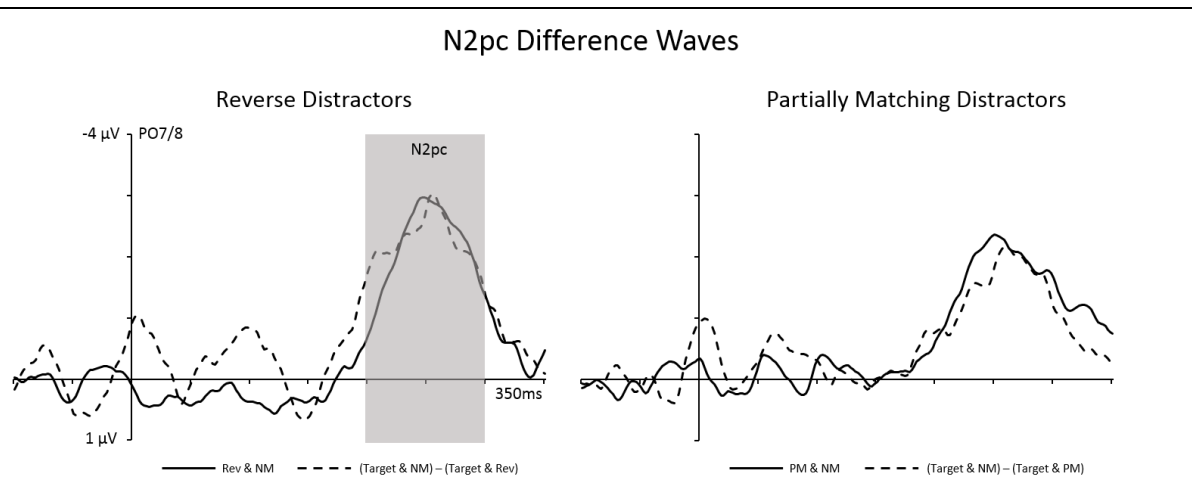


Figure 4. Left panel: N2pc difference waveforms showing that the difference of target N2pcs in the presence versus absence of a reverse distractor (dashed line) in Experiment 1 matched the size of the N2pc triggered by reverse distractors on target-absent trials (solid line). Right panel: N2pc difference waveforms showing the effect of partially matching distractors on target N2pc components (dashed line) matched the N2pc to partially matching distractors on target-absent trials (solid line).

2.2.3 Discussion of Experiment 1

The results of Experiment 1 demonstrate that the attentional selection of target objects defined by the configuration of two basic shapes is not entirely controlled by object templates that represent only the overall shape of targets and not their component parts. Distractor objects composed of both target shapes in the reverse spatial configuration produced clear behavioural costs and triggered substantial N2pc components, indicating that they were able to attract attention. Target-present RTs were delayed when targets were accompanied by a reverse distractor object, and the presence of these objects also produced the slowest RTs on target-absent trials. Reverse distractors not only triggered clear N2pc components in displays

where they appeared together with a nonmatching distractor, but their presence also strongly delayed and attenuated N2pcs to target objects in the same display. This attenuation of the target N2pc by reverse distractors matched the size of the N2pc elicited by reverse distractors alone, suggesting that targets and reverse distractors triggered simultaneous N2pcs of opposite polarity when they appeared on opposite sides of the same display. Partially matching distractor objects that contained one target shape also elicited reliable N2pcs on target-absent trials, and attenuated target N2pc components on target-present trials. The size of this attenuation matched the N2pc to partially matching distractors alone, again indicating that attention was allocated in parallel to both targets and partially matching distractors in the same display. If attention had been exclusively guided by an integrated template of the overall shape of the target object, neither reverse nor partially matching distractors should have been able to attract attention and to elicit N2pc components.

Another possibility is that attentional object selection was guided simultaneously and independently by the templates for each of the two target-defining shapes. This type of strictly part-based guidance would not have been able to discriminate between targets and reverse distractor objects. In fact, the results of Experiment 1 showed that attentional control processes were sensitive to the spatial configuration of shape components, but that this sensitivity emerged later than the effects of part-based attentional guidance. The presence of a reverse distractor on the opposite side of the same display delayed and attenuated target N2pc components, but an N2pc to targets did eventually emerge for these displays, at around 240 ms after display onset, demonstrating that from this point in time onwards, the attentional bias triggered by targets was stronger than the bias elicited simultaneously by reverse distractors. Further evidence for this was provided by the comparison of N2pc components to targets and reverse distractors in displays with a nonmatching distractor on the other side. During the early N2pc time window, these two components did not differ in size, but from

about 230-250 ms onwards, the target N2pc were reliably larger than N2pc to reverse distractors. Together, these observations suggest that attentional guidance processes became sensitive to shape configurations during this time period. The observation that N2pc components to distractors with one target-matching shape were larger when this shape appeared in its assigned vertical position than when it was presented at the other nonmatching position (PMw distractors) from about 230-240 ms post-stimulus is also in line with this hypothesis. Overall, this pattern of results suggests that attention was guided jointly by feature-specific templates for each target shape and by templates that represent the overall spatial configuration of target objects, and that the effects of part-based guidance precede the effects of guidance by shape configuration.

The configuration-based guidance processes revealed in Experiment 1 could be implemented by two different types of target template. One possibility is that these templates are genuinely object-based, representing the target shape as a whole by integrating across its two component parts. The fact that the displays used in Experiment 1 contained two spatially aligned shapes which formed two composite perceptual objects may have encouraged participants to employ such object templates. An alternative possibility is that targets were still represented in terms of their component shapes, together with the task-relevant locations of these shapes (i.e., templates for two shape/location combinations). This was investigated in Experiment 2, where stimulus displays were identical to the first experiment, except that the shape pairs on the left and right side were spatially separated, with one component shape presented in the upper and the other in the lower visual field (see Figure 1, right panel). If attentional guidance by shape configuration was based on integrated object templates, such guidance processes should be less efficient, or not be available at all, when target-defining shapes are not spatially contiguous. In this case, these processes should be more strongly part-based than in Experiment 1.

2.3 EXPERIMENT 2

2.3.1 Methods

Participants

Thirteen participants took part in Experiment 2, and one participant was excluded due to error rates over 3 SDs above the group mean. Of the 12 remaining participants, 4 were male and 3 were left handed (M age = 31, SD = 5). All participants had normal or corrected-to-normal vision. To assess that the sample size in Experiment 1 had been appropriately powered, an analysis was conducted on the previously observed effect sizes. In Experiment 1, the higher order interaction of Display Type x Laterality yielded a partial eta square effect size of .74, in fact larger than the effect size previously observed by Berggren and Eimer (2016b) which informed Experiment 1, and suggesting a minimum sample size of $N = 6$. Thus, there was no evidence to suggest that Experiment 1 was underpowered, and the same sample size in Experiment 2 was used to ensure comparability between these two experiments

Apparatus, Stimuli and Procedure

This experimental design was identical to Experiment 1, except that the two shapes on each side were now presented in the upper and lower visual field quadrant. The vertical gap between the centre of the upper shape and the centre of the lower shape was 4.32° (see Figure 1, bottom panel, for an example display). This distance was identical to the distance between the centres of the two shapes on the left and right side. As in Experiment 1, targets were defined by the spatial configuration of two specific shapes on the same side.

EEG Recording and Data Analysis

These procedures were all identical to Experiment 1.

2.3.2 Results

Behavioural Analysis

Table 1 (right panel) shows mean RTs and error rates for the six different target-present and target-absent displays. For target-present RTs, a main effect of Distractor Type (NM, Rev, PM) was present ($F(2,22) = 8.74, p = .002, \eta_p^2 = .44$). Targets were detected faster when they were accompanied by a nonmatching distractor ($M = 608$ ms) than when they appeared together with a reverse distractor ($M = 639$ ms; $t(11) = 2.91, p = .014, d = .27$) or with a partially matching distractor ($M = 640$ ms; $t(11) = 5.92, p < .001, d = .27$). Target RTs did not differ between displays with reverse or partially matching distractors ($t < 1$). Target-absent RTs were also affected by which type of target-matching distractor was present ($F(2,22) = 52.93, p < .001, \eta_p^2 = .83$). They were slower for displays that included a reverse distractor ($M = 660$ ms) relative to displays with a partially matching distractor ($M = 607$ ms; $t(11) = 4.74, p = .001, d = .70$) and displays with a PMw distractor ($M = 568$ ms; $t(11) = 6.56, p < .001, d = 1.30$). Furthermore, target-absent RTs were slower for displays containing a partially matching distractor with a target shape in its correct position than for displays with a PMw distractor ($t(11) = 10.21, p < .001, d = .56$).

The corresponding analyses of error rates showed no significant main effect of Distractor Type for target-present trials ($F(2,22) = 3.09, p = .066, \eta_p^2 = .22$). Mean error rate on these trials was 5%. On target-absent trials, error rates were reliably affected by the type of target-matching distractor in the display ($F(2,22) = 7.57, p = .003, \eta_p^2 = .41$). Paired

samples t -tests revealed fewer incorrect target-present responses for displays with a PMw distractor ($M = 0.84\%$) than for displays with reverse distractors ($M = 2.24\%$; $t(11) = 2.89$, $p = .015$, $d = .98$) or partially matching distractors ($M = 4.17\%$; $t(11) = 3.81$, $p = .003$, $d = 1.48$). Error rates for target-absent displays with reverse and partially matching distractors did not differ reliably ($t(11) = 1.75$, $p = .108$, $d = .75$).

ERP Analysis: N2pc Components

Target-present displays. Figure 5 shows ERPs elicited contralateral and ipsilateral to target objects on the three different types of target-present displays, with the corresponding N2pc difference waveforms. The presence of target N2pcs was confirmed by a main effect of Laterality ($F(1,11) = 27.82$, $p < .001$, $\eta_p^2 = .72$). A significant Distractor Type x Laterality interaction ($F(2,22) = 31.01$, $p < .001$, $\eta_p^2 = .74$) was due to the fact that these N2pcs were larger when targets were accompanied by a nonmatching distractor ($M = -2.65 \mu\text{V}$) relative to target displays that contained a reverse distractor ($M = -1.14 \mu\text{V}$; $t(11) = 6.03$, $p < .001$, $d = 1.25$) or a partially matching distractor ($M = -1.16 \mu\text{V}$; $t(11) = 5.94$, $p < .001$, $d = 1.12$). There was no target N2pc amplitude difference between displays with reverse and partially matching distractors ($t < 1$). Additional t -test analyses confirmed that significant target N2pc components were elicited for all three types of displays (all t 's > 4.16 , p 's $< .01$, d 's $> .25$). The onset latency of target N2pcs was reliably affected by Distractor Type ($F_c(2,22) = 9.20$, $p = .001$, $\eta_{pc}^2 = .46$), as these N2pcs emerged earlier in displays with nonmatching distractors ($M = 197$ ms) relative to displays with reverse distractors ($M = 249$ ms; $t_c(11) = 4.04$, $p = .002$, $\eta_{pc}^2 = .59$). Additionally, there was an earlier N2pc for targets accompanied by a partially matching distractor ($M = 227$ ms) relative to targets with reverse distractors ($t_c(11) = 2.49$, $p = .030$, $\eta_{pc}^2 = .36$). The target N2pc onset delay difference between displays with

nonmatching versus partially matching distractors narrowly failed to reach significance

($t_c(11) = 2.11, p = .058, \eta_{pc}^2 = .29$).

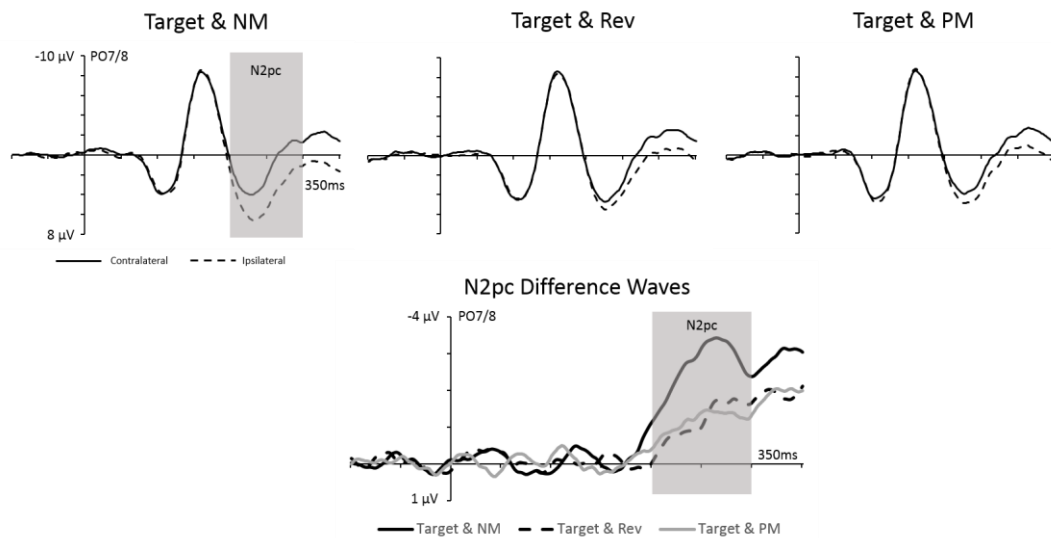


Figure 5. Top panel: Grand-average event-related brain potentials (ERPs) obtained in Experiment 2 on target-present trials at PO7/8 contralateral and ipsilateral to the side of the target object during the 350 ms interval after display onset. ERPs are shown separately for the three different types of target-present displays. Bottom panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for the three target-present display types.

Target-absent displays. Figure 6 shows ERPs elicited contralateral and ipsilateral to target-matching distractor objects in target-absent displays, with the corresponding N2pc difference waveforms. These objects elicited N2pc components, confirmed by a main effect of Laterality ($F(1,11) = 15.41, p = .002, \eta_p^2 = .58$). There was also a significant Distractor Type x Laterality interaction ($F(2,22) = 4.06, p = .032, \eta_p^2 = .27$), demonstrating that N2pc amplitudes differed between the different types of distractors in target-absent displays. N2pc components to PMw distractors ($M = -.83 \mu\text{V}$) were smaller than N2pcs to partially matching

distractors ($M = -1.40 \mu\text{V}$; $t(11) = 3.38$, $p = .006$, $d = .62$), and to reverse distractors ($M = -1.42 \mu\text{V}$), although the latter difference narrowly missed significance ($t(11) = 2.06$, $p = .06$, $d = .51$). N2pc amplitudes to reverse and partially matching distractors did not differ ($t < 1$). Additional analyses confirmed that significant N2pc components were elicited for all three types of target-matching distractors displays (all t 's > 3.27 , p 's $< .01$, d 's $> .19$). N2pc onset latencies did not differ between the three different types of target-matching distractors ($F_c < 1$).

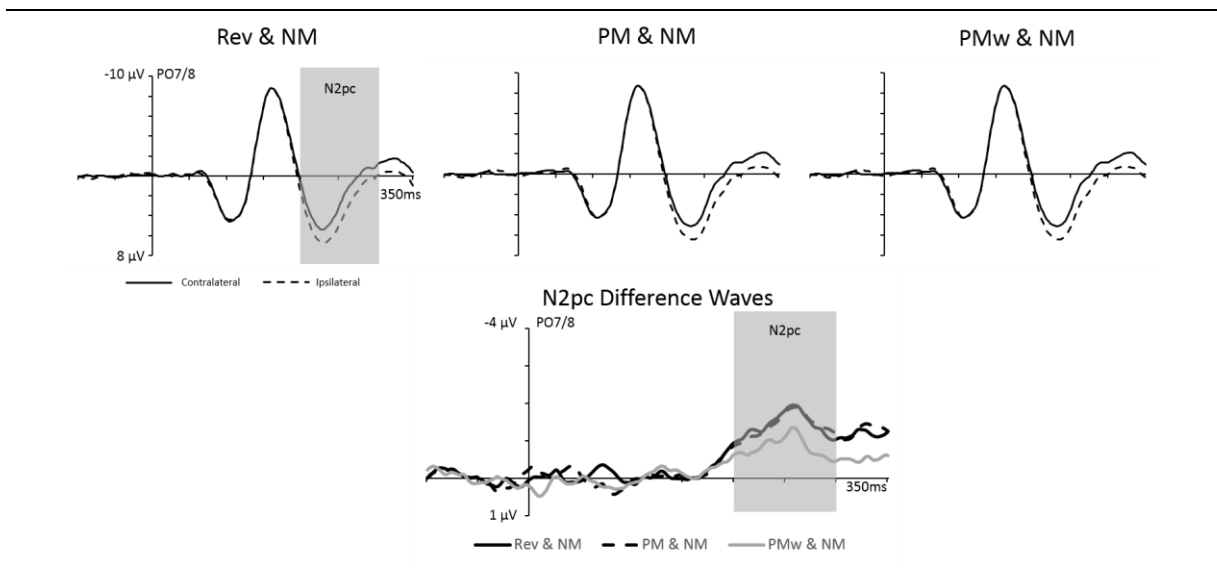


Figure 6. Top panel: Grand-average event-related brain potentials (ERPs) obtained in Experiment 2 on target-absent trials at electrode sites PO7/8 contralateral and ipsilateral to the side of the target object during the 350 ms interval after display onset. ERPs are shown separately for the three different types of target-absent displays. Bottom panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for the three target-absent display types.

N2pc analyses across target-present and target-absent trials. As in Experiment 1, N2pcs triggered by targets and reverse distractors in displays with nonmatching distractors

were compared to find out whether the spatial arrangement of the two target-matching shapes affected N2pc amplitudes. Across the whole N2pc measurement window, targets again triggered larger N2pcs than reverse distractor objects ($t(11) = 5.87, p < .001, d = .84$). Comparisons of N2pc difference waves for these two types of objects with successive one-tailed paired t-tests and with a jackknife-based analysis (using the same procedures and onset criteria as in Experiment 1) showed that target N2pcs started to become larger than N2pcs to reverse distractors at 220 ms (t-test analysis) or 222 ms (jackknife-based analysis) after display onset. The attenuation of target N2pc components in displays where targets were accompanied by reverse or partially matching distractors again matched the N2pc elicited by these two types of distractors on target-absent trials. As shown in Figure 7, the difference between N2pcs to targets presented with or without a reverse distractor N2pc was equal in size to the N2pc elicited by reverse distractors on target-absent trials (left panel), and the same result was found for partially matching distractors (right panel; both t 's < 1). The corresponding analyses comparing N2pc amplitudes to PM and PMw distractors found that the N2pc to PM distractors started to become larger than the N2pc to PMw distractors from 262 ms (t-test analysis) or 244 ms (jackknife analysis) post-stimulus.

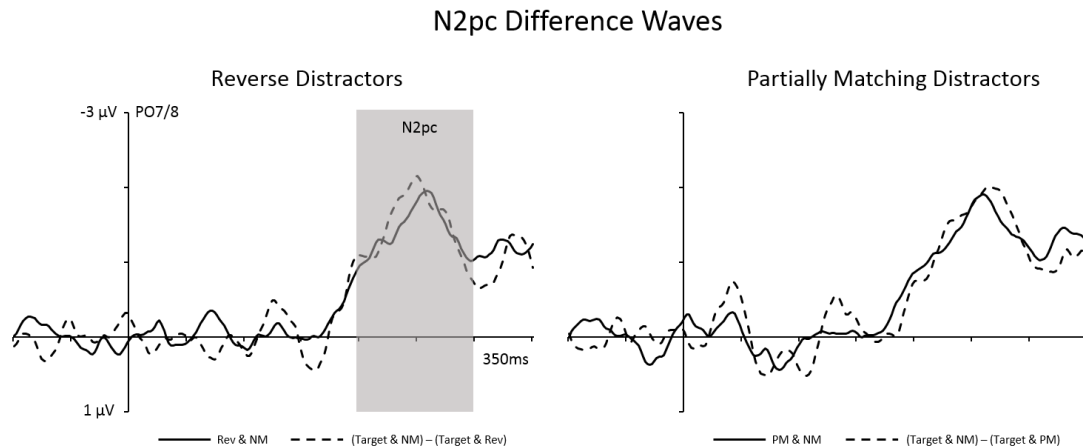


Figure 7. Left panel: N2pc difference waveforms showing that the difference of target N2pcs in the presence versus absence of a reverse distractor (dashed line) in Experiment 2 matched the size of the N2pc triggered by reverse distractors on target-absent trials (solid line). Right panel: N2pc difference waveforms showing the effect of partially matching distractors on target N2pc components (dashed line) matched the N2pc to partially matching distractors on target-absent trials (solid line).

2.3.3 Discussion of Experiment 2

As in Experiment 1, reverse and partially matching distractors triggered reliable N2pc components on target-absent trials, and their presence attenuated and delayed target RTs and target N2pc components. The reduction of N2pcs to targets by reverse and partially matching distractors in the same display again matched the size of the N2pc components elicited by these distractors on target-absent trials, suggesting that this reduction was due to two N2pc components of opposite polarity elicited at the same time. These results show that, as in Experiment 1, reverse and partially matching distractors were able to attract attention, in line with the assumption that object selection was guided by part-based feature templates for component shapes.

Critically, attentional guidance remained sensitive to the spatial arrangement of the two component target shapes in Experiment 2, in spite of the fact that these shapes were vertically separated and appeared in different quadrants. Analogous to Experiment 1, target objects elicited larger N2pc components than reverse distractors, and this amplitude difference emerged around 220 ms after display onset. Furthermore, a reliable N2pc was triggered contralateral to targets when they appeared together with a reverse distractor on the opposite side, demonstrating that targets triggered a stronger attentional bias than reverse distractors. As in Experiment 1, this N2pc emerged later than the N2pc to targets with nonmatching distractors, indicative of configuration-based guidance mechanisms that are activated later than part-based processes. Partially matching distractors again elicited larger N2pc components when the target-matching shape appeared at its assigned position than when it was presented in the opposite vertical position, and this difference now emerged around 250 ms post-stimulus. These results clearly show that, as in Experiment 1, attentional guidance was not fully part-based, but remained sensitive to the spatial arrangement of the two target-defining shapes even when these shapes were not spatially aligned and thus did not form composite perceptual objects. The implications of these findings will be further considered below.

2.4 Chapter 2 Discussion

The goal of the two Experiments reported in this Chapter was to investigate the guidance of attentional object selection in conjunction search tasks where target features come from the same dimension (shape) and target objects are defined by a particular spatial arrangement of two component shapes. Participants reported the presence or absence of targets in displays that contained two vertically arranged shapes on opposite sides. These

shapes were either spatially aligned (Experiment 1) or separated (Experiment 2). A previous N2pc investigation of colour/colour configuration search (Berggren & Eimer, 2016b) found that attentional guidance operated in a strictly part-based fashion, independently for both target colours, and was insensitive to the spatial configuration of these colours. The experiments reported in Chapter 2 demonstrated that this is not the case for the guidance of shape/shape configuration search. Regardless of whether objects were composed of spatially aligned or vertically separated shapes, targets triggered larger N2pc components than reverse distractors. In displays where targets and reverse distractors appeared on opposite sides, an N2pc was triggered contralateral to the target, confirming that targets triggered a stronger attentional bias. Distractors with one target-matching shape elicited larger N2pc components when this shape appeared in its assigned target-matching location. Together, these findings show that the guidance of attentional object selection during shape/shape configuration search was not entirely part-based, but was sensitive to the spatial arrangement of the two component shapes. The fact that this was also the case when the component shapes were spatially separated (Experiment 2) shows that the spatial arrangement of two task-relevant shapes influences attentional guidance even when these shapes do not form a single spatially contiguous perceptual object.

Even though attentional guidance was not completely part-based, separate feature templates for both target-defining shapes were clearly involved in the control of attentional object selection. Reverse and partially matching distractors triggered reliable N2pc components, and delayed N2pcs to targets in the same display, demonstrating that a target-matching shape remained able to attract attention even when it was part of a nontarget object. In both experiments, participants were slowest to report the presence or absence of a target when a reverse distractor was present in the same display, suggesting that these distractor objects triggered attentional biases that were at least initially similar to the biases triggered by

targets. The fastest RTs were observed for PM & NM and PMw & NM displays, presumably because these displays only contained a single target-matching shape and could thus be rapidly classified as target-absent trials. Because targets were defined by a combination of two shapes, these results also provide further evidence that search can be controlled by templates for multiple features from the same dimension. This is in line with the conclusion drawn in previous studies of colour/colour conjunction search (Irons et al., 2012; Grubert & Eimer, 2016; Berggren & Eimer, 2016a), but inconsistent with the hypothesis of the Guided Search model that only a single feature per dimension can be involved in attentional guidance (Wolfe, 2007).

If feature-based attentional guidance operates independently and concurrently for each target-matching shape, one would expect reverse distractors to trigger stronger early attentional biases than partially matching distractors, because the former contain both target shapes. The fact that the presence of a reverse distractor in the same display attenuated and delayed target N2pc components more strongly than the presence of a partially matching distractor is in line with this predictions. However, there were no reliable amplitude or latency differences between N2pcs to reverse and partially matching distractors on target-absent trials. This discrepancy could suggest that the difference in the attentional biases elicited by these two types of distractor objects is more pronounced when the competition for attention is high in displays that contain multiple candidate targets than when they are the only object with target-matching features. Because the similarity of N2pc components to reverse and to partially matching distractors in target-absent displays is not entirely in line with a parallel account of feature-based attentional selectivity, this result needs to be confirmed and accounted for in future studies.

Overall, the results of Experiments 1 and 2 show that shape parts and shape configurations are both employed in the control of attention during search for target objects

defined by a specific configuration of component shapes, and that these two types of attentional guidance appear to differ in their time course. In displays where targets were accompanied by reverse distractors, N2pc were delayed by about 40 ms relative to displays where targets appeared together with nonmatching distractors. As the onset latency of target N2pc marks the moment when an attentional bias for target objects emerges, the delay caused by the presence of reverse distractors indicates that such biases did not emerge during the early part of the N2pc time window, but only beyond 230 ms post-stimulus. The absence of a target N2pc before that point in time indicates that targets and reverse distractors elicited equivalent attentional biases which cancelled each other out, as would be the case if attentional guidance was entirely part-based during this time period. Following this initial feature-based phase, guidance became sensitive to the spatial arrangement of target-matching shape components, resulting in a net attentional bias towards target objects. Further evidence for these two phases in attentional guidance was provided by the observation that N2pc components to targets and to reverse distractors in displays with a nonmatching distractor on the opposite side were initially identical in size, before the target N2pc started to become larger than the distractor N2pc from about 230 ms post-stimulus. The hypothesis that the guidance of search for shape configurations is initially part-based may also explain why search for targets defined by the configuration of two shapes among distractor objects with the reverse spatial arrangement (e.g., snowmen among upside-down snowmen; Wolfe et al., 1999) is relatively inefficient. An analogous sequence of feature-based followed by object-based attentional selection mechanisms has been found in previous N2pc experiments investigating conjunction search tasks where target-defining features came from different dimensions (colour and shape: Eimer & Grubert, 2014; colour/shape and alphanumeric category: Nako, Grubert, & Eimer, 2016) or from the same dimension (colour: Berggren & Eimer, 2016a).

According to this biphasic account, an early strictly part-based selection phase is guided by separate templates for individual target shapes that bias attention towards any of these shapes, regardless of their location in the visual field and irrespective of their configural relationship with other spatially aligned or non-aligned shapes in the same display. During the second phase, attentional control starts to be affected by spatial-configural information, resulting in an attentional bias towards objects with shape components in the correct spatial arrangement. This configural guidance of attentional selectivity could be based on integrated target object templates that represent overall target shape rather than individual shape parts, or on separate templates for each target shape that also represent the assigned task-relevant locations of these shapes (e.g., circle in lower visual field). The fact that attentional biases towards objects with the relevant spatial arrangement of shape components emerged beyond 230 ms post-stimulus not only when target objects were composed of spatially aligned component shapes (in Experiment 1), but also when these shapes were spatially separated (in Experiment 2) suggests that this type of attentional control is more likely to be based on separate templates for specific shape/location conjunctions. Recent electrophysiological studies (Adamo, Pun, & Ferber, 2010; Berggren, Jenkins, McCants, & Eimer, 2017) have suggested that it is difficult to employ multiple templates for different target features at particular positions in order to restrict feature-based attentional guidance to specific locations. However, these experiments have only investigated task sets for specific colour/location combinations, and it therefore remains possible that such templates might be available in the shape domain.

The current results show that visual search for target objects defined by the vertical arrangement of two component shapes can be guided by the spatial arrangement of these shapes (albeit only after an initial part-based phase). In contrast, the previous N2pc experiment of colour/colour configuration search (Berggren & Eimer, 2016b, Experiment 3)

found that guidance was entirely part-based throughout the 500 ms interval after search display onset. This discrepancy might be partially due to procedural differences. The search display employed in this earlier experiment always contained four objects, and displays in which targets and reverse distractors appeared together also contained two other objects with one target-matching colour. The competitive effects of these partially matching distractor objects may have reduced the sensitivity of colour-based attentional control processes to spatial-configural information in this study. The differences between these previous and the current results may also reflect more general differences between the colour and shape domains. Attentional guidance based on the spatial arrangement of component shapes will be useful during search for many real-world objects, but there are few occasions where search targets are defined by particular configuration of different colours.

In summary, the two experiments reported in this Chapter have shown that search for target objects defined by the spatial configuration of two component shapes is initially guided in a part-based fashion by independent templates for each target shape. Following this early strictly feature-based selection phase, attentional control processes become sensitive to spatial-configural information, and are therefore able to distinguish target objects from objects with the same shape components in a different spatial arrangement. These results also underline that attentional object selection should not be conceptualized as a single discrete stage that is controlled by a fixed top-down task set, but instead a temporally extended process that can be guided by different types of target templates at different moments in time.

Chapter 3

**The control of working memory maintenance for
basic shapes and spatial configurations of shapes**

The experiments presented in this chapter have been submitted for publication in a peer-review journal.

Experiments 3 and 4:

McCants, C., Katus, T., & Eimer, M. The control of working memory maintenance for basic shapes and spatial configurations of shapes.

3.1 Chapter 3 Introduction

Chapter 2 investigated the role of spatial configuration information in the guidance of perceptual attention. Attentional selectivity was sensitive to spatial configuration, suggesting that this information was represented as part of an attentional template. Templates are held in working memory (WM), suggesting that shape-shape configuration information can be effectively represented in WM. But how is this information represented? Analogous to the questions addressed in Chapter 2 for perceptual attention, there are several possibilities. Consider the situation where observers have to encode and maintain the exact spatial configuration of a compound object that is composed of two basic shapes in a particular spatial configuration (e.g., hourglass above circle, as in the experiments reported in Chapter 2). One possibility is that each shape is represented separately in WM, together with a specification of the spatial location of each shape (e.g., hourglass/top; circle/bottom). Another possibility is that these two shapes are fully integrated during their encoding into WM, so that the resulting maintained object no longer represents each shape independently, but instead specifies a single compound object with its specific compound shape. These possibilities are analogous to the difference between integrated and part-based attentional templates investigated in Chapter 2. In the experiments reported in this Chapter, these alternatives will be studied in the context of a WM paradigm, using the same set of stimuli used in the experiments reported in Chapter 2.

To study the maintenance of shape parts and shape configurations in WM, brain activity elicited during visual WM maintenance was measured, in order to obtain ERP markers of visual WM storage processes. Earlier ERP studies (e.g., Vogel & Machizawa, 2004; McCollough, Machizawa, & Vogel, 2007) employed a lateralized change detection task where bilateral memory sample displays contained coloured objects in the left and right visual hemifield, and observers had to maintain the colours of sample stimuli on one side in order to compare them

to a subsequent test display. ERPs recorded during the delay period between the memory and test displays revealed an enhanced negativity at posterior electrodes contralateral to the to-be-remembered display side (contralateral delay activity, CDA). This activity started around 300 ms after the onset of the memory sample display, persisted throughout the retention interval, increased in amplitude when memory load was increased, and was sensitive to individual differences in WM capacity (e.g., Vogel & Machizawa, 2004). Based on these observations, it has been suggested that the CDA is an on-line neural marker of the storage of objects or object features in visual WM.

Other CDA experiments have shown that the activation of WM representations to the same memorized objects can vary as a function of which object attributes are currently task relevant. For example, Woodman and Vogel (2008) addressed the question whether non-spatial features (colour and orientation) can be represented separately in WM even when they belong to the same object. They measured CDA components to memory sample displays containing oriented coloured rectangles in tasks where observers had to memorize either colour, orientation, or the conjunction of both features. CDA amplitudes were larger when orientation as compared to colour was task-relevant, in spite of the fact that sample displays were identical. This observation is inconsistent with the hypothesis that objects are always represented fully and in an integrated fashion in WM, so that all of their features are coded, regardless of which of their features are task-relevant. If this was the case, no CDA amplitude differences to physically identical sample objects should have been present in the study by Woodman and Luck (2008). These authors therefore interpreted the presence of CDA differences produced by different task instructions as evidence that colour and orientation information can be represented independently in WM, even when the other feature is present in the same object. Similar CDA amplitude differences in response to physically identical sample stimulus displays have also been found in another ERP study (Luria, Sessa, Gottler, Jolicœur, &

Dell'Acqua, 2010) where observers had to memorize either the colours or the shapes of coloured polygons. These CDA results demonstrate that specific object features can be selectively prioritized in WM, and that other features of the same object that are currently not task-relevant may not be encoded at all. In other words, WM representations can be part-based when this is required by the specific demands of a WM task.

This raises an important question about the nature of WM representations of objects with multiple features. One possibility is that these objects are typically represented by default in a fully integrated fashion. Another possibility is that part-based representations are the norm in WM. A third possibility is that both part-based and integrated object representations can be effectively maintained in WM, and that the choice between these two types of representational formats depends on the nature of a particular WM task. The goal of the experiments reported in Chapter 3 was to investigate this third possibility. Instead of studying the more common situation where to-be-memorized object features come from different dimensions (such as colour and orientation, as in Woodman & Vogel, 2008), the present chapter focused on a task where these features come from the same dimension (shape). As in the experiments reported in Chapter 2, objects that were composed of two basic shapes that were aligned vertically were employed. Instead of instructing participants to activate attentional templates for specific target objects defined by a shape/shape combination in order to find these objects in search displays, as in Chapter 2, the same objects in the context of a lateralised change detection task were used. On each trial, a memory sample display containing objects in the left and right visual field was followed by a memory test display containing a single object at fixation (see Figure 8 for an illustration). The memory sample and test displays were separated by a delay period of 850 ms. Participants had to memorize the object or objects on one task-relevant side of the sample display, in order to compare them to the object in the subsequent test display. This test object was identical to an

object in the sample display on 50% of all trials, and different on the other 50%. Participants had to report the presence of a match or mismatch on each trial with a button press response. The task-relevant side of the memory sample display (left versus right) was varied between blocks, and remained the same within each experimental block.

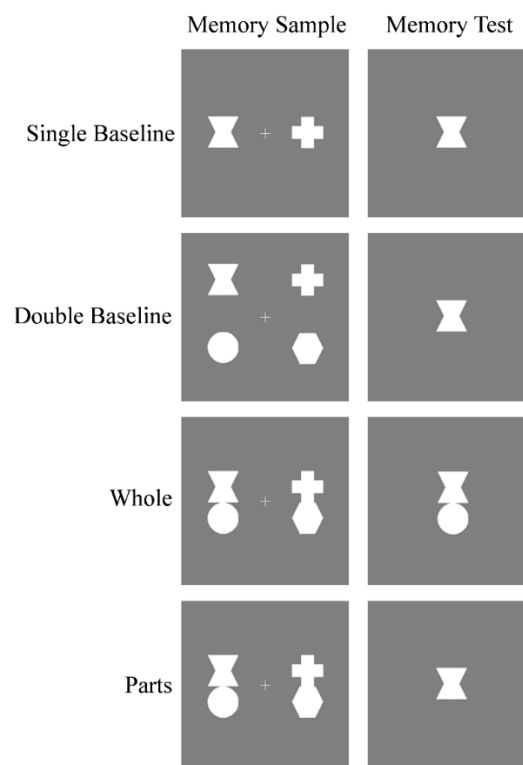


Figure 8: Illustration of the four conditions in Experiment 3. Memory sample and test displays are shown on the left and right, respectively. In the examples shown, the stimuli on the left of the fixation cross were designated as the target(s). In all conditions, participants were tasked with memorizing the target stimuli. In the Single Baseline condition, the target consisted of only one shape whilst in the other conditions, the target items were two shapes in vertical alignment. Memory test stimuli were always presented at fixation. In the Whole condition, the test item was composed of two vertically aligned shapes, whilst in the remaining conditions, the test item was a single shape.

Because participants had to maintain the shape(s) on the task-relevant side of the memory displays in WM throughout the delay period before the test display was presented, CDA components should be elicited during this delay period. In Experiment 3, these CDA components were measured in different task conditions that were designed to selectively invoke either part-based or integrated representations of object shapes in WM. The four task conditions employed in Experiment 3 are illustrated in Figure 8. There were two baseline conditions and two critical test conditions (Parts and Whole) where identical sample displays were used, but test displays and task instructions were different. These four task conditions were run in different blocks. In the Whole condition, memory sample displays contained two compound shapes (two vertically aligned basic shapes) on either side and test displays contained one compound-shape object at fixation. Participants had to memorize the compound shape of the object on the relevant side of the memory display, and to report whether the object in the test display was exactly identical to this shape or not. To encourage participants to represent the relevant memory sample object in an integrated fashion in this condition (and not in a part-based fashion), half of all test displays shown on mismatch trials contained the same two basic shapes as the memorized sample object, but in the opposite spatial configuration (e.g., circle-above-hourglass when hourglass-above circle was the currently memorized object). Because activating entirely part-based WM representations of sample objects would not enable participants to distinguish matching test objects from these inverted mismatching objects, the inclusion of these objects was expected to facilitate an integrated WM encoding and maintenance strategy.

This Whole condition was contrasted with a Parts condition, which employed physically identical memory sample displays. The critical difference between Whole and Parts conditions concerned the nature of the memory test displays. In the Parts condition, only one component shape was presented at fixation in these test displays. On half of all

trials, this shape matched one of the two basic shapes on the task-relevant side of the sample display. On the remaining mismatch trials, the test shape matched neither of the two relevant sample shapes. In this condition, participants were required to represent both of the component shapes in the sample display independently, as either of them was equally likely to re-appear in the subsequent test display. In contrast to the Whole condition, they had no incentive to form a compound WM representation that integrated across these two shapes, and compound objects never appeared in the test display. In fact, forming an integrated WM representation across both task-relevant shapes might be counterproductive in this task, as it might make it more difficult to correctly identify the subsequent simple test shape as either matching or mismatching.

In addition to the Whole and Parts condition, Experiment 3 also included two baseline conditions where WM was always tested with displays that contained a simple shape at fixation. In the Single Baseline, participants memorized a single simple shape on the task-relevant side. In the Double Baseline, they had to maintain two shapes on the relevant side, which now were no longer vertically aligned (as in the Whole and Parts conditions), but were spatially separated, in order to appear as two clearly distinct objects (see Figure 8).

The critical question addressed in Experiment 3 was whether participants would encode and maintain physically identical sample display objects in WM in a qualitatively different fashion in the Whole and Parts condition. In the Whole condition, these objects should be represented in an integrated fashion, that is, as a single compound shape. In contrast, the same objects should be represented in a part-based fashion (that is, as two separate basic shapes) in the Parts condition. To test this prediction, CDA components elicited during the delay period between memory sample and test displays were measured and compared between these two conditions. One critical property of the CDA is that it is sensitive to the number of objects that are currently maintained in WM, with CDA

amplitudes increasing as the number of memorized objects increases (e.g., Vogel & Machizawa, 2004). Thus, qualitative differences in the way that physically identical sample display objects are represented in WM in the Whole and Parts conditions should be reflected by systematic CDA amplitude differences between these two conditions. More specifically, if participants represent the two component shapes as a single integrated object in the Whole Task, the effective working memory load in this task would correspond to one object. In contrast, if participant represent the same memory sample display items as two separate objects in the Parts task, the effective WM load in this task would be two. In this case, CDA amplitudes in the Parts task should be significantly larger than in the Whole task, in spite of the fact that identical sample displays were shown in both tasks.

If WM contains a single compound shape object in the Whole condition, but two separate simple shape objects in the Parts condition, the CDA amplitude difference between these two conditions should be equivalent to the CDA amplitude difference observed between the Single and Double Baseline conditions. One could even postulate that the CDA observed in the Whole condition should be identical to the Single Baseline condition, and the CDA in the Parts condition should be the same as the CDA in the Double Baseline condition. However, these direct comparisons are problematic for several reasons. First, it has previously been shown that CDA amplitudes are larger for complex as compared to simple stimuli (e.g. polygons versus colours; Luria & Vogel, 2011), even when the number of items was held constant. Thus, CDA amplitudes are likely to be larger for compound objects in the Whole condition than for simple object shapes in the Single Baseline condition. Furthermore, the fact that sample display shapes appeared at different locations in the Double Baseline and Parts conditions (spatially separated versus aligned; see Figure 8), could also result in CDA amplitude differences between these two conditions that are unrelated to the number of objects that are currently maintained in WM.

3.2 EXPERIMENT 3

3.2.1 Methods

Participants

Fourteen participants were tested (mean age 30 years, 6 male, 1 left-handed). All participants were healthy and had no visual or neurological impairments at the time of testing and gave informed written consent prior to testing. The experiment was approved by the Ethics Committee of the Department of Psychological Sciences, Birkbeck, University of London.

Apparatus, Stimuli, and Procedure

This experiment was programmed and executed using Matlab software (MathWorks, Natick, MA). Stimuli were presented on a 24-inch BenQ widescreen monitor (60Hz, 1920 x 1080 screen resolution) at a viewing distance of approximately 60 cm. Participant responses were given via button press on a BlackBox Toolkit button system (The Black Box Toolkit Ltd, 2016) with a custom 4-button layout arranged in cardinal directions and equidistant from the centre of the box. In this experiment, only the top and bottom buttons were used. Reaction times were recorded starting from the onset of the memory display. If participants did not answer before the next trial commenced, their response was registered as incorrect.

In each trial, a bilateral sample memory display was displayed for 150 ms, followed by a delay period of 850 ms, and a central memory test display that was presented for 150 ms. A grey fixation cross subtending 0.31 x 0.31 degrees of visual angle was present throughout

each block. The central memory test display was superimposed on this fixation cross. The stimuli used in Experiment 3 were identical to those used in the two experiments reported in Chapter 2 (see also McCants, Berggren, & Eimer, 2018). All four possible shapes (hexagon, circle, hourglass and cross) were both vertically and horizontally symmetrical and were equal in size ($1.15 \times 1.15^\circ$). Each memory sample display contained objects in the left and right visual field, at a horizontal eccentricity of 2.16° from the central fixation cross.

Before each block, participants were instructed to memorize the object or objects on one task-relevant side (left or right), and to report on each trial whether the subsequent memory display object matched this memorized object(s). The task-relevant side changed from left to right, or vice versa, between each successive block. There were four task conditions, each delivered in four successive blocks. In the Single Baseline condition, memory displays contained a single geometric shape on each side, and participants had to report whether the shape presented on the task-relevant side was repeated in the test display (match trials) or not (mismatch trials). In the Double Baseline condition, sample displays contained two shapes on each side, which were separated by 4.32° (measured from the midpoint of both shapes). On match trials, one of the two shapes on the task-relevant side was shown again in the memory test display. On mismatch trials, the shape in the test display matched neither of these two memorized shapes. In the Whole and Parts conditions, memory sample displays contained two vertically aligned shapes on either side, which were now spatially aligned (one on top of the other, see Figure 8). These two conditions differed with respect to the memory test displays shown on every trial. In the Whole condition, the test display included two spatially aligned shapes at fixation, and participants had to report whether these shapes and their spatial arrangement matched the shape arrangement shown on the task-relevant side of the sample display. On half of all mismatch trials, one shape in the test display differed from the two memorized sample display shapes, while the other shape

appeared in the same location as in the sample display. On the other half, the test display contained both memorized shapes, but in the incorrect vertical configuration (e.g. cross above hexagon instead of hexagon above cross). This was done to encourage participants to memorize the task-relevant sample display items as a global object, and not as separate representations of simple shapes. In the Parts condition, the test display contained a simple shape at fixation. Test displays either showed one of the task-relevant sample shapes (match trials), or a different shape (mismatch trials).

In all four task conditions match and mismatch trials were equiprobable (50% each). Participants were required to press the top button to report a sample-test match, and the bottom button to report a mismatch. The assignment of different shapes to locations on the left and right side of the memory sample displays was randomly determined on each trial, without replacement. As a result, all four possible shapes appeared in each memory sample display in the Double Baseline, Whole, and Parts condition, whereas only two of these four shapes were shown in sample displays in the Single Baseline condition (see Figure 8). Each of the four successive blocks for each task condition consisted of 36 trials. The interval between the offset of a memory test display and the onset of a sample display on the next trial was 1500 ms. The order in which the four task conditions were delivered was counterbalanced across participants in the form of a size four Latin square (e.g. ABCD, CDAB, DCBA, BADC).

EEG Recording and Data Analysis

EEG was DC-recorded at 27 scalp electrodes on an elastic cap at sites Fpz, F7, F8, F3, F4, Fz, FC5, FC6, T7, T8, C3, C4, Cz, CP5, CP6, P9, P10, P7, P8, P3, P4, Pz, PO7, PO8, PO9, PO10, and Oz. A sampling rate of 500 Hz was used with a low-pass filter of 40 Hz. Channels were referenced online to an electrode on the left earlobe, and re-referenced to an average of

both the left and right earlobes offline. No other filters were applied following EEG acquisition. Trials were rejected for incorrect responses, eye-blinks ($> \pm 60 \mu\text{V}$ at Fpz), eye-movements ($> \pm 30 \mu\text{V}$ in the HEOG channels), or muscle movement artefacts ($> \pm 80 \mu\text{V}$ at all other channels), and these trials were not included in any analysis. The remaining trials were segmented into epochs from 100 ms before to 1000 ms after the onset of each memory sample display. Trials with left and right targets were collapsed and averaged ERP waveforms were then computed for each of the four conditions. CDA amplitudes were quantified as the difference between ERP mean amplitudes obtained between 350 and 950 ms after test display onset at lateral posterior electrode sites (PO7 & PO8) contralateral and ipsilateral to the currently task-relevant side of the sample displays. These CDA mean amplitudes were compared between the tasks employed in Experiment 3. Paired t-tests were used to compare CDA amplitudes between the Parts and Whole tasks, and between the two Baseline tasks. To test whether CDA amplitude differences between the Parts and Whole conditions were equivalent to those observed between the Single and Double Baseline conditions, Bayesian analyses (Rouder et al., 2009) analysed with the software Jasp (JASP team 2018) were used to calculate the Bayes factor for the comparison between these two CDA amplitude differences. Bayes factors denote the relative evidence for the null hypothesis as compared to the alternative hypothesis, and thus allow for statistical inferences regarding the absence of differential effects. The Bayes factor for the null hypothesis (BF_{01}) corresponds to the inverse of the Bayes factor for the alternative hypothesis (BF_{10}), and indexes the relative evidence in the data that an effect is absent rather than present. Reliable evidence for the null hypothesis is provided by a $\text{BF}_{01} > 3$ (Jeffreys, 1961), suggesting that the empirical data is at least 3 times more likely under this hypothesis as compared to the alternative hypothesis.

3.2.2 Results

Behavioural Analysis

Figure 9 shows reaction times (RT) and error rates for the four task conditions of Experiment 3. RTs were entered into a one-way ANOVA with factor Task (Single Baseline, Double Baseline, Whole, Parts). There was a highly significant effect of Task ($F(3,39) = 23.33, p < .001, \eta_p^2 = .64$). Responses were substantially faster in the Single Baseline condition (604 ms) relative to the Double Baseline condition (717 ms; $t(13) = 8.23, p < .001, d = 0.84$), the Whole condition (703 ms; $t(13) = 7.82, p < .001, d = 0.67$), and the Parts condition (702 ms; $t(13) = 6.06, p < .001, d = .73$). There were no significant RT differences between any of these other three task conditions (all $t(13) < 1.1$, all $p > .29$).

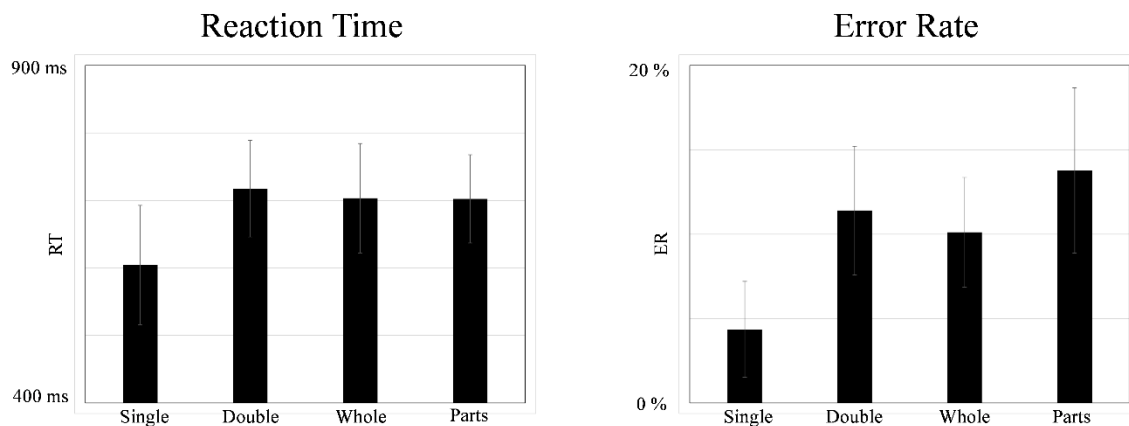


Figure 9: Reaction times (left panel) and error rates (right panel) in all four conditions in Experiment 3. Error bars in graphs indicate 95% confidence intervals (Cis) for the true population mean.

Error rates also differed between the four task conditions ($F(3,39) = 12.51, p < .001, \eta_p^2 = .490$). Errors were less frequent in the Single Baseline condition (5%) than in the

Double Baseline condition (12%; $t(13) = 4.69, p < .001, d = 1.26$), the Whole condition (10%; $t(13) = 3.63, p = .003, d = 1.08$), and the Parts condition (14%; $t(13) = 4.10, p < .001, d = 1.33$). Errors were more frequent in the Parts relative to the Whole condition ($t(13) = 2.63, p = .021, d = 0.49$). There were no error rate differences between the Double Baseline and Whole conditions ($t(13) = 1.21, p = .247, d = 0.21$) or the Double Baseline and Parts conditions ($t(13) = 1.58, p = .138, d = 0.31$).

ERP Analysis: CDA Components

Figure 10 shows ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to the task-relevant side of the memory displays, separately for each of the four task conditions (top panels), together with the corresponding contralateral-ipsilateral difference waves (bottom panel). Mean amplitudes in the range of 350 to 950 ms after sample display onset were entered into an ANOVA with factors Task (Single Baseline, Double Baseline, Whole, Parts) and Laterality (Contralateral, Ipsilateral). There was a significant main effect of Laterality ($F(1,13) = 25.33, p < .001, \eta_p^2 = .661$) indicating the presence of reliable CDA components. Paired samples t-tests confirmed that significant CDA components were elicited in all four task conditions (all t 's > 3.92 , all p 's $< .002$). Importantly, there was also an interaction between Task and Laterality ($F(3, 39) = 11.34, p < .001, \eta_p^2 = .466$), demonstrating that the size of the CDA differed between task conditions. To assess this further, difference waves were computed by subtracting ipsilateral from contralateral ERPs, separately for each task condition, and were then compared with planned post-hoc paired samples t-tests. The results for the two baseline conditions were as expected. CDA amplitudes were larger in the Double as compared to Single Baseline condition ($-1.55 \mu\text{V}$ versus $-0.90 \mu\text{V}$), although this difference was only marginally significant ($t(13) = 2.06, p = .03, d = 0.57$, one tailed). Critically, there was also a CDA amplitude difference between the Whole and Parts

condition. Larger CDA components were elicited in the Parts condition ($-2.30 \mu\text{V}$) than in the Whole condition ($-1.86 \mu\text{V}$), and this difference was reliable ($t(13) = 2.74, p = .017, d = .30$). Thus, the increase in the size of the CDA associated with memorizing two rather than just one simple shape in the two Baseline conditions ($.65 \mu\text{V}$) was numerically similar to the increase observed in the two critical tasks for the Parts condition relative to the Whole condition ($.44 \mu\text{V}$; $t(13) < 1$). A Bayesian t-test directly comparing the size of these two effects provided substantial but not fully conclusive evidence for the null-hypothesis ($\text{BF}_{01} = 2.916$). This suggests that the likelihood of CDA amplitude increases in the Double versus Single Baseline condition being identical to the CDA increase in the Parts versus Whole conditions was almost three times more likely than the alternative hypothesis.

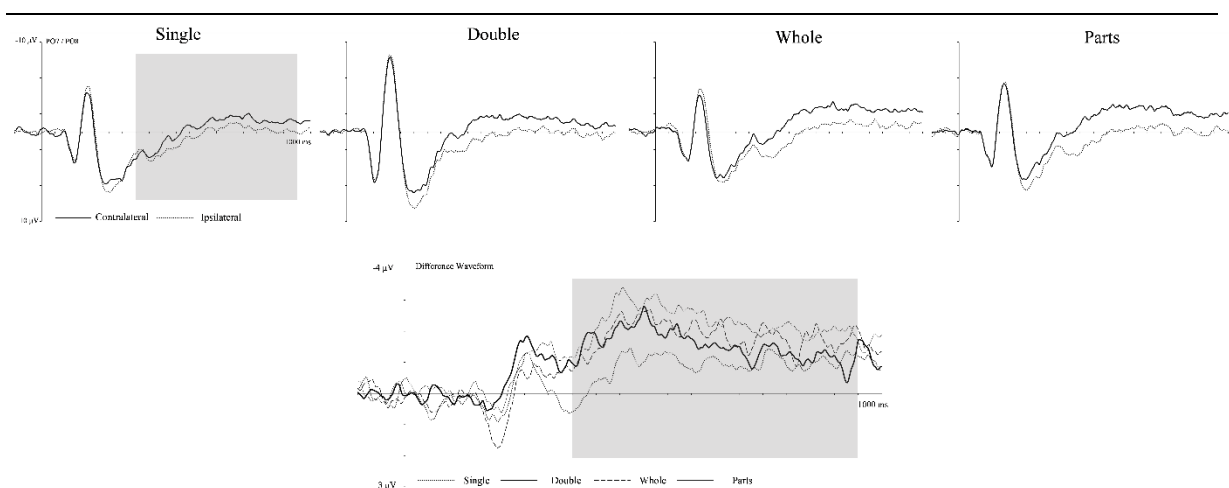


Figure 10: Top panel: Grand-average event-related brain potentials (ERPs) obtained in Experiment 3 at PO7/PO8 contralateral and ipsilateral to the side of the target object during the 1000 ms interval after memory sample display onset. ERPs are shown separately for the four different task conditions. Bottom panel: CDA difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for the four different task conditions.

3.2.3 Discussion of Experiment 3

The CDA results obtained in Experiment 3 provide new evidence that physically identical visual stimuli can be represented in different formats in WM, depending on current task demands. Although the sample stimulus displays were identical in the Whole and Parts condition, the subsequent test displays were different, and this difference required participants to represent the sample stimuli in different ways. In the Parts Condition, the two spatially aligned component shapes of the sample items had to be represented separately, because only one of these shapes could appear in the subsequent test displays. Representing the two shapes as a single integrated object was not adaptive in this task, as it would have made the matching process between the memorized sample object and the test display object more difficult. In contrast, participants had to represent these sample shapes in an integrated fashion in the Whole task, where test displays also contained compound objects with two aligned component shapes. Because both shapes of the task-relevant memory sample items could also re-appear on mismatch trials in this task, in the reverse spatial configuration, representing these items in a part-based fashion was not adaptive, since their spatial configuration was relevant to distinguish matching from mismatching test displays.

The fact that CDA amplitudes were larger in the Parts relative to the Whole Condition demonstrates that WM maintenance processes were sensitive to the difference in task demands between these two conditions. They suggest that physically identical visual objects that are composed of component shapes can be stored in two qualitatively different ways in WM – either in a part-based fashion, where their component parts are represented independently, or in an integrated fashion, by emphasizing the overall shape of the compound objects, without individuating their component parts. As a result of these differences, the

number of objects stored in WM should have been different in these two conditions – WM included a single object in the Whole task, and two separate objects in the Parts task. As CDA amplitudes are sensitive to the number of objects currently maintained in WM (e.g., Vogel & Machizawa, 2004), the CDA should therefore have been larger in the Parts condition, and this was exactly what was observed in Experiment 3.

To obtain an additional independent measure of the effects of WM load on CDA amplitudes, Experiment 3 also included the Single and Double Baseline conditions, where one versus two shapes had to be stored in order to be compared with a subsequent single-shape memory test display. As expected, CDA amplitudes were larger in the Double Baseline condition. Although this difference was somewhat less robust than expected, it was statistically significant in a one-tailed paired t-test. More importantly, the size of the CDA amplitude increase when two versus just one shape had to be maintained in these two baseline conditions was not statistically different from the CDA amplitude difference between the Parts and Whole conditions, and additional Bayesian analyses suggested that the CDA amplitude increases in the Parts versus Whole and in the Single versus Double Baseline conditions were likely to be equivalent in size. This provides additional evidence that identical compound-shape items can be stored in WM either as a single integrated object or as two separate objects, and that this can be controlled in a top-down fashion in line with the requirements imposed by the specifics of a WM task context. If the part-based versus integrated representation of compound objects in WM can be controlled flexibly in this way, changing the task demands for one of the two tasks used in Experiment 3 should also change the pattern of CDA differences between these tasks. This prediction was tested in Experiment 4.

3.3 EXPERIMENT 4

3.3.1 Introduction for Experiment 4

In Experiment 3, the CDA was significantly larger in the Parts versus Whole condition, suggesting that identical sample display objects were represented in WM as separate shapes in the former task, and as a single integrated shape in the latter task. If this is the case, decreasing the load imposed on WM storage in the Parts condition should reduce, eliminate, or even reverse the CDA amplitude differences between the two tasks observed in Experiment 3. In Experiment 4, a small but critical change was introduced to experimental procedures that was expected to affect WM storage load specifically for the Parts condition. In contrast to Experiment 3, where the two component shapes on the task-relevant side that had to be memorized were chosen randomly on each trial, one of these two shapes remained constant throughout each experimental block in Experiment 4. This constant shape was changed between each block. Previous CDA research (e.g., Carlisle, Arita, Pardo, & Woodman, 2011) has shown that when a to-be-memorized feature stays constant for longer periods, this feature is no longer represented in WM, but is transferred to a different long-term memory store. This was also predicted to be the case for the Parts task of Experiment 4, where the constant shape should not be maintained in WM for an entire block. As a result, CDA amplitudes in this task should be smaller than in Experiment 3, reflecting the maintenance of just one rather than two basic shapes in WM. To assess the transfer of the constant shape to a different long-term store in the course of an experimental block, separate CDA components were computed for the first versus second half of each block. If both shapes are initially held in WM for a number of trials before the constant shape is transferred

to a different store, CDA amplitudes should be larger in the first as compared to the second part of each experimental block.

Critically, keeping one component shape constant across all trials of a block should have no such consequences on WM maintenance in the Whole task, as this task requires the storage of integrated shape configurations rather than shape parts. Even when one of the two shapes stays constant, the overall shape configuration still varies across trials, and participants therefore still have to maintain this configuration in WM, as in Experiment 3. Therefore, there should be no CDA amplitude differences between Experiments 3 and 4 in the Whole condition. If the introduction of a constant target shape reduces CDA amplitudes in the Parts condition of Experiment 4, but has no effect on the size of the CDA in the Whole condition, a different pattern of CDA components between the two tasks should be observed in this experiment. CDAs should no longer be larger in the Whole as compared to the Parts condition, as in Experiment 3. Instead they should now be equal in size, reflecting the WM maintenance of a single shape object in both tasks. Previous CDA studies have shown that CDA amplitudes are sensitive to the complexity of memorized objects, with larger CDAs for more complex objects (e.g., Luria & Vogel, 2011). It is therefore also possible that CDA amplitude differences show the reverse pattern in Experiment 4 relative to Experiment 3, with larger CDAs in the Whole versus Parts tasks, as the shape held in WM is more complex in the former task.

Because the predictions of Experiment 4 all relate to the Parts and Whole conditions, the Single and Double Baseline conditions were not included in this experiment. Furthermore, in order to allow within-participant comparisons of CDA amplitude differences in the Parts and Whole conditions between Experiments 3 and 4, the same set of participants that was tested in Experiment 3 also took part in Experiment 4.

3.3.2 Methods

Participants

The same fourteen participants who were tested in Experiment 3 (mean age 30 years, 6 male, 1 left-handed) also took part in Experiment 4, in order to allow within-participants comparisons between these two experiments. Experiment 4 was conducted after all participants had completed Experiment 3. All participants gave informed consent, both written and orally, prior to testing.

Apparatus, Stimuli and Procedure

The stimuli and procedures used in Experiment 4 were identical to those used in Experiment 3 with a few notable exceptions. There were no Single and Double Baseline conditions, so that only two task conditions (Whole and Parts) remained. Each of these two task conditions was tested in 16 successive experimental blocks with 24 trials per block. Task order was counterbalanced across participants. The other important change relative to Experiment 3 was that one of the two spatially aligned component shapes on the task-relevant side of the memory sample displays remained constant for an entire experimental block. This constant shape changed across each successive block, so that each of the four component shapes was the constant shape in 8 of the total of 32 blocks included in Experiment 3. On each trial, the positions of the other three shapes in the sample displays were randomly selected, so that each of the three non-constant shapes was equally likely to be paired with the constant shape on the task-relevant side. Participants were informed about the constant shape

for each block by an instruction screen shown prior to each block that verbally specified this shape.

EEG Recording and Data Analysis

This experiment used the same EEG recording, filtering, and analysis methods as in Experiment 3. However, the behavioural and EEG analyses contained the additional factor Block Position (first 12 versus final 12 trials in each block), which was included to assess possible effects of learning the constant shape and transferring it to long-term memory on memory performance and CDA components. To achieve this, performance data and ERPs were computed separately for trials 1-12 and trials 13-24 in each block. For all comparisons across Experiments 3 and 4, performance and ERP data were computed across all trials, leaving out the factor Block Position.

3.3.3 Results

Behavioural Analysis

Figure 11 (left panel) shows RTs and error rates measured in the two task conditions of Experiment 4, separately for the first and second half of trials in each block. RT data were entered into an ANOVA with factors Task (Whole, Parts) and Block Position (First Half, Second Half). Unsurprisingly, RTs became faster in the second as compared to first half of each block (497 ms versus 545 ms; $F(1,13) = 16.62, p = .001, \eta_p^2 = .561$). There was however no main effect of Task ($F(1,13) < 1$) and no interaction between Task and Block Position ($F(1,13) = 1.45, p = .250, \eta_p^2 = .100$). The analysis of error rates revealed an increase in the percentage of errors in the second half of each block (9.67%, as compared to 8.31% in the first half; $F(1,13) = 7.06, p = .020, \eta_p^2 = .352$). A main effect of Task ($F(1,13) =$

6.79, $p = .022$, $\eta_p^2 = .343$) was due to the fact that errors were more frequent in the Parts condition (10.06%) relative to the Whole Condition (7.92%), analogous to what was observed in Experiment 3. There was no interaction between Task and Block Position for error rates ($F(1,13) < 1$).

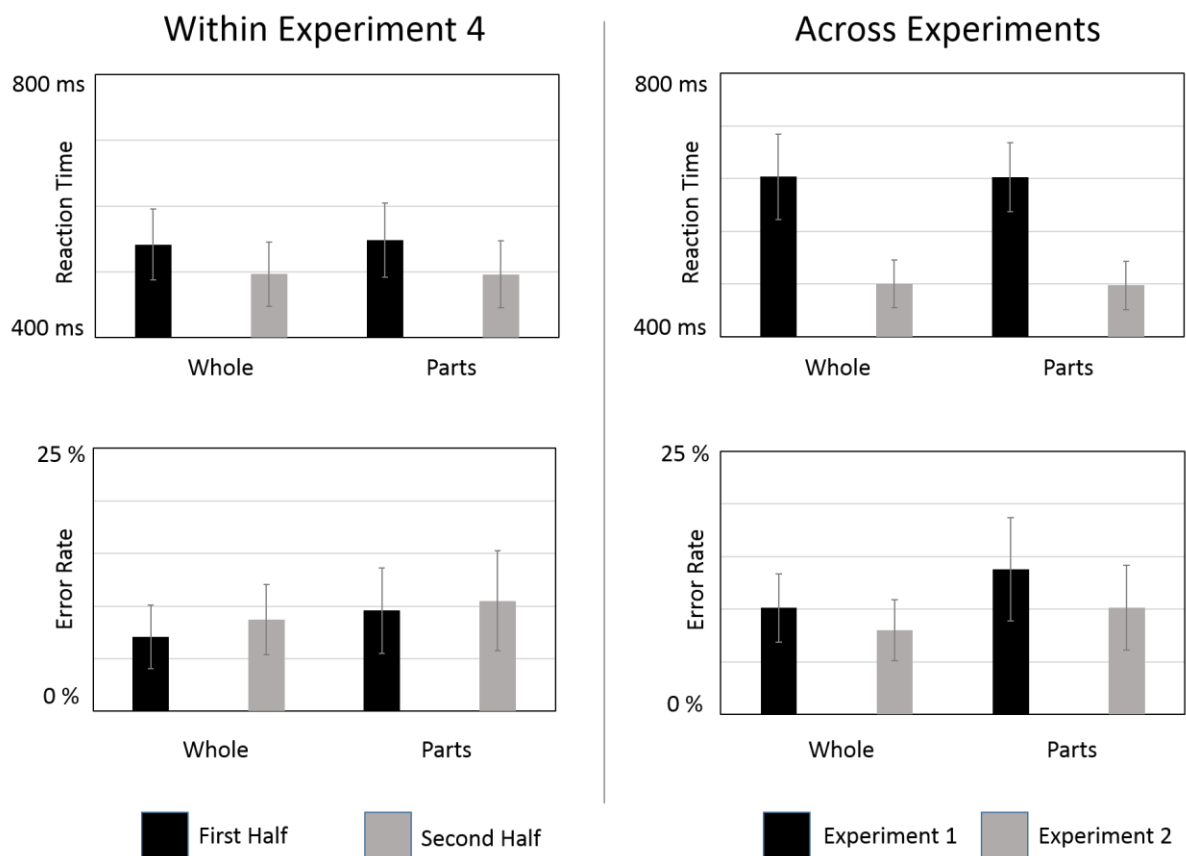


Figure 11: Left panel: Reaction times (top panel) and error rates (bottom panel) for Whole and Parts conditions in the First and Second Half of each block in Experiment 4. Right Panel: Reaction times (top panel) and error rates (bottom panel) for Whole and Parts conditions in Experiments 3 and 4. Error bars in graphs indicate 95% confidence intervals (CIs) for the true population mean.

Comparison of Behavioural Data in the Parts and Whole Tasks between Experiments 3 and 4

Figure 11 (right panel) shows RTs and error rates measured in the Parts and Whole conditions of Experiments 3 and 4. These data were entered into a two-way repeated-measures ANOVA with factors Experiment (Experiment 3, Experiment 4), and Task (Whole, Parts). RTs in Experiment 4 (499 ms) were much faster than in Experiment 3 (703 ms; main effect of Experiment: $F(1,13) = 53.87, p < .001, \eta_p^2 = .806$). There was no main effect of Task and no interaction between Task and Experiment (both $F(1,13) < 1$) for RTs. Errors were more frequent in Experiment 3 relative to Experiment 4 (12.0% versus 9.0; $F(1,13) = 8.87, p = .011, \eta_p^2 = .406$), and more frequent in the Parts as compared to the Whole condition (11.9% versus 9.1 %; $F(1,13) = 9.30, p = .009, \eta_p^2 = .417$). There was no interaction between Task and Experiment ($F(1,13) = 1.81, p = .201, \eta_p^2 = .122$).

ERP Analysis: CDA Components

Figure 12 shows ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to the task-relevant side of the memory displays, separately for the first and second half of each block in the Whole and Parts conditions (top left and middle panels), and collapsed across halves (top right panel). The corresponding contralateral-ipsilateral difference waves are shown in the bottom panels. The analysis of ERP mean amplitudes in the 350-950 ms time window following sample display onset revealed a significant main effect of Laterality ($F(1,13) = 39.16, p < .001, \eta_p^2 = .751$), reflecting the presence of reliable CDA components. However, and importantly, there was no interaction between Laterality and Task ($F(1,13) < 1$), demonstrating that in contrast to Experiment 3, CDA amplitudes were now equal in size in the Parts and Whole tasks. There was also no interaction between Laterality and Block

Position ($F(1,13) < 1$), and no three-way interaction between Laterality, Task, and Block Position ($F(1,13) < 1$), thus indicating that there was no difference in the amplitude of CDA components elicited during the first twelve and the final twelve trials of each block in either task condition.

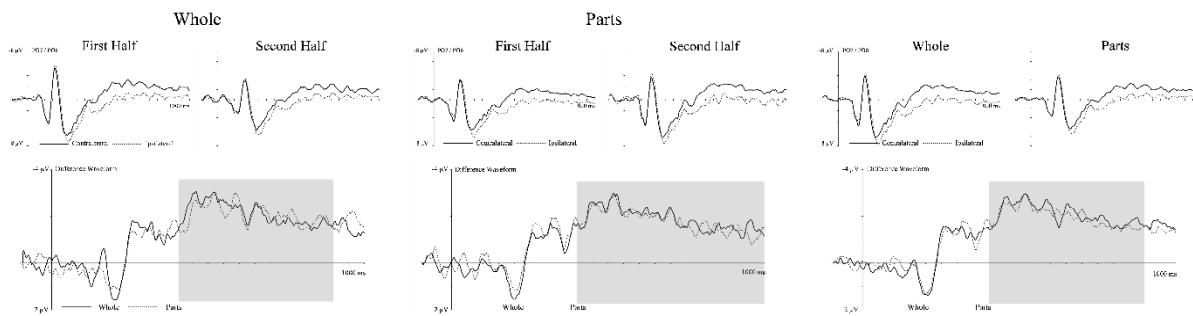


Figure 12: Top panel: Grand-average event-related brain potentials (ERPs) obtained in Experiment 4 at PO7/PO8 contralateral and ipsilateral to the side of the target object during the 1000 ms interval after memory sample display onset. ERPs are shown separately for the first and second half of blocks in the Whole (left panel) and Parts (middle panel) conditions and the average ERPs across Block Position (right panel). Bottom panel: CDA difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for the two halves of the Whole (left panel) and Parts (middle panel) conditions, and for the Whole versus Parts condition (averaged across all trials in each block; right panel).

Comparison of CDA Components in the Parts and Whole Tasks between Experiments 3 and 4

Mean amplitudes obtained in both experiments between 350 and 950 ms following sample display onset were analysed in a three-way ANOVA with factors Experiment (Experiment 3, Experiment 4), Task (Parts, Whole), and Laterality. There was a main effect of Laterality ($F(1,13) = 34.02, p < .001, \eta_p^2 = .724$), again reflecting the presence of CDA

components. There was no interaction between Experiment and Laterality ($F(1,13) = 1.63, p = .224, \eta_p^2 = .111$) or between Condition and Laterality ($F(1,13) = 1.40, p = .258, \eta_p^2 = .097$). Critically, however, a three-way interaction between Experiment, Task, and Laterality was present ($F(1,13) = 5.50, p = .036, \eta_p^2 = .297$). To assess this interaction, contralateral/ipsilateral CDA difference waveforms obtained in the Parts and Whole conditions were compared between Experiments 3 and 4 with two planned paired samples t-tests. As predicted, there were no CDA amplitude differences between these two experiments for the Whole Condition ($-1.86 \mu\text{V}$ versus $-1.92 \mu\text{V}$ in Experiments 3 and 4, respectively; $t(13) < 1$). In contrast, keeping one of the two to-be-memorized shapes in the Parts Condition constant in Experiment 4 led to a significant reduction of CDA amplitudes relative to Experiment 3 where both shapes changed unpredictably across trials ($-1.79 \mu\text{V}$ versus $-2.30 \mu\text{V}$; $t(13) = 1.94, p = .037, d = 0.39$, *one tailed*).

3.4 Chapter 3 Discussion

In Experiment 4, no CDA amplitude differences were observed between the Parts and Whole task. This finding, which differs from the results of Experiment 3 (as discussed below) is in line with the prediction that making one of the two shapes constant within each block changed the way that these shapes were stored, specifically in the Parts condition. Previous CDA evidence (e.g., Carlisle et al., 2011) suggested that features which stay constant for an extended period are no longer held in WM but are instead transferred to a different long-term store, and thus no longer affect CDA amplitudes. This was likely to be also the case in the Parts condition of Experiment 4, where only the shape that changed randomly across trials was maintained in WM. As a result, WM load was reduced to a single shape in this condition,

and was thus equal to the WM load in the Whole condition. As a result, CDA components were now equal in size in the two conditions.

It should be noted that the complexity of the item that was held in WM in the two conditions of Experiment 4 (a simple shape in the Parts task, a compound shape in the Whole task) could in principle have resulted in larger CDA amplitudes in the Whole task (see Luria & Vogel, 2011, for an effect of object complexity on the size of the CDA). This was not the case, as CDA amplitudes were equivalent in both conditions. The question whether and how the CDA reflects object complexity remains unresolved (see Luria et al., 2016, for a review), and a recent study (Balaban & Luria, 2015) also found no CDA amplitude differences between simple and more complex shape objects. Furthermore, CDA amplitudes in Experiment 4 did not differ between the first and second halves of each block, and this was the case also for the Parts condition where the constant shape was expected to be transferred from WM into a different long-term store after the first few trials of each block. A possible reason for the absence of any clear CDA amplitude decrease in the second half of each block (trials 13-24) in the Parts condition is that this transfer may have already occurred after one or two trials in this condition, so that a single shape object remained in WM even for most of the trials in the first half of each block (e.g., from trial 3 onwards).

The comparisons across Experiments 3 and 4 revealed the pattern that was predicted. There were no CDA amplitude differences between the two experiments for the Whole condition. This shows that whether one of the two component shapes on the task-relevant side varied unpredictably across trials (Experiment 3) or remained constant for an entire block (Experiment 4) had no impact on the way that the compound shape was stored in WM in the Whole condition. If shape information was maintained in an integrated fashion in this condition, so that only the overall compound shape was represented but not its component parts, the predictability versus unpredictability of one of these shape components should not

affect WM storage, and this was exactly what was found. In contrast, CDA components in the Parts condition were reduced in size in Experiment 4, where one component shape was constant, relative to Experiment 3, where both shapes changed randomly across trials. This CDA amplitude reduction in Experiment 4 was predicted by the hypothesis that variable features have to be maintained in WM while constant features can be stored in a different long-term system. The CDA amplitude comparison between the two experiments was only significant for a one-tailed t-test. However, the fact that the overall ANOVA revealed a significant interaction between Experiment, Task, and Laterality provides additional evidence that the critical difference between the two experiments (i.e., whether one of the relevant shapes in the sample display was constant or varied randomly) affected WM maintenance processes only in the Parts but not in the Whole condition.

Overall, the pattern of CDA components observed in the two experiments reported in this Chapter provides novel evidence that the format in which identical visual stimuli are represented in WM can vary in accordance with current task demands. To-be-memorized visual objects that are composed of two component shapes can be represented in an integrated or in a part-based fashion, depending on how WM is tested at the end of each trial. When memory is tested separately for one of the shape components, compound objects are represented in a part-based fashion. When memory is instead tested with compound objects in the test displays, and when these displays can also include non-matching objects that contain both component shapes in a different spatial configuration, physically identical compound objects in memory sample displays are represented in a qualitatively different integrated fashion. These conclusions underline the critical role of top-down control processes during the maintenance of visual information in WM. The storage of visual objects in WM does not merely involve the sustained maintenance of a copy of the sensory information that was received by the visual system. Instead, WM representations transform this sensory

information into a format that is most useful for the task at hand. When the component parts of visual objects are task-relevant, WM retains separate representations of these parts. When overall shapes are relevant, these component parts are integrated into a single representation of the combined compound shape.

These findings also have implications for current discussions about whether the features of visual objects are always represented in an integrated fashion or whether different features can also be represented independently (see Luck & Vogel, 1997; Wheeler & Treisman, 2002, for contrasting view on this issue). For example, a CDA study by Woodman and Vogel (2008) investigated whether colour and orientation can be represented separately in WM even when they belong to the same object. These authors measured CDA components to memory sample displays containing oriented coloured rectangles, and instructed observers to memorize either colour, orientation, or the conjunction of both features, in response to physically identical sample displays. CDA amplitudes were larger when orientation as compared to colour was task-relevant. No such CDA amplitude difference should have been present if colour and orientation were always stored in an integrated fashion in WM. These results thus provide evidence that colour and orientation information can be represented independently, depending on task instructions, even when both are present in the same object. The CDA results reported in this Chapter confirm and extend these previous findings. In line with Woodman and Vogel (2008), they demonstrate that task instructions can change the way in which the features of physically identical visual stimuli are represented in WM. Furthermore, this does not just apply to features from different dimensions (such as colour and orientation), but also to features from a single dimension (shape). Finally, the current findings show for this first time that task-dependent top-down control processes can determine how identical visual objects are segregated into chunks during WM maintenance.

Depending on task goals, they can either be stored as single objects or be parsed into different objects which are then maintained separately.

Chapter 4

Is space special?

The control of visual search by space-based and feature-based attention

The experiments presented in this Chapter have been submitted for publication in a peer-reviewed journal.

Experiments 5 and 6:

McCants, C., Berggren, N., & Eimer, M. Is space special?: The control of visual search by space-based and feature-based attention.

4.1 Chapter 4 Introduction

In the experiments reported in Chapters 2 and 3, the interplay between spatial and non-spatial factors during the control of attention in perception and working memory was investigated in situations where task-relevant visual objects were either defined by simple features (shapes) or by spatial configurations of these features (a specific spatial arrangement of basic shapes). However, links between space-based and feature-based attentional selectivity can also be studied more directly, by investigating and contrasting attentional control mechanisms that are based on the spatial location of visual objects or on specific non-spatial features of these objects. In Chapters 4 and 5 of this thesis, this will be addressed for the attentional guidance of selective attention during the perceptual processing of visual search displays (Chapter 4) and for the attentional activation of working memory representations of stimuli that are no longer physically present (Chapter 5).

The two experiments reported in this Chapter were conducted to investigate interactions between spatial and feature-based attention during visual search. Although it is generally agreed that spatial and feature-based attention both play important roles in the adaptive guidance of visual processing, the question whether and how these two types of attentional control are linked remains unresolved (e.g., Maunsell & Treue, 2006; Egner et al., 2008; Cohen & Maunsell, 2011). One possibility is that space-based and feature-based attention are entirely independent. Selective processing biases for objects at particular locations within the visual field produced by spatial attention could emerge irrespective of the features of these objects. Likewise, feature-based attentional biases for objects that have a particular non-spatial attribute (e.g., the colour red) may occur in a spatially global fashion, irrespective of whether these objects appear at attended or unattended locations (e.g., Martinez-Trujillo & Treue, 2004; Serences & Boynton, 2007). An alternative possibility is that these two attentional control

mechanisms interact. Feature-based attentional selectivity could be modulated by spatial attention, and spatial selection processes might be influenced by feature-based attention.

One reason why links between spatial and feature-based attention remain poorly understood is that these two aspects of attentional selectivity have typically been investigated independently, with different experimental procedures. Research on spatial attention is dominated by the spatial cueing paradigm developed by Posner and colleagues (e.g., Posner, Snyder, & Davidson, 1980). In this paradigm, spatial cues presented at the start of each trial inform participants about the likely location of an upcoming target object. Performance is generally better for targets at cued (spatially attended) as compared to uncued (unattended) locations. This has been attributed to preparatory shifts of a hypothetical attentional spotlight, which facilitate the processing of visual stimuli that appear within the current focus of spatial attention. In many spatial cueing experiments, there is no competition between objects for attentional selection, as only a single stimulus is shown on each trial, either at an attended or unattended location. This is different in visual search tasks, which are the main tool for investigating non-spatial attentional selectivity. Visual search displays contain multiple visual objects, of which one can be the target. Targets are defined by a particular feature or a feature combination, and can appear among distractors that share some of these target features (e.g., Treisman & Gelade, 1980). In search tasks, the location of target objects is not known in advance, and attention is assumed to be guided in a feature-based fashion towards objects with attributes that match the currently active target template (e.g., Duncan & Humphreys, 1992; Wolfe, 2007).

It is often assumed that space-based attentional selection operates more rapidly than feature-based attention. When the spatial location of an upcoming target object is known in advance, spatially selective processing biases for that location can be triggered even before this target is presented, in the form of preparatory baseline shifts of neural activity in retinotopic

visual areas (e.g., Driver & Frith, 2000). No such spatial preparation is possible in visual search tasks when target locations vary randomly and unpredictably across trials. Any feature-based guidance of attention will therefore have to follow an initial rapid parallel analysis of the whole search display, which can obtain evidence for the presence of objects with target-matching features within this display. For this reason, effects of feature-based attention should emerge more slowly than the effects of spatial attention. Visual processing is assumed to include an early rapid feedforward sweep of neural activity that proceeds in a bottom-up fashion from lower to higher levels of the visual hierarchy, as well as a subsequent recurrent stage of processing, where the activity of lower levels is modulated by top-down signals from higher levels (e.g., Lamme & Roelfsema, 2000; Hochstein & Ahissar, 2002). It is possible that spatial attention already operates during the early feedforward sweep, whereas feature-based modulations of visual selectivity only appear at a later stage of recurrent visual processing. Behavioural evidence for this hypothesis was reported by Theeuwes and Van der Burg (2007). In this study, where visual search displays that contained a target singleton object (defined by its unique colour or shape) were followed by masks, advance information about target locations improved perceptual sensitivity, whereas non-spatial cues that specified the likely target colour or shape did not.

More direct evidence that spatial attention operates at an earlier stage than feature-based attentional was found in event-related brain potential (ERP) studies (see Eimer, 2014, for review). In spatial cueing experiments, ERPs to target objects preceded by spatially predictive cue stimuli were measured for targets at cued/attended and uncued/unattended locations. With single-item displays, spatially attended targets triggered larger sensory-evoked P1 components than targets outside the cued focus of spatial attention (e.g., Mangun & Hillyard, 1991; Eimer, 1994). For displays containing two items in opposite hemifields, spatial cueing resulted in enhanced P1 amplitudes at electrodes contralateral to the object at the attended location

(Heinze, Luck, Mangun, & Hillyard, 1990). The P1 component is generated in low-level extrastriate regions of ventral visual cortex (Mangun & Hillyard, 1991). Spatial attention can affect the amplitude of this component within 90-100 ms after stimulus onset, which is consistent with an effect of space-based attention during the feedforward phase of visual processing. In contrast, effects of feature-based attention emerge considerably later. In single-item displays, ERP differences between objects in a task-relevant attended colour and objects in a different irrelevant colour can be observed from around 150 ms post-stimulus onwards (e.g., Eimer, 1995). In visual search tasks, the feature-based attentional selection of target objects among distractors is reflected by the N2pc component. As already described in the Introduction and in Chapter 2, the N2pc is an enhanced negativity at posterior scalp electrodes contralateral to objects with task-relevant features that typically emerges 180-200 ms post-stimulus, is generated in ventral extrastriate visual areas (Hopf et al., 2000), and is assumed to reflect the allocation of attention to objects with target-matching features in multi-stimulus displays (e.g., Luck & Hillyard, 1994a; Eimer, 1996; Woodman & Luck, 1999; see Eimer, 2014, for review). The fact that feature-based attentional selection processes reflected by the N2pc component appear to be activated about 100 ms later than the space-based attentional biases associated with enhanced P1 amplitudes suggests that feature-based attention operates during the later recurrent phase of visual processing. In line with the hypothesis, N2pc components are assumed to reflect an attentional bias in extrastriate visual cortex that is generated by top-down feedback signals from anterior attentional control regions (e.g., Cohen, Heitz, Schall, & Woodman, 2009).

If spatial and feature-based attention operate at different stages of visual processing, how do they interact when target objects are defined by a combination of spatial and non-spatial attributes, and both types of attentional control are required to select these targets? Results from an ERP study by Hillyard and Münte (1984) suggest that feature-based attentional biases

depend on a prior selection of visual objects by their spatial location. In this study, target stimuli were defined by a combination of colour and location (e.g., red stimuli on the left), and ERPs were recorded to single objects that either matched both, one, or neither target-defining attributes. ERP correlates of spatial attention (P1 and N1 amplitude enhancements) preceded ERP modulations of colour-based attention (an enhanced negativity for target-colour objects that emerged around 150 ms after stimulus onset). Critically, these colour-based attentional effects were only observed for stimuli at attended locations. Hillyard and Münte (1984) concluded that feature-based attentional selectivity is hierarchically dependent on spatial attention, and only operates for objects that have previously been spatially selected. However, this conclusion has not been generally accepted. In fact, several influential models of attentional selectivity (e.g., Bundesen, 1990; Duncan & Humphreys, 1992) postulate that space-based and feature-based attention play qualitatively similar roles in the control of attention. According to these models, spatial and non-spatial attributes can be given equal weight in determining the allocation of attention to particular objects. Behavioural evidence in line with this hypothesis was provided by Adams and Chambers (2012) in a task where spatial or non-spatial cues indicated the location versus colour of target objects that appeared in a subsequent search display, and the SOA between cues and targets was manipulated. Spatial and colour cues were equally efficient in facilitating target detection, and the time course of their effects was similar.

How can the evidence that spatial and feature-based attention operate at different processing stages be reconciled with claims that these two types of attentional control guide the selection of target objects in qualitatively similar ways? The goal of the experiments reported in this Chapter was to address this question. While it is clear that visual processing biases produced by spatial attention can emerge during the early feedforward sweep (as reflected by the P1 amplitude modulations observed in spatial cueing studies), the question

remains whether these biases are directly associated with attentional target selection mechanisms. An alternative possibility is that such selection processes always take place at the subsequent recurrent stage of visual processing, regardless of whether target objects are defined by their location or by non-spatial features. This is the stage that is associated with the N2pc component. If space-based and feature-based target selection both operate at this stage, N2pc components should be found not only in typical search tasks where the location of targets is unknown and their selection is guided by feature-based attention, but also when search targets are defined exclusively in terms of their spatial location. Furthermore, target N2pc components should emerge at the same time in both types of tasks.

Because no previous N2pc studies of visual search have investigated purely space-based target selection processes, these predictions have not been tested before. This was done in Experiment 5, where ERPs recorded during a feature-based and a space-based visual search task were compared. In both tasks, participants had to find a target object in a circular visual display containing eight Landolt C rings, in order to report the location of the gap in the target ring (Figure 13). The target object for an upcoming search display was indicated by an alphanumeric cue at the start of each trial. In the Colour Task, targets were defined by their colour, which was specified by a letter cue. In the Spatial Task, targets were defined by their position within the circular display, which was signalled by a digit cue. Cues were either presented prior to the onset of the search display, with a stimulus onset asynchrony (SOA) between cue and target of 250 ms, or simultaneously with the search display (SOA: 0 ms), and this was varied randomly across trials. Search displays were physically identical in both tasks.

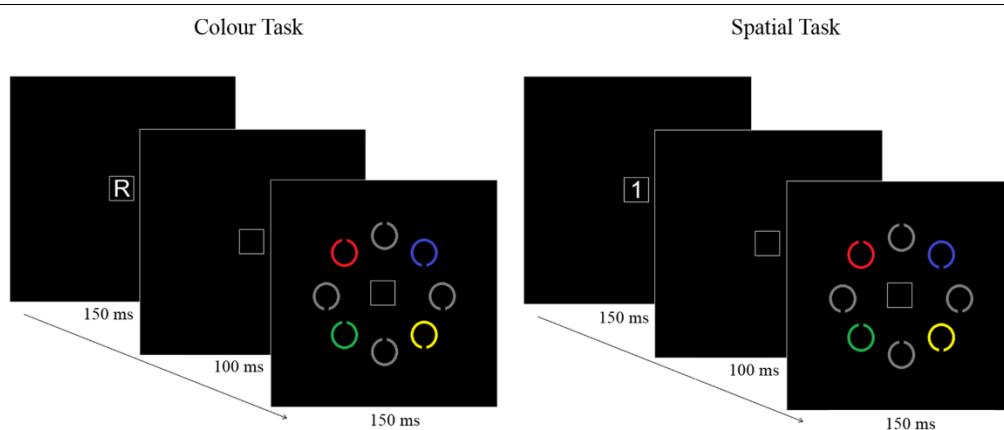


Figure 13: Illustration of the stimulus setup on SOA 250 trials in the Colour Task and the Spatial Task of Experiment 5. A letter cue or a digit cue that specified the target-defining colour or spatial location was followed after an SOA of 250 ms by a search display that contained four coloured and four grey Landolt rings. Participants’ task was to report the location of the cut in the target ring. On SOA 0 trials, the cue and the search display were presented simultaneously for 150 ms.

Target objects in the Colour Task were expected to trigger N2pc components, in line with earlier studies observing N2pcs to feature-defined targets. On trials where the colour cue preceded the search display, this target N2pc was expected to emerge at the typical latency of about 200 ms post-stimulus, as participants could activate a task set for the cued target colour prior to the onset of the search display. On trials where the colour cue and the search display appeared simultaneously, participants first had to identify the cue letter before being able to guide attention to the target-colour object in the search display. As a result, target N2pcs should emerge considerably later on these trials. The critical new question addressed in Experiment 5 was whether target objects in the Spatial Task that were defined exclusively by their location would trigger any N2pc components at all and, if they did, whether these N2pcs would differ from those measured in the Colour Task. If space-based attentional selectivity operated

exclusively at earlier feedforward stages of visual processing, no target N2pc should be found at all in the Spatial Task. Alternatively, if spatial and feature-based attentional selection both operate in a qualitatively similar fashion during the later recurrent stage of visual processing, target N2pc components should emerge at approximately the same time in both tasks. This was indeed what was observed in Experiment 5. In the second experiment of this Chapter, the fact that the N2pc reflects both feature-based and space-based target selection mechanisms was used to assess how these mechanisms interact when search targets are defined by a combination of colour and location.

4.2 EXPERIMENT 5

4.2.1 Methods

Participants

Fourteen participants were paid to take part in Experiment 5. Two of them were excluded from analysis because more than half of all trials were rejected due to eye blinks and saccades. The remaining 12 participants had a mean age of 30 years (2 males, none left-handed). All reported normal or corrected-to-normal vision.

Desired sample size was defined at 12 participants consistent with many previous N2pc studies (e.g., Berggren, Jenkins, McCants, & Eimer, 2017; Luck & Hillyard, 1994a). To assess the appropriateness of this sample size, as no previous study has examined spatial guidance of attention using the N2pc component, partial eta square effect sizes were used from a related previous study that examined feature-based attentional biases at specific spatial locations (Berggren et al., 2017). Across two experiments, effect sizes for modulations of feature biases by competing features at irrelevant spatial locations were used as the basis for power analysis

(.76 in Experiment 5, .60 in Experiment 6), where power of 0.95 and an alpha level of 0.05 was assumed. This suggested a minimum sample size of 4-7 participants was required to potentially find evidence of interactions between feature-based and space-based attention.

Apparatus, Stimuli and Procedure

The experiment was programmed and executed on-line using Matlab software (MathWorks, Natick, MA). Stimuli were presented on a 24-inch BenQ widescreen monitor (60 Hz, 1920 x 1080 screen resolution) at a viewing distance of approximately 90 cm. Participants responded by pressing one of two buttons on a standard PC keyboard. Reaction times (measured relative to the onset of each visual search display) and response accuracy were recorded by Matlab.

A grey fixation box subtending 0.31 by 0.31 degrees of visual angle was displayed in the centre of the screen throughout each block. In all trials, search displays contained eight equidistantly spaced Landolt rings (diameter of each ring: 0.91°) that were arranged in a circular fashion, at an eccentricity of 2.40° from the central fixation box. Each ring contained a gap at the top or bottom (size of each gap: 0.12°). All displays contained four rings with a gap at the top and four with a gap at the bottom. The location of the gap for the target object was randomly selected on each trial. The four items directly above, below, and to the left and right of the fixation box were grey. The remaining four items at the four diagonal locations appeared in four different colours. These colours were red (CIE x/y coordinates: .605 / .322), blue (CIE x/y coordinates: .169 / .152), yellow (CIE x/y coordinates: .405 / .470) and green (CIE x/y coordinates: .296 / .604), and the position of each colour was randomly determined for each trial. Search displays were presented for 150 ms. All items in these displays, including the grey items, were equiluminant (14 cd/m²).

The identity of the target item in the search display on any given trial was indicated by an alphanumeric cue stimulus (height: 0.25°) displayed for 150 ms. In different blocks, these cues defined either the colour or the location of the target (colour task and location task). In colour task blocks, the target colour was indicated by letter cues ('R': red; 'Y': yellow; 'G': green; 'B': blue). Here, the colour-defined target object was equally likely to appear at any of the four possible target locations. In location task blocks, target location was specified by digit cues ('1': upper left; '2': upper right; '3': lower left; '4': lower right). Here, the object at the cued target location was equally likely to appear in any of the four possible colours. Participants were instructed to find the target ring indicated by the cue, and to report the position of the gap for that ring (top or bottom) by pressing the up or down arrow keys on the keyboard. "Top" and "bottom" responses were assigned to the index fingers of the left and right hand, and these assignments were counterbalanced between participants. Responses were measured within a 1500 ms time window following search display onset.

There were two different cue-target SOAs that were intermixed randomly and unpredictably within each block. In SOA 0 trials, the cue and the search display were presented simultaneously for 150 ms. In SOA 250 trials, the cue was shown for 150 ms, and was followed by a blank interval of 100 ms before the search display was presented for 150 ms. The inter-trial interval between the offset of the search display and the onset of the first visual stimulus on the next trial was always 1600 ms. The experiment included 16 blocks, with 64 trials within each blocks. There were 8 successive blocks for the colour and location tasks, respectively, and task order was counterbalanced across participants. Each block included two trials for each of the 32 possible combinations of target colour, target location, and SOA.

EEG Recording and Data Analysis

EEG was DC-recorded at 27 scalp electrodes on an elastic cap at sites Fpz, F7, F8, F3, F4, Fz, FC5, FC6, T7, T8, C3, C4, Cz, CP5, CP6, P9, P10, P7, P8, P3, P4, Pz, PO7, PO8, PO9, PO10, and Oz. A sampling rate of 500 Hz was used, with a low-pass filter of 40 Hz. Channels were referenced online to an electrode on the left earlobe, and re-referenced to an average of both the left and right earlobes offline. No other filters were applied following EEG acquisition. Trials with incorrect responses, eye-blinks ($> \pm 60 \mu\text{V}$ at Fpz), eye movements ($> \pm 30 \mu\text{V}$ in the HEOG channels), or muscle movement artefacts ($> \pm 80 \mu\text{V}$ at all other channels) were not included in any analysis. The remaining trials were segmented into epochs from 100 ms before to 500 ms after the onset of each search display. Averaged ERP waveforms were then computed relative to a 100 ms baseline prior to search display onset, for SOA 0 and SOA 250 trials in the colour and location tasks, separately for trials where the target object appeared in the left and right visual field. N2pc components to targets were measured at lateral posterior electrode sites PO7 and PO8. For SOA 250 trials, where target N2pc components were elicited within their typical latency range, N2pc mean amplitudes were quantified on the basis of ERPs measured between 200 and 300 ms after search display onset. As predicted, target N2pc components emerged considerably later on SOA 0 trials. For these trials, a later time window (350 – 450 ms after search display onset) was used to quantify N2pc mean amplitudes. N2pc onset latencies were calculated by assessing grand averaged difference waveforms (contralateral minus ipsilateral ERPs), using a jackknife-based analysis method (Miller, Patterson, & Ulrich, 1998). In this analysis, 12 subsamples of grand-averaged difference waves were computed, each excluding a different participant from the original grand-averaged sample. N2pc onset was defined as the time at which each of these subsamples reached an absolute threshold of $-0.5 \mu\text{V}$. N2pc onset latency differences between task conditions were assessed using repeated-measures ANOVAs and paired-sample t-tests, with F- and t-values corrected according to the

formulas described by Ulrich and Miller (2001) and Miller et al. (1998). The corrected tests are indicated with F_c and t_c , respectively.

4.2.2 Results

Behavioural Performance

Reaction times (RTs) and error rates to search targets were assessed in two 2x2 repeated-measures Analysis of Variance (ANOVA) with factors SOA (SOA 0 and SOA 250) and Task (Colour Task, Spatial Task). RTs were much slower on SOA 0 trials relative to SOA 250 trials ($M = 838$ ms versus 620 ms; $F(1,11) = 738.30$, $p < .001$, $\eta_p^2 = .99$). There was no effect of Task ($F < 1$) and no interaction between SOA and Task ($F(1,11) = 1.98$, $p = .19$, $\eta_p^2 = .15$) for RTs. Errors were also more frequent in SOA 0 as compared to SOA 250 trials ($M = 7.4\%$ versus 2.6% ; $F(1,11) = 16.60$, $p = .002$, $\eta_p^2 = .61$). The main effect of Task was not significant ($F(1,11) = 4.28$, $p = .063$, $\eta_p^2 = .28$), but there was an interaction between SOA and Task for error rates ($F(1,11) = 7.76$, $p = .018$, $\eta_p^2 = .41$). Paired-sample t-tests revealed that when cues and search displays were presented simultaneously, incorrect responses were more frequent in the Colour Task than in the Spatial task ($M = 8.9\%$ versus 5.9% ; $t(11) = 2.79$, $p = .018$, $d = 0.59$). On SOA 250 trials error rates did not differ between the two tasks ($M = 2.6\%$ and 2.5% ; $t(11) < 1$).

ERP Analysis: N2pc Components

Figure 14 shows N2pc components triggered in response to target objects on trials where the SOA between cues and search displays was 250 ms (left side) and on trials where cues and search displays appeared simultaneously (right side), separately for the Colour and Spatial Task. ERPs elicited contralateral and ipsilateral to the target are shown together with

the corresponding contralateral-ipsilateral difference waves. As can be seen in this Figure, target N2pc components were elicited within the usual 200-300 ms post-stimulus time window on SOA 250 trials, but were strongly delayed by about 150 ms on SOA 0 trials. For this reason, N2pc mean amplitudes were computed within two different time windows for these two types of trials (200-300 ms and 350-450 ms post-stimulus, respectively), and were analysed separately in 2x2 ANOVAs with the factors Task and Laterality (electrode contralateral versus ipsilateral to a target). For SOA 250 trials, a main effect of Laterality ($F(1,11) = 37.04, p < .001, \eta_p^2 = .77$), reflecting the presence of N2pc components, was accompanied by an interaction between Task and Laterality ($F(1,11) = 9.66, p = .010, \eta_p^2 = .47$), as N2pc amplitudes were larger in the Colour Task than in the Spatial task (see Figure 14). However, follow-up comparisons of contralateral and ipsilateral ERPs confirmed that reliable N2pc components were elicited not only in the Colour Task ($M \text{ diff} = -1.53 \mu\text{V}; t(11) = 6.30, p < .001, d = 0.42$), but also in the Spatial Task ($M \text{ diff} = -0.91 \mu\text{V}; t(11) = 4.48, p < .001, d = 0.26$). For SOA 0 trials, a main effect of Laterality ($F(1,11) = 24.52, p < .001, \eta_p^2 = .69$) confirmed the presence of target N2pc components during the 350-450 ms analysis window. There was no interaction between Laterality and Task ($F(1,11) = 1.52, p = .243, \eta_p^2 = .12$), indicating that N2pcs of similar size were elicited to targets in the Colour Task and in the Spatial Task.¹

¹ As can be seen in the difference waveforms in Figure 14 (bottom right panel), a transient small but reliable contralateral negativity was elicited on SOA 0 trials in the 200-300 ms time interval after search display onset in the Spatial Task ($t(11) = 2.59, p = .025, d = .09$), but was absent in the Colour Task. To test whether this ERP modulation was linked to the processing of the search display, or was instead triggered by the spatial cues that appeared simultaneously with the search display on SOA 0 trials, an additional analysis of ERPs elicited on SOA 250 trials was conducted, for epochs that were time-locked to the onset of the cue on these trials. An enhanced negativity contralateral to the side of the target that was indicated by the spatial cue was again found during the 200 – 300 ms interval following cue onset ($t(11) = 2.97, p = .013, d = .16$), indicating that this effect was associated with cue-related rather than target-related processing. The processes responsible for this lateralisation following spatial cues will be considered in the General Discussion.

Jackknife-based comparisons of target N2pc onset latencies revealed no onset differences between the Colour and Spatial Tasks for SOA 250 trials ($M = 199$ ms versus 193 ms; $t_c < 1$). On SOA 0 trials, the N2pc emerged earlier in the Spatial Task relative to the Colour Task ($M = 343$ ms versus 384 ms), and this difference was significant ($t_c(11) = 2.96$, $p < .013$, $\eta_{pc}^2 = .44$).

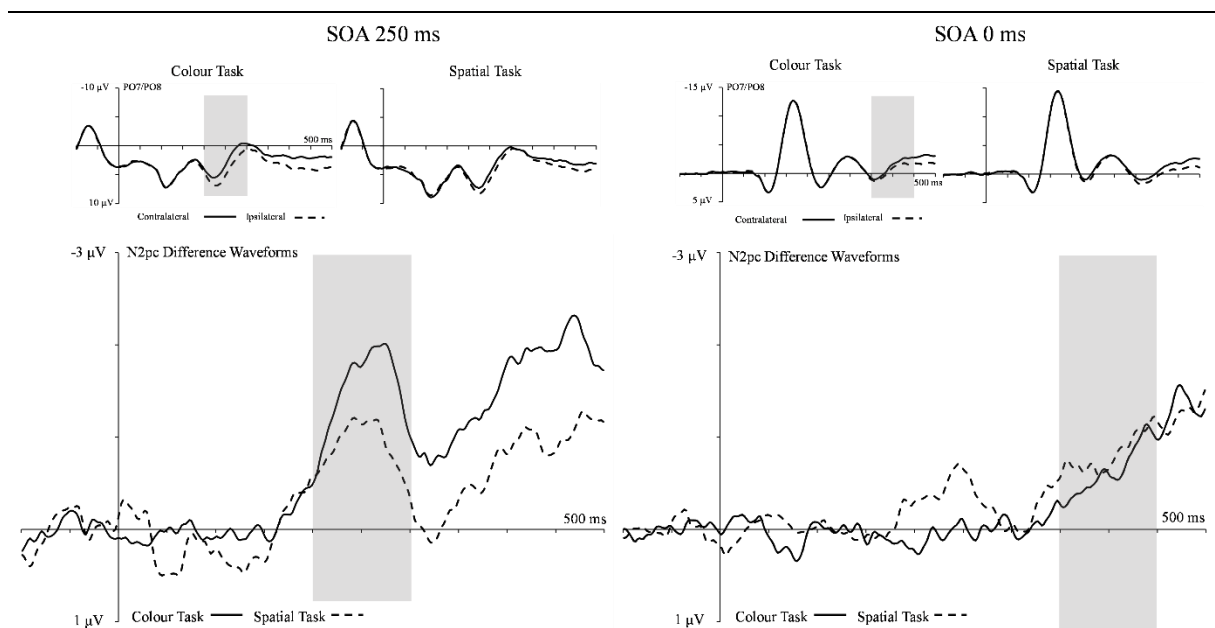


Figure 14. Top panel: Grand-averaged event-related brain potentials (ERPs) obtained in the Colour Task and Spatial Task of Experiment 5 at electrode sites PO7/8 contralateral and ipsilateral to the side of the target on SOA250 ms trials (left panel) and SOA0 ms trials (right panel). ERPs are shown for the 500 ms interval following search display onset. Bottom panel: N2pc difference waves obtained by subtracting ipsilateral from contralateral ERPs in the Colour Task and Spatial Task, shown separately for SOA250 and SOA0 trials. The grey areas mark the respective N2pc analysis windows.

4.2.1 Discussion of Experiment 5

Experiment 5 provided new electrophysiological evidence for qualitatively similar target selection processes during feature-based and space-based visual search. Reliable N2pc components were triggered by search targets not only in the Colour Task, but also in the Spatial Task. As the N2pc is assumed to reflect the attentional selection of target objects during the recurrent phase of visual processing, these results demonstrate that the same selection mechanisms operate for targets that are defined by a non-spatial feature (colour), and also for targets whose selection is exclusively space-based.

As predicted, target N2pcs were delayed on trials where cues and search displays were presented simultaneously relative to trials where cues were presented 250 ms prior to the onset of a search display. This N2pc delay was present in both tasks, and is likely to reflect the time demands associated with identifying the cue stimulus and activating a corresponding search template for a particular target colour or location. On SOA 250 trials, target N2pc components were triggered within 200 ms after search display onset, which is similar to many previous N2pc experiments where target-defining features were specified at the start of each block and then remained constant. This suggests that the 250 ms interval between the cue and target was sufficient for participants to fully prepare a spatial or feature-based task set for the upcoming search episode. Thus, the N2pc delay of approximately 150 ms observed for SOA 0 trials provides an estimate of the time demands of cue identification and search template activation processes.

If feature-based and space-based attentional selection processes operate in a qualitatively similar fashion, target N2pc components should emerge at the same time in the Colour and Spatial Tasks. This was indeed the case on trials where cues preceded search

displays by 250 ms, indicating that when participants are fully prepared for an upcoming selection task, colour-based and space-based target selection mechanisms are activated at the same time. When cues and targets appeared simultaneously, target N2pcs emerged 40 ms earlier in the Spatial Task relative to the Colour Task. This difference could indicate a slight speed advantage for space-based relative to feature-based attention. Alternatively, it may reflect differences between the digit and letter cues used in these two tasks. Digits might be slightly easier to decode, or more easily mapped to target locations than letters are mapped to target colours. This would reduce the time required to initiate target selection processes in the Spatial Task. Target N2pc amplitudes did not differ between the two tasks on SOA 0 trials, but were larger for the Colour Task than the Spatial Task on SOA 250 trials. This suggests that when observers are fully prepared for an upcoming target selection task, attentional biases elicited for colour-defined targets may be slightly stronger than biases associated with purely space-based attention (see Adams & Chambers, 2012, for corresponding behavioural evidence). This will be further investigated in Experiment 6.

4.3 EXPERIMENT 6

4.3.1 Introduction for Experiment 6

The N2pc results of Experiment 5 suggest that feature-based and space-based attentional target selection mechanisms operate at the same stage of visual processing. The presence of N2pc components to both colour-defined and spatially-defined search target objects opens up the possibility to use this component to investigate interactions between spatial and feature-based attention under conditions where both are required to identify target objects in visual search displays. This was done in Experiment 6. Search displays were identical

to Experiment 5, but there were no longer any cues, as target-defining attributes were now specified at the start of each block, and remained constant for this block.

In this experiment, there were three different search tasks. In the Colour Task and the Spatial Task, targets were defined by their colour or location, respectively, as in Experiment 5. These two tasks were included to confirm that N2pc components are elicited both during the feature-based and during the space-based selection of search targets, even when the target-defining attribute is not cued on a trial-by-trial basis but remains constant within a block of trials. Another goal was to find out whether spatial attention would also result in an earlier modulation of contralateral P1 amplitudes, as previously observed (Heinze et al., 1990). This could not be assessed in Experiment 5, where search displays appeared either concurrently with or immediately after centrally presented cue stimuli, producing overlapping early ERP components. In Experiment 6, P1 components should be enhanced at posterior electrodes contralateral to the target in the Spatial Task (reflecting an early effect of spatial attention on feedforward visual processing), but not in the Colour Task.

In the Conjunction Task of Experiment 6, target objects were defined by the combination of a specific colour and location (e.g., red objects at the top left position). On target-present trials, participants had to report the location of the gap in the target ring. There were also target-absent trials, where the object occupying the target-defining location had a nontarget colour, and no response was required (see Figure 15). In this task, both colour-based and space-based attention were required to find target objects. To investigate interactions between these two types of attentional control, N2pc components to target-present and three different types of target-absent search displays were measured. A clear N2pc should be elicited in response to target-present displays, where the target appeared at the attended location and had the attended colour. If feature-based and space-based attentional mechanisms operate jointly at the stage where N2pc components are generated, these target N2pcs will reflect the

combined contributions of these two mechanisms. The attentional biases associated with spatial and with feature-based attention were dissociated by assessing N2pc components to three different types of target-absent displays (illustrated in Figure 15). On one thirds of all target-absent trials, a target-colour object was present in the search display, but appeared at a nontarget location, on the same (ipsilateral) side as the specified target location (colour-ipsi displays). On another third, the target-colour object appeared on the side contralateral to the spatially attended location (colour-contra displays). In the final third of all target-absent trials, no target-colour object was present at all (colour-absent displays).

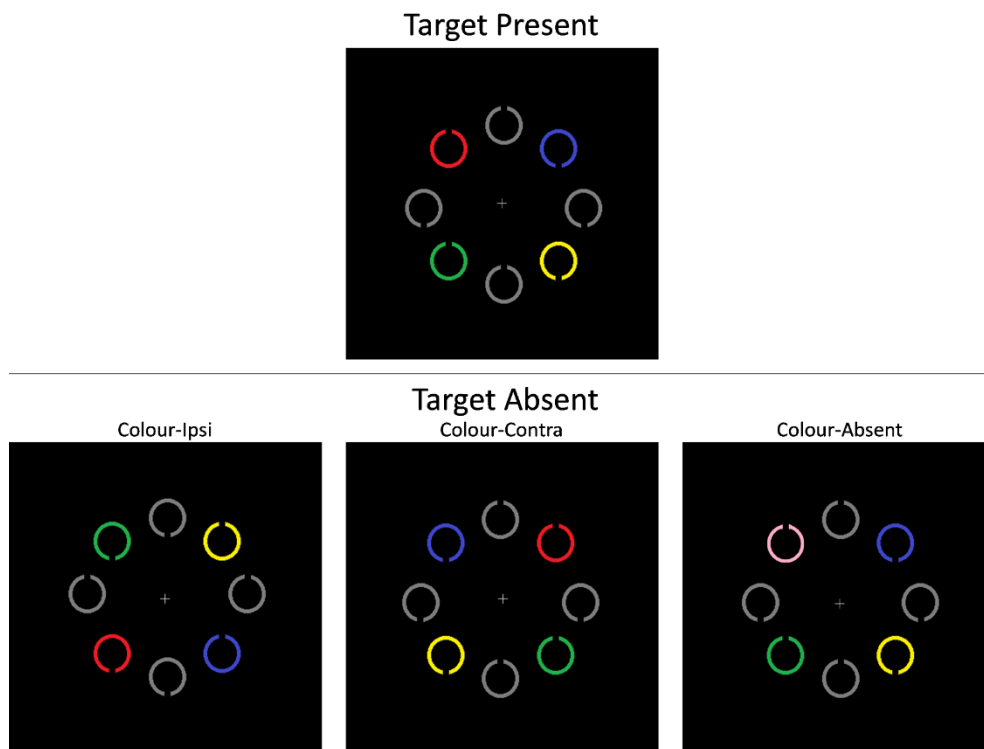


Figure 15. Illustration of target-present (top panel), colour-ipsi, colour-contra, and colour-absent search displays (bottom panel) in the Conjunction Task of Experiment 6. In the examples shown here, the target was the red object at the top left position. In colour-ipsi and colour-contra displays, a target-colour object was present at a task-irrelevant location on the same side or the opposite side as the attended location. Colour-absent displays included four objects in different nontarget colours.

There are several ways in which spatial and feature-based attention might interact in the Conjunction Task. One possibility is that target selection is determined jointly by both types of attentional control. In this case, attention will be allocated to an object only if it appears at the attended location and also matches the current target colour. This joint control hypothesis predicts that an N2pc will only be elicited by target objects, but not for any of the three types of target-absent displays. A second possibility is that attentional target selection processes are determined entirely by spatial attention. In this case, N2pc components should always be elicited contralateral to the attended location, irrespective of whether the object at this location matches the target colour, or whether a target-colour object is present elsewhere in the display. If attentional control was purely space-based, identical N2pc components should be found for target-present and all target-absent displays. It is also possible that feature-based attention is hierarchically dependent on spatial attention, with colour-based attentional biases only elicited by objects at the currently attended location (e.g., Hillyard & Münte, 1984). In this case, N2pc components should be larger for target-present as compared to target-absent displays, reflecting the combined attentional biases elicited by spatial and feature-based attention. If there are no feature-based attentional modulations for target-colour objects at unattended locations, identical N2pcs should be elicited on all three types of target-absent trials, representing purely space-based biases triggered by the nontarget-colour object at the attended location.

Finally, it is also possible that spatial and feature-based attentional control processes operate independently and in parallel, and contribute separately to the attentional biases reflected by N2pc components. This hypothesis predicts a very specific pattern of N2pc amplitude differences between the three types of target-absent displays. For displays where a nontarget-colour object at the attended location is accompanied by a target-colour object on the same side (colour-ipsi displays), N2pc amplitudes will reflect the joint additive effects of

feature-based and spatial selectivity. N2pcs elicited by these displays should therefore be larger than for the other target-absent displays. If feature- and space-based attention operate fully independently, N2pc components to colour-ipsi displays should be identical to N2pc elicited by target-present displays, as both types of displays contain a target-location and a target-colour object on the same side. There should also be an N2pc for colour-absent displays, reflecting the pure effect of space-based control on attentional selectivity. However, this N2pc should be smaller than the N2pc to colour-ipsi displays, due to the absence of any additional feature-based attentional biases. Finally, feature-based and spatial attentional biases will be triggered by objects on opposite sides in colour-contra displays. This should result in N2pcs of opposite polarity and thus in a strong attenuation of overall N2pc amplitudes. If these two types of biases were equally strong, they should cancel each other out, and no measurable N2pc will be observed at all in response to colour-contra displays.

4.3.2 Methods

Participants

Fourteen paid participants were tested in Experiment 6. One participant was excluded due to the loss of more than half of trials of all trials because of eye blinks, and another was excluded because of poor task performance (their response accuracy more than 3 SDs below the mean of all other participants). The remaining 12 participants had a mean age of 32 years (6 male, 1 left-handed). All reported normal or corrected-to-normal vision.

To assess whether the sample size obtained in Experiment 6 had provided appropriate statistical power for the significant results found, a new analysis was conducted on the partial eta square effect size for the interaction between Task and Laterality in the SOA 250 condition of Experiment 6, using the same parameters as for the previous experiment. This suggested a

minimum sample size of 6 participants was appropriate for contrasting the time-course of spatial and feature-based attention using the N2pc component. Thus, there was no evidence to suggest that Experiment 6 was underpowered, and the same desired sample size of 12 participants was retained to have comparable signal-to-noise ratios across experiments.

Apparatus, Stimuli and Procedure

Procedures were similar to Experiment 5, with the following exceptions. There were no longer any cue stimuli, as target-defining attributes were specified at the start of each block via instructions on the computer screen. The central fixation box was replaced by a central fixation cross ($0.31^\circ \times 0.31^\circ$) that remained continuously present throughout each block. On every trial, a search display was presented for 150 ms, followed by a 1450 ms blank interval prior to the onset of the search display on the next trial. Search displays were identical to Experiment 5, except that an additional possible colour (pink; CIE coordinates: .270 / .134; identical luminance to the other colours: 14 cd/m²) was used. This was required to include target-absent displays with four different nontarget colours in the Conjunction Task (see below).

There were three different tasks that were presented in different blocks. In the Colour and Spatial Tasks, targets were defined by one particular colour or as appearing in one specific location. There were four consecutive blocks of 64 trials in each of these two tasks. A target Landolt ring was present in each search display, and participants had to report the location of the gap on each trial, as in Experiment 5. A different target colour or location was specified at the start of each block. In the Conjunction Task, targets were defined by the combination of a particular colour and location (e.g., red items in the top left position). Participants were instructed to only respond to Landolt rings in the target colour when they appeared in the specified location, and to refrain from responding on all other trials. This task included eight successive experimental blocks with 72 trials per block. A different target-defining

colour/location combination was specified at the start of each block. Target objects that matched this specification were present in the search display on 24 trials per block. There were three different types of target-absent trials. On 16 trials, search displays included four different nontarget-colour items (colour-absent). On the remaining trials, a target-colour item was present, but it appeared at an irrelevant location, either on the same side (ipsilateral) as the specified target location (colour-ipsi; 16 trials), or on the opposite contralateral side (colour-contra; 16 trials). In these colour-contra displays, the target-colour item always appeared in the same horizontal hemifield (above or below fixation) as the current target-defining location. The three tasks in Experiment 6 were counterbalanced by forming a Latin Square (ABC, BCA, CAB), with each of the three task sequences assigned to three participants.

EEG Recording and Data Analysis

These were similar to Experiment 5. As above, only correct trials were analysed. N2pc components were computed for the Colour, Spatial, and Conjunction Tasks (separately for target-present, colour-ipsi, colour-contra, and colour-absent trials). N2pc mean amplitudes were measured within a fixed time window (200 - 300 ms after search display onset). In addition to the analyses of N2pc components, possible early attentional modulations of P1 components and their specificity for spatial attention were also assessed. P1 peak amplitudes (defined as the maximum positive amplitude value in the 90 – 160 ms post-stimulus time window) were measured at electrodes PO7 and PO8 for the Spatial and Colour Tasks, and were compared separately for both tasks between electrodes contralateral and ipsilateral to the side where the target object was presented.

4.3.3 Results

Behavioural Analysis

RTs on target-present trials were compared in a one-way ANOVA with the factor Task (Spatial Task, Colour Task, Conjunction Task). There was a significant effect of Task ($F(2,22) = 12.61, p < .001, \eta_p^2 = .66$), due to the fact that RTs in the Colour Task ($M = 454$ ms) were faster than RTs in the Spatial Task and Conjunction Task ($M = 528$ ms and 527 ms, respectively; both $t(11) > 4.62$, both $p < .002$), which did not differ from each other ($t(11) < 1$). An analogous ANOVA for response errors on target-present trials also obtained a main effect of Task ($F(2,22) = 7.53, p = .003, \eta_p^2 = .41$), as incorrect responses to targets were less likely in the Conjunction task where targets only appeared on one third of all trials ($M = 1.4\%$) than in the Colour and Spatial Tasks where a target was present on all trials ($M = 5.1\%$ and 4.1% , respectively). Finally, the percentage of responses between the three different types of target-absent trials in the Conjunction task were repaired. Such False Alarms were more likely when a target-colour object was presented at the other position on the same side as the specified target location (colour-ipsi trials: $M = 3.3\%$) relative to trials where a target-colour object was absent or appeared on the opposite side ($M = 1.2\%$; and $M = 0.9\%$; both $t(11) > 4.31$, both $p < .01$). There was no difference in error rate, however, between Colour Contra and Colour Absent conditions ($t(11) = 1.25, p = .236, d = 0.27$).

ERP analysis: N2pc Components

Figure 16 shows N2pc components triggered in the Conjunction Task, separately for target-present, colour-ipsi, colour-contra, and colour-absent trials. For all trial types, contralateral and ipsilateral ERPs were defined relative to the target-defining location specified at the start of each block, regardless of whether a target-colour item was actually presented at

this location (on target-present trials) or not (on all other types of trials). They are shown together with the corresponding contralateral-ipsilateral difference waves. Clear N2pc components were elicited for three of the four trial types. They appear to be largest on target-present trials, slightly reduced on colour-ipsi trials, and more strongly attenuated on colour-absent trials. No N2pc was apparent for colour-contra trials.

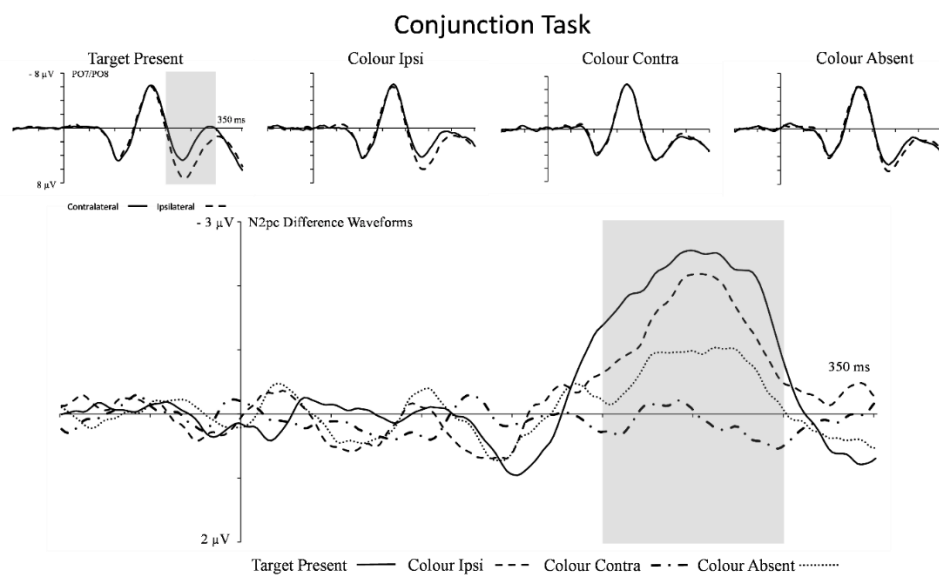


Figure 16. Top panel: Grand-averaged event-related brain potentials (ERPs) obtained at electrode sites PO7/8 contralateral and ipsilateral to the side of the target object in the Conjunction Task of Experiment 6. ERPs are shown for the 350 ms interval after search display onset, separately for the four different search display types (target-present, colour-ipsi, colour-contra, colour-absent). Bottom panel: N2pc difference waves obtained by subtracting ipsilateral from contralateral ERPs, shown separately for all four search display types. The grey areas mark the N2pc analysis window.

These differences were assessed in a 4x2 ANOVA of N2pc mean amplitudes with factors Trial Type (target-present, colour-ipsi, colour-contra, colour-absent) and Laterality. A significant main effect of Laterality ($F(1,11) = 16.00, p = .002, \eta_p^2 = .60$) confirmed that N2pcs were generally present in the Conjunction Task. Importantly, there was an interaction effect between Trial Type and Laterality ($F(3,33) = 25.27, p < .001, \eta_p^2 = .70$), confirming that N2pc amplitudes differed between the four different types of trials. Follow-up analyses comparing contralateral and ipsilateral ERPs showed that no N2pc was present at all on colour-contra trials ($M \text{ diff} = .15 \mu\text{V}; t(11) < 1$). In contrast, reliable N2pcs were elicited on target-present trials ($M \text{ diff} = -2.38 \mu\text{V}; t(11) = 5.74, p < .001, d = 1.39$), colour-ipsi trials ($M \text{ diff} = -1.46 \mu\text{V}; t(11) = 3.73, p = .003, d = 1.10$), and colour-absent trials ($M \text{ diff} = -0.72 \mu\text{V}; t(11) = 2.64, p = .032, d = 0.53$). The N2pc amplitude differences between each of these three trial types were all reliable (all $t(11) > 3.15$, all $p < .01$). Analyses of N2pc onset latencies (again using a jackknife procedure with a threshold criterion of $-0.5 \mu\text{V}$) showed that the N2pc on colour-absent trials ($M = 217 \text{ ms}$) was delayed relative to the N2pc onset on target-present trials ($M = 183 \text{ ms}; t_c(11) = 2.91, p = .013, \eta_{pc}^2 = .43$) and colour-ipsi trials ($M = 192 \text{ ms}; t_c(11) = 2.33, p = .039, \eta_{pc}^2 = .33$). The N2pc onset latency difference between target-present and colour-ipsi trials was not reliable ($t_c(11) < 1$).

Figure 17 shows N2pc components elicited by target items in the Spatial and Colour Tasks with their corresponding difference waves. The N2pc to colour-defined targets was slightly larger than the N2pc to spatially-defined targets. In contrast to Experiment 5, this amplitude difference was not reliable ($M = -2.05 \mu\text{V}$ versus $-1.57 \mu\text{V}; t(11) = 1.14, p = .178, d = 0.33$). Target N2pcs also tended to emerge earlier in the Colour as compared to the Spatial Task, but this difference was not significant ($M = 183 \text{ ms}$ versus $202 \text{ ms}; t_c(11) = 1.69, p = .119$). As can also be seen in Figure 17, there was a tendency in the Spatial Task for P1 amplitudes to be larger at electrodes contralateral to the side of the target as compared to

ipsilateral electrodes, while no such lateralised P1 modulation was present in the Colour Task. A planned comparison of contralateral versus ipsilateral P1 peak amplitudes did confirm the presence of a reliable difference in the Spatial Task ($t(11) = 2.02$; $p = .034$, one-tailed; $d = 0.22$), but not in the Colour Task ($t(11) < 1$).

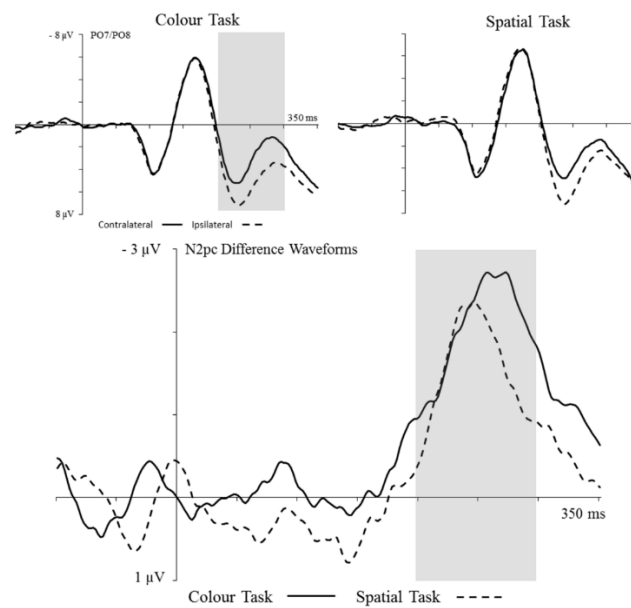


Figure 17. Top panel: Grand-averaged event-related brain potentials (ERPs) obtained in the Spatial Task and Colour Task of Experiment 6 at electrode sites PO7/8 contralateral and ipsilateral to the side of the target. ERPs are shown for the 350 ms interval following search display onset. Bottom panel: N2pc difference waves obtained by subtracting ipsilateral from contralateral ERPs in the Colour Task and Spatial Tasks. The grey areas mark the N2pc analysis window.

4.3.3 Discussion of Experiment 6

In the Conjunction Task of Experiment 6, targets were defined by a colour/location combination. By measuring N2pc components separately for target-present and three different types of target-absent displays, four different hypotheses about how spatial and feature-based mechanisms interact during the control of attentional target selection were assessed. Three of these hypotheses were conclusively ruled out by the pattern of N2pc components found in this task. If target selection was determined jointly by space-based and feature-based control, attention should only be allocated to objects that appear at the attended location and have the target-defining colour, but not to any objects that match only one of these two attributes. In this case, N2pcs should have been triggered exclusively by target-present displays. This was obviously not the case, as clear N2pc components were also found for two of the three types of target absent displays. The second hypothesis assumes that attentional selectivity is controlled in an exclusively space-based fashion. In this case, identical N2pc components should have been elicited on target-present and all types of target-absent displays. Again, this was clearly not the case in the Conjunction Task. A third alternative is that feature-based attention is hierarchically dependent on spatial attention (e.g., Hillyard & Münte, 1984), so that feature-based attentional biases are only triggered for target-present displays where a target-colour object appears at the attended location, but not by any target-absent displays. If this was correct, identical N2pc components reflecting exclusively space-based attentional selectivity should have been observed for all target-absent displays. In fact, there were systematic N2pc differences between the three different types of target-absent displays, thus ruling out this hierarchical selection hypothesis.

The fourth and final hypothesis tested was that space-based and feature-based attentional control mechanisms contribute independently to target selection processes in visual

search. This hypothesis makes very specific predictions about the pattern of N2pc components in the Conjunction Task, and the results matched these predictions almost perfectly. Reliable N2pc components were elicited by target-present displays as well as by colour-ipsi and colour-absent displays, whereas no N2pcs were observed at all for colour-contra displays (see Figure 16). The N2pc to target-absent displays where an object at the attended location was accompanied by a target-colour object on the same side (colour-ipsi displays) was twice as large compared to the N2pc for target-absent displays without a target-colour object ($-1.46 \mu\text{V}$ versus $-0.72 \mu\text{V}$). If feature-based and space-based control processes both produce attentional biases during target selection that are reflected by N2pc amplitudes, the N2pc to colour-ipsi displays will reflect the joint contributions of both processes, while the N2pc to colour-absent displays exclusively reflects the effect of spatial attention. The N2pc amplitude difference between these two types of displays thus demonstrates that feature-based and space-based attention both contributed to the attentional selection of objects with target-matching attributes in the contralateral hemisphere. Moreover, the size of this difference suggests that feature-based and space-based attentional biases were equally strong. If this was the case, the effects of these biases on N2pc amplitudes should cancel each other out for colour-contra displays where the target-colour object and the spatially attended object were located in opposite visual fields. The absence of any reliable contralateral negativity for these displays confirmed this prediction.

If feature-based and spatial attention operated entirely independently and in parallel at the stage where N2pc components are generated, N2pc amplitudes should have been identical for target-present and colour-ipsi displays, because both contained a target-matching colour and an object occupying the currently attended location in the same visual hemifield. The fact that these two attributes belonged to the same object on target-present trials, but to two different objects on colour-ipsi trials, should not have affected the net attentional biases produced by

strictly separate space-based and feature-based attentional control systems. This was not the case. N2pc amplitudes on target-present trials were reliably larger than on colour-ipsi trials, suggesting that spatial and feature-based attention did not operate strictly independently, but interacted with each other to some degree. The nature of this interaction will be further considered below.

The N2pc results observed in the Colour Task and Spatial Task of Experiment 6 confirmed the findings of the first experiment. Reliable N2pcs were elicited by colour-defined as well as by spatially-defined target objects under conditions where these target definitions were not cued on a trial-by-trial basis, but remained constant within blocks of trials. This provides additional evidence that the target selection processes reflected by the N2pc operate in a similar fashion, regardless of whether they are guided by non-spatial features and by spatial location. Numerical tendencies for N2pcs to emerge earlier and be larger in the Colour Task were present, similar to Experiment 5, but these differences were not reliable. Notably, P1 components triggered by search displays in the Spatial Task were larger contralateral to the currently attended target location, indicative of a space-based attentional bias during early feedforward stages of visual processing. As expected, no such early modulation was found for feature-based attention in the Colour Task. Although it was statistically reliable, the contralateral P1 enhancement observed in the Spatial Task was smaller than in previous ERP experiment with single-item or two-item displays (e.g., Mangun & Hillyard, 1991; Heinze et al., 1990). This is likely to be due to the fact that multi-stimulus search displays were employed where spatially attended targets were accompanied by a task-irrelevant distractor object on the same side, which should attenuate the effects of space-based attention on contralateral P1 amplitudes.

3.5 Chapter 4 Discussion

The question whether spatial and feature-based attentional target selection processes operate in a qualitatively similar fashion or are fundamentally different remains unresolved. In the two experiments reported in this Chapter, electrophysiological markers of selective biases on visual processing produced by space-based and feature-based attention were used. These two types of attentional control were found to produce very similar effects. It was also found that when they are activated concurrently, they operate in parallel and largely independently.

Previous ERP studies have suggested that space-based and feature-based attention affect different stages of visual processing. In spatial cueing tasks (e.g., Heinze et al., 1990; Mangun & Hillyard, 1991), spatial attention was found to modulate early sensory-evoked P1 components, suggesting that space-based attentional control modulates the initial feedforward sweep of visual processing. In contrast, the attentional selection of feature-defined targets in visual search tasks is associated with the N2pc component, which emerges about 100 ms later, and is assumed to reflect an attentional bias in retinotopic extrastriate visual areas during the subsequent recurrent phase of visual processing (e.g., Cohen et al., 2009). Experiment 5 compared target selection processes in visual search under conditions where target objects were defined by a non-spatial feature (a specific colour) or exclusively by their spatial location. The main new finding was that N2pc components were not only elicited in response to search targets specified by colour cues, but also when target objects were defined by spatial cues. The existence of N2pc components during both feature-based and space-based target selection was confirmed in the Colour and Spatial Tasks of Experiment 6, where the target colour or location was specified at the start of each block, and remained constant for this block. N2pc components were generally similar during the spatial and colour-based selection of target objects, except for a small tendency for N2pc amplitudes to colour-defined targets to be larger than to spatially-

defined targets, which was reliable in the SOA 250 condition of Experiment 5, but not in Experiment 6. Overall, these results demonstrate that attentional target selection processes guided by feature-based and by space-based mechanisms both operate during the recurrent phase of visual processing.

In addition to target N2pc components in the Colour and Spatial tasks, Experiment 6 also found a small but reliable early attentional enhancement of P1 components contralateral to the target, which was present only in the Spatial but not in the Colour Task. This observation that effects of space-based attention were present at the level of the P1 component as well as at the level of the subsequent N2pc shows that these effects are not confined to a single stage within the visual hierarchy, but can affect both early feedforward and later recurrent processing. This raises the important question which of these effects should be interpreted as an electrophysiological marker of space-based attentional target selection processes. It was suggested that modulations of P1 components elicited by spatial attention are not directly associated with the attentional selection of visual objects. These early spatial biases should instead be interpreted as the results of preparatory baseline shifts of visual activity that occur in a spatially specific fashion prior to the onset of a visual search display in tasks where the location of an upcoming task-relevant object is known in advance (e.g., Driver & Frith, 2000). As a result of these baseline shifts, any object that appears at a spatially attended location will elicit a stronger visual response relative to objects at other locations. The selection of search targets occurs at a later stage where recurrent top-down signals trigger visual processing biases for objects that match a target-defining spatial or non-spatial attribute. These visual biases are reflected by N2pc components.

Although the experiments reported here are the first to demonstrate the existence of N2pc components to search targets that are defined exclusively by their spatial location, two previous ERP studies have reported findings that are consistent with the presence of N2pc

components during space-based attentional target selection. In one study (Kiss, Van Velzen, & Eimer, 2008), visual search displays were preceded by spatial cues that indicated the hemifield where a feature singleton target object could appear. On target-absent trials, a small but reliable sustained negativity contralateral to the cued hemifield emerged around 200 ms after search display onset. A similar sustained negativity was observed by Woodman, Arita, and Luck (2009) contralateral to placeholder boxes that were present during the interval between a spatial cue and a subsequent target display. The fact that these lateralised ERP modulations were smaller and temporally more diffuse than the N2pcs observed during space-based target selection in the experiments reported here may be due to the fact that they were elicited by objects at spatially attended locations in displays that were otherwise entirely task-irrelevant.

In the Conjunction Task of Experiment 6, the sensitivity of the N2pc to both space-based and feature-based target selection processes were utilised to investigate how these two types of attentional control interact when both are required to find search targets, and to dissociate their respective effects on visual processing. Results demonstrated that spatial and feature-based attention operated largely independently and in parallel, and that the visual processing biases produced by these two attentional mechanisms were very similar in magnitude. N2pc amplitudes were twice as large on target-absent trials where a target-colour object and an object at the currently attended location appeared on the same side than on trials without a target-colour object, suggesting that N2pc components associated with spatial and feature-based selection combined additively. For displays where a target-colour object and a spatially-attended object were presented on opposite sides, no N2pcs were present at all, indicative of attentional biases in opposite hemifields that cancelled each other out. This apparent independence of space-based and feature-based attention demonstrated by these results is obviously inconsistent with the hypothesis that feature-based attention is hierarchically dependent on spatial selectivity, as was claimed in the basis of previous ERP

results (Hillyard & Münte, 1984). This apparent discrepancy may be due to the fact that in this earlier study, single-object displays were used. It is possible that spatial filtering can prevent feature-based attentional modulations for single objects that appear in an otherwise empty display. For visual search displays that contain multiple items, feature-based attention operates in a spatially global fashion, irrespective of the current focus of spatial attention (e.g., Berggren et al., 2017; Serences & Boynton, 2007).

Even though spatial and colour-based attentional control mechanisms operated in parallel in the Conjunction Task of Experiment 6, they appear to be not entirely unconnected. N2pc amplitudes elicited by target-present displays were larger than N2pcs in response to displays that contained a spatially attended object and a target-colour object at different locations on the same side. If space-based and colour-based attention were completely independent, identical contralateral visual processing biases should have been observed for both types of displays. The fact that the target objects triggered larger N2pc components suggests that attentional control processes were not entirely insensitive to the fact that the attended colour belonged to the object at the attended location. The nature of this interactive effect remains to be clarified. In previous N2pc studies that investigated the selection of search target objects defined by two non-spatial features (e.g., a red square) attentional biases for each of these features were initially triggered independently and in parallel (e.g., Eimer & Grubert, 2014; Berggren & Eimer, 2016a). N2pcs to target objects were identical in size to the sum of the N2pc components triggered by partially matching nontargets (e.g., blue squares and red circles) until about 230-250 ms post-stimulus. Beyond this point in time, target N2pc amplitudes became superadditive (i.e., larger than the summed N2pcs to feature-matching nontargets), suggesting an interaction between different feature-based attentional control processes. No such transition from parallel to interactive attentional control was apparent in the temporal pattern of N2pc components observed in in the Conjunction Task of Experiment

6. Here, N2pc components were larger for target-present as compared to colour-ipsi displays throughout the N2pc time window (see Figure 16). This indicates that colour-based and space-based attention interacted already at the start of the target selection process. One way of explaining this early emergence of such interactions is to assume that spatial attention facilitated the effects of feature-based attention, resulting in stronger attentional modulations for target-colour objects at currently attended versus unattended locations. Another possibility is that this facilitation was bidirectional, with feature-based attention enhancing the effects of spatial attention on visual processing. These alternatives need to be dissociated in future research.

Overall, the results of the two experiments reported here have shed new light on current debates about the roles of space-based and feature-based control during the attentional selection of target objects in visual search displays. Some have argued that these two types of control are qualitatively different, with spatial attention operating at an earlier stage than feature-based attention (e.g., Theeuwes & Van der Burg, 2007), and feature-based attention depending hierarchically on spatial filtering (Hillyard & Münte, 1984). Others have claimed that space-based and feature-based attention contribute in similar ways to target selection (e.g., Bundesen, 1990; Duncan & Humphreys, 1992; Adams & Chambers, 2012). The current findings support the latter view. Both types of attentional control produced very similar selective biases during the recurrent stage of visual processing reflected by N2pc components, and they operated concurrently and largely (but not entirely) independently. These results suggest that spatial location does not play a special role in the guidance of attention during visual search, but is just one of several attributes that contribute to the adaptive control of target selection processes.

Chapter 5

The capacity and resolution of spatial working memory and its role in the storage of non-spatial features

The experiments presented in this Chapter have been submitted for publication in a peer-reviewed journal.

Experiments 7 and 8:

McCants, C., Katus, T., & Eimer, M. The capacity and resolution of spatial working memory and its role in the storage of non-spatial features.

5.1 Chapter 5 Introduction

In the experiments reported in the previous Chapter, N2pc components were employed to study interactions between spatial and feature-based attention during the guidance of attention towards potential target objects in visual search displays. In this final Chapter, two experiments are reported that investigated similarities and differences in the storage of spatial and non-spatial features in WM. As outlined in Chapter 1, attention is likely to play an important role in the maintenance of visual objects in WM (see Awh et al., 2006, for discussion). Investigating the mechanisms involved in the storage of spatial and non-spatial attributes of visual objects is therefore likely to provide further insights into space-based and feature-based attentional control processes.

At the most general level, WM is responsible for the active short-term maintenance of information that is no longer perceptually available, and for making this information accessible to ongoing cognitive activities. The classic multiple-component model of WM (e.g., Baddeley & Hitch, 1974) postulates the existence of separate storage systems for verbal and visual information (the phonological loop and the visuospatial scratchpad), and a central executive that allocates attention and controls the activation states of representations in these storage systems. More recent extensions of this model (e.g., Baddeley, 2003) include the addition of a third independent storage system (the episodic buffer), as well as an important distinction within the visuospatial scratchpad between the storage of spatial locations and the maintenance of other types of non-spatial visual information (e.g., Logie & Pearson, 1997; Zimmer, 2008).

The question whether and how visual WM for locations differs from WM for other visual attributes such as colour or shape is important for understanding how WM is organised, and of how WM storage is implemented in the brain. Early neural models of WM assumed that memorized objects are maintained in a modality-unspecific fashion in prefrontal cortex (e.g., Goldman-Rakic, 1990). In contrast, more recent sensory recruitment accounts of WM (e.g.,

Postle, 2006) postulate that WM storage is primarily implemented by the modality-specific sensory brain areas that are also involved in the on-line perceptual analysis of incoming information. Evidence for such sensory recruitment mechanisms was provided by studies that found sustained activations during the delay period of visual WM tasks within extrastriate visual-perceptual areas (e.g., Emrich, Riggall, LaRocque, & Postle, 2013; Ranganath, Cohen, Dam, & D'Esposito, 2004). In these areas, visual information is represented in a spatiotopic fashion in two-dimensional maps (e.g., Franconeri, Alvarez, & Cavanagh, 2013), and the active maintenance of this information is assumed to be controlled by the selective allocation of attention to particular locations within these maps. Evidence for such links between spatial attention and visual WM storage comes from studies investigating memory for spatial locations (e.g., Awh, Anllo-Vento, & Hillyard, 2000), but it is plausible that attention is also involved in the maintenance of non-spatial visual attributes (see Awh, Vogel, & Oh, 2006, for discussion). If WM maintenance is based on the allocation of attention to features or objects that are represented at particular locations within extrastriate visual maps, location information may always be explicitly represented, regardless of whether observers have to remember object positions or other non-spatial attributes of these objects (e.g., Foster, Bsales, Jaffe, & Awh, 2017). More generally, this would also be in line with the suggestion that visual WM contains object-based representations where all features of a memorized object (including its spatial location) are stored in a fully integrated fashion (e.g., Luck & Vogel, 1997).

The idea that visual WM representations integrate the location and other non-spatial attributes of visual objects is not universally accepted. An alternative possibility is that spatial locations and other non-spatial object features can also be represented in functionally and anatomically independent WM stores. This was suggested by Wheeler and Treisman (2002) on the basis of behavioural experiments that used variations of the change detection task introduced by Luck and Vogel (1997). A set of coloured squares was presented in memory

sample displays, and participants had to report whether or not there was a change in the memory test display that was presented after a delay period. In the colour task, only the square colours could change, while only location changes were present in the location task. In another condition (either task), both colour changes and location changes were possible and were randomly intermixed, so that participants had to independently memorize both dimensions of the sample stimuli on each trial. Performance was better in the location task than in the colour task, but, critically, performance in the task in which either colour or location could change was identical to the colour task. Wheeler and Treisman (2002) interpreted the absence of any costs in this task relative to the colour task as evidence that colours and spatial locations can be held independently in parallel systems with separate storage capacities. In a fourth task where observers had to remember colour/location conjunctions, performance costs were observed when memory test displays contained multiple objects. This suggests that colours and locations can also be represented in an integrated fashion, but that this type of storage requires additional attentional resources.

It is difficult to dissociate the integrated versus separate maintenance of spatial locations and non-spatial object features in visual WM exclusively on the basis of behavioural measures. For example, the performance costs found by Wheeler and Treisman (2002) in their colour/location conjunction tasks are likely to be associated not with WM storage, but with subsequent sample-test comparison processes. An alternative approach is to measure brain activity elicited during visual WM tasks as a marker of WM maintenance processes. Previous event-related potential (ERP) studies (e.g., Vogel & Machizawa, 2004; McCollough, Machizawa, & Vogel, 2007) have employed a lateralized change detection task where bilateral memory sample displays contained coloured objects in the left and right visual hemifield, and observers had to maintain the colours of sample stimuli on one side in order to compare them to a subsequent test display. ERPs recorded during the delay period between the memory and

test displays revealed an enhanced negativity at posterior electrodes contralateral to the to-be-remembered display side (contralateral delay activity, CDA). This activity started around 300 ms after the onset of the memory sample display, persisted throughout the retention interval, increased in amplitude when memory load was increased, and was sensitive to individual differences in WM capacity (e.g., Vogel & Machizawa, 2004). These observations support the view that the CDA is an on-line neural marker of the storage of objects or object features in visual WM.

To address the question whether non-spatial features (colour and orientation) can be represented separately in WM even when they belong to the same object, Woodman and Vogel (2008) measured CDA components to memory sample displays containing oriented coloured rectangles in tasks where observers had to memorize either colour, orientation, or the conjunction of both features. CDA amplitudes were larger when orientation as compared to colour was task-relevant, in spite of the fact that sample displays were identical. Because no such CDA amplitude difference should have been present if colour and orientation were always stored in an integrated fashion in WM, Woodman and Luck (2008) interpreted this result as evidence that colour and orientation information can be represented independently, even when the other feature is present in the same object. Here, CDA measures were employed to investigate whether spatial and non-spatial features are stored in WM in an integrated or independent fashion.

In line with the sensory recruitment model of WM, CDA components observed during the retention of visual stimuli show a modality-specific topography CDA over contralateral posterior visual areas, suggesting that they reflect the activation of visual-perceptual brain regions during the maintenance of visual information. During the retention of tactile stimuli presented to the left versus right hand, a similar sustained contralateral component is elicited (tactile CDA; e.g., Katus, Grubert, & Eimer, 2015; Katus & Eimer, 2016), with a modality-

specific topography over central somatosensory cortex. Given their likely origin in spatiotopic visual and somatosensory cortex, it is plausible to assume that the visual and tactile CDA components reflect the attentional activation of particular locations within the cortical maps in these areas (e.g., Berggren & Eimer, 2016c; Katus & Eimer, 2015). If this was the case, load-related CDA amplitude differences should primarily reflect how many different locations that are currently attended, rather than the number of features that are currently maintained in WM. In line with this hypothesis, visual CDA amplitudes were found to be similar when one feature (orientation) or two features (orientation and colour) of the same object had to be memorized, and larger when the memorized orientation and colour were presented at different locations (Luria & Vogel, 2011). However, results from another CDA study (Ikkai, McCollough, & Vogel, 2010, Exp. 2) suggest that this component does not directly reflect the number of attended spatial positions. In this experiment, two sample displays that each contained two task-relevant coloured stimuli were presented sequentially, and the relevant stimuli either appeared at the same locations or at different locations in these two displays. CDA amplitudes increased in the interval following the second sample display, and this was the case not only on different-location trials, but also, critically, on same-location trials. This suggests that the CDA reflects how many objects are represented in WM, rather than the number of object locations.

Overall, current evidence about the link between CDA components and the storage of object features versus spatial locations in visual WM is inconclusive. Until now, visual CDA components have been exclusively measured under conditions where participants had to maintain non-spatial attributes of visual objects such as their colour or shape, but not in purely spatial WM tasks. In order to understand whether the retention of spatial locations and non-spatial object attributes operates in an integrated or separable fashion, it is important to directly compare CDA components in both types of tasks. This was done in the two experiments

reported in this Chapter. In Experiment 7, CDAs in a standard colour change detection task were measured, and compared to lateralized ERP components measured during the delay period of an exclusively location-based WM task where only spatial positions had to be retained. In both tasks, physically identical memory sample displays were shown, which contained one, two, three, or four coloured items on the left and right side (see Figure 18). The items on both sides differed in their shape (circles versus squares), and participants had to encode and maintain items in the pre-defined target shape in order to compare them to the subsequent bilateral test display that contained a single item on either side. The side on which the relevant sample and test stimuli appeared varied randomly across trials. In the Colour Task, participants memorized the colours of the task-relevant sample items, and reported whether the test item on the same side matched or did not match one of the sample items. The locations where the sample stimuli appeared were irrelevant, as the test items were always presented at a different location as any of the samples. In the Location Task, participants were instructed to maintain the locations of the task-relevant samples, and match them to the location of the subsequent test item on the same side. The colours of the samples were now task-irrelevant, as the test items were always white. WM load was manipulated in the same way for both tasks, by presenting sample displays with 1, 2, 3, or 4 task-relevant items.

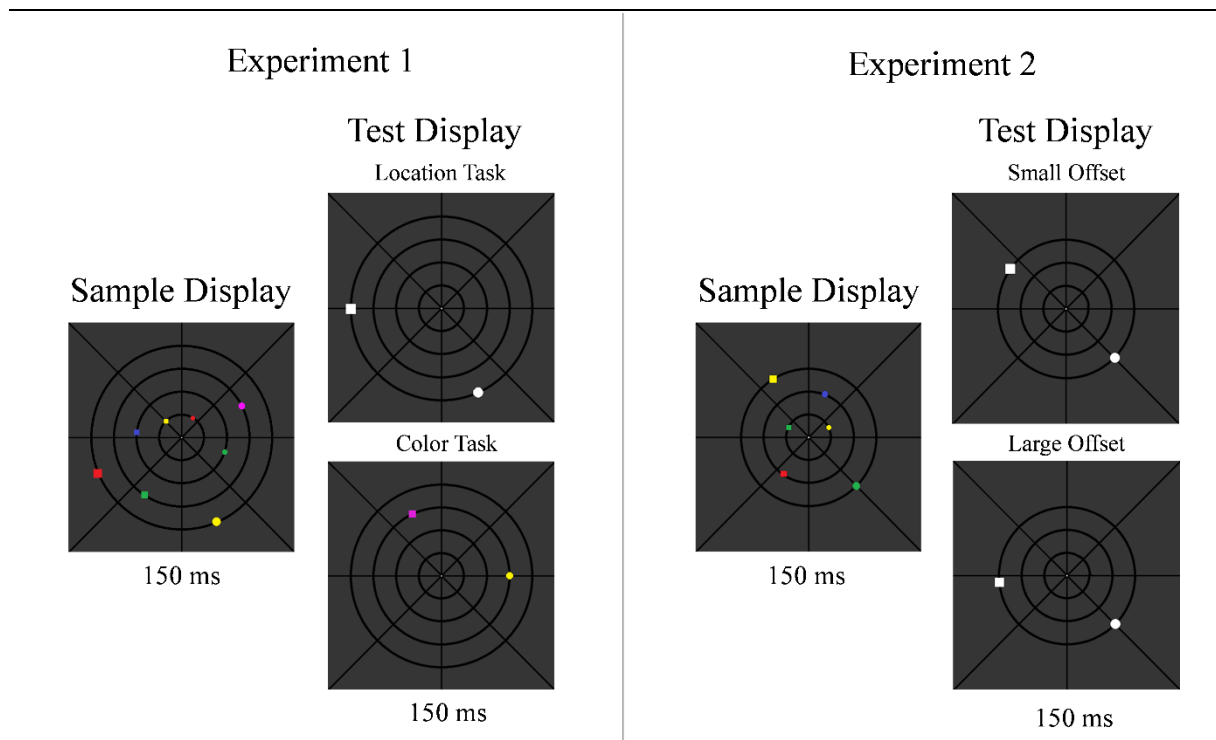


Figure 18. Examples of memory sample and test displays in Experiment 7 (left panel) and Experiment 8 (right panel). In these examples, participants had to encode the locations or colours of the squares on the left side of the memory displays, in order to match the location/colour of the square in the test display to one of the sample items. In Experiment 8, only stimulus locations had to be memorized. On mismatch trials, the spatial distance between the relevant item in the test display and the nearest item in the sample display was either small (Small Offset Task) or large (Large Offset Task). Only mismatch trials are shown in Figure 18.

CDA components were measured during the retention interval between the memory sample and test displays, separately for the Colour and Location tasks, and for each level of WM load. For the Colour Task, results were expected to be similar to previous ERP studies using analogous colour change detection procedures (e.g., Vogel & Machizawa, 2004; McCollough et al., 2007; Ikkai, McCollough, & Vogel, 2010). CDA amplitudes should increase with increasing WM load, and reach asymptote at the typical WM capacity limit of 3 items. The critical new question was which pattern of CDA components would be observed in

the Location Task. One possibility is that CDAs elicited during the retention of spatial locations are not sensitive to how many locations have to be maintained. This would suggest that in contrast to the storage of object colours, where the CDA reflects the number of individual objects that are currently maintained in WM, objects are not represented in an individuated fashion when only their locations have to be memorized. For example, they might be grouped and stored as a single spatial pattern, irrespective of how many individual locations contribute to this pattern. The presence of load effects for CDA components in the Colour Task and the absence of such effects in the Location Task would be indicative of fundamental qualitative differences between the storage of features and spatial locations in WM. Another possibility is that CDA components show load-dependent amplitude increases not only in the Colour Task but also in the Location Task, but that these load effects differ systematically between the two tasks. For example, CDA amplitudes might reach asymptote earlier in the Colour Task relative to the Location Task. This would point towards quantitative differences between WM storage mechanisms for colours and locations, in line with the suggestion by Wheeler and Treisman (2002) that these attributes are maintained independently in parallel stores with separate capacities. A third possible outcome is that the effects of WM load on CDA components are identical in both tasks, but that CDA amplitudes are generally larger in the Colour Task. Such a result could indicate that locations are always represented explicitly even when they are irrelevant (e.g., Foster et al., 2017) whereas object colours are only maintained when WM for colour is subsequently tested. In this context, a larger CDA in the Colour Task would reflect stronger activations during the retention of two attributes for each memorized object (colour and location) than when just the spatial locations of objects are maintained. This would be problematic for the hypothesis that visual WM always represents spatial and non-spatial features in a fully integrated fashion, irrespective of which attribute has to be memorized (see Woodman & Luck, 2008, for the same logic applied to the storage of colour and orientation).

A final possibility is that there are no CDA differences at all between the Colour and Location tasks. This would be consistent with the hypothesis that the maintenance of spatial locations and non-spatial features of objects are equally based on the allocation of spatial attention to specific locations in visual cortical maps. CDA amplitudes directly reflect the number of currently attended objects at particular locations within these maps. Because all features of these objects, including their spatial locations, are represented in an integrated fashion, WM maintenance processes will remain unaffected by whether object colours or locations are currently task-relevant.

5.2 EXPERIMENT 7

5.2.1 Methods

Participants

Sixteen participants were tested for Experiment 7 (mean age 28 years, 10 male, 2 left-handed), All participants were neurologically unimpaired, had normal or corrected-to-normal vision, and gave informed written consent prior to testing. The experiment was approved by the Psychology Ethics Committee, Birkbeck, University of London.

Apparatus, Stimuli and Procedure

The task was based on the visual task used in a previous multisensory WM experiment (Katus & Eimer, 2018). Visual stimuli were presented at a viewing distance of 100 cm against a dark grey background on a 22 inch monitor (Samsung SyncMaster 2233; 100 Hz refresh rate, 16 ms response time). Throughout the experiments, the monitor showed black crosshairs (three lines at 0°, 45° and 90° polar angle; horizontal/vertical eccentricity: 9° of visual angle) and four

black rings centred on the fixation dot (see Figure 18, left panel). The eccentricity of the four rings was 2.18°, 4.24°, 6.41°, and 8.46°; respectively. Visual sample and test stimuli (circles and squares) were presented on top of these rings, and their size was scaled for eccentricity (circles: 0.34°, 0.40°, 0.52°, and 0.57°; squares: 0.30°, 0.36°, 0.46°, and 0.51°, from the innermost to outermost ring). On each trial, a memory sample display was followed by a retention period and then by a memory test display. Sample and test displays were each presented for 150 ms, and were separated by a period of 850 ms where only the rings/crosshair display was visible. Thus, the stimulus onset asynchrony (SOA) between memory sample and test displays was 1000 ms. Memory displays contained a set of coloured circles and squares. Stimulus colours of the stimuli were drawn from a set of five equiluminant colours (~11.8 cd/m²; CIE colour coordinates, red: .627/.336; green: .263/.568; blue: .189/.193; yellow: .422/.468; magenta: .289/.168).

There were two tasks (Colour Task and Location Task). Participants had to memorize the sample stimuli in a predefined task-relevant shape (circles or squares), and to judge whether the test stimulus with the task-relevant shape matched the colour or the location of one of the task-relevant items in the sample display (match trials) or not (mismatch trials). They responded by pressing one of two vertically aligned response buttons (top for match, bottom for mismatch) with the index finger of the left or right hand during a 1500 ms response period starting at the onset of each test display. In each memory sample display, squares and circles were always presented on opposite sides, to ensure that participants would always encode and maintain stimuli in one hemifield only. Sample displays with squares on the left and circles on the right, and vice versa, were randomly intermixed in each block. For eight participants, squares were task-relevant and circles had to be ignored, and this assignment was reversed for the other eight participants.

The number of to-be-memorized items in the sample display (WM load: one, two, three, or four items) was varied randomly across trials. Task-relevant sample stimuli were always accompanied by the same number of stimuli with the task-irrelevant shape on the opposite side. Memory sample displays for a given WM load (N) were generated by randomly selecting N colours and N locations on each trial, independently for the samples on the left and right side. Locations were sampled from 240 angular positions (in polar coordinates, left side: 120° to 240°, right side: 300° to 60°), with the constraint that any two sampled positions were at least 20° apart. Pairs of positions on the left and right side were assigned to the same concentric ring. N rings were selected without replacement to ensure that no ring contained more than one item on each side.

Test displays contained one circle and one square on the same side where circles and squares had appeared in the preceding memory sample display. In the Colour task, participants judged whether the colour of the test stimulus in the task-relevant shape matched the colour of one of the task-relevant sample stimuli (50% match/mismatch). Sample stimulus locations were irrelevant, as this test stimulus appeared on the same side as the relevant sample stimuli, but at a randomly selected position. In the Location task, test displays always contained a white circle and a white square on opposite sides. Participants had to judge whether the location of the task-relevant test item matched the location of one of the relevant items in the preceding sample display, which was the case on match trials (50% of all trials). On mismatch trials, the location of this test item was shifted to a different location on the same ring that was previously occupied by a task-relevant sample item (25° angular offset relative to the original sample location; with upwards or downwards shifts equiprobable and randomly mixed across trials).

The experiment contained 20 blocks with 40 trials per block, resulting in a total of 100 trials for each WM load condition in either task. Task order was randomly determined for each participant, and varied in an ABBA fashion (i.e., the task changed after block five and after

block 15). One training block was run prior to the start of the first experimental block. Feedback about the proportion of correct responses was given after each experimental block.

EEG Recording and Data Analysis

EEG data, sampled at 500 Hz using a BrainVision amplifier, were DC-recorded from 32 electrodes at standard locations of the extended 10-20 system. Two electrodes at the eyes' outer canthi monitored horizontal eye movements (horizontal electro-oculogram, HEOG). Continuous EEG data were referenced to the left earlobe during recording, and re-referenced to the arithmetic mean of both earlobes for data pre-processing. Data were offline submitted to a 20 Hz low-pass filter (Blackman window, filter order 2000). To confirm that this specific filter setting did not affect the pattern of CDA effects, additional analyses were conducted on EEG data sets that were low-pass filtered at 40 Hz. Statistical results were virtually identical for both filter settings. Epochs were computed for the 1000 ms interval following the onset of a memory sample display, relative to a 200 ms pre-stimulus baseline.

Trials with saccades were rejected using a step function that ran on the bipolarized HEOG (step width 200 ms, threshold 25 μ V). Independent Component Analysis (ICA) (Delorme, Sejnowski, & Makeig, 2007) was used to correct for frontal artefacts such as eye blinks, and residual traces of horizontal eye movements that had not been detected by the step function. Trials were rejected when EEG amplitudes at any electrode exceeded a 100 μ V threshold, and when amplitudes in the time window of interest (i.e., between 300 and 1000 ms following sample display onset) exceeded a 20 μ V threshold in difference waveforms for lateral electrode pairs (such as O1 vs. O2). Trials with incorrect behavioural responses were also excluded from EEG analysis. Following trial rejection, an average of 75.6% of all trials were retained.

EEG was averaged separately for all four WM load conditions in the Colour and Location tasks, for trials where the task-relevant memory samples appeared on the left or right side. CDA components were computed on the basis of mean amplitudes measured during the 300-1000 ms interval after sample display onset. The CDA was measured at lateral occipital electrodes PO7 and PO8 where this component is usually maximal. This was confirmed by quantifying mean CDA amplitudes across all task conditions separately for all four lateral posterior electrode pairs (mean CDA amplitudes at PO7/8: $-1.18 \mu\text{V}$, P7/8: $-1.05 \mu\text{V}$, PO9/10: $-1.0 \mu\text{V}$, P9/10: $-0.94 \mu\text{V}$). CDA mean amplitude differences between tasks and WM load conditions were assessed in a repeated measures ANOVA. To test whether the effects of manipulating WM load on WM accuracy and CDA amplitudes were identical or differed between the Colour and Location tasks, Bayesian analyses (Rouder et al., 2009) and the software Jasp (JASP team 2018) were used to calculate Bayes factors for interactions between the factors Task and WM Load. Bayes factors denote the relative evidence for the null hypothesis as compared to the alternative hypothesis, and thus allow for statistical inferences regarding the absence of differential effects. The Bayes factor for the null hypothesis (BF_{01}) corresponds to the inverse of the Bayes factor for the alternative hypothesis (BF_{10}), and indexes the relative evidence in the data that an effect is absent rather than present. Reliable evidence for the null hypothesis is provided by a $\text{BF}_{01} > 3$ (Jeffreys, 1961), suggesting that the empirical data is at least 3 times more likely under this hypothesis as compared to the alternative hypothesis.

5.2.2 Results

Behavioural Analysis

Memory accuracy was assessed in an ANOVA with the factors Task (Colour versus Location) and WM Load (1, 2, 3, or 4 items). As can be seen in Figure 19 (top left panel), accuracy was generally higher in the Colour Task than in the Location Task (87.1% versus 80.6% correct responses), as reflected by a main effect of Task ($F(1, 15) = 6.201, p = 0.025, \eta_p^2 = .292$). Unsurprisingly, accuracy dropped when WM load increased (main effect of WM Load: $F(1.55, 23.27) = 41.58, p < .001, \eta_p^2 = .735$). This effect of WM load on accuracy was similar in the Colour and Location tasks, as reflected by the absence of an interaction between WM Load and Task ($F(3, 45) = 1.32, p = 0.279, \eta_p^2 = .081$). This hypothesis that the manipulation of WM load affected the accuracy of WM for colours and for locations in an essentially identical fashion was confirmed by the corresponding Bayesian analysis ($BF_{01} = 7.25$).

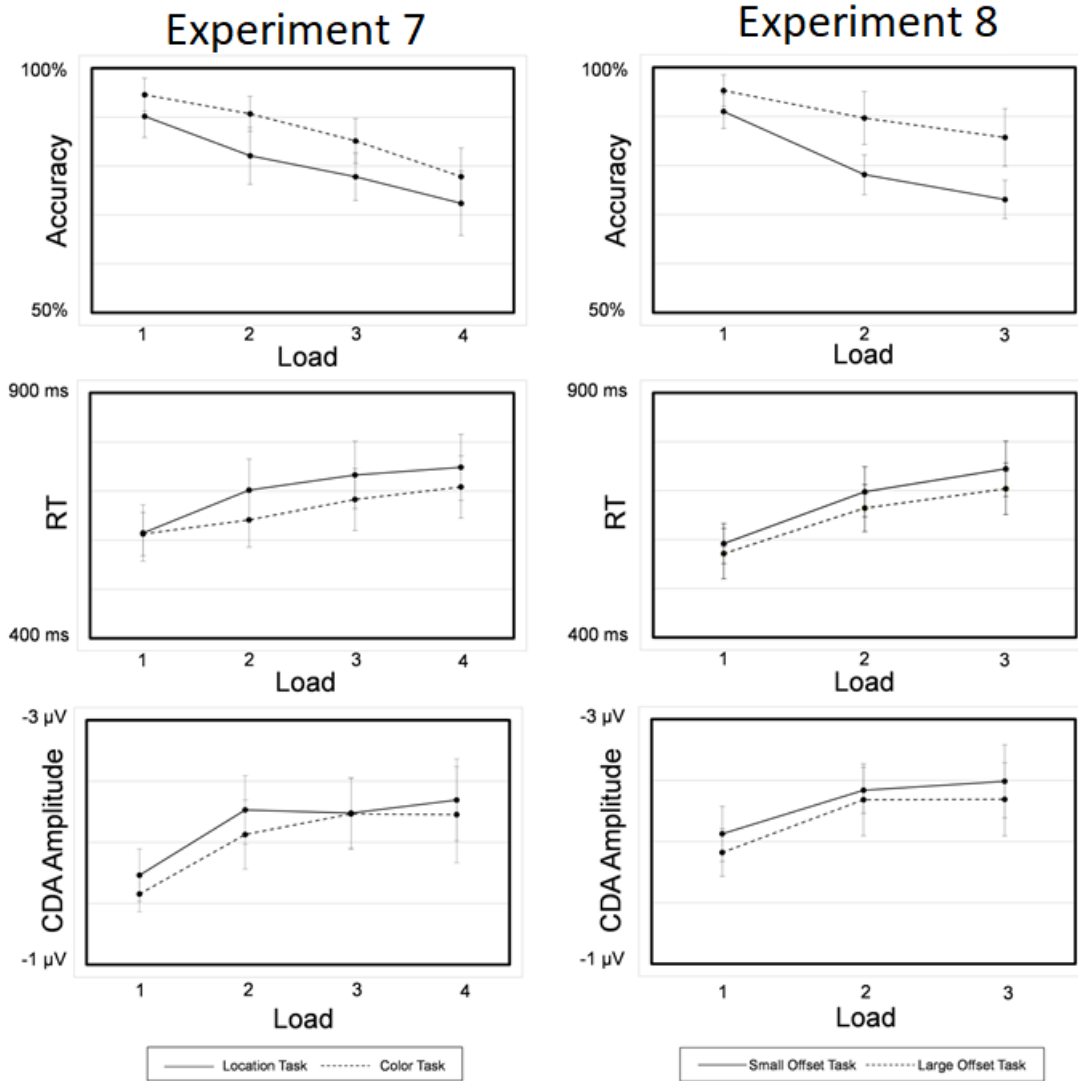


Figure 19. Accuracy of WM performance (top panels), RTs to memory test displays (middle panels), and CDA amplitudes (bottom panel), shown separately for the two tasks and all WM load conditions in Experiment 7 (left) and Experiment 8 (right). Error bars in graphs indicate 95% confidence intervals (CIs) for the true population mean.

Reaction times (RTs) to memory test displays were slower in the Location Task than in the Colour Task (699 ms vs. 661 ms), but this difference only approached significance ($F(1, 15) = 4.41, p = 0.053, \eta_p^2 = .227$). A main effect of Load ($F(1.37, 21.24) = 36.73, p < .001, \eta_p^2$

= .710) confirmed that RTs increased with increasing WM load. There was also an interaction between WM Load and Task $F(1.42, 21.24) = 6.01, p = 0.002, \eta_p^2 = .286$. This was due to the fact that increasing WM load from one to two items had a stronger effect on RTs in the Location Task relative to the Colour Task (87 ms versus 29 ms; $t(15) = 4.72, p < .001, d = 1.19$).

ERP Analysis: CDA Components

Figure 20 shows CDA components elicited in the 1000 ms interval after memory sample display onset for displays containing one, two, three, or four lateralized task-relevant items, separately for the Location and Colour Tasks. ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to the task-relevant sample items are shown together with the corresponding contralateral-ipsilateral difference waveforms. CDA components were elicited in both tasks, and CDA amplitudes increased with increasing WM load. This is further illustrated by the topographical scalp distribution maps of lateralized ERP activity during the 300 – 1000 ms interval after sample display onset shown in Figure 20. These spline-interpolated voltage maps were obtained by subtracting ERPs ipsilateral to the task-relevant target stimuli from contralateral ERPs, and flipping electrode coordinates over the midline for sample displays with task-relevant items on the left side. As a result, CDA components are reflected by negative potentials over the left hemisphere in these maps.

The analysis of CDA mean amplitudes with the factors Task, WM Load, and Laterality (electrode contralateral versus ipsilateral to the task-relevant samples) obtained a main effect of Laterality ($F(1,15) = 28.32, p < .001, \eta_p^2 = .654$), confirming the presence of reliable CDA components in Experiment 7. As expected, there was also an interaction between Laterality and WM Load ($F(3, 45) = 18.72, p < .001, \eta_p^2 = .555$), reflecting the increase of CDA amplitudes when WM load was increased. Importantly, there was also an interaction between Task and Laterality ($F(1, 15) = 8.66, p = 0.010, \eta_p^2 = .366$), as there was a small but systematic

tendency for CDA amplitudes to be larger in the Location Task than in the Colour Task. This difference remained reliable when CDA components were measured across all four lateral posterior electrode pairs (PO7/8, P7/8, PO9/10, P9/10; $F(1, 15) = 7.30, p = 0.016, \eta_p^2 = 0.327$), as larger CDA amplitudes in the Location task were present at all four pairs. This CDA enhancement in the Location Task is also illustrated in Figure 19 (bottom left panel), which shows mean CDA amplitudes for each WM Load condition in both tasks. Finally, there was no three-way interaction between Laterality, Task, and WM load ($F(3, 45) = 0.594, p = 0.622, \eta_p^2 = .038$), suggesting that the impact of increasing WM load on CDA amplitudes did not differ between the Colour and Location tasks. The hypothesis that the manipulation of WM load had identical effects on CDA components in both tasks was confirmed by the corresponding Bayesian analysis ($BF_{01} = 7.545$).

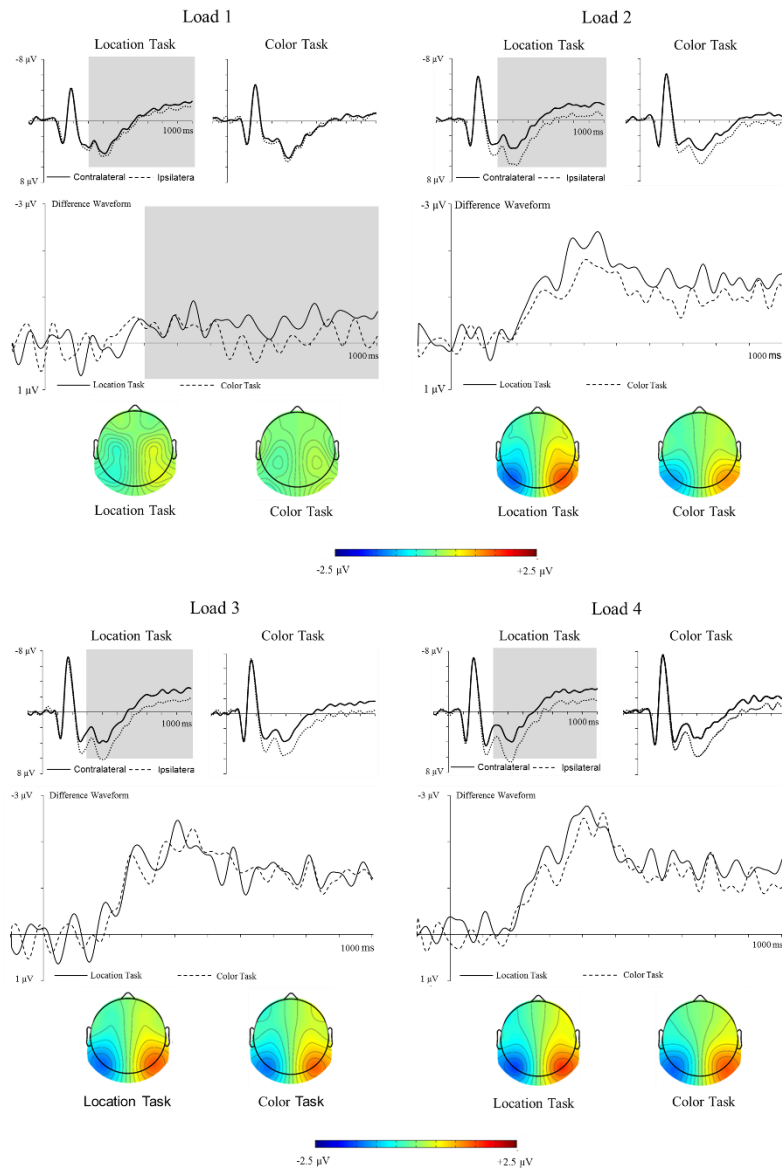


Figure 20. Grand-averaged ERPs elicited in Experiment 7 in response to memory sample displays at electrodes PO7/8 contralateral and ipsilateral to the task-relevant sample display items. ERPs are shown separately for the Location and Colour Tasks, together with difference waveforms obtained by subtracting ipsilateral from contralateral ERPs. Topographic maps show the scalp distribution of CDA components during the 300-1000 ms interval after memory display onset for both tasks. Data are shown separately for WM loads of 1, 2, 3, or 4 items.

5.2.3 Discussion of Experiment 7

Experiment 7 demonstrated that CDA components are not only triggered during the maintenance of non-spatial features of visual objects, but also when only the locations of these objects have to be retained in WM. Moreover, and importantly, the effects of increasing WM load on CDA amplitudes were identical in both tasks. These findings are in line with the hypothesis that the storage of colours and locations in visual WM is mediated by shared mechanisms. Object colours and spatial locations may both be maintained by allocating spatial attention selectively to those locations within visual cortical maps that represent the currently task-relevant objects in a memory sample display. In this scenario, WM capacity limitations would reflect limitations in the ability to maintain multiple independent foci of spatial attention that are independent of which attributes are currently task-relevant (e.g., Franconeri et al., 2013). The observation that WM load had identical effects on WM accuracy and CDA amplitudes the Colour and Location Tasks of Experiment 7 does indeed show that, at least for the task parameters of this experiment, WM for colours and locations did not differ in their capacities. The fact that increasing WM load from one to multiple items affected RTs to test displays more strongly in the Location Task than in the Colour Task is unlikely to be linked to differences in storage capacity. Instead, it could reflect differences in WM retrieval and sample-test comparison processes between the two tasks.

These findings of Experiment 7 did not provide support for the hypothesis that colours and locations are stored in parallel in separate stores with independent capacities (Wheeler & Treisman, 2002). However, another aspect of the CDA results suggests that WM maintenance processes did not operate in an identical fashion in the two tasks. If locations are always maintained in an obligatory fashion even when colours have to be memorized, while colours are only retained if they are task-relevant, CDA amplitudes might have been generally larger

in the Colour Task relative to the Location Task, reflecting the maintenance of two versus just a single attribute for each stored sample object. This was clearly not the case. In fact, the opposite pattern was obtained, as CDA amplitudes were generally larger in the Location Task. Even though this effect was small, it was reliably present, and was independent of WM load. If the CDA reflects visual processing biases for task-relevant objects at currently attended locations that are elicited in the same way when colours or locations have to be memorized, no such CDA amplitude difference should have been observed. One possibility is that the storage of spatial and non-spatial information is based on partially separate mechanisms, with spatial WM associated with larger activation levels during the retention period. Alternatively, the presence of larger CDAs in the Location Task could be due to the fact that this task was generally harder than the Colour Task. This was reflected by reduced WM accuracy in the Location Task and a tendency towards slower RTs to test displays. As this task was apparently more demanding than the Colour Task, it may have required participants to retain more precise WM representations, and this could have resulted in larger CDA amplitudes (see Reinhart et al., 2012, for links between CDA amplitudes and the spatial precision of memory-based behaviour in humans and non-human primates). In this case, this CDA amplitude difference would not reflect qualitative differences between the WM storage of colours versus spatial locations, but rather a quantitative difference in the difficulty of these two WM tasks. This possibility was further investigated in Experiment 8.

5.3 EXPERIMENT 8

5.3.1 Introduction for Experiment 8

CDA components may have been larger in the Location Task than in the Colour Task of Experiment 7 because the former task was harder, thus suggesting that maintaining sufficiently precise WM representations of spatial locations was more demanding than retaining object colours. The possibility that CDA amplitudes reflect task difficulty and/or the resolution with which objects are stored in WM has been investigated in several studies, which have generally obtained negative results (see Luria, Balaban, Awh, & Vogel, 2016, for review). Although the CDA increases in size when the complexity of memorized visual objects increases (Luria & Vogel, 2011), studies that manipulated the difficulty of colour change detection tasks found no differential effects on CDA components (e.g., Ikkai et al., 2010; Ye et al., 2014). One notable exception is a study by Machizawa, Goh, and Driver (2012), who investigated how the difficulty of WM tasks involving line orientations affected CDA amplitudes. Participants had to memorize the orientations of two or four sample lines and to report whether a line in a subsequent test display was shifted in a clockwise or counter-clockwise directions. CDA amplitudes were larger in blocks where the line rotations in the test display were small, relative to blocks where this rotation was larger. This CDA amplitude increase was only found when WM load was small (2 sample items) but not when four line orientations had to be memorized. This suggests that voluntary adjustments of WM activation processes in line with the anticipated difficulty of subsequent memory-test comparison processes only take place under conditions where WM load remains below capacity. To confirm that the CDA amplitude increase in blocks with small line rotations was associated

with more precise WM representation of line orientations, Machizawa et al. (2012) conducted another behavioural experiment where line colours in sample displays indicated whether the subsequent line orientation discrimination would be difficult or easy on most trials. On a minority of trials, test displays contained a line with an intermediate orientation shift. Performance on these critical trials was better when observers expected a difficult discrimination, demonstrating that they were able to vary the precision of WM representations in line with anticipated task demands.

The goal of Experiment 8 was to test whether the anticipated difficulty of location discriminations between memory and test displays would also affect CDA amplitudes, using a similar logic as Machizawa et al. (2012). Procedures were similar to the Location Task of Experiment 7, except that on mismatch trials, the spatial separation between the task-relevant item in the test displays and one of the relevant items in the sample displays was manipulated. In different blocks, this distance was either 40° (Large Offset Task) or 15° (Small Offset Task). The critical question was whether this difference in the difficulty of comparing spatial locations between sample and test displays would affect CDA components, with larger CDA amplitudes in the more difficult Small Offset Task. WM load (1, 2, or 3 relevant sample items) was also manipulated. Because Machizawa et al. (2012) found that task difficulty only modulated CDA amplitudes when WM load was low, WM load was blocked in Experiment 8. Foreknowledge about how many locations would have to be memorized for each sample display should maximize the chances to find load-related differences in the effects of task difficulty on CDA components in the Small versus Large Offset Task.

5.3.2 Methods

Participants

Sixteen volunteers participated in Experiment 8 (mean age 29 years, 8 male, none left-handed). All participants were neurologically unimpaired and gave informed written consent prior to testing.

Stimuli, Procedure, and Analyses

These were the same as in the Location Task of Experiment 7, with the following exceptions. First, sample and test items now only appeared at one of three possible eccentricities (2.81°, 5.67°, 8.46°; stimulus size for circles: 0.40°, 0.52°, 0.57°; for squares: 0.35°, 0.46°, 0.54°, for the innermost to outermost eccentricity). The constant rings/crosshair display used in Experiment 7 was adjusted accordingly (see Figure 18, right panel). Two versions of the Location Task were run, which only differed with respect to the size of spatial offset between a task-relevant sample and test location on mismatch trials. In the difficult Small Offset Task, this angular offset was 15°. In the easier Large Offset Task, it was 40°. Even though the colour of memory sample stimuli was entirely irrelevant, the same stimulus colours for these displays that were used in Experiment 7 were retained. There were three WM load conditions (one, two, or three). Load now remained constant within each block, and changed every two blocks, with the sequence of WM load conditions randomized for each participant. The task-relevant shape (circle versus square) in the memory sample and test displays was randomly determined for each participant before the first block, and changed after every 6 blocks (i.e., after block 6, 12, and 18). 24 blocks with 32 trials per block were run, resulting in a total of 128 trials for each WM load condition in the Small and Large Offset tasks. Eight participants first completed 12 Small Offset blocks prior to 12 blocks for the Large Offset task, and this order was reversed for the other eight participants.

EEG processing and analysis procedures were the same as in Experiment 7. Following trial rejection, an average of 80.4% of all trials were retained for EEG analyses. The CDA was

measured at electrodes PO7 and PO8 where CDA amplitudes were again maximal (PO7/8: -1.52 μV , P7/8: -1.38 μV , PO9/10: -1.06 μV , P9/10: -0.91 μV). Analogous to Experiment 7, Bayes factors were computed for interactions between the factors Task and WM Load to assess whether increasing the number of memorized locations had identical or different effects on WM accuracy and CDA amplitudes when the demands on spatial precision were either high (Small Offset Task) or low (Large Offset Task).

5.3.3 Results

Behavioural Analysis

As predicted, accuracy was impaired in the Small Offset Task relative to the Large Offset Task (80.7% vs. 90.2% correct responses; main effect of Task: $F(1, 15) = 28.55, p = .001, \eta_p^2 = .656$; see Figure 19, top right panel). There was also a main effect of WM Load ($F(2, 30) = 70.35, p < .001, \eta_p^2 = .824$), as accuracy decreased when the number of locations that had to be memorized increased. Finally, there was an interaction between Task and WM Load ($F(2, 30) = 13.48, p = .001, \eta_p^2 = .473$). This is due to the fact that the reduction in WM accuracy in the Small Offset Task relative to the Large Offset task was much larger when two or three locations had to be memorized (12.7% and 11.5%, respectively) than when just one location had to be maintained (4.3%; both $p < 0.01$).

RTs to memory test displays (shown in Figure 19, middle right panel) increased when WM load was increased ($F(1.46, 28.63) = 78.71, p < .001, \eta_p^2 = .840$). There was also a tendency for RTs to be slower in the Small Offset Task (678 ms vs. 647 ms in the Large Offset Task), but the main effect of Task only approached significance ($F(1, 15) = 3.90, p = 0.067, \eta_p^2 = .206$). There was no interaction between Task and WM Load for RTs ($F(2, 30) = 0.735, p = 0.488, \eta_p^2 = .047$).

ERP Analysis: CDA Components

Figure 21 shows CDA components elicited in response to memory sample displays containing one, two, or three lateralized task-relevant items in the Small and Large Offset Task at electrodes PO7/8 contralateral and ipsilateral to these items. The corresponding contralateral-ipsilateral difference waveforms and topographical maps are also shown. As expected, CDA amplitudes increased with the number of locations that had to be memorized. More importantly, CDA components also appear to be generally larger in the more difficult Small Offset Task. These observations were confirmed by an ANOVA with the factors Task (Small Offset, Large Offset), WM Load, and Laterality. There was a main effect of Laterality ($F(1,15) = 60.50, p < .001, \eta_p^2 = .654$), confirming the presence of reliable CDA components in Experiment 8. A significant interaction between WM Load and Laterality ($F(2, 30) = 16.14, p < .001, \eta_p^2 = .518$) reflected the increase of CDA amplitudes with increasing WM load. Critically, there was also an interaction between Task and Laterality ($F(1, 15) = 5.26, p = 0.037, \eta_p^2 = .260$), confirming that CDA components were larger in the Small Offset Task. This is also illustrated in Figure 19 (bottom right panel), which shows mean CDA amplitudes for each WM Load condition in both tasks, and suggests that CDAs were larger in the Small Offset Task relative to the Large Offset Task irrespective of whether one, two, or three locations had to be memorized. Accordingly, there was no three-way interaction between Task, Load and Laterality ($F(2, 30) = 0.18, p = .83, \eta_p^2 = .012$). This observation that the increase of CDA amplitudes in the more difficult Small Offset Task was independent of WM load was confirmed by the corresponding Bayesian analysis ($BF_{01} = 5.705$).

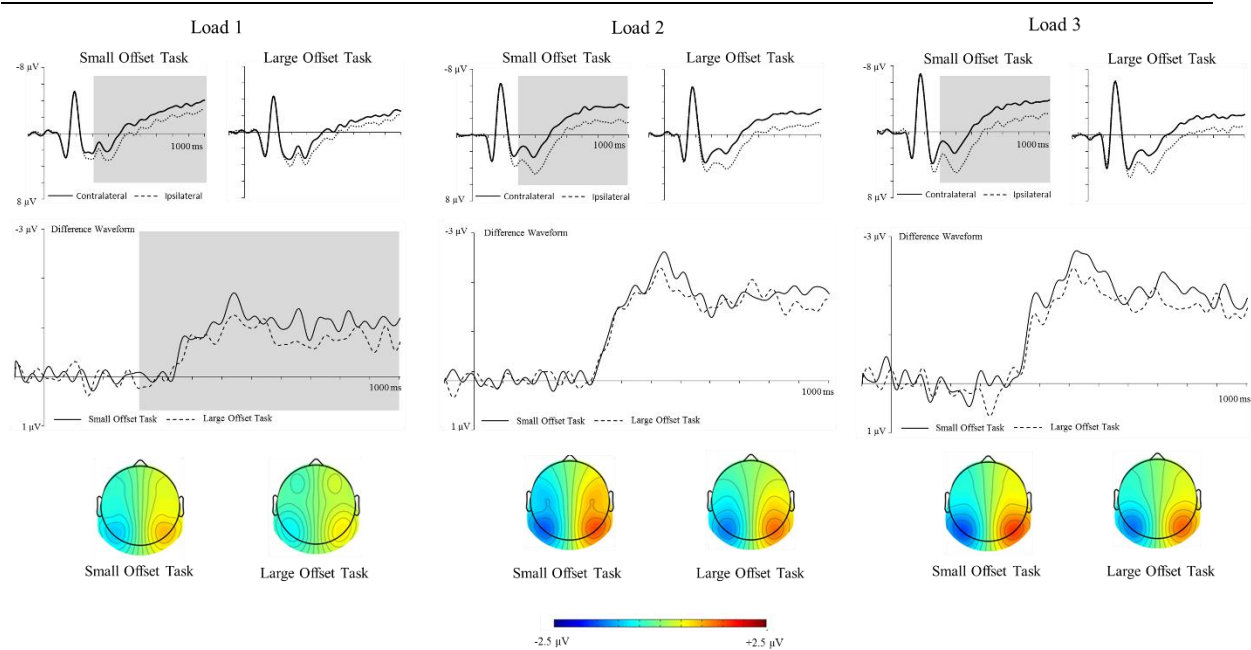


Figure 21. Grand-averaged ERPs elicited in Experiment 8 in response to memory sample displays at electrodes PO7/8 contralateral and ipsilateral to the task-relevant sample display items. ERPs are shown separately for the Small Offset and Large Offset Tasks, and for WM loads of 1, 2, or 3 items, together with difference waveforms obtained by subtracting ipsilateral from contralateral ERPs. Topographic maps show the scalp distribution of CDA components during the 300-1000 ms interval after memory display onset for both tasks and each WM load condition.

5.3.4 Discussion of Experiment 8

Experiment 8 demonstrated that CDA amplitudes measured in spatial WM tasks are sensitive to the difficulty of these tasks. When the spatial separation between sample and test items on mismatch trials was small (Small Offset blocks), WM performance was impaired relative to Large Offset blocks. This impairment was particularly pronounced when two or three locations had to be memorized, showing that reducing the spatial offsets of sample and test stimulus locations on mismatch trials had the desired effect of increasing task difficulty.

Critically, CDA components were generally larger in the Small Offset Task as compared to the Large Offset Task. This is in line with earlier observations by Machizawa et al. (2012), who found an analogous CDA amplitude increase when the difficulty of a WM task for line orientations was increased, as reflected by decrements of WM performance. Interestingly, and in contrast to Machizawa et al. (2012), Experiment 8 found no evidence for an effect of WM load on CDA amplitude differences between the two tasks, in spite of the fact that WM load was blocked, so that participants always knew how many locations they had to retain. CDAs were consistently larger in the Small Offset Task, regardless of whether one, two, or three spatial locations had to be memorized (see Figure 19, bottom right panel). This will be further discussed below. More generally, the central finding of Experiment 8 is that CDA amplitude differences reflect differences in the anticipated difficulty of spatial comparisons between sample and test display locations. Based on an analogous pattern of CDA results, Machizawa et al. (2012) concluded that task difficulty affects the precision with which visual attributes (in their case, line orientations) are represented in WM, and provided additional support for this conclusion with their additional behavioural experiment (as described above). It is likely that this also applies to the results of Experiment 8, with larger CDA amplitudes in the Small Offset Task reflecting an increase in the spatial precision with which locations are represented in WM. As was also the case in Machizawa et al. (2012), any such improvement in the precision of WM representations was not sufficient to fully counteract the effects of increasing task difficulty on WM performance, which was worse in the more difficult Small Offset Task.

The fact that CDA amplitudes in Experiment 8 were sensitive to task difficulty also has implications for the interpretation of the fact that CDA amplitudes were larger in the Location Task of Experiment 7. This difference is likely due to the fact that spatial task demands were higher in this task than in the Colour Task where the locations of sample items were irrelevant and thus could be ignored.

5.4 General Discussion for Chapter 5

The goal of the two experiments reported in this Chapter was to use CDA components as electrophysiological markers of WM maintenance processes to investigate the mechanisms involved in the storage of spatial locations, and compare them to the maintenance of non-spatial features (colours) of visual objects. In Experiment 7, CDA components to physically identical sample displays which contained coloured shapes were measured under conditions where participant memorized either the locations of task-relevant sample items and ignored their colours, or vice versa. Clear CDA components that were sensitive to WM load were found in both tasks, and load-dependent CDA amplitude modulations were identical. This suggests that similar if not identical mechanisms are responsible for the storage of object locations and object colours in WM. However, CDA amplitudes were generally larger in the Location Task. To account for this unexpected result, Experiment 8 investigated whether CDA components are sensitive to the precision of WM representations for spatial locations. Participants memorized one, two, or three locations in blocks where the spatial offset between memorized and tested locations on mismatch trials was either small or large. Relative to Large Offset blocks, CDA amplitudes were larger in Small Offset blocks where the precision of represented sample locations in WM had to be higher. Thus, the CDA amplitude differences observed in Experiment 7 between the Location and Colour Tasks are unlikely to reflect qualitative differences in the storage of spatial and non-spatial visual information. They are likely to be due to higher demands on spatial resolution in the former task.

The current results have implications both for understanding spatial WM, and links between the maintenance of spatial and non-spatial attributes of visual stimuli. With respect to the mechanisms involved in the representation of spatial locations in WM, Experiment 8

showed that activation states of these representations can be adjusted in line with task demands, as reflected by corresponding CDA amplitude modulations. This is in line with previous findings by Machizawa et al. (2012) in a task that required WM for line orientation. In contrast to this earlier study, Experiment 8 found no evidence that such strategic adjustments are restricted to conditions where WM load is low. This could either be due to differences in the mechanisms involved in maintaining spatial locations and stimulus orientations, or to the fact that manipulated WM load was only manipulated up to a maximum of three locations in Experiment 8. It is possible that CDA components will no longer be sensitive to differential task demands when the number of sample locations clearly exceeds WM capacity, and this should be studied in future research. It is important to note that previous attempts to demonstrate analogous associations between task difficulty and CDA amplitude modulations in non-spatial WM tasks involving coloured objects have generally been unsuccessful (e.g., Ye et al., 2014; see Luria et al., 2016, for review). This suggests that in contrast to spatial WM, the activation and/or precision of WM for non-spatial features such as colours can either not be regulated at all, or, if it can, that such adjustments are not reflected by the CDA. It is possible that voluntary control over the activation of visual WM representations is only available for WM tasks that have a strong spatial component. This was obviously the case in the Location tasks employed in the present experiments, but also in the study by Machizawa et al. (2012) where observers had to memorize line orientations. WM for orientations can be regarded as a variant of spatial WM, as observers might represent the orientation of lines in terms of the locations of cardinal points, such as line endings. The presence of task difficulty effects on CDA amplitudes in such spatial WM tasks, and their apparent absence in colour change detection tasks that lack a spatial component could point to a special role for space-based executive control processes in the regulation of visual WM.

This would be entirely consistent with the suggestion that spatial attention is responsible for the activation and maintenance of visual WM representations (e.g., Awh et al., 2006) that are held in two-dimensional maps in visual cortex (Franconeri et al., 2013). In such maps, representations of visual objects are addressed by their spatial location, irrespective of whether spatial positions or other non-spatial features are currently task-relevant. If top-down attentional control processes operate on the basis of spatial coordinates, it should be relatively straightforward to regulate their sensitivity in response to changing demands on the spatial precision of WM storage. The sensitivity of CDA amplitudes to task difficulty and thus to the required precision of spatial WM observed in Experiment 8 could reflect stronger attentional processing biases at object locations that have to be retained with high resolution. However, it is much more difficult to envisage how such space-based attentional control mechanisms might adjust the resolution with which non-spatial features such as object colours are stored in WM.

With respect to links between the storage of spatial and non-spatial information in WM, the current findings are in line with the hypothesis that memorized spatial and non-spatial features of visual objects are represented in an integrated fashion in visual cortical maps where these representations are maintained through the allocation of focal attention. There is however a possible alternative interpretation of the CDA results of Experiment 7. Previous research has shown that location information is encoded into WM even when it is entirely task-irrelevant (Foster et al., 2017), and it is possible that CDA components may exclusively reflect the spatial attributes of visual objects held in WM. The CDA components observed in the Colour Task of Experiment 7 could reflect this obligatory maintenance of object locations, and the fact that CDA amplitudes were larger in the Location Task might be the result of spatial location now being task-relevant. While this interpretation is consistent with the pattern of CDA results observed in Experiment 7, findings from previous CDA experiments do not support the hypothesis that this component only reflects the representation of the spatial properties of

objects in WM. For example, several studies (Woodman & Luck, 2008; Luria, Sessa, Gottler, Jolicœur, & Dell'Acqua, 2010) have found systematic CDA amplitude differences in response to physically identical sample stimulus displays containing orientated coloured rectangles or coloured polygons between blocks where either colour or orientation/shape was task-relevant. These results demonstrate not only that specific non-spatial features can be selectively prioritized in WM, but also that the CDA component is sensitive to this feature selectivity of WM storage processes. If the CDA exclusively reflected the representation of object locations in WM, it should not be affected by instructions to attend to different non-spatial feature of identical sample display objects.

In summary, the results of Experiments 7 and 8 have provided new electrophysiological evidence that the maintenance of spatial locations and non-spatial features in visual WM is based on overlapping neural mechanisms. This conclusion was supported by the similarity of CDA components elicited during the storage of object colours and object locations, and by the fact that increasing WM load in both tasks had equivalent effects on CDA amplitudes. These observations are in line with the suggestion that different features of visual objects, including their spatial location, are represented in an integrated fashion in WM, and that the maintenance of these features is facilitated by the allocation of spatial attention to specific locations within spatiotopic maps in visual cortex. In spite of these similarities between the storage of spatial and non-spatial attributes, spatial WM may be special in one important aspect. In apparent contrast to non-spatial features, the resolution with which spatial locations are represented can be strategically adjusted in line with current demands on the precision of spatial WM.

Chapter 6

General Discussion

6.1 Summary

Altogether, this thesis has investigated two avenues regarding the utilisation of space-based and feature-based attention in the guidance of perceptual attention processes and maintenance in visual working memory. Firstly, the nature of spatial-configural properties in feature-based target representations was explored. Chapter 2 investigated how attentional selection operates for targets defined by a conjunction of a particular spatial configuration of features. Chapter 3 further explored the organization of spatial-configural information by investigating how visual working memory representations are affected by the task demands in an expected test display.

Secondly, qualitative similarities and differences between space-based and feature-based attentional control mechanisms were examined. Chapter 4 compared the neural correlates of perceptual attentional selection of targets that were defined by either spatial or featural properties. Chapter 5 explored how visual working memory representations differ between tasks requiring maintaining either the featural or spatial properties of objects. Investigations into perceptual aspects of attention (Chapters 2 and 4) used the N2pc as a marker for attentional selection, whilst those which focused on visual working memory (Chapters 3 and 5) used the CDA as a marker for visual working memory maintenance.

Chapter 2 tested whether attentional templates of same-dimension feature conjunctions include spatial-configural information. Attentional templates guide attentional object selection during many types of visual search. In many real world situations, target objects are defined not just by a single feature, or even a combination of features, but by the spatial configuration of their component parts. In Experiments 1 and 2, electrophysiological markers of attentional selection processes were used to determine whether the guidance of shape configuration search is entirely part-based or sensitive to the spatial relationship between shape features. Participants searched for targets defined by the spatial arrangement

of two shape components (e.g., hourglass above circle). N2pc components were triggered not only by targets but also by partially matching distractors with one target shape (e.g., hourglass above hexagon) and by distractors that contained both target shapes in the reverse arrangement (e.g., circle above hourglass), in line with part-based attentional control. Target N2pc components were delayed when a reverse distractor was present on the opposite side of the same display, suggesting that early shape-specific attentional guidance processes could not distinguish between targets and reverse distractors. The control of attention then became sensitive to spatial configuration, which resulted in a stronger attentional bias for target objects relative to reverse and partially matching distractors. The results reported in Chapter 2 demonstrated that search for target objects defined by the spatial arrangement of their component shapes is initially controlled in a feature-based fashion but can later be guided by templates for spatial configurations.

These findings of Chapter 2 demonstrate that attentional selectivity is sensitive to spatial configuration, which suggests that configural information was represented in attentional templates in WM. The experiments reported in Chapter 3 investigated the nature of such configural representations in WM. Each component shape may be represented separately along with a specification of the spatial location of each shape (e.g., hourglass/top; circle/bottom). Alternatively these two shapes may be represented in a fully integrated fashion. In the two experiments reported in Chapter 3, these alternatives were studied in the context of a WM paradigm, using the same set of stimuli used in the experiments reported in Chapter 2. The contralateral delay activity (CDA) was measured as a marker of WM maintenance, in the context of a lateralised change detection task. On each trial, a memory sample display containing objects in the left and right visual field was followed by a memory test display containing a single object at fixation. The two critical tasks (Whole and Parts conditions), employed physically identical memory sample displays, but, critically, different

memory test displays. In the Parts condition, only one component shape was presented at fixation in these test displays, so that participants were required to represent both of the component shapes in the sample display independently. In the Whole condition, test displays contained compound shapes, so that integrated WM representations of a single object had to be formed. CDA amplitudes in Experiment 3 were indeed larger in the Parts task than in the Whole task, demonstrating that physically identical visual stimuli can be represented in different formats in WM (integrated versus part-based), depending on current task demands. In Experiment 4, one of the to-be-memorized two shapes remained constant throughout each experimental block, thus reducing WM load specifically for the Parts task. As predicted, in this experiment, there was no longer a larger CDA for the Parts relative to the Whole task, suggesting that a single object was now maintained in WM in both tasks. Overall, these results illustrate how task-dependent top-down control processes determine whether identical visual objects are stored as single objects in WM or are separately maintained as different objects.

Chapter 4 compared the attentional selection of targets defined by spatial and non-spatial properties in terms of onset latency and amplitude differences of target N2pc components. A commonly held view is that spatial attention plays a special role during the selection of task-relevant visual objects. It has been claimed that space-based attentional selectivity operates at earlier stages of visual processing than feature-based attention, and that feature-based attention is hierarchically dependent on spatial attention. The experiments reported in Chapter 4 demonstrated with electrophysiological markers of attentional target selection processes in visual search that spatial and feature-based attention operate in qualitative similar ways at the same stage of visual processing. N2pc components were measured to target objects in visual search displays in tasks where these targets were either defined by their colour or exclusively by their spatial location. Very similar N2pcs were

triggered during the space-based and feature-based selection of these target objects. In a conjunction search task where targets were defined by a colour/location combination, N2pc components demonstrated that feature-based and spatial attentional control processes operated simultaneously and largely independently. These results challenge the view that spatial location has a special role in the top-down attentional control of target selection processes. The contributions of space-based attentional mechanisms to the guidance of visual search are not qualitatively different from those of feature-based attention.

Finally, in Chapter 5 of the present thesis, qualitative differences in visual working memory maintenance between representations for spatial and non-spatial information were investigated. The question whether the storage of spatial locations and other non-spatial features in visual working memory is based on shared or separate processes remains unresolved. CDA components were recorded as on-line electrophysiological markers of WM maintenance in two tasks where observers had to retain either the colours or locations of sample stimuli. In Experiment 7, participants were presented with a display consisting of a number of coloured shapes at variable eccentricities to fixation and were required to remember either the colours (Colour Task) or the locations (Spatial task) of the shapes on a particular side of fixation. Participants were required to respond, via button press, whether a subsequent test item matched either one of the colours or locations of the objects in the memory sample display depending on the task. Working memory maintenance was examined via the CDA component during the delay period between memory and test displays. The results revealed that there were no differences in CDA load enhancement between the Colour and Spatial tasks, suggesting that both types of information have similar capacity limitations. However, the CDA amplitude in the Spatial Task was enhanced relative to the Colour Task. This was further investigated in Experiment 8 by testing whether the degree of spatial offset between the memory and test samples in a spatial working memory task would affect CDA

amplitudes. It was found that in tasks with a smaller mismatch offset, which required a greater precision of representation, CDAs were larger in amplitude compared to the CDA elicited in a task with larger mismatch offsets. This suggests that the greater precision requirement of the Spatial Task in Experiment 3 may have influenced the greater CDA amplitude compared to the Colour Task.

6.2 Contrasting Spatial and Non-Spatial Attention and Working Memory

The current literature has rarely provided integrative direct comparisons of space-based and feature-based attentional selection and visual working memory storage. In the present thesis, it was found that the electrophysiological correlates of visual attention selection and working memory maintenance for spatial and non-spatial attention are qualitatively similar in many contexts. In Chapter 4, N2pcs elicited by spatially defined targets were of equivalent amplitude in the 0 SOA condition and the same onset latency in the 250 SOA condition as those to the colour-defined targets. Similarly, in Chapter 5, there was no interaction in CDA load enhancements from loads 1 to 4 between tasks requiring the maintenance of either locations or colours, suggesting that both dimensions had similar capacity limitations. Together, these results suggest that space-based and feature-based attentional control processes that guide the perceptual selection of target objects and the maintenance of specific objects in WM operate in qualitatively similar ways.

However, it was also reported in Chapter 4 that whilst there was no difference in onset latency of the N2pc between the tasks requiring maintenance of locations and colours in the 250 SOA condition, the N2pc elicited by the spatial task had an earlier onset than in the colour task in the 0 SOA condition. It was concluded that in the latter condition, in which both the cue and target display were shown simultaneously, there was greater time pressure to rapidly

decode the symbolic cue in order to be able to select the target. Under these conditions, it appears that the top-down control is more efficient in activating an attentional template for a spatial location than for a non-spatial feature. However, when adequate time was given to prepare the relevant template, attentional target selection processes, as reflected by N2pc elicited by spatial and colour targets, occurred with similar time-courses.

Another distinction between the spatial and non-spatial control of attention in perception and working memory was revealed in Chapters 4 and 5. In Experiment 5 reported in Chapter 4, the N2pc elicited by the colour target was significantly larger than the N2pc yielded by the spatial target in the 250 SOA condition. Interestingly, the opposite pattern was observed for the CDA component in Experiment 7 (Chapter 5). Here, the CDA elicited during the maintenance of locations was larger in amplitude than the CDA triggered during the maintenance of colours. According to the results of the Experiment 8 (Chapter 5), however, the latter effect may have been primarily due to the greater required precision in the spatial task relative to the colour task. In this experiment, the CDA was found to be sensitive to manipulations involving the required precision of the location representations. When the offset in the mismatch trials was larger, the precision requirements were lower and the CDA amplitude was attenuated compared to a condition with smaller mismatch offsets. Given that the spatial task had a greater precision requirement than in the colour task in Experiment 7, it is possible that the larger CDA amplitude yielded by the spatial task may have been primarily linked to this difference in precision demands.

Importantly, one specific observation reported in this thesis has revealed that space-based attention and feature-based attention can act independently. In Experiment 6 of Chapter 4, there was no N2pc in trials with colour-location conjunction targets in displays consisting of partially-matching nontarget objects on opposing sides of fixation which match either the target colour or location, suggesting that space-based and feature-based selection processes were

activated in parallel and independently, and cancelled each other out at the level of the N2pc. This observation counters previous ERP work which suggests that attention selection to target features are hierarchically dependent on spatial selection (Hillyard & Münte, 1984).

6.3 Spatial Configuration

Another goal of the present thesis was to investigate how spatial-configural information affects the control of perceptual attention and working memory maintenance. Using tasks where a search target composed of two vertically-aligned and fused shapes was either present or absent, the experiments reported in Chapter 2 examined whether attention is equally attracted by objects formed from the same two shapes in the reverse configuration. Berggren and Eimer (2016b) found that spatial configural information did not influence attentional guidance to colour-colour conjunction objects as reverse-configuration non-targets elicited identical N2pcs. In the present thesis, however, it was observed that although reverse non-targets and partially matching non-targets with one target-matching shape yielded reliable N2pcs, they were significantly attenuated compared to that elicited by correct-configuration targets. This provides strong evidence that although attentional templates for colour-colour conjunction representations apparently do not include any configural information, templates for shape-shape conjunctions maintained spatial information in order to guide attention. Furthermore, these data also demonstrated that attention can be efficiently guided towards targets that are defined by a conjunction of features from the same dimension. This finding argues against a central claim of Wolfe's (2007) Guided Search model of attention, which postulates that search can only be guided by features from different dimensions, but not by multiple features from the same dimension.

In Chapter 3, the influence of spatial-configural information on shape-shape conjunction representations in working memory was investigated. Using the same stimuli as Chapter 2, participants were tasked with remembering an object on either the left or right side of fixation and deciding, after a delay period, whether a subsequent test item matched the target. In the Parts condition, the matching test item was a single shape which was a component of the target, whilst in the Whole condition, the matching test item was an object composed of two fused shapes in the correct spatial configuration. Importantly, both conditions had identical sample stimuli. Therefore, differences observed in the CDA between these two conditions was related to this manipulation in task demands. In Experiment 3, CDA mean amplitude was greater in the Parts condition than in the Whole condition. Given the classic observation that the CDA amplitude is sensitive to the number of objects held in working memory (e.g., Vogel & Machizawa, 2004), this result suggested that participants in the Parts condition held the two component shapes of the target separately, thereby increasing memory load to 2 items, whilst in the Whole condition, participants held the target representation as a fused object, corresponding to a memory load of 1 item. This difference demonstrates that working memory representations of identical stimuli can be stored differently, depending on the properties of the test display. In Experiment 4, one component shape on the target side was repeated throughout blocks. It was expected that when one shape was known in advance, the CDA difference between the Parts and Whole conditions would decrease, as one of the individually-maintained shapes in the Parts task could be held in long term memory. This appeared to be the case, as the significant difference in CDA observed in Experiment 3 was no longer present in Experiment 4.

6.4 Similarities between Attention and Working Memory

The results reported in this thesis also helped to shed new light on the relationship between attentional control processes involved in perception and working memory. In Chapters 4 and 5, there were significant differences for both the N2pc and CDA components, respectively, for colour-based and space-based tasks. The direction of this difference, however, was not consistent, as discussed previously. In Chapter 4, attention to spatially-defined targets yielded attenuated N2pcs compared to attention to colour-defined targets. In Chapter 5, working memory representations for spatial locations elicited greater CDA components than those for colours. This suggests that the relationship between spatial and non-spatial attentional control might vary between perception and working memory. However, given the finding in Experiment 8 that precision demands of a spatial working memory task can affect the CDA, it is possible that the difference in CDA between the colour and spatial tasks in Experiment 7 might be influenced by the unequal precision requirements of the two tasks. Future investigations should further examine the relationship between memory representations for colour and spatial locations, using alternative designs which eliminate this precision confound.

In contrast, attentional control mechanisms in perception and working memory were revealed to be similarly affected by spatial configuration information. In Chapter 4, it was reported that attention to shape-shape conjunction targets in the correct configuration yielded greater N2pcs than reverse-configuration non-targets. This observation led to the conclusion that spatial configuration can guide perceptual attention selection when it is an important dimension of the target representation. In Chapter 5, spatial configuration information was only maintained in the Whole condition, as shape representations were individually maintained in the Parts condition. This demonstrates that identical targets can be maintained differently

depending on the task demands, and that holding an integrated object rather than its individual components reduces working memory load, as reflected by reduced CDA components.

6.5 Future Directions

The present thesis has described a body of work which has examined the relationship between space-based and feature-based attention in perception and working memory. In some circumstances, space-defined and feature-defined targets have been found to be attentionally selected in similar manners, suggesting that spatial information may be regarded as simply one of many possible feature dimensions that can be employed by attentional guidance processes. However, other findings in this thesis have revealed important differences in terms of template preparation processes and target selection efficiency between spatial and feature-based attention tasks. Future studies could systematically examine the contexts in which spatial templates differ from featural templates. For example, it is intriguing that spatial-configural properties influence the attentional selection of shape-shape conjunction targets (Chapter 4) but not the selection of colour-colour conjunction targets (Berggren & Eimer, 2016b). Given that the spatial relationship between component shapes that are parts of a compound shape object are a crucial component of the spatial definition of this object, whereas colour information has no inherent spatial qualities, it is possible that spatial- configural information can be employed by attentional guidance only for feature dimensions with essential spatial properties. Future studies could examine other features with the expectation that attention to those with intrinsic spatial characteristics like orientation and size would be guided by configuration whilst features without such intrinsic properties like luminance and texture would not be guided by configural information.

Another direction for future work would be to examine the qualitative differences between space-based and feature-based perceptual attention and working memory with other methodologies. Whilst this thesis illuminates key delineations between attention for spatial and featural templates, it is not possible to reliably determine the relative cortical sources of associated electrophysiological activity, due to the spatial limitations of the EEG methods employed here. The present studies have exclusively used EEG caps with only 32 electrodes. It is possible that a denser spatial sampling of EEG signals could yield more precise topographies of space-based and feature-based attentional effects and also reveal subtle topographic differences. Furthermore, due to the inherently poor source localization of EEG, future studies should use fMRI or MEG to investigate the relative origins of these two types of attention. An alternative EEG-based method that might be useful for revealing potential difference between feature-based and space-based attention is multivariate pattern analysis (MVPA; see Fahrenfort et al., 2017), which can take into account signals from multiple channels simultaneously, and may therefore be more sensitive to small differences between these two types of attentional control than standard univariate ERP markers.

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