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Attending to Multiple Objects: The
Dynamics of Attentional Control in Multi-
target Stimulus Arrays

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A thesis submitted for the degree of
Doctor of Philosophy
September 2017

Originality Statement

I, Michael Jenkins, declare that the work in this submitted thesis is my own.

Signed,

A red rectangular box intended for a signature.

10th September 2017

ABSTRACT

In this thesis, the cognitive and neural mechanisms of attentional control are examined, with a specific focus on investigating the temporal dynamics of these mechanisms in scenarios where multiple objects must be attended. Event-related potential (ERP) measures are used to track the continuous time course of visual responses in the brain, and the N2pc component is employed as a marker for the attentional selection of target objects. Two broad lines of research are presented. The first line examines the attentional selection of multiple rapidly presented instances of a single target object defined by varying properties, revealing very rapid and flexible brain responses triggered independently to the appearance of each target. The second line investigates the speed and qualitative nature of strictly serial attention shifts when they are guided by stimulus features or only by location information, revealing the availability of different attentional control mechanisms for these different shifts. In the context of these findings, this thesis attempts to improve the cognitive and neural understanding of how attentional control operates. The attentional template, a working memory representation of currently task-relevant properties, is proposed to flexibly allow for the preparatory enhancement of the activity of neurons that respond to these target-defining properties, allowing for the independent allocation of attention to each instance of a target in real-time. The properties that can be maintained by the attentional template are not restricted to being visual in nature, but can consist of more complex semantic and category-related information. Importantly, the experiments of this thesis demonstrate that attentional control is a highly flexible cognitive mechanism that can be rapidly altered on the basis of current goals, and can rapidly influence the processing of incoming visual information.

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Chapter 1

General Introduction

1.1 Chapter Overview

This chapter begins by clarifying what is meant by visual attention, particularly in the context of cognitive neuroscience. Upon distinguishing goal-directed attentional control from other forms of attention, this chapter then elaborates on the basic cognitive architecture of attentional control by describing the attentional template as a crucial tool in guiding attention to task-relevant information. I then go on to outline some of the outstanding issues in the visual attention literature, highlighting the need for continuous electrophysiological measurements to address these issues. Following this, I provide an introduction to the electrophysiological method used throughout this thesis, the event-related potential (ERP) technique, and establish how this technique can be employed to address the current issues in the literature by tracking multiple attentional deployments in real time. Finally, I outline the core research aims of this thesis.

1.2 What is Attention?

The concept of attention is very familiar to most people. Someone who fails to pay attention to the movie being played in front of them will be much less likely to be aware of what happened in that movie, despite the fact that it appeared in its entirety before your eyes. Thus, attention is crucial in allowing us to make use of information that arrives in our brain.

From the perspective of cognitive psychology, attention is a powerful and necessary tool in everyday life. At any given moment, the human brain is inundated with external sensory information (e.g., sights, sounds and smells). Though the world is constantly rich with this information, the brain does not have the resources to deal with all of it, and must manage these resources to effectively make sense of the surrounding environment (Sperling, 1960; Irwin and Andrews, 1996; Luck and Vogel, 1997; Vogel et al., 2001; Cowan, 2010).

Doing this requires an attentional system which must be able to select only the most important information for further processing; this function has led to the term ‘selective attention’, and the colloquial term ‘gatekeeper’, being used by many to describe this system (e.g., Awh, Vogel, & Oh, 2006; Koch & Ullman, 1984; Wolfe, 2000).

From a neuroscientific perspective, how does the attentional system select the most relevant information? The most basic explanation is that attended information receives more neural processing, and this facilitates awareness of this information, and ultimately, action on the basis of this information. However, before doing this, the attentional system must determine which information is most important. It is much less clear how this is done, but there is a vast array of research investigating the many factors that influence how attention chooses what information to select. Despite the intensive research done in this field, there is a notable lack of clarity in understanding these factors. This thesis aims to contribute to these investigations.

While attention is an important tool in all sensory modalities, this thesis will focus on visual attention. Humans are highly dependent on visual information, with a large proportion of the brain dedicated to visual processing (Fixot, 1957). Vision is highly spatially precise (unlike audition), and temporally precise (unlike olfaction), which means that it provides detailed information about when and where we see something, which in turn can be used by the visual attentional system. Because the visual world is particularly rich and continuous, it benefits most from a powerful and flexible attentional system. When considering the concept of attention in a visual context, it is important to bear in mind the retinotopic nature of visual processing; the visual cortex employs what is called a retinotopic map (Holmes, 1918, 1944; Horton and Hoyt, 1991), which corresponds to the spatial layout of the visual field on the brain; in other words, neighbouring locations in the visual field are represented at neighbouring locations in the visual cortex. However, this information is in fact represented

contralaterally, meaning that neural activity corresponding to the left visual hemifield will be processed in the right hemisphere of the visual cortex, and vice versa. The idea of enhanced neural processing that reflects attentional selection can be thought of, then, as enhancements in the processing of specific regions in the retinotopic map. When paying attention to an object or a region in the visual field, such as a bright colour in the corner of one's eye, this is ultimately reflected in increased neural activity in the area of the visual cortex that corresponds to this location. Of course, this is not to say that other brain regions are not involved in visual selective attention.

Finally, it is important to clarify that this thesis is concerned specifically with covert, rather than overt, attention (see Posner, 1980, for a distinction between these forms of attention). Overt attention corresponds to eye movements; and while this is an important constraint in the way attention operates (being aware of something strongly encourages eye movements towards it in order to take advantage of high-acuity foveal vision), these mechanisms rely on the operations of covert attention that come before them. In other words, eye movements towards objects deemed important are preceded by enhancements of neural activity in the retinotopic map that corresponds to the location of these objects in the visual field (Wurtz & Goldberg, 1972). An important reason for focusing on covert attention will be explained later in this chapter (see 'Electrophysiological Measures of Attention').

1.3 Bottom-up and Top-down Attention

As mentioned in the previous section, it is unclear how the attentional system is able to determine which information is important and which is not. The most basic and evolutionally relevant examples of what makes an event important include potential danger or threat; information of this sort may appear at any time, and the attentional system must be equipped

to rapidly respond to these stimuli regardless of the context in which they appear. Generally, this kind of information is highly salient – it may be a bright light, or a looming object, or something that uniquely stands out among its surroundings. Objects such as these will generally elicit enhanced processing regardless of the task at hand, in what is called a bottom-up fashion (Egeth & Yantis, 1997).

However, another reason for the existence of the attentional system is to enable the efficient processing of only the information that is most relevant to a person's goals. For example, if the goal is to begin driving when a traffic light turns green, the traffic light in the visual field is relevant to this goal, while other regions in the visual field are not, or are less, relevant. The ability to achieve this goal relies on the enhanced processing of these relevant regions and features relative to other regions and features. In another scenario, the goal might be to find a red purse on a kitchen counter. The exact location of this purse may be unknown, but because its colour is known, it is beneficial for the attentional system to enhance the processing of red objects in the visual field in order to make finding it easier – any objects that are not red do not need to be searched, since they are not goal-relevant and are not selected by the attentional system. These are examples of attentional control, or top-down control (e.g., Folk, Remington, & Johnston, 1992); when a goal emerges, the attentional system is able to control which incoming information is selectively enhanced, on the basis of the current goal. While both bottom-up attention and top-down control are important facets of visual attention, the latter requires more complex high-level cognitive processing, and studying its mechanisms may provide more fruitful insights into how we can process and filter the information-rich world around us. This thesis will focus on investigating attentional control.

1.4 The Attentional Template

How is attentional control able to alter which incoming visual information selectively receives enhanced neural processing? This is a major question in the visual attention literature. From the examples given in the previous section, it is clear that properties such as colour can be used to guide attention on the basis of specific goals: searching for an object defined by a known colour is generally very easy, and this is supported by a host of research (e.g., Treisman & Souther, 1985; Treisman & Gormican, 1988; Nagy & Sanchez, 1990; D’Zmura et al., 1991; Bauer, Jolicœur, & Cowan, 1996). When considering the cognitive mechanisms by which processing of a specific property can be selectively enhanced, especially in the context of a task involving visual search, it becomes clear that this task-relevant information must be represented in some way. When an observer knows that they are looking for a red object, a representation of the property of ‘red’ needs to be maintained in working memory in a way that allows efficient search for this property. While the neural correlates of such a representation are far from clearly understood (e.g., Fannon, Saron, & Mangun, 2007), there is general agreement that this representation is held in visual working memory (e.g., Chelazzi et al., 1998), can be activated before relevant objects are physically present in the visual field (Chawla et al., 1999; Giesbrecht et al., 2006; Shibata et al., 2008), and is actively used by the attentional system to enhance neural responses to any matching incoming visual information. This is believed to be done by activating neurons that selectively respond to task-relevant properties in a preparatory fashion, known as ‘baseline shifts’ in neural activity (Chelazzi et al., 1998). Returning to the example of searching for a red object, the maintenance of a working memory representation of red in preparation for such a search means that, from a very early stage, the neural response to this object will be enhanced relative to neural responses to other objects; this itself reflects attentional selection of the red object.

This representation of an object's properties is a necessary process in successfully attending to task-relevant objects, and reflects a core component of attentional control. This goal-oriented representation is known as a task set (Folk, Remington, & Johnston, 1992), attentional set (Theeuwes, 1992), or attentional template (Desimone & Duncan, 1995). Throughout this thesis, the term 'attentional template' will be used to describe this representation. It is important to note that such a representation is believed to be qualitatively different from other working memory representations, as it actively guides attention to specific properties (Olivers et al., 2011), and is therefore thought to hold a special status in visual working memory (Cowan, 2001; Oberauer, 2002; Nee & Jonides, 2011).

1.5 Current Issues in Attention Research

A wide range of issues have emerged throughout the study of visual attention; while some of these issues have been resolved, others have been under long-standing debate (see Townsend, 1990, for a review of one such debate). This thesis addresses two of the most active issues still under scrutiny, within the context of top-down attentional control. The first of these issues concerns the content of the attentional template, in other words, the type of information that can be represented by the attentional template to guide search. Can this working memory representation only store visual information, making efficient search for descriptive or categorical targets difficult? What are the limits to the complexity and detail of information that can be represented by the attentional template? The other issue concerns the time course of attention; how quickly can the focus of attention move from one location to another? Can attention be deployed to more than one location at any given moment? Both of these issues are heavily interlinked; answering questions about the content of the attentional template can provide valuable insights into the factors that constrain the temporal dynamics of attention.

But these questions, when brought together, are also most relevant in scenarios where multiple task-relevant objects are present in the visual field. It is in these scenarios that the relationship between the attentional template and the temporal dynamics of attention can be uncovered.

1.5.1 The Content of the Attentional Template

While there is generally agreement regarding the existence of the attentional template, the type of information that this template can represent to efficiently guide attention to task-relevant objects is less clearly understood. While some features such as colour can clearly guide attention rapidly and efficiently, other features such as letter identity or alphanumerical category show mixed evidence for this kind of guidance, and yet others, such as faces or intersections, appear unable to guide attention in this way at all (see Wolfe & Horowitz, 2004, for a review). Current evidence that supports these claims about which properties guide attention generally comes from behavioural paradigms which provide visual stimulation to observers. Visual search tasks are particularly common, and involve presenting objects in an array, with participants being asked to report the presence or absence of a particular target in this array. To gain insight into whether certain properties in these visual search tasks can guide attention, reaction times (RTs) are often used in these tasks. One such method of employing RT data in this way is the use of search slopes, which plot the RT as a function of the number of task-irrelevant distractors in the search array (set size). In some cases, RTs increase linearly with more distractors, while in others, no such 'slope' exists and RTs remain fairly constant regardless of the number of distractors presented. A common interpretation of these qualitative differences is that the focus of attention in scenarios producing steep search slopes must be deployed in a sequential fashion to individual objects in the search array,

serially shifting between objects until the target is detected, while it can be more rapidly and directly guided towards task-relevant objects in scenarios that produce flat search slopes, without the need to deploy attention to task-irrelevant objects (Wolfe & Horowitz, 2004). The idea of attentional guidance to task-relevant features is directly linked to the concept of the attentional template; if a feature can be visually represented, the attentional template is assumed to enhance neural responses to this feature, and it is therefore intuitive that the presence of this feature will immediately attract the focus of attention. Despite the fact that many studies have demonstrated flaws in the validity of search slopes as a measure of the guidance of attention towards targets (Wolfe, 1998a; Haslam, Porter, & Rothschild, 2001), this technique has been employed across many studies of visual attention, in which targets are defined by different visual features, as a diagnostic tool for determining the guiding power of these features, and thus, whether these features can be represented in an attentional template.

Regardless of whether or not search slope measures provide clear and distinctive constraints in determining whether a particular feature can guide attention or not, a critical issue is that these measures only provide estimates of the nature of attentional deployments, and crucially do not track the allocation of attention separately to different objects. This lack of precision has led to many alternative interpretations of search slope data; for example, steep search slopes may not represent serial shifts of attention between objects, but perhaps may result from increased competition between targets and distractors that are processed in parallel (this will be discussed in more detail in the next subsection). In order to provide more compelling evidence for the guiding power of different features, and to gain deeper insight into the content of the attentional template, electrophysiological measures must be employed to track observable brain responses to individual objects defined by different features. These electrophysiological methods will be discussed later in the General Introduction.

To a large extent, the most vaguely understood aspect of the attentional template is its neural correlates. Cognitive questions about what information can be represented by the attentional template rely heavily on neuroscientific questions about the brain processes involved in forming these representations, and in using them to guide attention. The enhancement of neural processing of basic, low-level features (such as colour and orientation) has been thought to result from relatively straightforward mechanisms in a process referred to as ‘feature-based attention’ (Treue & Trujillo, 1999). Essentially, successful and rapid visual detection of targets defined by such low-level features can be explained by preparatory neural baseline shifts (controlled by the attentional template) that in turn facilitate spatially global (i.e., across the visual field) enhancements of the processing of task-relevant objects as they appear. These baseline shifts are believed to occur in visual feed-forward neural streams to brain regions that receive input directly from visual neurons, in neuronal populations that respond selectively to specific features (Chelazzi et al., 1998), and therefore directly influence the visual processing of target objects. On the basis of this theoretical framework, it is less clear how successful attentional selection of more complex objects could be possible. Feature-based attention alone cannot facilitate the preparatory enhancement of the processing of higher-level features or properties (such as shapes or categories), and this itself may explain why behavioural measures such as search slopes tend to find little evidence for guidance by these more complex objects. However, if rapid detection of objects defined by high-level features is indeed possible, this would suggest that the attentional template can indeed represent more complex information, and new accounts of selective attention will need to be explored. In particular, additional brain regions would likely be involved in the selective enhancement of high-level objects; for example, a working memory representation of complex information, which is able to effectively guide the deployment of attention to the presence of this information, may require long-range

interactions between prefrontal regions and visual cortex (e.g., Freedman et al., 2001; Miller, Brody, et al., 2003). This thesis will build on recent evidence for successful rapid attentional selection of complex features and objects (e.g., Peelen & Kastner, 2011; Peelen, Fei-Fei, & Kastner, 2009; Maxfield, Stadler, & Zelinsky, 2014), will provide novel evidence for this across a range of feature complexity, and will formulate a basic interpretation of these findings to bridge cognitive and neuroscientific accounts of attentional control.

1.5.2 The Time Course of Attention

Another major issue in the field of visual attention concerns the time course of attentional selection. In real-world scenarios, many objects require the focus of attention in rapid succession, or even simultaneously, and the attentional system must effectively deal with rapidly emerging task-relevant information in real time. This thesis will investigate the temporal dynamics of attentional control in scenarios containing multiple task-relevant stimuli.

How quickly can the focus of attention be deployed to different task-relevant objects?

With the use of the attentional template, the attentional system is able to elicit observable brain responses that are biased toward the location of a task-relevant object relative to other irrelevant objects (these brain responses are discussed later in this chapter). While the time course of these responses is generally reliable and robust in scenarios where objects are defined by properties that can be effectively represented by the attentional template (Eimer, 1996; Luck & Hillyard, 1994), the temporal dynamics of multiple deployments of attention to multiple task-relevant objects in the visual field have been under much debate. One of the most active debates in this context has concerned whether focused attention can be deployed

in parallel to multiple objects at any given moment in time, or whether this focus must be shifted serially between single objects or locations in the visual field.

Models and theories of visual attention that argue for a single, unitary focus of attention at any given point in time include the Guided Search theory (e.g., Wolfe, 1994; 2007), which attempts to provide a model for the cognitive systems involved in allocating attention to objects, both in terms of bottom-up and top-down guidance. According to Guided Search, when an object's property is available to guide attention, the presence of this property receives enhanced processing, but attentional selection occurs in serial to each of several potential objects possessing this property. Thus, in search for one of two red objects among green distractors, Guided Search assumes that attention can rapidly distinguish these red objects from green objects (rather than searching every object at random), but must select each of the red objects in serial. While the model claims that subsequent object recognition processes can take place in parallel for multiple selected objects, the core argument is that at any point in time, only one object can receive focused attention. This has been likened to a 'car wash' (Moore & Wolfe, 2001; Wolfe, 2003), in which only one car can enter at a time, but multiple cars can be going through the carwash at the same time. Essentially, the Guided Search model proposes that while multiple locations containing task-relevant features can be pre-attentively marked in parallel, there is an attentional bottleneck at the stage of attentional selection itself, implying serial deployments of attention to each task-relevant object.

Another theory supporting the proposal of serial, focused attention is Treisman & Gelade's (1980) Feature Integration Theory (FIT). FIT proposes that while features are initially registered automatically and in parallel across the visual field, objects as a whole are identified at a later stage in attentional processing, requiring focused attention. This focused attention is claimed in FIT to be strictly serial in nature; similarly to the proposals of Guided Search, the deployment of spatial attention to specific objects, while based on the presence of

features processed in parallel, can only take place sequentially between objects with only one object receiving focused attention at any moment in time. According to FIT, in a typical visual search task, the presence of all task-relevant features can be detected at an early parallel stage of attentional processing, but the selection of each of these objects is limited by a late serial stage of focused attention.

Alternatively, other research proposes that focused attention can in fact be allocated to multiple separate regions of the visual field in parallel, and that search slopes produced in visual search tasks reflect delays in responses as a result of competition between items attended in parallel, rather than accumulated sequential serial attention shifts. One such model is the Biased Competition account of visual attention (Desimone & Duncan, 1995); according to this model, several objects can receive focused attention in parallel, but there is a limited capacity to these parallel processes. As more objects are simultaneously attended, competition for attentional resources increases, and performance decreases. This account was supported by physiological research in monkeys (Chelazzi et al., 1998) and behavioural research in humans (e.g., Duncan, Ward, & Shapiro, 1994), which found sustained interference (lasting for several hundred milliseconds) in the attentional demand of several temporally separated objects. These studies concluded that attention should be considered as a sustained state rather than a high-speed switching mechanism, and that the parallel processing of several objects results in increased competition, which in turn results in reduced performance accuracy.

These directly competing theories and models of the time course of visual attention represent different interpretations of observed results, the majority of which is behavioural. Why do these interpretations differ so much? A major reason put forward by this thesis is that behavioural measures, such as search slopes described earlier, only provide estimates of the speed and nature of multiple attentional deployments by producing data that reflects the result

of many possible attentional processes (such as RTs). Without the ability to track independent observable attentional processes, it is very difficult to settle the debate of whether deployments of focused, spatial attention are necessarily restricted to being serial in nature or whether multiple such deployments can be made in parallel. In the following section, the advantages of using electrophysiological measures in combination with behavioural measures will be explored in detail.

It is important to acknowledge that evidence supporting the possibility of parallel deployments of attention does not preclude the possibility of attention being deployed in serial; in fact, some scenarios may necessitate serial sequential shifts of attention. In these scenarios, questions about the speed of attention have led to varying answers, both from behavioural data (e.g., Wolfe, 1998b) and electrophysiological data (e.g., Woodman & Luck, 1999; Grubert & Eimer, 2016b). One major reason for the vast differences observed across these studies is that different attentional control mechanisms may be at play depending on the information available during attention shifts; a fundamental difference that has been known as early as 1980 (e.g., Posner, 1980), is between exogenous attention shifts that are guided by stimulus properties (for example, when a cue appears at the target's location) and endogenous attention shifts (for example, when an arrow dictates where the target will be). In the first case, stimulus properties are available to determine the movement of attention; it can be said that "the focus of attention is changed for us" (Horowitz et al., 2009). In the latter, the endogenous shift of attention must be voluntary, without the aid of stimulus properties or onset. While many behavioural studies have shown support for considerable differences in the speed of exogenous and endogenous attention shifts (e.g., Horowitz et al., 2009; Jonides, 1981), the electrophysiological evidence to support this is sorely lacking. As such, these findings are open to many alternative interpretations regarding whether the speed of attentional selection is truly being measured, or whether they are confounded by additional

processes such as stimulus identification. Again, the advantages of using electrophysiological measures alongside the behavioural data in these cases will be put forward in the following section.

1.6 Electrophysiological Measures of Attention

A host of electrophysiological techniques are available to provide information that would otherwise be unavailable through behavioural measures alone. Specifically, electrophysiological measures allow an insight into the neural and cognitive processes that ultimately result in behavioural output observed in visual attention experiments, as measured by RTs and accuracy. In other words, they allow researchers to understand what processes are taking place in the brain prior to action.

In the context of visual attention, electrophysiological measures provide the chance to observe changes in the brain's response to visual input. As discussed previously, selective attention itself is thought of ultimately as enhancements in neural processing at specific regions of the retinotopic visual cortex that correspond to regions in the visual field (e.g., Treue & Trujillo, 1999; Chelazzi, 1998). Directly measuring these enhancements is vital to understanding the nature, both spatial and temporal, of attentional processing and attentional control.

Measurements of brain activity that can help to uncover and distinguish the different brain regions involved in attentional control primarily include functional magnetic resonance imaging (fMRI). This technique involves measuring and imaging subtle changes in blood flow to different regions of the brain, generally referred to as the blood-oxygen-level-dependent (BOLD) signal. Because changes in brain activity are highly correlated with changes in blood supply to regions exhibiting this activity (Logothetis & Wandell, 2004), the

BOLD signal can be very useful in determining, with relatively high spatial resolution, which brain regions are more highly activated during an experimental condition.

Several visual attention studies have employed the fMRI technique to investigate the different localised and connected brain regions involved in allocating attention to objects and locations in visual space. Indeed, neural enhancements in feed-forward regions of visual cortex that are thought to directly reflect the resulting deployment of attention have been observed, for example in V1, V2, and V3 (Liu, Pestilli, & Carrasco, 2005), and even in pre-cortical regions such as the lateral geniculate nucleus (LGN; O'Connor, Fukui, Pinsk, & Kastner, 2002). Other fMRI studies have attempted to shed light on the attentional template itself, using the spatial resolution of fMRI signals to identify potential brain regions responsible for maintaining such guiding representations. Some of these studies have suggested that the left prefrontal cortex (e.g., Bledowski et al., 2004) may be a candidate for this maintenance, while others have distinguished stimulus-driven and top-down controlled preparatory representations and posited that the frontomedian cortex may be specifically involved in the latter (Weidner, Pollman, Müller, & von Cramon, 2002).

While fMRI studies are useful in that they highlight the brain regions responsible for attentional control and for deployments of attention, they lack temporal precision, and thus provide limited information about the time course of visual attention. This is important because visual input is continuous and rapidly changing, so it is intuitive to assume that attention is equipped to deal flexibly with this rapid input. To investigate the continuous time course of attention, a continuous measure is required, and electroencephalography (EEG) is ideal for this. EEG measures the overall electrical activity of populations of neurons using electrodes placed on the scalp. Each electrode receives the summed electrical activity generated by neurons in the brain in a continuous fashion, on a millisecond-by-millisecond basis. Thus, EEG signals provide a continuous measure of changes in electrical activity

(reflecting changes in neuronal activity) across different areas of the brain. Despite the low spatial resolution of EEG, many insights can be gained about when neural enhancements of visual processing emerge, as well as measuring the strength of these responses.

A major obstacle in EEG research is distinguishing between signal and noise. Because EEG signals reflect all neural activity at corresponding regions on the scalp, these signals reflect not only the systematic brain responses to visual events that occur (the signal), but also all other concurrent brain activity that is unrelated to these visual events (the noise). An effective method for dealing with this problem is to produce many visual events across a series of experimental trials, and average the EEG responses across these trials. Because the signal is directly related to the onset of the visual event in each trial, this signal will be highly similar in terms of both electrical amplitude and time course on every such trial. Averaging across these trials will produce data that largely reflect the signal on any given trial (as averaging many instances of the same value will produce this same value). Conversely, because the noise is not related to these visual events, it will vary randomly from trial to trial, and will thus average out at a value that approaches zero. As more trials are averaged together, the noise will continue to reduce to negligible levels, while the signal will remain. These remaining EEG signals are known as event-related brain potentials (ERPs), and are highly measurable relative to raw EEG data as they reflect activity that is systematically related to the experimentally applied visual event. A typical ERP response to a visual event (i.e., the onset of a visual display) will include peaks and troughs of activity in positive and negative directions (usually measured in microvolts; μV) that emerge in the first few hundred milliseconds after a visual event (see Luck, 2005, for an introduction to the ERP technique).

How can ERPs be used to provide a continuous measure of visual attention? Since attentional selection is thought to be directly reflected in neural enhancements of visual processing at corresponding areas of the retinotopic map, measurements of ERP signals in

visual cortex, and their changes over time, can provide insights into the time course of attentional selection. In other words, ERPs can be used to track the point in time when a location in the visual field receives the focus of spatial attention. Because these deployments of spatial attention are by definition sensitive to locations in the visual field, differences in neuronal activity (and thus different ERP responses) should be seen when comparing this activity across different regions of visual cortex. For example, if an object in the left visual field receives the focus of attention, there should be observable enhancements of neural activity in the corresponding region of the retinotopically organised visual cortex (i.e., the right hemisphere), relative to regions that correspond to unattended locations in the visual field (i.e., the left hemisphere). Indeed, despite its poor spatial resolution, ERP measures can reveal these differences, and importantly, can continuously track their time course.

1.6.1 The N2pc Component

If an observer is fixating on the centre of a screen, and a stimulus display appears on this screen, observable ERP responses will be elicited in the visual cortex, starting from as early as around 60 ms after the display appears (Luck, 2005). These ERP components may vary depending on a host of factors, including the number of stimuli that appear (Gebuis & Reynvoet, 2013), the locations in which they appear (Carrasco, Evert, Chang, & Katz, 1995), or the task that observers are performing (Eimer & Kiss, 2010). Presenting an equal number of stimulus objects in the left and right visual hemifield will produce ERP responses of equal amplitude on electrode sites over the left and right hemispheres of the visual cortex, since an equal amount of visual information will be received by these hemispheres. However, it has been found that the allocation of spatial attention to one of the objects in this display results in the neural enhancement of visual processing at the corresponding region of the retinotopic

map. In other words, if the attended object is on the left side of the observer's visual field, enhanced ERP activity will be seen in electrodes over the right (contralateral) visual hemisphere relative to the left (ipsilateral) hemisphere, and vice versa. This difference in activity across visual hemispheres is known as the N2pc component, because it is an enhanced negativity that typically emerges around 200 ms after visual onset in posterior electrodes over contralateral regions of the brain. The neural substrates of the N2pc component are thought to be generated in extrastriate areas of the ventral visual processing stream (Hopf et al., 2000), and reflect the attentional selection of a candidate target object among distractors in the visual field (e.g., Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999).

The reason that the N2pc is known to reflect cognitive attentional processing, rather than visually evoked responses to the appearance of stimuli, is that its emergence depends on task demands. For example, in a display containing a red digit in the left visual field and a green digit in the right, and there is no task for an observer to perform, no N2pc component (i.e., no difference in ERP activity between left- and right-hemisphere electrodes) will emerge, because attention will not reliably be allocated to the left or right side (provided both objects are equally salient). However, if this same display is presented to participants whose task is to report the value of the red digit (thus requiring a deployment of spatial attention to this object), an N2pc component will emerge in the form of more negative activity over contralateral (right-hemisphere) electrodes, reflecting increased activity of neurons over the region of the visual cortex that corresponds to the location of the attended object. Conversely, if the task were to report the value of the green digit, an N2pc component would emerge as a difference in the opposite direction (left-hemisphere). The fact that the N2pc component is sensitive to the location of task-relevant objects in the visual field demonstrates that it reflects the emergence of spatially selective, focused attention. Thanks to the extremely high

temporal resolution of EEG, the emergence of the N2pc component, and thus the point in time when spatial attention is deployed to a particular object, can be tracked in real time.

An important obstacle in using the N2pc component to track the deployment of spatial attention arises in scenarios where more than one object needs to be attended. Solving this issue is critical because many of the current issues in attention research, as previously discussed, concern the time course of attention in these multi-target scenarios. The problem is that since the N2pc is computed by taking the difference in ERP activity between contralateral and ipsilateral electrode sites, this difference will include a combination of all neural enhancements across the visual cortex that may be taking place as a result of multiple deployments of attention. These attentional processes, whether concurrent or separate, may produce ERP modulations that interact and cannot be disentangled. This problem can be demonstrated in a simple example: In a task requiring the attentional selection of two red objects, if these target objects both appear in the left visual field (with differently coloured distractors appearing elsewhere), an N2pc response will be observed as an enhanced negativity over the right visual hemisphere. This response may reflect simultaneous attentional selection of both red objects, selection of only one of these objects, or temporally separated sequential deployments of attention to each object. Distinguishing between these possibilities is impossible in this scenario, because the ERP activity elicited by separate attentional processes at different regions in the left visual field will merge together. If the two red objects were to be placed on opposite sides of the visual field (again, among differently coloured distractors), N2pc components of opposite polarity will be elicited and will essentially cancel each other out. While it may be possible to determine whether the emergence of one such N2pc response is earlier or later than the other, it is extremely difficult to provide any useful conclusions about the time course of the attentional responses to these task-relevant objects.

To remedy this issue, a simple experimental technique can be employed: By presenting one of two task-relevant objects directly on the vertical midline (i.e., at any point directly above or below an observer's fixation), this vertical target will not elicit any lateralised ERP activity (Eimer & Grubert, 2014a; Eimer, Kiss, & Nicholas, 2011; Hickey, Di Lollo, & McDonald, 2009; Hickey, McDonald, & Theeuwes, 2006; Woodman, & Luck, 1999). In other words, because the vertical midline in the visual field corresponds to the centre of the retinotopic map in visual cortex (i.e., directly between the two hemispheres of the brain), any neural enhancements of visual cortex processing that reflect the attentional selection of this vertical target will emerge equally in electrode sites over the left and right visual hemisphere, and computing the difference in activity between these electrode sites will produce roughly zero. Thus, regardless of whether or not this object is attended, no observable N2pc response will be elicited. This is useful because it means that when another target is also presented laterally (i.e., to the left or right of fixation), any N2pc response observed in response to such a display will only reflect the attentional selection of the lateral target, thus isolating one specific deployment of attention. By reversing the arrangement of these two targets in separate visual events, the N2pc responses to each target can be separated and directly compared. Independently tracking the attentional selection of each of multiple objects in real time allows questions about the time course of attention in multi-target arrays to be investigated.

1.7 Using ERPs to Address Issues in Attention Research

Returning to the issues discussed in the previous sections of this chapter, the temporal advantages of ERPs and their ability to capture attentional processing in real time can be applied to these issues. By tracking the point in time when attentional mechanisms facilitate

changes in neuronal activity at the level of the visual cortex, more confident answers can be given about the time course of attentional deployments to specific objects, and the constraints that limit the efficiency and flexibility of these deployments.

What can the N2pc component tell us about the content of the attentional template? Because the N2pc simply reflects the neural enhancement of visual processing at specific regions of the retinotopic map, regardless of what causes these enhancements, it is not necessarily linked to the attentional template. In other words, it is possible for attentional selection to take place without prior knowledge of upcoming task-relevant features, for example when attending to a specific location, or when attention is attracted to a salient but task-irrelevant object. However, experimental paradigms can be devised that control for salience and for spatial predictability in order to rule out the possibility of selection on the basis of these factors. In such paradigms, a visual target can be made equally salient to distractors by ensuring that it does not uniquely stand out and that all objects are, for example, equiluminant and similar in size; in addition, its location can be randomised on each trial. In this way, successful attentional selection of the target must rely on the preparatory representation of its features, which are known in advance; in other words, the observation of N2pc responses in these trials can be assumed to directly result from the preparatory maintenance of an attentional template in working memory.

Using tightly controlled experimental paradigms in this way, targets can be defined by different features and properties to investigate the time course of the attentional selection of objects, strictly on the basis of the ability to represent these features and properties. If temporally reliable N2pc responses are observed when targets defined by particular features are presented in unpredictable locations, it can be concluded that it is possible to prepare in advance for this feature to appear, with the use of the attentional template. If, however, these N2pc responses are reduced in amplitude, delayed, or absent, constraints can be applied to the

type, quality and complexity of information that can be represented by the attentional template. Thus, using the N2pc is a valuable method for uncovering the attentional template's possible content.

Early ERP studies have demonstrated attentional responses to targets defined by colour, orientation, size and spatial frequency (Harter & Guido, 1980; Aine & Harter, 1986; O'Donnell et al., 1997), providing electrophysiological evidence for the ability to enhance the processing of spatially unpredictable targets defined by these features as they emerge. Further ERP research (Eimer, 1996; Luck & Hillyard, 1994) has solidified the N2pc specifically as a marker for the selection of a feature-defined target among task-irrelevant distractors, indicating that it arises only when spatially selective neural enhancements of objects are necessary (e.g., when a target needs to be distinguished from many distractors), and thereby providing more support for the claim that the N2pc can be reliably used to measure the selection of task-relevant objects on the basis of their distinguishing features. These studies demonstrate the critical value of N2pc measures in understanding which types of information can be employed by the attentional control system. However, the paradigms employed in these experiments shed light only on the dynamics of attentional responses to single task-relevant objects. While useful in understanding the content of the attentional template, it provides little insight into the time course of attentional processing in response to multiple objects; for example, they provide no new answers to the parallel/serial debate introduced earlier in this chapter. Experiments that seek to utilise the N2pc to address this debate must present multiple targets, either simultaneously or in rapid succession. By isolating N2pc responses to individual objects by using the previously described vertical/horizontal target arrangement, clear hypotheses can be generated about the time course of attention, with particular regard to the speed of attentional deployments and whether they can operate in parallel. If multiple N2pc responses overlap in time, this would provide strong evidence for

the availability of multiple attentional selection processes occurring in parallel; if delays are observed in the selection of two rapidly presented targets, this would support the notion of a serial limitation on the deployment of focused spatial attention.

This thesis uses such multi-target paradigms to address the critical issues of the content of the attentional template and the time course of attention. By varying target-defining features across several experiments, and thus varying the information that can be used to prepare for and detect upcoming targets, answers will be provided about what content can be represented by the attentional template. In addition, by presenting multiple such feature-defined targets, these experiments can concurrently investigate the temporal dynamics of attentional deployments when they are guided by the attentional template, thus uncovering the power and flexibility of attentional control.

1.8 Research Aims and Thesis Outline

The overarching aim of this thesis is to provide a clear understanding of the temporal dynamics of top-down attentional control in scenarios where multiple task-relevant objects are present. To achieve this aim, electrophysiological evidence from ERPs (specifically the N2pc component) will be provided to clarify the quality, complexity, and nature of information that can be represented by the attentional template, and to determine the limits of the speed and flexibility of multiple deployments of attention, when they are facilitated by the attentional template. In investigating these temporal properties of attention, this thesis aims to provide further insights into the neural basis of top-down attentional control that can explain its high speed and flexibility. In Chapter 2, N2pc evidence for the availability of very rapid selection processes operating in parallel in scenarios with multiple colour- and shape-defined targets will be demonstrated, indicating that the attentional template can represent relatively

complex visual images beyond colour to guide attention in this way. Chapter 3 extends these findings to category-defined targets, where no visual information can be employed to detect targets, and presents implications for the neural architecture of top-down attentional control. In Chapter 4, guidance of attention to several conjunctively-defined targets will be investigated, and will employ the ERP technique to provide deeper insights into the continuous transition from feature-based to object-based attentional processing. Chapter 5 will examine scenarios where attentional deployments are restricted to operating serially and sequentially through task demands, highlighting the effectiveness of the N2pc component in understanding the speed of exogenous and endogenous attention shifts. Chapter 6 continues these novel N2pc findings by investigating the spatial properties of endogenous and voluntary attention and offering a novel ERP technique for tracking continuous movements of attention across the visual hemifields. Finally, Chapter 7 integrates the work reported in this thesis and argues for the existence of a highly flexible and interconnected attentional control system that can represent complex visual and non-visual information, and can use and manipulate this information in a continuous fashion to facilitate multiple rapid and concurrent deployments of attention to several instance of task-relevant objects in the visual field.

Chapter 2

Rapid and Parallel Attentional Allocation to Features

The experiment presented in this chapter has been published in a peer-reviewed journal.

Experiment 1:

Jenkins, M., Grubert, A., & Eimer, M. (2016). Rapid parallel attentional selection can be controlled by shape and alphanumeric category. *Journal of Cognitive Neuroscience*, 28, 1672-1687.

2.1 Chapter Overview

To begin the process of concurrently investigating the two interlinked questions of what information can be represented in attentional templates and how template-guided attentional deployments operate in real time, the first step is to examine N2pc responses to multiple instances of a target defined by a simple feature that is known to guide attention efficiently. Colour is perhaps the best example of such a feature; introspectively, it is clear that finding colour-defined targets among differently coloured distractors is very easy, and this is supported by a host of research (see Wolfe & Horowitz, 2004, for a review). Observing N2pc responses to colour-defined targets should therefore allow for an understanding of the temporal dynamics of attentional deployments when they can be guided by a visual working memory representation.

This was done by Eimer and Grubert (2014), by measuring the time course of N2pc responses to colour-defined targets in rapidly presented displays. In as little as 10 ms, a display containing a horizontal target was either preceded or succeeded by a display containing a vertical target, thus isolating N2pc components to either the first or second of two rapidly presented targets. N2pc components to each spatially separate target heavily overlapped in time, and emerged 200 ms after each respective target's display appeared; in other words, the N2pc components were separated by 10 ms, matching the delay in presentation of the two targets. These results provide strong evidence that when an object's colour is represented in the attentional template, rapid and parallel deployments of attention are possible. Crucially, these deployments appear to operate entirely independently of each other.

While these results demonstrate the existence of fast and flexible independent attentional selection processes facilitated by the attentional template, it is possible that these

processes are only possible when very basic features such as colour are used to guide attention. Since colours can be discriminated at an extremely early stage in the processing of visual input, it remains to be determined whether more complex representations, such as shape, are able to guide attention in a qualitatively similar way. Experiment 1 addresses this issue by investigating whether N2pc responses to shape-defined targets, which possess no colour, are also elicited rapidly and in parallel.

2.2 Experiment 1: Rapid Parallel Attentional Allocation to Shapes

2.2.1 Introduction

In real-world visual scenes, there is a vast amount of accessible information competing for perceptual processing and access to conscious control. Selective attention acts as a filter that allows us to resolve this competition, favouring those objects that are most relevant to our current task goals. In visual search tasks where observers must find a specific target object among several distractors, internal representations of target-defining features (attentional templates) in working memory can be employed to guide the allocation of attention (e.g., Duncan & Humphreys, 1989; Wolfe & Horowitz, 2004; Olivers et al., 2011). These attentional templates are set up before the onset of the visual search display, and facilitate visual processing of template-matching objects in a spatially selective fashion (e.g., Desimone & Duncan, 1995; Eimer, 2014, 2015). In most visual search experiments, search targets are presented simultaneously with multiple task-irrelevant distractors in the same display. When the target is defined by a known simple visual feature (such as the colour red), the search template will bias attention towards any object in the search display that possesses this feature. However, there are real-world contexts where multiple feature-defined target

objects or events can appear simultaneously or in rapid succession. In such situations, observers might encounter a new object that requires immediate attention (e.g., traffic lights changing to red) while their attention is already focused elsewhere (e.g., on the car in front). To facilitate the adaptive control of behaviour in such situations, attentional control processes should be able to allocate attention rapidly and flexibly to such new target objects.

There is continuing debate as to whether attention can be allocated simultaneously to multiple objects at different locations. Serial visual search models (e.g., Treisman & Gelade, 1980; Wolfe, 1994, 2007) claim that focal attention can be directed only to one object at any given moment, and that the selection of several objects requires sequential movements of a unitary focus of attention. In other words, the deployment of attention to a new target object requires that attention is withdrawn from its previous location. On the other hand, parallel models of attention (e.g., Desimone & Duncan, 1995) assume that attention can be allocated simultaneously to several objects in a scene, and that multiple parallel foci of attention can operate concurrently at different locations in the visual field. The availability of such a parallel selection mechanism would be particularly useful in situations where a new attention-demanding event arrives while attention is focused at a different task-relevant location. Drivers will want to maintain an attentional focus on the traffic in front of them while simultaneously deploying their attention to a changing traffic light.

In a recent study, we investigated the processes responsible for the rapid allocation of attention to new target objects with event-related brain potential (ERP) markers of attentional object selection (Eimer & Grubert, 2014a; see also Grubert & Eimer, 2015 for extended findings). This study demonstrated that attention can be allocated in parallel and independently to multiple objects at different spatial locations. Two search displays, each containing one colour-defined target object (e.g., a red item) and one distractor object in a different task-irrelevant colour (e.g., a green, blue, or yellow item) were presented in rapid

succession on opposite sides of central fixation. Participants were asked to report whether the two target-colour items in the two successive displays belonged to the same alphanumerical category (both letters or both digits) or not (one letter and one digit). The stimulus onset asynchrony (SOA) between the two displays was either 100 ms or 10 ms. To track the speed of the attentional selection of the two target-colour objects in the first and second display in real time, the N2pc component of the event-related potential was measured in response to both successively presented search displays. The N2pc is an enhanced negativity that is elicited at posterior electrodes contralateral to the visual field of a target object in multi-stimulus visual displays. This component typically emerges 180-200 ms after stimulus onset, is generated in extrastriate areas of the ventral visual processing stream (Hopf et al., 2000), and reflects the attentional selection of a candidate target object among distractors in the visual field (e.g., Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999). Because the N2pc is computed by comparing contralateral and ipsilateral ERP waveforms to targets in the left versus right visual field, no N2pc is elicited for target objects appearing on the vertical meridian (Eimer & Grubert, 2014a; Eimer, Kiss, & Nicholas, 2011; Hickey, Di Lollo, & McDonald, 2009; Hickey, McDonald, & Theeuwes, 2006; Woodman, & Luck, 1999). This fact makes it possible to use the N2pc to measure the attentional selection of a particular target object independently from the selection of another target that appears simultaneously or in close temporal proximity. When one of these two target objects is presented on the horizontal midline (to the left or right of fixation) and the other on the vertical midline (above or below fixation), the N2pc will exclusively reflect the selection of the horizontal target, irrespective of any parallel attentional processing of the other (vertical) target object.

This logic was applied in our previous study (Eimer & Grubert, 2014a), where one target/nontarget pair was always presented on the vertical meridian, and the stimulus pair in the other display was presented on the horizontal midline. On half of all trials, the horizontal

target/nontarget pair preceded the vertical stimulus pair (horizontal target first: H1 targets), while this order was reversed in the other half of all trials (horizontal target second: H2 targets). Because the positions of the two targets were not predictable, participants could not allocate attention in advance to specific spatial locations, and attentional selection of each target could only commence once the respective stimulus displays had been presented. By comparing the onset latency of N2pc components on H1 and H2 trials, we determined how rapidly attention was deployed to the target object in the second display after the initial attentional selection of the target in the first display. When the two displays were separated by an SOA of 100 ms, N2pc components elicited by H2 targets were delayed by almost exactly 100 ms relative to the N2pc components triggered by H1 targets. When both displays were separated by only 10 ms, the onset latency difference between N2pc components to H1 and H2 targets was 10 ms, again matching the objective SOA time separating the two target objects precisely. In other words, both H1 and H2 targets always elicited an N2pc approximately 200 ms after they were presented, regardless of whether they appeared nearly simultaneously (SOA10 condition) or were separated by a longer temporal interval (SOA100 condition). With an SOA of 10 ms, N2pc components to H1 and H2 targets were equal in size and overlapped in time, suggesting that focal attention was allocated to the newly arriving second target while the previously established focus of attention on the first target location remained active. In the SOA 100 condition, N2pc components to H1 and H2 targets were again equal in size, but did not overlap in time, indicating that two temporally separate attentional selection processes can be triggered within 100 ms of each other. Overall, these findings suggest that focal attention can be allocated rapidly and in parallel to multiple target objects, and that each of the two selection processes follows its own independent time course (see also Grubert & Eimer, 2015, for similar results in experiments where two successively presented target objects were defined by two different colours).

These observations provide strong evidence for parallel attentional selection mechanisms, and challenge the hypothesis that attention must always be allocated sequentially to multiple targets. However, it remains possible that this type of parallel selection can only be observed in the specific type of tasks that were employed in our previous studies (Eimer & Grubert, 2014a; Grubert & Eimer, 2015). In these experiments, target objects were always defined in terms of their colour. Because colour is known to facilitate highly efficient search performance (e.g., Wolfe & Horowitz, 2004), multiple target objects may be selected in a rapid parallel fashion when these processes can be based on colour, but not when they have to be controlled by other target-defining visual features.

Colour is a powerful guiding feature for visual search, and this may be linked to a special status of colour signals during the perceptual processing of visual input. Colour discriminations take place as early as the lateral geniculate nucleus of the thalamus (see Sincich & Horton, 2005, for a review), and colour is perceived faster than other visual attributes such as orientation or motion (Moutoussis & Zeki, 1997, Moutoussis, 1997; Arnold, Clifford, & Wenderoth, 2001; see also Zeki, 2015, for a review). If colour signals are generally processed more rapidly and become available earlier than information about other visual features, the rapid parallel attentional selection processes observed in previous N2pc studies (Eimer & Grubert, 2014a; Grubert & Eimer, 2015) may be specific to situations where participants search for colour-defined targets. To test this hypothesis, the target objects in the current experiment were defined by their shape. In contrast to colour, the status of shape for the control of attentional object selection is less clear (e.g., Wolfe & Horowitz, 2004). Although some aspects of shape can facilitate efficient search (e.g., Treisman & Gormican, 1988), the exact featural properties that guide attention towards shape targets have not been fully specified (see Cheal & Lyon, 1992). While colour signals are extracted rapidly, shape information is processed more gradually, starting in V1 with orientation detectors

(Hubel & Wiesel, 1962, 1968) and texture segregation processes (Lamme et al., 1992), and continuing in V2 with illusory contour processing (e.g., Kanizsa, 1979; von der Heydt & Peterhans, 1989), and in V4 with the segregation of shapes from their backgrounds (Desimone & Schein, 1987). The perceptual presence of illusory contours, in the absence of a physical basis for a resulting percept, reflects the complexity of shape processing, and the absence of dedicated shape-detecting units in the brain. Such differences in the functional architecture of neural systems processing colour and shape might be mirrored by systematic differences in the effectiveness of attentional guidance by these two feature dimensions in a task where two task-relevant objects are presented in rapid succession.

To test this hypothesis, participants had to attend to two successively presented target objects that were defined by a specific shape, and to report whether a gap in the contour of these two target objects was located on the same side or on opposite sides (see Figure 1.1). Four blocked SOA conditions were tested (10, 20, 50, and 100 ms, respectively), and procedures were otherwise identical to those used in our earlier experiments with colour-defined targets (Eimer & Grubert, 2014a; Grubert & Eimer, 2015). Behavioural performance and N2pc components observed in this experiment can therefore be directly compared to the results obtained in these earlier studies. When attention is guided by shape rather than colour, the attentional selection of two targets presented in rapid succession may operate more slowly. If this were the case, the time interval between the two N2pc components to H1 and H2 targets should not match the objective SOA between the two targets (as was observed for colour-guided selection), but should be substantially increased. It is also possible that there are fundamental qualitative differences between colour-guided and shape-guided attentional selection processes, in that the former can operate in parallel while the latter have to take place in a strictly sequential fashion. If this were the case, attention would have to be withdrawn from the first target object before being allocated to the second target object,

which would result in two N2pc components to H1 and H2 targets that do not overlap in time. In particular for short SOAs, a serial selection mode could imply that attention will only be allocated to the first target object, because the second target may have already disappeared from view before attention can be deployed to its location. In this case, behavioural performance should be severely impaired in blocks with short SOAs between the two displays, and N2pc components to H2 targets should be strongly attenuated or entirely absent. Even if serial selection processes operated extremely rapidly, the fact that attention would have to be withdrawn from the first target in order to be allocated to the second target object would imply that for short SOAs, the N2pc components to H1 targets should be strongly attenuated or absent. Thus, regardless of its speed, a serial attentional selection mechanism should be reflected by a marked attenuation of one of the two N2pc components in the short SOA conditions.

Alternatively, a rapid mechanism of allocating attention in parallel and independently to multiple target objects may not only be available in selection tasks where colour is the target-defining feature, but may also operate in a similar fashion for other target attributes, such as shape. If attention can be allocated rapidly and in parallel to shape-defined target objects, the pattern of N2pc results in the current experiment should be qualitatively the same as the pattern reported by Eimer and Grubert (2014) with colour-defined targets.

2.2.2 Methods

Participants

Thirteen participants were paid to take part in the experiment. One of them was excluded from analysis due to excessive eye movement activity. The remaining twelve

participants were aged between 21 and 41 years (mean age 31 years). Eight were female and three were left-handed. All participants had normal or corrected-to-normal vision.

Stimuli and procedure

Stimuli were presented on a 22-inch Samsung wide SyncMaster 2233 LCD monitor (resolution of 1280x1024 pixels, 100 Hz refresh rate; 16ms black-to-white-to-black response time, as verified with a photodiode). Participants were seated in a dimly illuminated cabin and viewed the screen at a distance of approximately 100 cm. Stimulus presentation, timing, and response recollection were controlled by a LG Pentium PC running under Windows XP, using the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.).

Stimuli were grey outline shapes (circles, squares, or triangles; 0.2° line width), subtending 1.1° x 1.1° of visual angle. The contour of each shape had a gap on the left or right side. The size of this gap was of 0.6°, and it was always centred in the middle between the top and bottom of each shape (as illustrated in Figure 1.1). All stimuli were presented at an eccentricity of 3.0° from central fixation against a black background. A central grey fixation point (0.2° x 0.2°) remained continuously present throughout each experimental block. Each stimulus display contained one object in the target shape and another distractor object in a randomly selected nontarget shape (Figure 1.1). The nontarget shapes were never repeated within a trial. Each participant was assigned a specific target shape that remained constant throughout the experiment. Their task was to report whether the position of the gap on the two successively presented target shapes was the same side (both gaps left, or right) or opposite sides (one gap left, one gap right) by pressing one of two purpose-built vertically aligned response keys. The response-to-key mapping, as well as the hand-to-key mapping,

was counterbalanced across participants. Trials requiring a same or different response were equiprobable and randomly intermixed in each block. Each of the three shapes (circle, square, and triangle) served as target shape for four participants.

On each trial, the two successive stimulus displays were each presented for 50 ms. One target-nontarget pair was presented on the horizontal meridian (left and right of fixation), and the other pair appeared on the vertical meridian (above and below fixation). In half of all trials, the horizontal stimulus pair was presented first (horizontal target first: H1 targets). In the other half, the vertical target/nontarget display preceded the horizontal display (horizontal target second: H2 target). These two display sequences were presented in randomly intermixed trials in each block. The position of the two target objects in these two displays (left/right; top/bottom) was randomly and independently determined on each trial. There were four blocked SOA conditions. In SOA 10 blocks, the onset of the first display preceded the onset of the second display by only 10 ms (i.e., there was a 40 ms overlap between these two displays). In SOA 20 blocks, this overlap was 30 ms. In SOA 50 blocks, the onset of the second display coincided in time with the offset of the first display. In SOA 100 blocks, the two consecutive displays were separated by a 50 ms blank interval. In all blocks, the interval between the offset of the second display and the onset of the first display on the next trial was 1900 ms. There was no mask display after stimulus presentation.

The experiment contained 24 blocks, with 64 trials per block (8 trials for each combination of display sequence [H1 target, or H2 target], side of horizontal target [left, or right], and side of vertical target [top, or bottom]). Each SOA condition was run in 6 successive blocks, and the order of SOA conditions was counterbalanced across participants. Each SOA condition was preceded by one practice block.

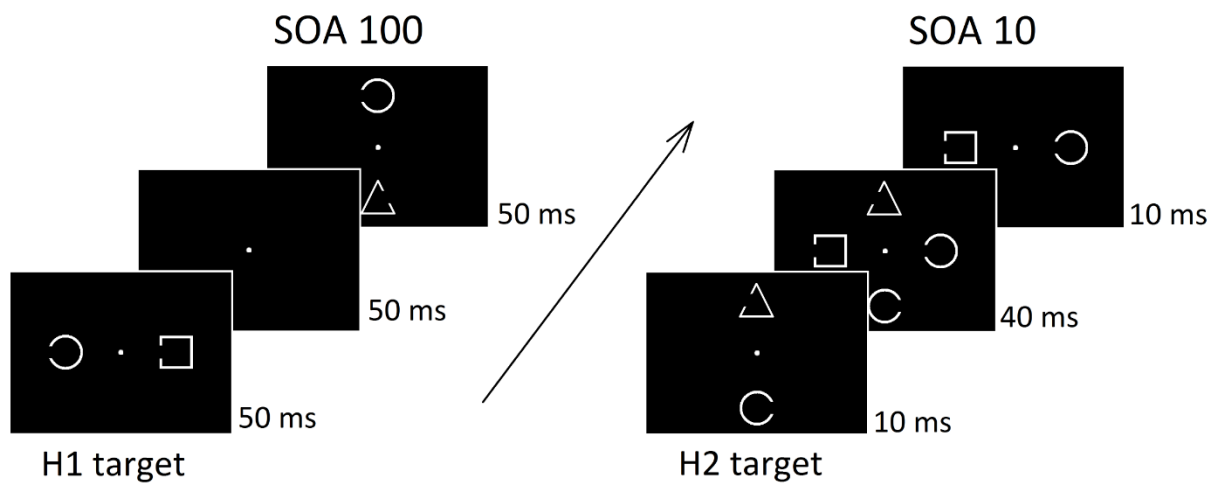


Figure 1.1: Schematic illustration of the search displays and the time course of events in the SOA 100 and SOA 10 conditions of Experiment 1. On each trial, two consecutive search displays were presented for 50 ms each. In different blocks, the SOA between these two displays was 100, 50, 20, or 10 ms (the SOA 50 and 20 conditions are not shown). Both displays contained a target/distractor pair on the horizontal or vertical meridian. On half of all trials, a horizontal target appeared in the first display and a vertical target in the second display, and this order was reversed in the other half (horizontal target first: H1 target; horizontal target second: H2 target). Stimuli were shapes with a gap on their left or right side, and participants' task was to decide whether the target shapes in the two displays (circles in Figure 1) had a gap on the same or on different sides.

EEG recording and data analyses

The continuous EEG was DC-recorded from 27 scalp electrodes at standard positions of the extended 10/20 system, sampled at a rate of 500 Hz, and digitally low-pass filtered at 40 Hz. No other offline filters were applied. All channels were online referenced to the left earlobe and re-referenced offline to the average of both earlobes. Trials contaminated with artifacts (eye movements exceeding $\pm 30 \mu\text{V}$ in the HEOG channels; eye blinks exceeding $\pm 60 \mu\text{V}$ at

Fpz; muscular movements exceeding $\pm 80 \mu\text{V}$ in all other channels), and trials with incorrect, anticipatory (faster than 200 ms), very slow (slower than 1500 ms), or missing responses were excluded from EEG analyses. This led to an exclusion of an average of 8.9%, 10.4%, 11.7% and 16.4% of all trials in the SOA 10, SOA 20, SOA 50, and SOA 100 conditions, respectively. For the remaining trials, EEG was segmented into epochs ranging from 100 ms prior to 500 ms after the onset of the first stimulus display, and was baseline corrected relative to the 100 ms interval prior to the onset of the first display. EEG was averaged separately for each of the sixteen combinations of SOA (100 ms, 50 ms, 20 ms, or 10 ms), horizontal display sequence (H1 targets or H2 targets) and location of the horizontal target (left or right).

N2pc components were quantified on the basis of ERP waveforms measured at lateral posterior electrodes PO7 and PO8. N2pc onset latencies were measured on the basis of difference waveforms, computed by subtracting ipsilateral from contralateral ERPs at PO7 and PO8. Onset latencies were determined with a jackknife-based procedure (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). Twelve grand-average difference waves were computed for each experimental condition, each excluding one different participant from the original sample. N2pc onset latency was defined as the point in time when each subsample difference wave reached a relative onset criterion of 50% (i.e., the point in time when 50% of the peak amplitude was reached in these difference waves), as described by Miller et al. (1998). Differences in N2pc onset latencies between H1 and H2 targets were assessed with repeated-measures ANOVAs and *t*-tests, with *F*- and *t*-values corrected according to the formulas described by Ulrich and Miller (2001) and Miller et al. (1998), respectively. The corrected statistical values are indicated with *F_c* and *t_c*, respectively. All *t*-tests were two-tailed and Bonferroni corrected where necessary. To measure effect sizes, Cohen's *d* (Cohen, 1988) was computed for all *t*-tests which returned a *t* value larger than 1,

and partial eta-squared (labelled η_p^2) was computed for all ANOVAs which returned an F value larger than 1. As no standardised formula exists for correcting individual group means and standard deviations of jackknifed samples to calculate effect size measures such as Cohen's d , jackknifed group means of N2pc latency and peak amplitude values were fed into repeated-measures ANOVAs where the error variance can be corrected according to the formula described by Ulrich and Miller (2001) to calculate corrected partial eta-squared values for all t-tests on N2pc latency and peak amplitude measures (reported as η_p^{2c}). When N2pc latency comparisons are based on fractional peak amplitude measures, it has to be shown that there are no systematic N2pc peak amplitude differences between conditions, because such differences can affect onset latency estimates. To assess whether this condition was met, we computed N2pc peak amplitudes for H1 and H2 targets, separately for the four SOA conditions, using a jackknife-based approach analogous to that employed for determining N2pc onset latencies. Peak amplitudes for H1 targets were determined within a 150 -350 ms post-stimulus latency window for all SOA conditions. For H2 targets, these windows were 150 – 350 ms (SOA 10 and SOA 20 conditions), 200 – 400 ms (SOA 50 condition) and 250 – 450 ms (SOA 100 condition). There were no reliable differences between H1 and H2 targets for any SOA condition ($t_c(11) < 1$, for the SOA 10, SOA 20, and SOA 50 conditions; $t_c(11) = 1.95$, $p = .077$, $\eta_p^{2c} = .26$, for the SOA 100 condition). The absence of systematic N2pc peak amplitude differences between H1 and H2 targets justifies our choice of a 50% peak amplitude criterion to define N2pc onset latencies.¹

N2pc mean amplitudes were computed within 100 ms post-stimulus time intervals. For H1 targets, a constant time window (210-310 ms) was employed for all four SOA conditions. Because N2pc components to H2 targets emerged at different latencies relative to

¹ All N2pc onset latency analyses reported in this article were also run using a fixed onset criterion of $-1\mu\text{V}$. The results of these analyses confirmed those obtained with the 50% relative onset criterion.

the onset of the first display in the different SOA conditions (reflecting the difference in the onset of H2 displays), the time intervals used for measuring N2pc mean amplitudes for H2 targets were determined separately for each SOA condition on the basis of the grand-averaged N2pc peak latency for this condition. Measurement windows were defined relative to a 100 ms interval centred on the N2pc peak latency (from 50ms before to 50ms after the N2pc peak for a particular SOA condition), rounded to the nearest 5 ms. The resulting H2 N2pc mean amplitude windows were 210-310 ms (SOA 10), 220-320 ms (SOA 20), 270-370 ms (SOA 50), and 320-420 ms (SOA 100).

2.2.3 Results

Anticipatory or exceedingly slow reaction times (RTs; faster than 200 ms or slower than 1500 ms after onset of the second display) were removed from analysis, resulting in the exclusion of less than 0.3% of all trials. A repeated-measures ANOVA with the factors SOA (10, 20, 50, and 100 ms) and displays sequence (H1 versus H2 targets) revealed a main effect of SOA on RTs, $F(3,33) = 5.93$, $p < .01$, $\eta_p^2 = .35$. Paired t -tests showed that RTs in the SOA 100 (714 ms) were slower relative to the three other SOA conditions (SOA 50: 663 ms, SOA 20: 660 ms, SOA 10: 654 ms; all $t(11) > 2.64$, all $p < .05$, all $d > .41$). RTs did not differ between the three shorter SOA conditions, all $t(11) < 1$. There was no main effect of display sequence on RTs, $F < 1$. Although the interaction between SOA and display sequence reached significance, $F(3,33) = 2.99$, $p < .05$, $\eta_p^2 = .21$, follow-up analyses conducted separately for each SOA showed no reliable RT differences between H1 and H2 targets for any SOA condition. A repeated-measures ANOVA on error rates with the factors SOA and display sequence also showed a main effect of SOA, $F(3,33) = 12.20$, $p < .001$, $\eta_p^2 = .53$. Error rates were higher in the SOA 100 condition (9.1%) relative to the three shorter SOA conditions

(SOA 50: 3.4%, SOA 20: 2.3%, SOA 10: 2.7%, all $t(11) > 3.64$, all $p < .01$, all $d > 1.17$), and did not differ between these three short SOA conditions, all $t(11) < 1$. There was no main effect of display sequence on error rates, $F < 1$. Even though the interaction between SOA and display sequence was significant, $F(3,33) = 3.35$, $p < .05$, $\eta_p^2 = .23$, follow-up analyses conducted separately for each SOA condition found no reliable differences in error rates between trials with H1 and H2 targets for any SOA.

N2pc components

Figure 1.2 (left and middle panels) shows ERPs at posterior electrodes PO7/8 contralateral and ipsilateral to the side of the horizontal shape target for trials where this target appeared in the first display (H1 targets) or in the second display (H2 targets). ERPs are shown separately for each SOA condition. The right panel of Figure 1.2 shows N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for H1 and H2 targets, for all four SOA conditions. In all SOA conditions, solid N2pc components were elicited to both H1 and H2 targets. N2pc components to both types of targets were similar in size. In the three shorter SOA conditions, there was considerable overlap in time between the N2pc components to H1 and H2 targets, and the onset latencies of these N2pcs appeared to match the objective SOA between the two displays.

These observations were confirmed by analyses of N2pc amplitudes and onset latencies. In a repeated-measures ANOVA of N2pc mean amplitudes with the factors display sequence (H1 versus H2 targets), SOA (10, 20, 50, or 100 ms), and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target) a main effect of laterality, $F(1,11) = 59.21$, $p < .001$, $\eta_p^2 = .84$, confirmed that N2pc components were reliably elicited by horizontal shape-defined target items. There were no main effects of SOA or display

sequence, $F < 1$, and no significant interactions between SOA and laterality, $F(3,33) = 1.31$, $p = .287$, $\eta_p^2 = .11$, or between display sequence and laterality, $F(1,11) = 3.64$, $p = .083$, $\eta_p^2 = .25$, indicating that the size of the N2pc did not differ systematically between SOA conditions, or between H1 and H2 targets. As can be seen in Figure 1.2, the N2pc to H2 targets tended to be larger than the N2pc to H1 targets in the SOA 100 condition, but an analysis conducted separately for this condition showed that this difference was not statistically reliable, $F(1,11) = 3.72$, $p = .08$, $\eta_p^2 = .25$. Follow up t -tests comparing contra- with ipsilateral activity separately for H1 and H2 targets and all four SOA conditions confirmed that all eight N2pc components were reliably present, all $t(11) > 6.29$, all $p < .001$, all $d > .36$.

A repeated-measures ANOVA of N2pc onset latency values with the factors SOA and display sequence (H1 versus H2 targets) revealed a significant interaction between these two factors, $F_c(3,33) = 28.98$, $p < .001$, $\eta_p^2 = .72$, showing that N2pc onset latency differences between H1 and H2 targets differed across SOA conditions. N2pc latencies in response to H1 and H2 targets were compared using paired t -tests, separately for each SOA condition. In blocks where both displays were separated by a 100 ms SOA, N2pc components to H1 and H2 targets emerged at post-stimulus latencies of 211 ms and 341 ms, $t_c(11) = 19.60$, $p < .001$, $\eta_p^2 = .97$. In the SOA 50 condition, the respective N2pc onset latencies were 231 ms and 274 ms, $t_c(11) = 2.78$, $p < .01$, $\eta_p^2 = .41$. For the two shortest SOA conditions, N2pc components to H1 and H2 targets emerged at post-stimulus latencies of 217 ms and 228 ms (SOA 20 condition) and 215 and 225 ms (SOA 10 condition). However, these two onset latency differences failed to reach significance, both $t_c(11) < 1.4$, both $p > .20$, both $\eta_p^2 < .15$.

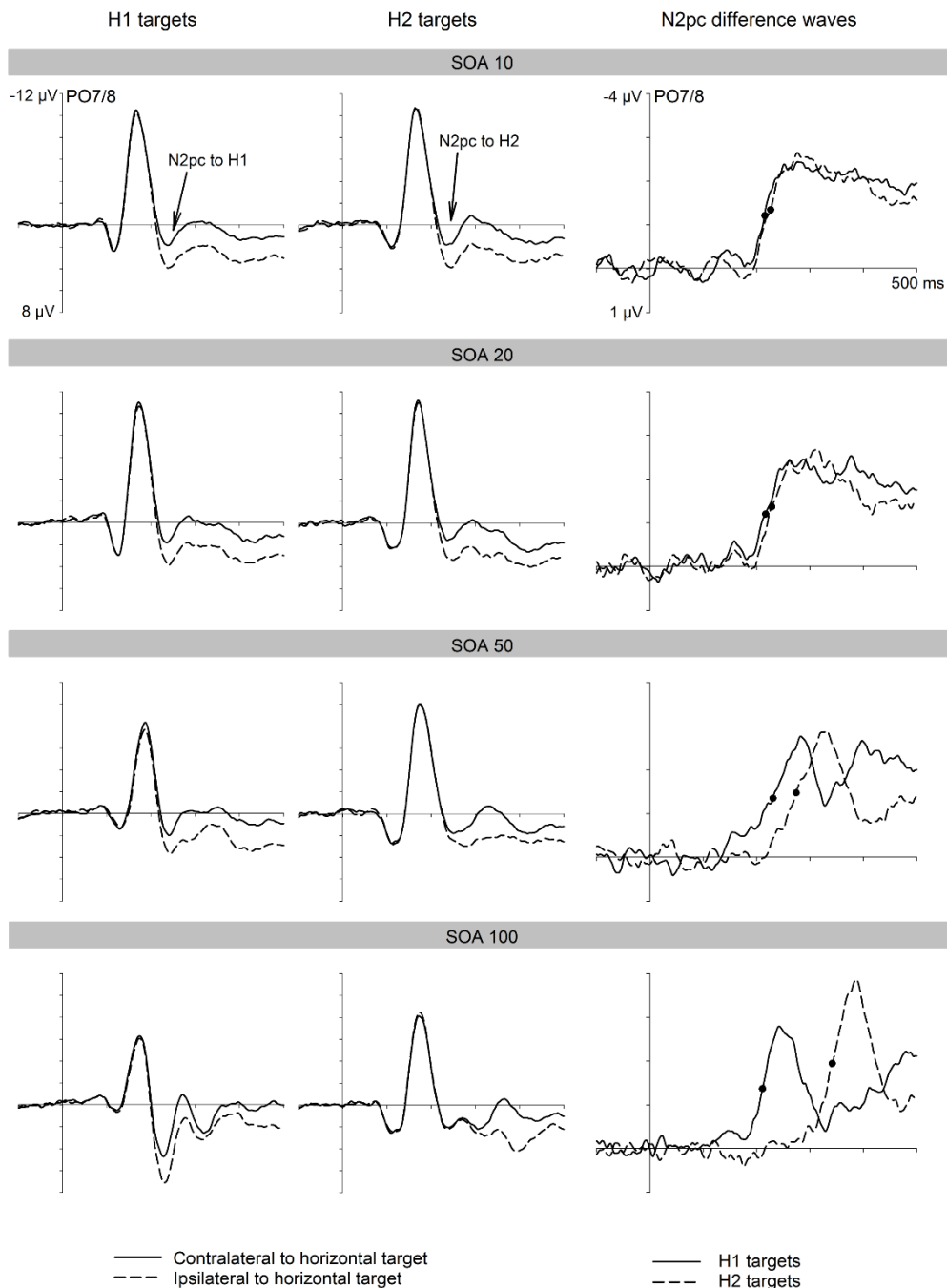


Figure 1.2: N2pc results in Experiment 1. The left and middle panels show grand-average ERP waveforms measured in the 500 ms interval after the onset of the first search display at posterior electrodes PO7/PO8 contralateral and ipsilateral to a horizontal target in the first display (H1 targets) or second display (H2 targets), separately for all four SOA conditions. The right panel depicts N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for H1 and H2 targets, and all four SOA conditions. The circles mark the point where N2pc difference

amplitudes reach the onset criterion value (50% of maximum amplitude). N2pc onset latency differences between H1 and H2 targets closely matched the objective time interval between the two displays.

2.2.4 Discussion

The current experiment investigated the speed with which attention is allocated to two shape-defined targets when these targets are presented in rapid succession. In all four SOA conditions, H1 and H2 targets elicited solid N2pc components. The onset delay between these two N2pc components (130 ms in the SOA 100 condition, 43 ms in the SOA 50 condition, and 10 ms in the SOA 20 and SOA 10 conditions) approximately matched the objective SOA between the two search displays. This temporal pattern of N2pc components was very similar to the results previously observed for colour-defined targets (Eimer & Grubert, 2014a), and provides no evidence that the shape-guided selection of multiple targets operates more slowly than target selection processes that are guided by colour. If this had been the case, attentional target selection as reflected by the N2pc should have been substantially delayed, in particular for targets in the second display. In fact, across all four SOA conditions, N2pc components to H1 and H2 targets were both elicited approximately 220 ms after the onset of the search display that included the respective target. This was confirmed by an additional analysis where N2pc onsets in response to H1 and H2 targets (averaged across all four SOA conditions) were computed relative to onset of the first and second display, respectively. N2pc onset latencies were nearly identical for H1 and H2 targets (219 ms versus 222 ms; $t_c(11) < 1$).

In the SOA 100 condition, non-overlapping N2pc components were observed (analogous to previous findings for colour-defined targets; see Eimer & Grubert, 2014a),

which would be consistent with two temporally separate serial selection processes. To dissociate serial and parallel selection, the results from the three shorter SOA conditions are critical. N2pc components to H1 and H2 targets in these conditions were identical in size and overlapped in time (see Figure 1.2, right panels), which strongly suggests that two attentional selection processes were elicited in parallel. The hypothesis that, in contrast to colour-guided selection processes, the attentional selection of shape-defined targets operates in a serial fashion would have predicted no overlap between N2pc components to H1 and H2 targets in any of the SOA conditions, as focal attention would need to be withdrawn from the first target location in order to be re-allocated to the second target. This was clearly not the case. If the shape-guided selection of multiple targets was a serial process, two possible outcomes would have been expected. Firstly, if serial selection was relatively slow, allocating attention to H2 targets should have been particularly difficult for the shortest SOA conditions, where these targets may have already disappeared before attention could be deployed to their location. This should have resulted in impaired performance and strongly attenuated N2pc components to H2 targets, in particular in the SOA 10 and SOA 20 conditions. Secondly, if serial selection processes were very fast, it may have been possible to shift attention extremely rapidly from the first to the second target in these short SOA conditions. Although performance may be spared in this case, N2pc components to H1 targets should have been severely attenuated in the SOA 10 and 20 conditions. No support for either of these predictions was obtained in the current experiment. There were no reliable N2pc amplitude differences between H1 and H2 targets in any of the four SOA conditions (see Figure 1.2), demonstrating that the deployment of attention to either of these two targets was not impaired when they followed each other in rapid succession. Furthermore, task performance was not impaired with short SOAs. In fact, performance was better in the three shorter SOA conditions relative to blocks where the two displays were separated by a 100 ms SOA. These

performance costs in the SOA 100 condition are likely due to the fact that a perceptual comparison between the two successively presented target shapes was required, as participants had to decide whether these shapes had a gap on the same side or on opposite sides. Previous research investigating the mechanisms of matching successively presented visual stimuli (e.g., Brockmole, Wang, & Irwin, 2002; Dalvit & Eimer, 2011) have found good matching performance when the interval between the two stimuli was either very short (below 100 ms) or long (300 ms or longer), but strongly impaired performance for intermediate intervals. This pattern of results was interpreted as evidence for the existence of two qualitatively different types of matching processes. With very short intervals between two targets, a sensory-perceptual representation of the first target is still available when a visual representation of the second target is generated, and both representations can be directly compared (percept-percept matching). With longer intervals, a representation of the first target has been encoded in working memory, and can be compared with a perceptual representation of the second target (image-percept matching). When the interval between both targets is intermediate, the sensory representation of the first target is no longer available and a working memory representation of this target has not yet been formed, resulting in strong impairments for matching performance. It is likely that the behavioural costs observed for the SOA 100 condition are due to the fact that a sensory representation of the first target shape had already faded at the time when a perceptual representation of the second target was formed, and a working memory representation was not yet available.

It should be noted that the N2pc onset latencies to H1 versus H2 targets did not match the objective onset difference between the two successive displays as precisely as was previously found for colour-guided target selection (Eimer & Grubert, 2014a; see also Experiment 1 of Grubert & Eimer, 2015). In these previous studies, the N2pc to H2 targets was significantly delayed relative to the N2pc to H1 targets even when the SOA between

these two targets was only 10 ms. Although N2pc components to H1 targets also emerged numerically earlier than the N2pc to H2 targets in the SOA 10 and SOA 20 conditions, these onset latency differences were not statistically reliable. This may suggest that attentional selection processes based on shape signals may be temporally less precise (i.e., less exactly coupled to the objective onset of a particular target stimulus) than colour-guided selection processes, perhaps because colour signals become available more rapidly than information about other sensory attributes such as form or motion direction (e.g., Zeki, 2015). The existence of even a small temporal jitter across trials may result in some temporal smearing of N2pc components to H1 and H2 targets when SOAs are very short. In the two longer SOA conditions, reliable N2pc onset latency differences between H1 and H2 targets were observed.

Overall, the results from this experiment demonstrate that the time course of the attentional selection of two target objects defined by their shape is very similar to the time course of colour-guided target selection (Eimer & Grubert, 2014a). They strongly suggest that attention can be allocated rapidly and in parallel to successively presented target objects, regardless of whether these targets are defined by a particular colour or a specific shape. Such rapid parallel attentional selection processes are clearly not restricted to situations where targets are defined by their colour.

2.3 General Discussion

By revealing almost identical N2pc responses to shape-defined as compared with colour-defined targets, Experiment 1 crucially demonstrates not only that the attentional template is able to successfully represent shape as an attention-guiding feature, but that this representation is equally effective in facilitating fast and flexible deployments of attention in

rapidly changing stimulus arrays, despite the fact that these representations necessarily consist of more complex information. Unlike colours, even basic shapes, as presented in this experiment, consist of specific combinations of more basic information such as intersections, angles, curvature, and size.

How are shapes represented in attentional templates? One possibility is that they simply consist of a veridical image of the shape itself (akin to an image in the mind's eye), which is then matched with incoming visual information. An alternative possibility is that this representation is not directly visual in this sense, but rather involves communication with lower-level visual regions that respond to basic properties such as intersections and angles. This latter possibility would not only provide a neural framework for rapid and flexible guidance towards visual features on the basis of task demands, but would also demonstrate the interconnected nature of the attentional template.

From this, some interesting questions arise. Is the attentional template restricted to representing only visual information, or can it guide attention to non-visually defined properties, such as semantic category? If such category-based representations are possible, do they guide attention in a similarly fast and flexible way as compared with visual representations? Answering these questions would help to understand the way in which guiding representations are made, and may shed further light on the information in the brain that is accessible to the attentional template.

Chapter 3

Rapid and Parallel Attentional Allocation to Categories

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

Experiment 2:

Jenkins, M., Grubert, A., & Eimer, M. (2016). Rapid parallel attentional selection can be controlled by shape and alphanumerical category. *Journal of Cognitive Neuroscience*, 28, 1672-1687.

3.1 Chapter Overview

In this chapter, the notion of rapid parallel attentional selection, that appears to take place for objects defined by visual properties, is tested in scenarios where objects are instead defined by categorical properties. Here, no low-level visual information can be used to distinguish targets from distractors, and as such, the results from this chapter suggest that the attentional template is not restricted to purely visual information but can also represent categorical information, and can communicate with high-level prefrontal brain regions that discriminate this categorical information.

3.2 Experiment 2: Rapid Parallel Attentional Allocation to Alphanumeric Categories

3.2.1 Introduction

When the physical features of target objects are known in advance, their attentional selection can be guided by search templates that represent these features. Although there may be substantial differences in the ability of different visual features to guide attention (e.g., Wolfe & Horowitz, 2004), it is generally assumed that target selection processes operate more rapidly and more efficiently when search targets are defined by one or more visual-perceptual attributes than under conditions where these targets are defined at a more abstract level in terms of their category membership. In fact, Wolfe and Horowitz (2004) have argued that information about the category membership of target objects (e.g., their alphanumeric or semantic category) is unlikely to guide the deployment of spatial attention in visual search

tasks. Many studies have demonstrated that search for specific visual target features is much more efficient than search for category-defined targets (e.g., Malcolm & Henderson, 2009; Yang & Zelinsky, 2009). When targets are defined by visual features, their selection can be based on a direct match between a stored feature template and the physical attributes of particular objects. During category-based search, objects within the current target category will often differ substantially with respect to their physical features, ruling out the possibility of a feature-based match with a particular target template as the mechanism of target selection. The important role of visual representations of target-defining properties for fast attentional selection has been demonstrated by behavioural and ERP visual search studies which have shown that search targets are detected more rapidly when they are specified by visual as compared to verbal descriptions (Wolfe, Horowitz, Kenner, Hyle, & Vasan, 2004; Nako, Smith, & Eimer, 2015).

If there are such qualitative differences in the control of attentional selection between feature-based and category-based search tasks, this may affect the availability of rapid parallel target selection mechanisms in situations where multiple targets are encountered in rapid succession. Such mechanisms may operate only under conditions where targets are defined by particular visual attributes such as their colour (Eimer & Grubert, 2014a) or shape (Experiment 1 of this thesis), but not in tasks where different possible target objects are physically dissimilar and their status as targets depends on their category membership, thus leading to delayed or absent N2pc responses to these targets. This prediction was tested in the present experiment, which used the same procedures as Experiment 1 of this thesis, except that targets were now defined by their alphanumeric category. One each trial, two successively presented displays contained one letter and one digit on opposite sides (Figure 2.1). Half of all participants were instructed to select the two digits and to decide whether or not these target objects belonged to the same sub-category (odd versus even digits). The other

six participants had to select the two successively presented letters to make an analogous judgment (vowels versus consonants). The two displays were separated in different blocks by SOAs of 100, 50, 20, or 10 ms, and N2pc components were measured in response to horizontally presented category-defined target objects in the first or second display (H1 and H2 targets). If the mechanism of guiding attention rapidly and in parallel to multiple target objects when targets are defined by colour or shape is not available when target selection has to be based on alphanumerical category, the pattern of N2pc components to H1 and H2 targets should be very different from the pattern observed in our previous study (Eimer & Grubert, 2014a) and in Experiment 1 of this thesis. A delay of N2pc components to H1 targets when searching for objects defined by alphanumerical category, rather than by colour or shape, would show that the deployment of attention to these category-defined targets operates more slowly than the allocation of attention to feature-defined target objects. Critically, if category-guided attention cannot be allocated rapidly and in parallel to multiple targets, N2pc components to H2 targets should be considerably delayed or attenuated, especially for the shorter SOA conditions, and task performance should be impaired when the SOA between the two targets is short. Alternatively, if rapid and parallel attentional allocation to multiple objects is a general mechanism of target selection that is even available when selection processes are category-based, this experiment should reveal a qualitatively similar temporal pattern of N2pc components as was observed in Experiment 1 of this thesis.

3.2.2 Methods

Participants

Thirteen participants were paid to take part in this experiment. One of them was excluded from analysis due to excessive eye movement activity. The remaining twelve

participants were aged between 20 and 40 years (mean age 30 years). Eight were female and four were left-handed. All participants had normal or corrected-to-normal vision.

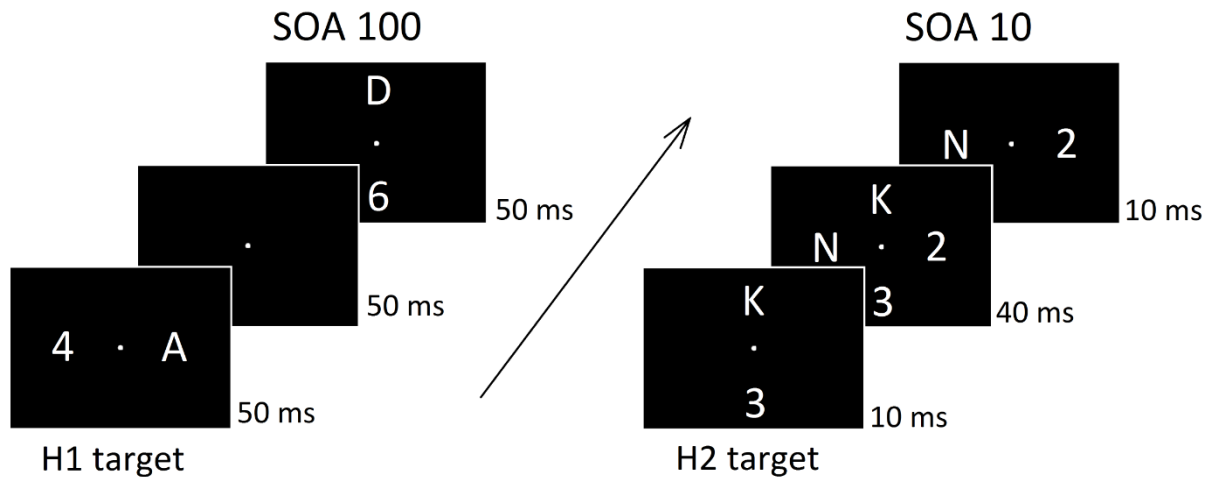


Figure 2.1: Schematic illustration of the search displays and the time course of events in the SOA 100 and SOA 10 conditions of Experiment 2. On each trial, two consecutive search displays were presented for 50 ms each. In different blocks, the SOA between these two displays was 100, 50, 20, or 10 ms (the SOA 50 and 20 conditions are not shown). Both displays contained a target/distractor pair on the horizontal or vertical meridian. On half of all trials, a horizontal target appeared in the first display and a vertical target in the second display, and this order was reversed in the other half (horizontal target first: H1 target; horizontal target second: H2 target). Stimuli were letters and digits, and participants' task was to decide whether the two objects in the target category (letters or digits) belonged to the same sub-category (vowels/consonants; odd/even digits) or not.

Stimuli and procedure

The procedure was identical to that of Experiment 1 of this thesis, except that stimuli were grey letters (A, D, E, K, N or U) and digits (2, 4, 5, 6, 7, or 9), and the target was

defined by its alphanumerical category (letter or digit). All digits and letters were matched in height and width ($0.8^\circ \times 0.8^\circ$). Target objects were all objects in one category and distractor objects were all objects in the other category (Figure 2.1). Each participant was assigned a target category that remained constant throughout the entire experiment. For half of the participants, the target items were letters, for the other half they were digits. Participants' task was to report whether the two successively presented category-defined targets belonged to the same sub-category (for letter targets, both vowels or both consonants; for digit targets, both odd or both even) or a different sub-category (one vowel and one consonant, or one odd and one even digit) by pressing one of two purpose-built vertically aligned response keys. Every other aspect of stimulus presentation and procedure was identical to Experiment 1 of this thesis.

EEG recording and data analyses

All EEG recording and data analyses were identical to those used in Experiment 1 of this thesis. The fixed N2pc mean amplitude window for H1 targets was 210-310 ms, and H2 mean amplitude windows were again defined as four 100 ms intervals centred on N2pc peak latencies for each SOA condition, rounded to the nearest 5 ms. These windows were 215-315 ms (SOA 10), 235-335 ms (SOA 20), 280-380 ms (SOA 50), and 335-435 ms (SOA 100). To justify the use of a 50% peak amplitude criterion to define N2pc onset latencies, it was again tested whether N2pc peak amplitudes differed reliably between H1 and H2 targets. N2pc peak amplitudes for these two types of targets were computed and compared with jackknife-based analyses within 200-300 ms post-stimulus time windows. No reliable peak amplitude differences between H1 and H2 targets were present for any SOA condition ($t_c(11) = 1.99, p$

= .072, $\eta_p^2 = .22$, for the SOA 10 condition, $t_c(11) = 1.31$, $p = .217$, $\eta_p^2 = .14$, for the SOA 20 condition, and $t_c(11) < 1$, for both the SOA 50 and SOA 100 conditions).

3.2.3 Results

Behavioural performance

Anticipatory or exceedingly slow responses (RTs faster than 200 ms or slower than 1500 ms) were removed from analysis, resulting in the exclusion of less than 0.3% of all trials. The repeated-measures ANOVAs with the factor SOA (10, 20, 50, 100 ms) and display sequence (H1 versus H2 targets) revealed no significant main effect of SOA on RTs (SOA 100: 667 ms, SOA 50: 688 ms, SOA 20: 710 ms, SOA 10: 710 ms; $F(3,33) = 2.35$, $p = .091$, $\eta_p^2 = .18$). Subsequent paired t -tests found a non-significant trend for faster RTs in the SOA 100 than SOA 10 and 20 conditions (SOA 10 vs. SOA 100: $t(11) = 1.95$, $p = .077$, $d = .48$; SOA 20 vs. SOA 100: $t(11) = 2.14$, $p = .056$, $d = .45$), which suggested an opposite direction of effect compared to Experiment 1, where responses were slower in the SOA 100 condition. There was no main effect of display sequence on RTs, and no interaction between SOA and display sequence, both $F < 1.6$. Error rates were statistically identical across SOA conditions (SOA 100: 3.1%, SOA 50: 3.0%, SOA 20: 3.3%, SOA 10: 3.0%), $F(3,33) < 1$. There was no main effect of display sequence and no interaction between SOA and display sequence on error rates, both $F < 1$.

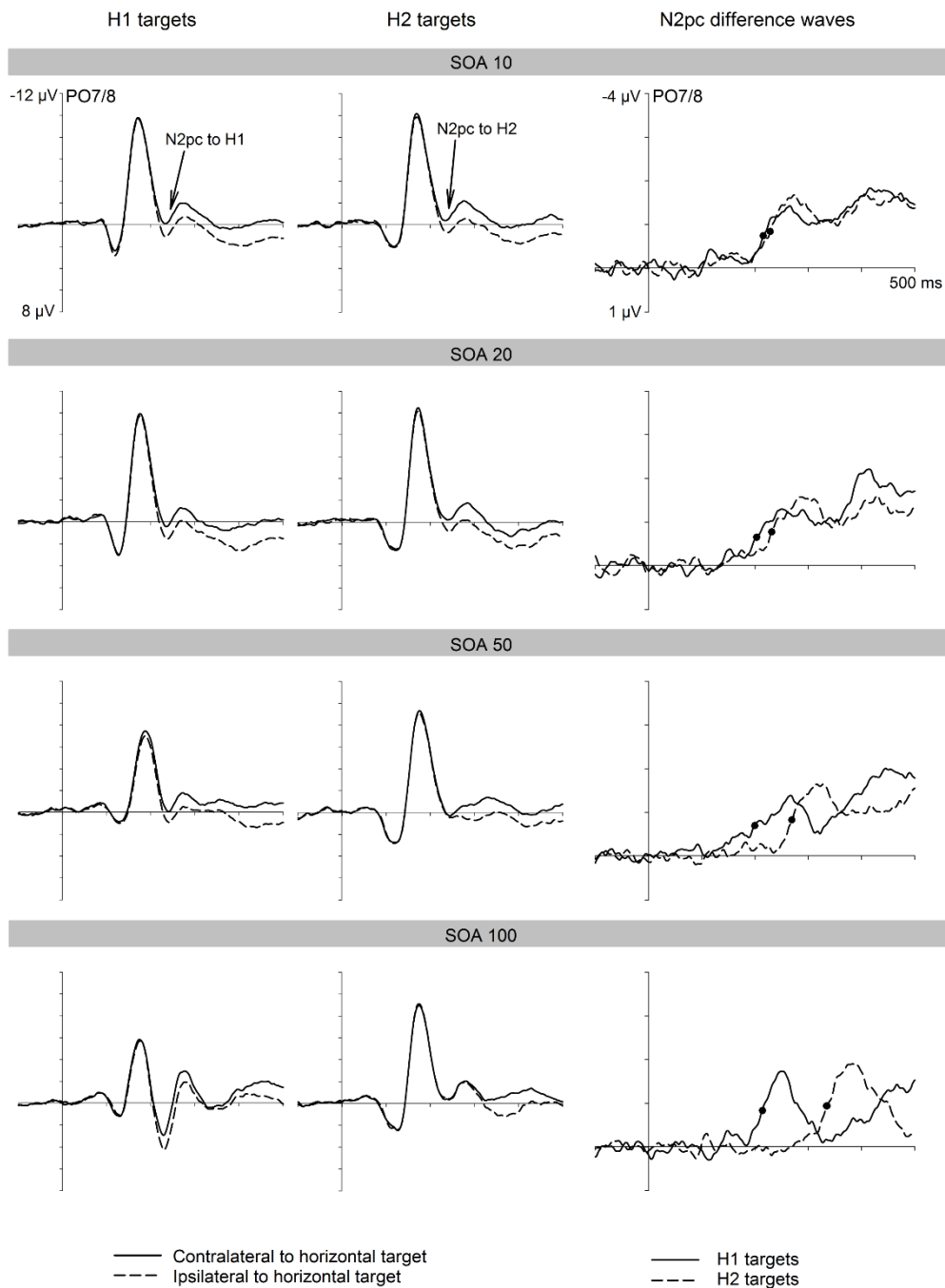


Figure 2.2: N2pc results in Experiment 2. Grand-average ERP waveforms measured in the 500 ms interval after the onset of the first search display at posterior electrodes PO7/PO8 contralateral and ipsilateral to a horizontal target in the first display (H1 targets) or second display (H2 targets), shown separately for all four SOA conditions, together with the corresponding N2pc difference waveforms (right panel). The circles mark the point where N2pc difference amplitudes reach the onset criterion.

N2pc onset latency differences between H1 and H2 targets again matched the temporal delay between the two search displays.

N2pc components

Figure 2.2 (left and middle panels) shows ERPs at posterior electrodes PO7/8 contralateral and ipsilateral to the side of the horizontal alphanumerically defined target in the first display (H1 targets) or in the second display (H2 targets). ERPs are shown separately for each SOA condition, together with N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for H1 and H2 targets. N2pc components of similar size were elicited to both H1 and H2 targets in all four SOA conditions, with onset latencies that mirrored the objective SOA between the two displays. N2pc components to H1 and H2 targets again overlapped in time for the three shorter SOA conditions.

These observations were confirmed by analyses of N2pc amplitudes and onset latencies. In a repeated-measures ANOVA of N2pc mean amplitudes with the factors display sequence (H1 versus H2 targets), SOA (10, 20, 50, or 100 ms), and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target) a main effect of laterality, $F(1,11) = 37.45$, $p < .001$, $\eta_p^2 = .77$, confirmed that N2pc components were reliably elicited by horizontal category-defined target items. There were no main effects of SOA or display sequence, and no significant interaction between SOA and laterality, all $F < 1$. The interaction between display sequence and laterality reached significance, $F(1,11) = 5.24$, $p < .05$, $\eta_p^2 = .32$, suggesting that there was a small but reliable tendency for N2pc amplitudes to be larger for H2 relative to H1 targets (see Figure 2.2). However, additional analyses conducted separately for each SOA condition did not find any significant interactions between laterality and display sequence, all $F(1,11) < 2.78$, all $p > .123$, $\eta_p^2 < .21$. Eight

follow up *t*-tests revealed that N2pc components to both H1 and H2 targets were reliably present in all four SOA conditions, all $t(11) > 3.33$, all $p < .01$, all $d > .21$.

A repeated-measures ANOVA of N2pc onset latencies with the factors SOA and horizontal display sequence revealed a significant interaction between both factors, $F_c(3,33) = 21.46$, $p < .001$, $\eta_p^2 = .66$, demonstrating that the onset of N2pc components to H1 and H2 targets was sensitive to the objective time interval between the two displays. Four follow-up *t*-tests compared N2pc onset latencies to H1 and H2 targets for each SOA condition. In the SOA 100 condition, where the two N2pc components showed no temporal overlap, their onset latency difference was 121 ms (214 vs. 336 ms; $t_c(11) = 13.22$, $p < .001$, $\eta_p^2 = .94$). In the SOA 50 condition, this difference was 71 ms (199 vs. 270 ms), $t_c(11) = 6.48$, $p < .001$, $\eta_p^2 = .79$). In contrast to Experiment 1 of this thesis, there was now also a significant N2pc onset latency difference between H1 and H2 targets of 29 ms in the SOA 20 condition (203 vs. 231 ms; $t_c(11) = 2.48$, $p < .05$, $\eta_p^2 = .36$). In the SOA 10 condition, the N2pc to H1 targets preceded the N2pc to H2 targets by 13 ms (215 vs. 228 ms), and this difference approached significance, $t_c(11) = 2.09$, $p = .061$, $\eta_p^2 = .28$.

3.2.4 Discussion

The temporal pattern of N2pc components to H1 and H2 targets in the current experiment was very similar to the pattern found in Experiment 1 of this thesis, in spite of the fact that target selection could no longer be guided by a visual feature (shape), but was instead determined by the alphanumeric category of target objects. The onset latency of the N2pc to horizontal targets in the first display (208 ms, averaged across all four SOA conditions) was similar to the corresponding N2pc latency for H1 targets in Experiment 1 of this thesis (219 ms), demonstrating that the attentional selection of category-defined targets was not

systematically delayed relative to the selection of shape targets. N2pc components triggered by H1 and H2 targets were equal in size and overlapped in time in the SOA 10, 20, and 50 conditions (see Figure 2.2). The onset delay between these two N2pc components (129 ms, 71 ms, 29 ms, and 13 ms, for the SOA 100, 50, 20, and 10 conditions) approximately matched the objective SOA between the two search displays, indicating that the attentional selection of each of the two targets followed its own independent time course. However, and in contrast to Experiment 1 of this thesis, there was a small but reliable delay in the onset of the N2pc to H2 targets (measured relative to the onset of the second display) relative to the onset of the N2pc to H1 targets (208 ms versus 221 ms; averaged across all four SOA conditions; $t_c(11) = 2.61$, $p < .01$, $\eta_p^2 = .54$).² This suggests that when two category-defined targets are presented in rapid succession, the deployment of attention to the second target object may be slightly but systematically delayed relative to the initial attentional selection of the first target.

Overall, the results of this experiment provide strong evidence that the rapid parallel selection of multiple target objects is not restricted to situations where targets are defined by specific visual features such as colour or shape, but also operates when it has to be based on the alphanumeric category of visual objects. If the category-based attentional deployment to target objects presented in rapid succession was based on slow serial attentional selection mechanisms, N2pc components to H2 targets should have been strongly delayed and attenuated in the current experiment, particularly for the short SOA conditions, and behavioural performance should have been strongly impaired in these conditions. No

² To determine whether this N2pc onset delay to H2 versus H1 targets in Experiment 2 differed across SOA conditions, we ran an additional ANOVA of these latency values with the factors SOA (10, 20, 50, or 100 ms) and display sequence (H1 versus H2). There was a main effect of display sequence, $F_c(1,11) = 11.43$, $p < .01$, $\eta_p^2 = .51$, reflecting the delayed N2pc to H2 targets, but no interaction between display sequence and SOA, $F_c < 1$, demonstrating that this delay was unaffected by the SOA between H1 and H2.

evidence for this was found in the N2pc waveforms, or in the pattern of behavioural results. There were no systematic differences in RTs or error rates between the four SOA conditions, demonstrating that decreasing the interval between the two category-defined targets did not impair participants' ability to select and identify both of them.

The rapid selection of category-defined targets is in line with previous behavioural studies demonstrating that information about category membership can affect attentional control processes. Nontarget objects which are physically dissimilar but semantically linked to current targets can attract attention during visual search (e.g., Moores, Laiti, & Chelazzi, 2003; Belke, Humphreys, Watson, Meyer, & Telling, 2008; see also Telling, Kumar, Meyer, & Humphreys, 2010, for ERP evidence). Along similar lines, images of real-world visual objects that match the current search target category can capture attention even when they are presented at task-irrelevant locations (Wyble, Folk, & Potter, 2013), indicating that information about object categories can be encoded rapidly and can affect the deployment of attention in a task-set contingent fashion (see also Castelhano, Pollatsek, & Cave, 2008, and Maxfield, Stadler, & Zelinsky, 2014, for evidence that the typicality of target objects in terms of their category can affect visual search performance). The speed of such category-based attentional selection processes has been investigated in recent N2pc studies from our lab which used category-based visual search tasks where a single target object appeared together with multiple distractor objects. N2pc components to target objects appeared approximately 200 ms after display onset when observers searched for any letter among digits, or vice versa (Nako, Wu, & Eimer, 2014), and around 240 ms post-stimulus in a task where targets were line drawings of real-world objects from a specific category (kitchen objects among items of clothing, or vice versa; Nako et al., 2015). While these findings demonstrate that the category-based selection of single target objects can be triggered remarkably rapidly, the

results of this experiment show that multiple category-guided selection processes can be elicited in parallel and independently.

Perhaps the most surprising outcome of the present experiment was that essentially the same temporal pattern of N2pc components to H1 and H2 targets was observed as compared to Experiment 1 of this thesis, where target objects were defined by a specific visual feature (shape). These N2pc components were again equal in size and overlapped in time in the short SOA conditions, which suggests that the selection of category-defined targets that appear in rapid succession is based on the same fast parallel attentional processes that are activated when targets are defined by a visual feature. In contrast to N2pc results obtained in response to shape-defined targets, there was a small but systematic delay in the onset of N2pc components to H2 versus H1 targets (relative to the onset of their respective stimulus displays) in the current experiment, which suggests that the two successive target selection processes may not be entirely independent, but that the category-guided allocation of attention to a new target object starts slightly later when attention has already been deployed to another category-defined target at a different location. The fact that the selection of the second target was delayed relative to the selection of the first target by approximately 10 ms for category-defined, but not feature-defined targets, mirrors similar observations from previous N2pc experiments where the two target objects were defined either by the same colour or two different colours (Grubert & Eimer, 2015). In this study, there was a small but systematic delay of the N2pc to H2 targets on trials where the two targets differed in colour. This was attributed to costs that arise when there is a feature change between these targets, so that the selection of the second target cannot be guided by the same feature-specific template that was activated during the selection of the first target object. An analogous explanation may also account for the small delay of the N2pc to H2 targets in the current experiment, where the two target objects belonged to the same category but were physically different.

Overall, these results indicate that alphanumerical category may be just as efficient as colour and shape in controlling the rapid parallel allocation of attention to multiple target objects. The behavioural results also suggested that attention was deployed rapidly and in parallel to category-defined objects. There were no systematic performance differences between this experiment and Experiment 1 of this thesis, as confirmed by between-participant analyses across both experiments, which found no reliable differences in RTs, $F(1,22) < 1$, or error rates, $F(1,22) = 1.78$, $p = .196$, $\eta_p^2 = .07$, between the shape and category selection tasks. If the allocation of attention to shape- or category-defined target objects was slow or operated in a serial fashion, the selection of target objects in the second display should have been particularly challenging when the SOAs between the two displays were very brief, and this should have been reflected by impaired performance in the short SOA conditions. No such performance costs were observed in any of the SOA conditions of this experiment.

If attention can be allocated rapidly and in parallel to multiple target objects not only when these objects are defined by a specific visual attribute, but also when they are defined by their alphanumerical category, which attentional control mechanisms are responsible for these remarkably fast and flexible selection processes? One possibility to account for the current findings is to assume that alphanumerical category is equivalent to visual features such as colour and shape in its ability to guide attention rapidly and flexibly to candidate target objects. In line with this assumption, visual search for letters among digits, or vice versa, is remarkably efficient (Egeth, Jonides, & Wall, 1972; Duncan, 1980), even when the physical similarity between and within these two categories is matched (Dixon & Shedden, 1987). If information about alphanumerical category is extracted rapidly during the early parallel processing of visual input (as proposed by Duncan, 1980), this information might be employed just as effectively in the guidance of attentional target selection as signals related to basic physical stimulus attributes such as colour and shape. Initial evidence for the

involvement of object categories in the top-down control of visual search comes from fMRI studies that investigated distributed patterns of brain activity elicited in visual cortex during search for category-defined target objects in real-world visual scenes (e.g., people or cars). Activation patterns selective to the current target category were found during both the preparation for an upcoming search task (Peelen & Kastner, 2011), and also during the subsequent processing of search displays, even when category-matching objects appeared at task-irrelevant ignored locations in these displays (Peelen, Fei-Fei, & Kastner, 2009). Such findings suggest that preparatory attentional templates and spatially global feature-based attentional modulations in visual cortex may be involved in the control of attentional target selection not only when targets are defined by simple visual attributes, but also during search for target objects that belong to more abstract but presumably highly overlearned categories (e.g., people, animals, cars, or letters versus digits).

Instead of assuming that the rapid parallel attentional selection of multiple category-defined target objects revealed by the N2pc results of this experiment is based on attentional control processes that operate primarily within posterior visual cortical areas, an alternative possibility is that these selection processes are based on long-range interactions between visual cortex and prefrontal areas involved in top-down attentional control. If information about the alphanumeric category of specific stimuli is extracted rapidly during the initial parallel processing of visual input, these signals may then be transmitted to prefrontal cortex which is known to be involved in category-based object discrimination processes (e.g., Freedman et al., 2001; Miller, Nieder, et al., 2003). The detection of a target category match in prefrontal cortex would then trigger recurrent feedback signals to spatially corresponding locations in visual cortex, resulting in enhancements of visual activity at these locations, and the emergence of N2pc components to category-defined targets (see Hochstein & Ahissar, 2002, and Bundesen et al., 2005, for similar ideas about the role of recurrent feedback

pathways in the control of attentional target selection). In this context, the temporal pattern of N2pc components to H1 and H2 targets observed in the current experiment would suggest that individual target selection processes controlled by recurrent interactions between visual and prefrontal cortex can be triggered in rapid succession, with each process following its own independent time course.

The central new insight of the present study is that processes involved in the rapid attentional selection of successive category-defined target objects show an extremely similar temporal profile to the processes previously observed during colour-based selection (Eimer & Grubert, 2014a) and shape-based selection (Experiment 1 of this thesis). This similarity strongly suggests that the same attentional control processes operate in all these selection tasks, thereby providing important constraints for the type of neural mechanisms that are likely to be involved. The rapid parallel attentional selection of targets defined by their alphanumeric category in visual areas may be mediated by category-sensitive areas of prefrontal cortex, and thus involve long-range recurrent interactions between prefrontal and visual cortex. The fact that the time course of selecting successive category-defined targets is virtually identical to the time course of allocating attention to multiple targets in colour or shape selection tasks suggests that the same recurrent interactions between posterior and anterior cortical areas are involved in the control of attention when targets are defined by simple visual attributes or by their alphanumeric category.

However, a critical issue that needs to be addressed is whether the rapid parallel attentional selection of alphanumeric categories truly reflects category-based processes (such as long-range recurrent interactions with prefrontal cortex), or whether this flexibility in attentional selection exists only because overlearned categories such as alphanumeric category can be represented in an equivalent fashion to features. If the latter is true, the attentional selection of objects defined by more complex, high-level categories (which are

less overlearned) should be qualitatively different, and the rapid parallel selection mechanisms available for features and overlearned categories should break down. This was tested in Experiments 3a and 3b.

3.3 Experiments 3a & 3b: Rapid Parallel Attentional Allocation to Real-world Objects

3.3.1 Introduction

While the guidance of spatial attention by attentional templates has been clearly demonstrated as a powerful and flexible mechanism when such templates represent visual features, there is evidence to suggest that category-based templates may not guide attention as effectively. Category information is not necessarily defined by visual properties at all; it may instead be defined by more abstract semantic properties such as functional purpose. For example, a hat and a shoe are in no way visually similar, but both are used as clothing. Wolfe and Horowitz (2004) have argued that category information is unlikely to act as a guiding feature in visual search, and others have demonstrated that search for categories is less efficient than search for specific visual features (e.g., Malcolm & Henderson, 2009; Yang & Zelinsky, 2009). It is likely that this reduction in efficiency is caused at least partially by the lack of any target-defining visual feature that can be matched with a stored feature template; this notion is supported by behavioural and ERP evidence for faster selection of targets when they are defined by visual versus verbal descriptions (Nako, Smith, & Eimer, 2015; Wolfe, Horowitz, Kenner, Hyle, & Vasan, 2004).

To determine whether the reduced efficiency of category search is due to differences in the ability to represent category information in attentional templates, the rapid parallel selection paradigm from our lab, in which two targets are presented in rapid succession, was

applied to targets defined by alphanumerical category (Experiment 2 of this thesis). Participants' task was to compare the alphanumerical subcategory of the two targets (vowels/consonants in letter search, odd/even in digit search). In line with the previous studies using this paradigm, this experiment revealed overlapping N2pcs with onset delays closely matching the objective SOA between the targets. This provides strong evidence that an attentional template for alphanumerical category, which is not defined by visual properties, can be used to guide attention rapidly and effectively to multiple targets in parallel. Interestingly, there was a small but reliable delay in the onset of the N2pc component in response to the second target, relative to that in response to the first target, and the amplitude of the N2pcs in this experiment was significantly reduced relative to feature-based target N2pcs. These reduced amplitudes may have resulted from temporal smearing of the N2pc responses across trials, which would suggest temporally less precise allocation of attention to the target. This evidence appears to suggest that category-based templates guide attention less efficiently than feature-based templates, but allow attention to operate in a qualitatively similar fashion (namely in a rapid and parallel fashion).

Despite these compelling results, they do not truly confirm the existence of rapid and parallel guidance by category information; alphanumerical category is highly overlearned and has been suggested to be pre-attentively classified (e.g., Egeth, Jonides, and Wall, 1972; Duncan, 1980, 1983; Bundesen, 1990; Jonides & Gleitman, 1972; see also Nako, Wu, Smith, et al., 2014, 2016; Wu et al., 2013, for recent supporting N2pc evidence). Thus, alphanumerical category in particular may represent a special case which does not reflect the actual mechanisms of category-guided search. To address this, a similar paradigm can be used with stimuli that do not share basic visual features, such as real-world objects. Indeed, such stimuli have been employed in a recent N2pc experiment (Nako, Wu, Smith et al., 2014). In this study, participants were presented with line drawings of kitchen and clothing objects in four

different search tasks. In two tasks, participants searched for one pre-specified target object which either appeared as a precise identical image, or in two possible orientations (single-target exemplar search); in another task, two particular objects from the same category were used as targets (dual-target exemplar search); in the remaining task, any object from one of the categories could appear as the target (category search). While the results of this study showed relatively fast category-based selection, this was delayed compared to exemplar-based selection. Do these findings demonstrate qualitative differences in category versus feature search, or simply reduced efficiency of the same attentional mechanisms? The current study tested this by means of the rapid parallel selection paradigm to determine whether multiple targets defined by category can be selected independently and in parallel, or whether this fast and flexible mechanism breaks down under such circumstances.

Experiment 3a used line drawings of real-world objects from two different functional categories: kitchen objects (e.g., cups, pans, irons), and clothing objects (e.g., hats, shoes, shirts). Two rapidly presented displays each contained one object from each category. Targets were defined by their membership of one particular category, so that participants searched for two different and randomly selected objects from either the kitchen or the clothing category. Importantly, 1-Target (1T) trials, where only one of the two displays contained a target-category object, were included along with 2-Target (2T) trials containing a category target in each display. If the selection of multiple targets defined by object category is difficult, this may lead to strong attenuation of N2pc components in 2T trials as compared to 1T trials, particularly in response to the second target, since selection may no longer take place independently and in parallel for multiple targets. If rapid and parallel attentional selection is indeed not possible in category search, this would lead to either delayed serial selection of the second target in 2T trials as reflected by late N2pc onset, or failure to select this second target, as reflected by impaired behavioural performance in 2T trials relative to 1T trials, and

severely attenuated or entirely absent N2pc components to the second target. Alternatively, if such an attentional mechanism can indeed be employed in category search, results should mirror those from previous studies in our lab, where N2pc components are clearly elicited in 2T trials, and there is no difference in N2pc amplitude for first and second targets. Crucially, the delay between onset of the N2pc components to first and second targets should match the objective SOA between the two targets.

In Experiment 3b, the same procedure and stimuli were used but with a specific exemplar image defined as the target, in order to directly compare category-based and exemplar-based selection of multiple targets. As well as determining the availability of rapid parallel attentional mechanisms in category search, the efficiency of these mechanisms can be tested by comparing the results of the two experiments. If efficiency is impaired (e.g., if attentional selection is temporally less precise), this should be revealed by decreased amplitude of N2pc components and a general delay in N2pc onset in Experiment 3a relative to Experiment 3b, but if rapid parallel attentional mechanisms are still available in category search, the relationship between the N2pcs to first and second targets should not differ across the experiments. However, if efficiency is not impaired in category search, the results should be similar in both experiments.

3.3.2 Experiment 3a: Objects Defined by Category Membership

3.3.2.1 Methods

Participants

Twelve participants, aged 25-38 years ($M = 30.58$ years, $SD = 4.44$), were paid to take part in Experiment 3a. Seven participants were female, three were left-handed, and all had normal or corrected-to-normal vision. The choice of this particular sample size ($n=12$) was based on a power analysis that employed the effect size obtained from a previous N2pc experiment in our lab (Experiment 1 of this thesis), in which the same sample size was used to compare N2pc onset latencies for different SOA conditions in response to two successively presented displays that included category-defined target stimuli.³

Stimuli and Procedure

Stimuli were presented on a 22-inch Samsung wide SyncMaster 2233 LCD monitor (resolution of 1280 x 1024 pixels, 100 Hz refresh rate; 16ms black-to-white-to-black response time, verified using a photodiode). Participants were seated in a dimly lit cabin and viewed the screen from an approximate distance of 100 cm. Stimulus presentation, timing, and response recollection were controlled by a LG Pentium PC operating under Windows XP, using the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.). Stimuli were black line drawings (12 clothing objects and 12 kitchen objects; angular size: $4.5^\circ \times 4.5^\circ$; see Figure 3.1) from the Bank of Standardised Stimuli (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010). The same set of stimuli was used in a recent publication from our lab (Nako, Wu, Smith, & Eimer, 2014). All stimuli were presented at an eccentricity of 4.0° from central fixation (with respect to the object centre)

³ To ensure a large enough sample size providing enough power to reliably exclude false rejection of the null hypothesis, power ($1-\beta$) was calculated using the G*Power program (Faul, Erdfelder, Lang, & Buchner, 2007), using the a priori option and the η_p^2 effect size (.66) of the SOA * Display sequence interaction of Experiment 2 in Jenkins et al. (2016; $n=12$). Power analysis revealed a test power of .998 (with an effect size f determined according to Cohen, 1988, of 1.39) and suggested that a sample size of $n=6$ was sufficient to achieve the desired effect size of .66.

against a white background (see Figure 3.1). A central black fixation point ($0.2^\circ \times 0.2^\circ$) remained continuously present for the duration of each experimental block.

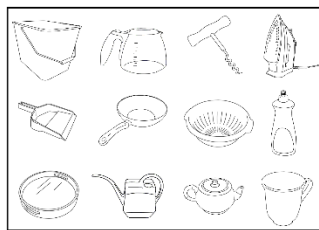
In each trial, two successive stimulus displays were each presented for 200 ms. Each stimulus display contained two objects on opposite sides of fixation. One stimulus pair was presented on the horizontal meridian (left and right of fixation), and the other pair was presented on the vertical meridian (above and below fixation). In half of all trials, the horizontal stimulus pair preceded the vertical stimulus pair (horizontal display first: H1 trial). In the other half of trials, this horizontal/vertical display presentation order was reversed (horizontal display second: H2 trial). These two display sequences were randomly intermixed in each block. The onset of the first display preceded the onset of the second display by 10 ms. Since displays were presented for 200 ms, there was a 190 ms overlap between the two displays. The interval between the offset of the second display and the onset of the first display on the next trial was 1700 ms.

There were three different trial types: In one-target (1T) trials, one display contained one object from the target category and one object from the nontarget category, and the other display contained two different nontarget category objects. In two-target (2T) trials, each display contained one object from the target category and one from the nontarget category. Each block also contained catch trials in which no targets were present and both displays contained two different nontarget category objects. Target and nontarget category objects were randomly selected on each trial, and no objects were repeated within a trial. The horizontal and vertical positions of the target object/objects (left or right; top or bottom) were randomly and independently determined on each trial.

Possible Target Objects



Clothing Objects



Kitchen Objects

Stimulus Displays

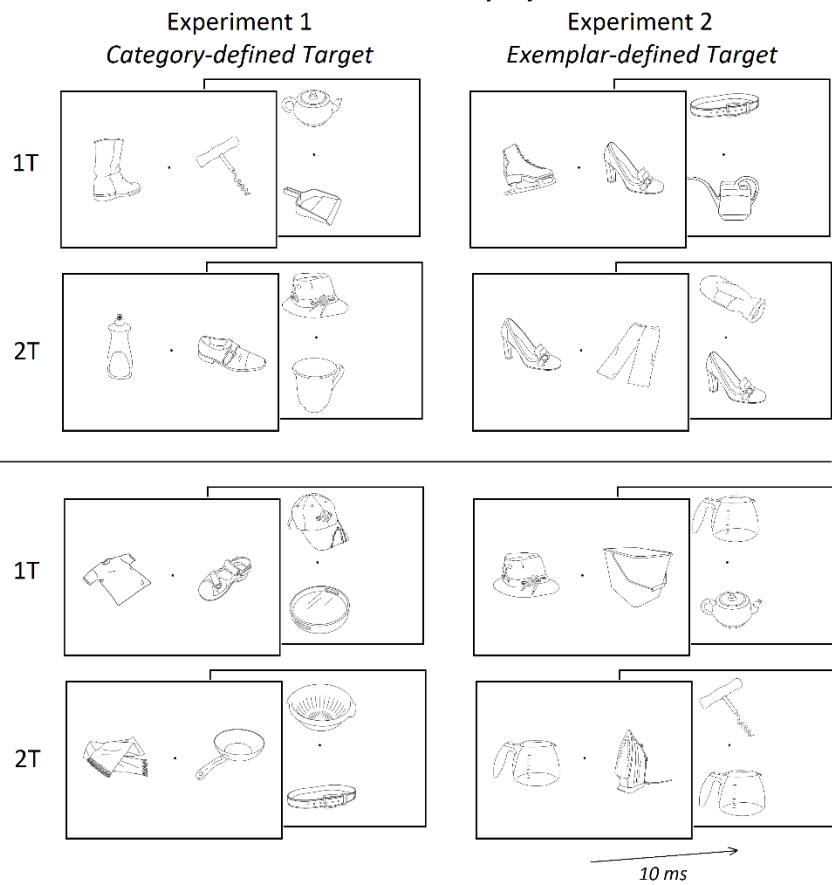


Figure 3.1: Schematic illustration of the possible stimuli and search displays, and the time course of events in Experiments 3a and 3b. On each trial, two consecutive search displays were presented for 200 ms each. Both displays contained a target/distractor pair on the horizontal or vertical meridian. On half of all trials, a horizontal target appeared in the first display and a vertical target in the second display, and this order was reversed in the other half (horizontal target first: H1 target; horizontal target second: H2 target). On each trial, the stimuli were selected from 12 clothing objects and 12 kitchen objects. In Experiment 3a (middle panels), targets were defined as any object from either the clothing category (top panels) or the kitchen category (bottom panels); critically, no two objects were presented twice in a single trial. In Experiment 3b, targets were defined as a specific exemplar object from either category. In both experiments, participants' task was to report the number of targets (one or two).

Each participant was assigned one of the two possible target categories (clothing or kitchen objects) for the first half of the experiment, and then assigned the other target category for the second half. Six participants searched for kitchen objects first, and six searched for clothing objects first. Participants were instructed to report the number of objects belonging to the target category presented in each trial (one or two) by pressing one of two purpose-built vertically aligned response keys, and to refrain from responding if no targets were present in a trial (catch trials). The response-to-key mapping, as well as the hand-to-key mapping, was counterbalanced across participants.

The experiment contained 16 blocks of 80 trials. In each block, there were 48 one-target (1T) trials and 24 two-target (2T) trials, meaning that trials requiring “one target” responses were twice as likely as trials requiring “two target” responses. In addition, there were 8 catch trials in which no target appeared. There were three 1T trials for each combination of display sequence (H1 trial, H2 trial), target display (first, second) and target position (left, right, top, bottom). There were three 2T trials for each combination of display sequence, position of horizontal target (left, right) and position of vertical target (top, bottom). Participants completed one practice block prior to the experiment, and another practice block after 8 experimental blocks (when the target category assignment was changed).

EEG recording and data analyses

The continuous EEG was DC-recorded from 27 scalp electrodes at standard positions of the extended 10/20 system, sampled at a rate of 500 Hz, and digitally low-pass filtered at 40 Hz. No other offline filters were applied. All channels were online referenced to the left earlobe and re-referenced offline to the average of both earlobes. Trials contaminated with

artifacts (eye movements exceeding $\pm 30 \mu\text{V}$ in the HEOG channels; eye blinks exceeding $\pm 60 \mu\text{V}$ at Fpz; muscular movements exceeding $\pm 80 \mu\text{V}$ in all other channels), and trials with incorrect, anticipatory (faster than 200 ms), very slow (slower than 1500 ms), or missing responses were excluded from EEG analyses. This led to an exclusion of an average of 11.5% of all trials (9.4% and 15.5% of 1T and 2T trials, respectively). For the remaining trials, EEG was segmented into epochs ranging from 100 ms prior to 500 ms after the onset of the first stimulus display, and was baseline corrected relative to the 100 ms interval prior to the onset of the first display. EEG was averaged separately for each of the eight combinations of display sequence (H1, H2), trial type (1T, 2T) and position of horizontal target (left, right; excluding 1T trials where the target appeared on the vertical midline).

N2pc components were quantified on the basis of ERP waveforms measured at lateral posterior electrodes PO7 and PO8. N2pc onset latencies were measured based on difference waveforms, computed by subtracting ipsilateral from contralateral ERPs at PO7 and PO8. Onset latencies were determined with a jackknife-based procedure (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). Twelve grand-average difference waves were computed for each experimental condition, each excluding one different participant from the original sample. N2pc onset latency was defined as the point in time when each subsample difference wave reached an absolute onset amplitude of $-1 \mu\text{V}$. Differences in N2pc onset latencies between different combinations of display sequence and number of targets were assessed with repeated-measures ANOVAs and *t*-tests, with *F*- and *t*-values corrected according to the formulas described by Ulrich and Miller (2001) and Miller et al. (1998), respectively. The corrected statistical values are indicated with F_c and t_c , respectively. All *t*-tests were two-tailed and Bonferroni corrected where necessary. To measure effect sizes, Cohen's *d* (Cohen, 1988) was computed for all *t*-tests, and partial eta-squared (labelled η_p^2) was computed for all ANOVAs. In order to correct individual group means and standard

deviations of jackknifed samples, the N2pc latency group means obtained through the jackknife procedure were fed into repeated-measures ANOVAs from which the error variance was corrected according to the formula described by Ulrich and Miller (2001). For this reason, effect sizes from N2pc latency analyses are reported as η_p^2 .

N2pc mean amplitudes were computed within 100 ms time intervals. A 220-320 ms time interval after the onset of the horizontal display was employed for both 1T and 2T trials.

3.3.2.2 Results

Behavioural performance

Anticipatory or exceedingly slow RTs (faster than 200 ms or slower than 1500 ms) were removed from analysis, resulting in the exclusion of 1.1% of all trials. A repeated-measures ANOVA with the factors trial type (1T versus 2T trials) and display sequence (H1 versus H2 trials) was run separately for RTs and error rates. Analysis of RTs revealed no effect of trial type, $F(1,11) = 2.10, p = .175, \eta_p^2 = .16$ (878 ms and 855 ms for 1T and 2T trials), no effect of display sequence, $F(1,11) = .04, p = .842, \eta_p^2 = .00$, and no interaction between these two factors, $F(1,11) = .44, p = .175, \eta_p^2 = .04$. The same analysis on error rates revealed a main effect of trial type, $F(1,11) = 39.41, p < .001, \eta_p^2 = .78$, as errors were more frequent in 2T relative to 1T trials (9.1% versus 3.1%). There was no effect of display sequence, $F(1,11) = 1.50, p = .247, \eta_p^2 = .12$, and no interaction, $F(1,11) = .85, p = .375, \eta_p^2 = .07$, for error rates. On catch trials, the rate of False Alarms was 4.9%.

N2pc components

Figure 3.2 (left and middle panels) shows ERPs at posterior electrodes PO7/8 contralateral and ipsilateral to the side of the horizontal target for trials where this target appeared in the first display (H1 targets) or in the second display (H2 targets). The right panel of Figure 3.2 shows N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for H1 and H2 targets. ERPs are shown separately for 1T (top) and 2T (bottom) trials. In both 1T and 2T trials, clear N2pc components of similar size were elicited to both H1 and H2 targets. A repeated-measures ANOVA of N2pc mean amplitudes was run with the factors trial type (1T versus 2T), display sequence (H1 target versus H2 target), and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target). This analysis revealed a main effect of laterality, $F(1,11) = 41.71, p < .001, \eta_p^2 = .79$, confirming the reliable presence of N2pc components in response to category-defined horizontal target objects. Trial type interacted with laterality, $F(1,11) = 8.58, p < .05, \eta_p^2 = .44$, as N2pc components were larger on 1T trials than on 2T trials (mean amplitudes $-1.56 \mu\text{V}$ and $-1.15 \mu\text{V}$, respectively). Display sequence did not interact with laterality, $F(1,11) = 1.00, p = .340, \eta_p^2 = .08$, indicating that N2pc components of similar size were elicited by horizontal target objects in the first and second display. There was no three-way interaction (laterality x trial type x display sequence), $F(1,11) = .10, p = .749, \eta_p^2 = .01$. Follow up t -tests comparing contra- with ipsilateral activity in response to H1 and H2 targets separately for 1T and 2T trials confirmed that N2pc components were reliably present in all four task conditions, all $t(11) > 4.39, p < .01, d > .24$. Mean N2pc amplitudes for H1 and H2 targets were $-1.65 \mu\text{V}$ and $-1.47 \mu\text{V}$ on 1T trials, and $-1.20 \mu\text{V}$ and $-1.10 \mu\text{V}$ on 2T trials.

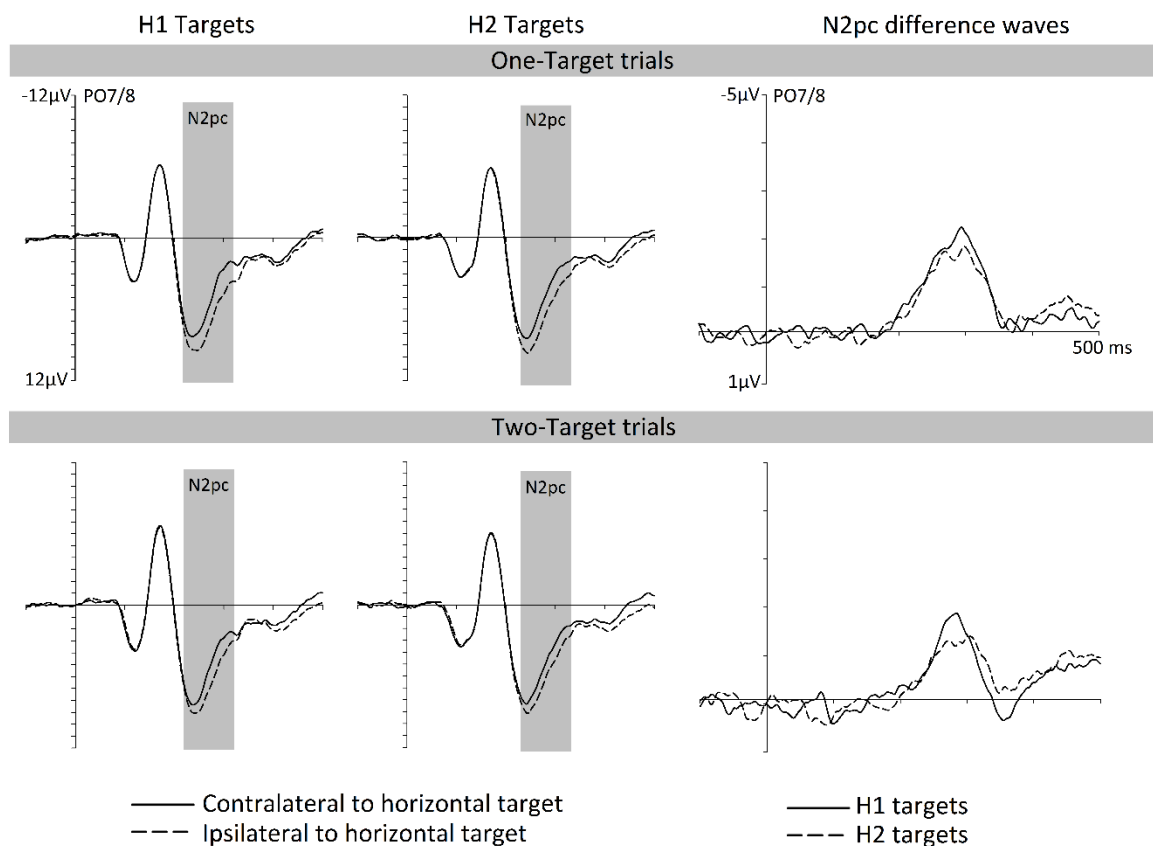


Figure 3.2: N2pc results in Experiment 3a. The left and middle panels show grand-averaged ERP waveforms in the 500 ms interval after the onset of the first search displays at posterior electrodes PO7/PO8 contralateral and ipsilateral to a horizontal category-defined target in the first display (H1 targets) or second display (H2 targets), shown separately for one-target trials and two-target trials. The right panels show corresponding N2pc difference waveforms. N2pc onset latency differences between H1 and H2 targets matched the temporal delay between the two search displays. Grey bars mark the analysed N2pc time-windows.

A further repeated-measures ANOVA was run on N2pc onset latency values determined with a jackknife-based procedure (see Methods) with the factors trial type and display sequence. Even though there was a tendency for N2pc components to emerge earlier

on 1T trials than on 2T trials (234 ms versus 250 ms), the main effect of trial type only approached significance, $F_c(1,11) = 3.42$, $p = .092$, $\eta_p^2 = .24$. There was no main effect of display sequence, $F_c(1,11) = .00$, $p = .926$, $\eta_p^2 = .00$, indicating that the onset of N2pc components to H1 and H2 targets was not sensitive to the objective 10 ms onset latency difference between the first and second display. There was no interaction between trial type and display sequence for N2pc onset latencies, $F_c(1,11) = .00$, $p = .869$, $\eta_p^2 = .00$. Follow-up paired t-tests compared H1 and H2 N2pc onset latency separately for 1T and 2T trials, to confirm whether an effect of display sequence existed for either of these trial types. In both trial types, no difference between H1 and H2 onset latency was observed, both $t_c(11) < 1$, both $p > .827$, both $\eta_p^2 < .01$. N2pc onset latencies for H1 and H2 targets were 233 ms versus 235 ms on 1T trials, and 250 ms for both types of targets on 2T trials.

3.3.2.3 Discussion

Experiment 3a revealed clear and reliable N2pc components to both H1 and H2 targets which completely overlapped in time, not only for 1T trials but also for 2T trials, presenting clear evidence for the availability of rapid parallel selection mechanisms in response to category-defined real-world objects. However, compared with previous studies of rapid parallel feature-based selection (Eimer & Grubert, 2014a; Grubert & Eimer, 2015, 2016) and also alphanumerical category selection (Experiment 2 of this thesis), N2pc onset latencies were generally more delayed (230 ms as compared to an approximate typical onset of 200 ms), indicating reduced efficiency of selection. This was further supported by the lack of an effect of display sequence on N2pc onset latency, suggesting more temporal variance in the speed of selection. Because the effect of display sequence was absent in both 1T and 2T trials, it is

unlikely to be due to any interactions in the concurrent selection of two objects, but rather the result of reduced temporal efficiency of selection in response to category-defined objects.

Despite the reliable presence of N2pc components in all trial types, the fact that N2pc mean amplitudes were smaller in 2T trials relative to 1T trials provides some evidence that the selection of two category-defined targets is not entirely independent. This amplitude reduction in 2T trials reflects an influence of the vertical target on selection of the horizontal target, and was not observed in a previous study of colour-based selection (Grubert & Eimer, 2016a, see also the General Discussion of this article).

Overall, this experiment suggests that while rapid parallel selection mechanisms are still available for category-defined objects, it is more difficult and less efficient than when targets are defined by their features. To determine more clearly to what extent the efficiency of category search is reduced, Experiment 3b was conducted using the same objects, procedures and participants, but with specific objects defined as exemplar targets. If search efficiency is indeed reduced as a result of targets being defined by category membership relative to specific visual properties, and not simply because of the visual complexity of the stimuli used, Experiment 3b should result in N2pcs emerging earlier, with no reduction of amplitude in 2T trials compared to 1T trials.

3.3.3 *Experiment 3b: Exemplar Objects Defined by Visual Properties*

3.3.3.1 Methods

Participants

For Experiment 3b, the same participants were tested as in Experiment 3a, to allow for within-participant comparisons across experiments. However, participants were tested in a separate session on a different day.

Stimuli and Procedure

Stimuli were identical to Experiment 3a. However, participants were now assigned a specific target object from one category (one particular exemplar of clothing or kitchen objects) for the first half of the experiment, and then assigned a target object from the other category for the second half of the experiment. Six participants searched for a specific kitchen object first, and six searched for a specific clothing object first, with the randomisation of task order across participants conducted independently of the individual task order assignment in Experiment 3a. To ensure that target selection in Experiment 3b was exemplar-based rather than category-guided, all target objects were accompanied by a nontarget object from the same category on the opposite side. On 1T trials where one of the two displays contained two nontarget objects, one of these objects was drawn from the same category as the target and the other from the other category. Objects were randomly selected on each trial, and no nontarget objects were repeated within a trial. All other aspects of stimulus presentation and procedure were identical to Experiment 3a.

EEG recording and data analyses

EEG recording, analysis and trial exclusion procedures were identical to Experiment 3a. On average 11.5% of all trials were excluded from analysis (10.9% and 12.6% of 1T and 2T trials, respectively). For all remaining trials with horizontal targets, EEG was averaged separately for each of the eight combinations of display sequence (H1, H2), trial type (1T,

2T) and position of horizontal target (left, right). N2pc mean amplitudes were computed within 100 ms time intervals. Because target N2pc components emerged earlier in the exemplar-based selection task of Experiment 3b than in the category-based task of Experiment 3a (see “comparisons across experiments” below), an earlier N2pc time window (200-300 ms time interval after the onset of the horizontal display) was employed in Experiment 3b. This earlier time-window relative to Experiment 3a was chosen on the basis of N2pc onset latency comparisons across experiments demonstrating significantly earlier N2pc onset in Experiment 3b.

3.3.3.2 Results

Behavioural performance

Exclusion of anticipatory and slow responses removed less than 0.1% of trials. A repeated-measures ANOVA on RTs with the factors trial type (1T versus 2T trials) and display sequence (H1 versus H2 trials) revealed no main effects and no interaction between factors, all $F(1,11) < 1.79$, $p > .256$, $\eta_p^2 < .14$. RTs were 515 ms on 1T trials and 526 ms on 2T trials. The same analysis of error rates also revealed no main effects and no interaction, all $F(1,11) < 3.84$, $p > .076$, $\eta_p^2 < .26$ (error rates on 1T and 2T trials: 1.2% and 2.9%). The False Alarm rate on catch trials was 1.1%.

N2pc components

Figure 3.3 shows ERPs for trials with horizontal targets, separately for H1 and H2 targets on 1T and 2T trials, with the corresponding N2pc difference waveforms. Clear N2pc components were triggered by H1 and H2 targets in both types of trials. A repeated-measures

ANOVA examined mean N2pc amplitudes with the factors trial type (1T versus 2T), display sequence (H1 versus H2), and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target). A main effect of laterality, $F(1,11) = 44.47, p < .001, \eta_p^2 = .80$, confirmed the presence of N2pc components in response to horizontal targets. There was also an interaction between trial type and laterality, $F(1,11) = 9.33, p < .05, \eta_p^2 = .46$. In contrast to Experiment 3a, N2pc amplitudes on 1T trials were now smaller than on 2T trials (mean amplitudes $-2.46 \mu\text{V}$ and $-3.21 \mu\text{V}$, respectively). The interaction between display sequence and laterality approached significance, $F(1,11) = 4.13, p = .067, \eta_p^2 = .27$, reflecting a tendency towards larger N2pc components for H2 targets (see Figure 3.3). There was no three-way interaction between trial type, display sequence, and laterality, $F(1,11) = .32, p = .584, \eta_p^2 = .03$. Follow up *t*-tests comparing contra- with ipsilateral activity in response to H1 and H2 targets, separately for 1T and 2T trials, confirmed that reliable N2pc components were present in all four task conditions, all $t(11) > 5.28, p < .001, d > .51$. Mean amplitudes in 1T trials were $-2.37 \mu\text{V}$ and $-2.55 \mu\text{V}$ for H1 and H2 trials, respectively. In 2T trials, these mean amplitudes were $-3.04 \mu\text{V}$ and $-3.38 \mu\text{V}$.

For N2pc onset latencies, a repeated-measures ANOVA with the factors trial type and display sequence revealed no main effect of trial type, $F_c(1,11) = 1.50, p = .247, \eta_p^2_c = .12$ and no main effect of display sequence, $F_c(1,11) = 3.09, p = .107, \eta_p^2_c = .22$. However, there was an interaction between these two factors, $F_c(1,11) = 5.36, p < .05, \eta_p^2_c < .33$. On 1T trials, there was no N2pc onset latency difference between H1 and H2 targets (210 ms and 212 ms; $t_c(11) = .52, p = .612, \eta_p^2_c = .02$). On 2T trials, the N2pc to H2 targets was delayed by 12 ms relative to the N2pc to H1 targets (201 ms versus 213 ms; $t_c(11) = 2.35, p < .05, \eta_p^2_c = .33$), mirroring the objective 10 ms SOA between the two successive displays.

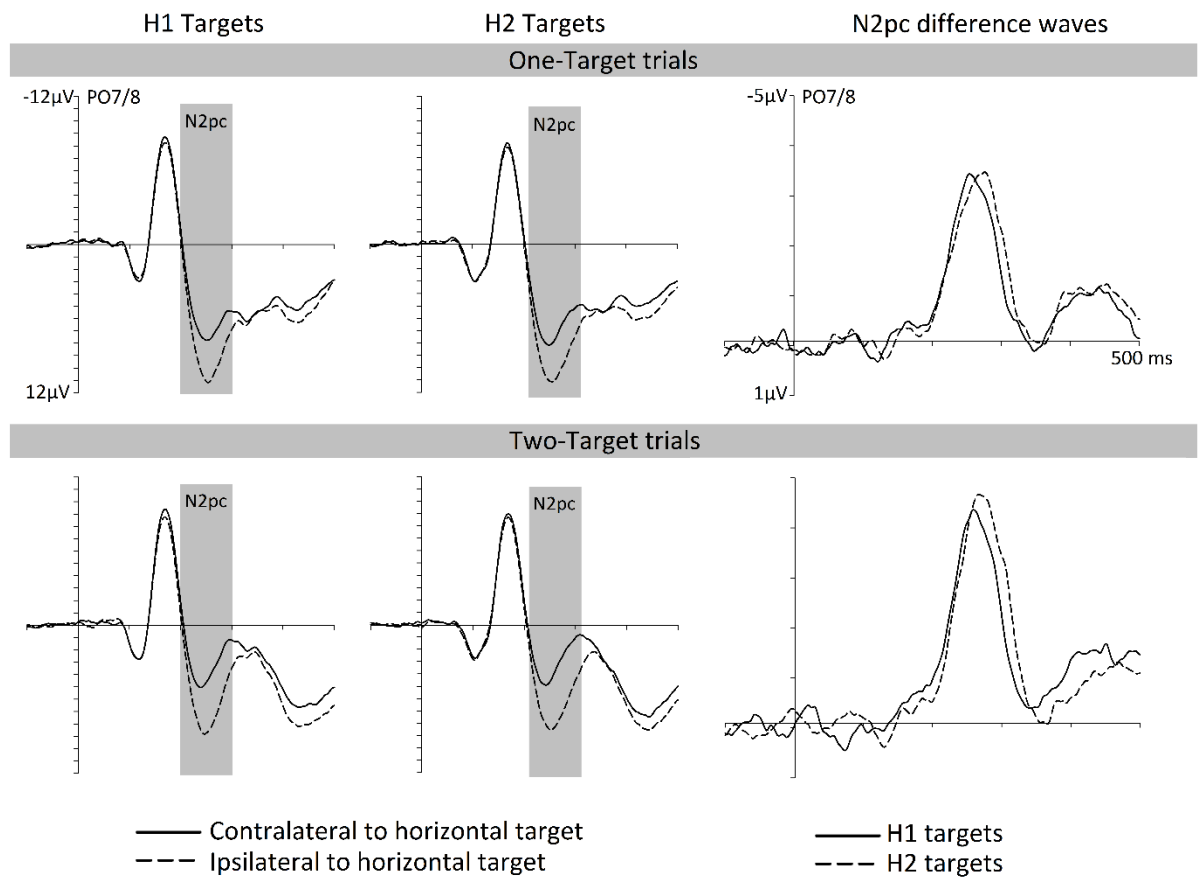


Figure 3.3: N2pc results in Experiment 3b, shown in an identical fashion to Experiment 3a. Again, N2pc onset latency differences between H1 and H2 targets matched the SOA delay between the two search displays. Grey bars mark the analysed N2pc time-windows.

Comparisons across experiments

Because the same participants were tested in Experiments 3a and 3b, additional within-participant comparisons of behavioural performance and N2pc components were conducted to assess differences between the category-based and exemplar-based selection of target objects.

Behavioural performance. Repeated-measures ANOVAs with the factors trial type (1T versus 2T trials), display sequence (H1 versus H2 trials) and selection task (category selection: Experiment 3a versus exemplar selection: Experiment 3b) were conducted for RTs and error rates. RTs were much slower for the category-based selection task (Experiment 3a) than with exemplar-based selection in Experiment 3b (866 ms versus 521 ms), as reflected by a main effect of selection task, $F(1,11) = 166.03, p < .001, \eta_p^2 = .94$. There were no significant interactions involving the factor selection task for RTs, all $F(1,11) < 2.93, p > .115, \eta_p^2 < .21$. Along similar lines, errors were more frequent during category selection than during exemplar selection (6.2% versus 2.1% in Experiments 3a and 3b, respectively; main effect of selection task), $F(1,11) = 15.90, p < .01, \eta_p^2 = .59$. Apart from an interaction between selection task and trial type, $F(1,11) = 10.33, p < .01, \eta_p^2 = .48$, reflecting the fact that errors were more frequent on 2T relative to 1T trials in Experiment 3a but not in Experiment 3b, no other interactions involving the factor selection task were present for error rates, all $F(1,11) < 1.67, p > .223, \eta_p^2 < .14$.

N2pc components. N2pc components were larger for exemplar targets (Experiment 3b; mean amplitude $-2.84 \mu\text{V}$) than for category-defined targets (Experiment 3a; mean amplitude $-1.36 \mu\text{V}$), as confirmed by an interaction between selection task and laterality, $F(1,11) = 10.97, p = .01, \eta_p^2 = .50$. There was also a three-way interaction between selection task, trial type, and laterality, $F(1,11) = 15.44, p < .01, \eta_p^2 = .58$, reflecting the fact that N2pc components were larger on 1T than on 2T trials in Experiment 3a, but larger on 2T relative to 1T trials in Experiment 3b. An analysis of N2pc onset latencies across both experiments confirmed that target N2pc components emerged earlier in the exemplar-based selection task of Experiment 3b relative to the category based selection task of Experiment 3a (209 ms versus 242 ms; main effect of selection task), $F_c(1,11) = 19.65, p < .01, \eta_p^2_c = .64$.

3.3.4 Interim General Discussion

The current experiments aimed to determine the availability of rapid parallel selection mechanisms in search for real-world objects defined by their category membership, and to assess the efficiency of such mechanisms. By measuring N2pc responses to candidate target objects presented in extremely rapid succession, both experiments were able to measure the speed of target selection, as well as the influence of one selection process on another concurrent selection process, in trials where two targets were presented. Experiment 3a revealed the availability of rapid parallel selection of category objects as demonstrated by overlapping N2pc components, suggesting that real-world categories can be represented in attention guiding target templates. This experiment also provided initial evidence for reduced efficiency of category search by showing general delays and temporal variance in N2pc onset as compared to feature based search (Experiment 2 of this thesis, and Experiment 3b of this chapter). In Experiment 3b, where targets were defined by a specific visual image, the same qualitative mechanisms of selection were found, but N2pcs were larger in amplitude and emerged earlier in time as compared to Experiment 3a, confirming the superior efficiency of feature templates over category templates reflected by increased temporal precision. In addition, there was no interference in the selection of horizontal targets by a concurrent vertical target in 2T trials, as was demonstrated by reduced N2pc amplitudes in these trials in Experiment 3a. The critical difference between 1T and 2T target-horizontal trials in these experiments is the additional presence of a second target on the vertical midline; thus, the reduction of N2pc amplitudes in 2T trials relative to 1T trials that is observed in Experiment 3a is indicative of interference in the allocation of attention to the horizontal target as a result of the concurrent presence of a vertical target. However, N2pc amplitudes in Experiment 3b were in fact significantly larger in 2T than in 1T trials. These reversed effects may be due to a boost in the N2pc response when two identical targets are presented in rapid succession; such

an effect may occur because the attentional selection of each target is facilitated not only by the currently held attentional template, but also by a direct perceptual match with the other currently visible target (note that while these targets did not appear at precisely the same time, they were simultaneously present on the screen for 190 ms).

It is important to address the lack of significant effects of display sequence in most conditions of the current study; only in 2T trials in Experiment 3b was a significant delay found between N2pc onset in response to H1 and H2 trials. The fact that such differences were also absent in Experiment 2 of this thesis, where targets were also category defined, supports the possibility that there is more temporal variance in selection when targets are not defined by a precise visual feature template. In some trials, target selection may take place more rapidly, resulting in earlier N2pcs, while in other trials this selection may be more delayed. Averaging across these two types of trials will result in an attenuation of the pooled N2pc component. Further support for this comes from the lack of a display sequence effect in 1T trials in the current study, indicating generally increased temporal variance in selection regardless of whether one or two objects are being selected.

The fact that target objects in Experiment 3b were always accompanied by a same-category distractor object in the same display implied that target selection could not be based on category, but had to be guided by an attentional template for this particular object. However, the possibility remains during this type of exemplar-based search that a template for the category of the target object may also have been activated (see Nako, Wu, & Eimer, 2014, for their use of a “foil” N2pc which was elicited in response to target-category matching items that were not part of the current target set). To assess this possibility, we computed N2pc components elicited on those 1T trials where a display with a vertical target/nontarget pair was preceded or followed by a display that contained two nontarget objects on the horizontal midline. One of these nontarget objects shared the target category,

whereas the other object belonged to the other category. Any residual category-based attentional guidance in Experiment 3b should have resulted in a tendency to direct attention towards the category-matching nontarget object in these displays, which should have resulted in an N2pc to these objects. As shown in Figure 3.4 (which shows ERP waveforms collapsed across H1 and H2 trials, time-locked to the onset of the horizontal display), this was indeed the case. A small but significant N2pc was elicited contralateral to the object that matched the target category (main effect of laterality: $F(1,11) = 5.77, p < .05, \eta_p^2 = .34$), demonstrating that even during this exemplar-based selection task, the category of the current target object was partially activated and affected the distribution of spatial attention (see also Nako, Wu, & Eimer, 2014, for analogous observations).

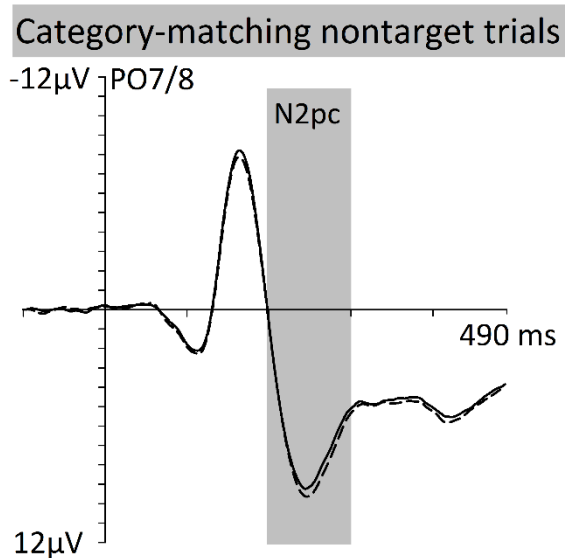


Figure 3.4: ERP waveforms elicited by horizontal category-matching nontargets in Experiment 3b. A small but significant N2pc response was observed in trials where the target appeared vertically, and a nontarget that matched the task-irrelevant category of the exemplar target was presented horizontally along with a nontarget that was a member of the other category.

The results of the current study directly answer questions concerning the cognitive mechanisms involved in category-based attentional guidance, but also lead to insights into the neural basis of such mechanisms, particularly regarding possible differences in the representation of alphanumeric and real-world categories. When searching for objects defined

by alphanumeric category, specific brain regions may be available to represent this information; in particular, the left middle fusiform gyrus is thought to represent meaningful objects such as words (visual word form area; e.g., Cohen & Dehaene, 2004), and more anterior regions of the left fusiform gyrus may be involved in specific representations of single letters (James, James, Jobard, Wong, & Gauthier, 2005). In real-world category search, where differences between objects are not based on alphanumerical properties but on more abstract, semantic categorisations, these regions would not be available to assist in the formation or maintenance of target representations. However, it is possible that other brain regions in the inferior temporal cortex, which are not specific to alphanumerical representations, may still aid in categorisation judgements (e.g., Freedman, Poggio, Riesenhuber, & Miller, 2001; see also Miller, Nieder, Freedman, & Wallis, 2003, for a review), and such occipitotemporal areas involved in object recognition are known to be directly linked to the ventrolateral prefrontal cortex (see Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013, for a recent review). The N2pc responses observed in Experiment 3a of the current study reflect spatially selective enhancements of processing in extrastriate visual areas, which are triggered by recurrent feedback signals from such category-sensitive brain regions via the prefrontal cortex.

In summary, despite the fact that category-based selection has been shown to be slower and temporally less precisely guided than exemplar-based selection, guidance by category information can still facilitate rapid and (largely but not entirely) parallel selection of two objects presented in rapid succession. Together, these experiments provide further evidence for the remarkable speed of category guidance.

3.4 General Discussion

Experiments 2 and 3 both demonstrated rapid and parallel attentional selection of multiple objects presented in rapid succession, when these objects were defined by category information. Crucially, the fact that qualitatively similar results were found in both experiments, when targets were defined by alphanumeric category and by semantic category with more visually complex stimuli, suggests that such rapid parallel attentional mechanisms can be employed even without the possibility of feature-based attentional processing. In other words, even when stimuli cannot in any way be detected on the basis of their visual properties, but instead (as in Experiment 3a) must be looked for using semantic representations of the purpose of these stimuli (e.g., whether they are used as clothing or as kitchen objects), the attentional selection of these targets can take place as each target appears.

It is clear from these experiments that different mechanisms must be available in feature and category search, as necessitated by the respective availability or absence of visual information in guiding these types of search. Despite this, such different mechanisms allow for similarly flexible deployments of attention. How do these mechanisms differ? It has been previously discussed that feature-based modulations of neural processing in visual cortical brain regions allow for the rapid parallel selection of multiple instances of feature-defined targets. In the context of the attentional template, it can be argued that when an object is defined by visual properties, these properties can be visually represented by the template to efficiently guide search in the ways that have been observed so far. Similarly efficient search for real-world categories in Experiment 3a implies that the attentional template can also represent more complex, semantic information that cannot be represented visually. The long-range recurrent interactions between prefrontal cortex and visual cortical regions that have been discussed in this chapter may have important implications for the flexibility of the

content of the attentional template; in other words, the attentional template may communicate with more high-level brain regions than has previously been assumed, and this may allow it to represent complex, non-visual information in a way that allows rapid and efficient attentional selection of multiple instances of category-defined targets.

In terms of the quality and complexity of a single property, attentional templates appear to have little limit. However, in many real-world scenarios, a single property (no matter how complex) is not sufficient to guide search. For example, when searching for a coin of particular value (e.g., a five pence coin), it may not be helpful to simply represent the colour silver in the attentional template, because other silver coins may also be present (e.g., a ten pence coin). Likewise, an attentional template for small size would not distinguish the target coin from other small coins (e.g., a one pence coin). In this situation, and many others, the need arises for conjunctions of features to be looked for – the target may share properties on one dimension (silver) with some distractors, and properties on another dimension (small) with other distractors, but it is the only object that possesses a specific combination of these properties (both small and silver). How can attentional templates represent these conjunctions? Are there flexible attentional control mechanisms that allow for efficient search for conjunctions? The following chapter will investigate these questions.

Chapter 4

Rapid and Parallel Attentional Allocation to Conjunctions

The experiments presented in this chapter have been accepted for publication in a peer-reviewed journal:

Experiments 4 & 5:

Jenkins, M., Grubert, A., & Eimer, M (in press-a). Target objects defined by a conjunction of colour and shape can be selected independently and in parallel. *Attention, Perception, & Psychophysics*.

4.1 Chapter Overview

As described in the end of Chapter 3, this chapter focuses on the attentional selection of multiple objects that are each defined by a specific conjunction of features from different dimensions. While the results from this chapter are qualitatively similar to those from the previous chapters, and reflect the availability of rapid parallel selection mechanisms in guiding the allocation of attention to conjunctively-defined targets, they do not support the notion that the attentional template can represent bound conjunctions of features (i.e., full object representations). Instead, the results from Experiment 5 indicate that information across separate feature dimensions is rapidly integrated during the process of attentional selection, reflecting a transition from spatially-global feature-based attention to spatially-local object-based attention.

4.2 *Experiment 4: Attentional Selection of Conjunctively Defined Targets*

4.2.1 Introduction

The successful detection of a looked-for target object among irrelevant distractors in a visual scene requires top-down attentional control. When some or all features of such a target are known in advance, these features are represented internally as attentional templates (Duncan & Humphreys, 1989; Desimone & Duncan, 1995). Activating such templates during the preparation for visual search will prioritize the visual processing of template-matching features, and can guide selective attention towards the location of candidate target objects in the visual field (e.g., Wolfe, 2007; Olivers, Peters, Houtkamp, & Roelfsema, 2011). The time course and nature of such template-guided attentional selection processes remains a topic of lively debate. One important controversial issue concerns the question whether these

processes operate in a strictly sequential fashion, with serial shifts of attention between successively selected objects, or whether attention can be allocated to multiple objects simultaneously. Leading models of visual search (e.g., Treisman & Gelade, 1980; Wolfe, 1994, 2007) postulate that attentional object selection is a serial process, particularly in situations when target objects are defined by a combination of features, and some of the distractor objects in the search display also possess target-matching features (conjunction search). In contrast, other models of attentional control (e.g., Desimone & Duncan, 1995) and accounts of the role of attention in multiple object tracking tasks (e.g., e.g., Cavanagh & Alvarez, 2005; see also Niebergall, Khayat, Treue, & Martinez-Trujillo, 2011) assume that attention can be allocated in parallel to several objects in the visual field.

Previous observations from our lab (e.g., Eimer & Grubert, 2014a; Grubert & Eimer, 2015; Grubert & Eimer, 2016a; Experiment 1 of this thesis) suggest that attention can be allocated rapidly and independently to multiple target objects in tasks where these objects can be discriminated from nontargets based on one particular feature. However, in real-world environments, it is often not possible to distinguish a relevant object from irrelevant distracting objects on the basis of a single feature. For example, search for large silver coins among small silver coins and large bronze coins has to be based on two target-defining attributes from different feature dimensions (colour and size). Behavioural studies have demonstrated that this type of conjunction search is typically less efficient than search for targets that are defined by a single feature (e.g., Treisman & Gelade, 1980). According to Feature Integration Theory (e.g., Treisman, 1988), this is because feature search can operate in parallel for multiple objects, whereas conjunction search requires serial shifts of spatial attention between individual objects. Response times (RTs) in conjunction search tasks increase with the number of distractor objects possessing one target-defining feature, but remains unaffected by the number of nontarget objects without task-relevant features (Egeth,

Virzi, & Garbart, 1984), suggesting that search can be restricted to the subset of objects with target features, but that search within this subset is conducted serially. Others (e.g., Wolfe, 1998b) have argued that the serial/parallel dichotomy is misleading, and that search efficiency varies continuously between different types of search tasks. According to the Guided Search model (Wolfe, 1994, 2007), search performance depends on the efficiency with which attentional object selection can be guided towards the location of target objects. Guidance is controlled by a spatiotopic salience map where information about the location of target-defining attributes is combined. Attention is then directed serially to those locations that are most likely to contain a target object.

The goal of the present study was to investigate the speed with which attention can be allocated to two target objects presented in rapid succession under conditions where these targets are defined by a conjunction of features. We employed the same rapid sequential presentation paradigm as in our previous studies of feature-guided attentional selection processes (e.g., Eimer & Grubert, 2014a), except for the fact that targets were now defined by a particular combination of colour and shape. In Experiment 4, targets were always accompanied by a distractor object in the same display that either matched the target colour or the target shape. Two target/distractor displays were presented successively for 50 ms each, and were separated by an SOA of 10 or 100 ms (in different blocks). The target/distractor pair was presented on the horizontal midline in one of these displays and on the vertical midline in the other display (see Figure 4.1). The order in which these two displays were presented (horizontal first or second: H1 or H2 targets) varied unpredictably across trials. Participants had to attend to the two target objects defined by a specific colour/shape conjunction (e.g., blue circles), and to report whether the gaps in their contours were located on the same side or on opposite sides. To assess the time course with which

attention was allocated to the two conjunctively defined target objects, we measured N2pc components, separately for H1 and H2 targets and for the two SOA conditions.

Because one target was accompanied by a colour-matching distractor and the other by a shape-matching distractor on each trial, target selection could not be based on a single search template for a particular feature. According to Feature Integration Theory (Treisman & Gelade, 1980), the identification of these target objects will have to be based on the integration of signals across the colour and shape dimensions, and this requires focal attention that can only be allocated in a serial fashion to one object at a time. In the Guided Search model, different features can guide attention independently and in parallel, but the resulting feature-guided attentional selection of objects is assumed to operate in a serial fashion (Wolfe, 2007). Both models predict that the selection of the target object in the second display can only commence after attention is withdrawn from the first target. If N2pc components mark the points in time when attention is allocated to H1 and H2 targets, respectively, their temporal pattern should differ from the pattern observed in our previous studies where these targets were defined by a single feature. It is possible that serial attention shifts can take place within 100 ms. In this case, both H1 and H2 targets should trigger N2pc components of similar size in blocks where the two displays are separated by 100 ms (SOA 100 condition), and their onset latency difference should match the objective SOA between the two displays. Critically, qualitatively different results should be observed in blocks with a 10 ms SOA between the two displays. In these blocks, the time required to initiate a shift of attention from the first to the second target should be considerably longer than the SOA between these targets. Given that each display was presented for only 50 ms, this might make it difficult to allocate attention to the second target at all while it is still perceptually available. As a result, N2pc components to H2 targets should be delayed, attenuated, or perhaps even entirely absent in the SOA 10 condition of Experiment 4. In addition, there

should also be performance costs relative to the SOA 100 condition, where more time is available to complete serial attention shifts.

The alternative possibility is that attention can be allocated independently and in parallel to both target objects even when these targets are defined by a feature conjunction. In this case, temporally overlapping N2pc components of similar size should be elicited by H1 and H2 targets in the SOA 10 condition, as was observed previously with feature-defined targets (e.g., Eimer & Grubert, 2014a). To preview the results, this was indeed what was found in Experiment 4. The feature-based versus object-based nature of these parallel attentional processing biases was investigated in Experiment 5.

4.2.2 Methods

Participants

Fifteen participants were paid to take part in Experiment 4. Three of them were excluded from analysis due to excessive eye movement activity. The remaining twelve participants were aged between 20 and 41 ($M = 30.25$, $SD = 6.52$). Eight were female, three were left-handed. All participants had normal or corrected-to-normal vision. This choice of sample size ($n=12$ after excluding three participants) was based on a power analysis that employed the effect size obtained from a previous N2pc experiment in our lab (Experiment 1 of this thesis), in which the same sample size was used to compare N2pc onset latencies across multiple displays and SOA conditions in response to rapidly presented shape-defined target stimuli.⁴

⁴ To ensure a large enough sample size providing enough power to reliably exclude false rejection of the null hypothesis, power ($1-\beta$) was calculated using the G*Power program (Faul, Erdfelder, Lang, & Buchner, 2007), using the a priori option and the η_p^2 effect size (.72) of the SOA * Display sequence interaction of Experiment 1 in Jenkins, Grubert, &

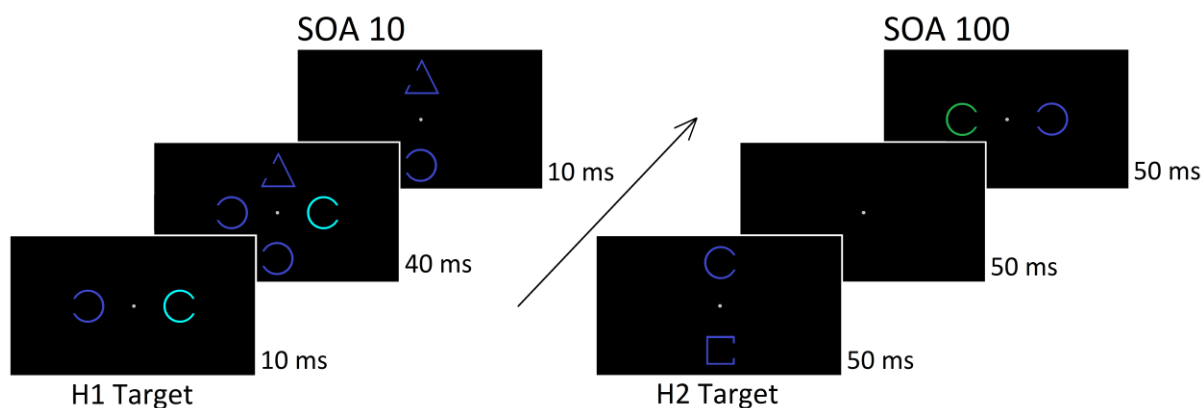


Figure 4.1: Schematic illustration of the search displays and the time course of events in the SOA 10 and SOA 100 conditions of Experiment 4. On each trial, two consecutive search displays contained a target defined by a specific colour/shape conjunction (a blue circle in the examples shown here) and a colour-matching or shape-matching distractor on opposite sides. Participants' task was to decide whether the two target objects had a gap on the same or on different sides. Displays with horizontal target/distractor pairs preceded vertical displays (H1 target) or vice versa (H2 target).

Stimuli and Procedure

Stimuli were presented on a 22-inch Samsung wide SyncMaster 2233 LCD monitor (resolution of 1280x1024 pixels, 100 Hz refresh rate; 16ms black-to-white-to-black response time, verified using a photodiode). Participants were seated in a dimly lit cabin and viewed the screen from an approximate distance of 100 cm. Stimulus presentation, timing, and response recollection were controlled by a LG Pentium PC operating under Windows XP, using the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks,

Eimer (2016; n=12). Power analysis revealed a test power of .872 (with an effect size f determined according to Cohen, 1988, of 1.60) and suggested that a sample size of $n=4$ was sufficient to achieve the desired effect size of .72.

Inc.). Stimuli were coloured outline shapes (circles, squares, or triangles; 0.2° line width), subtending $1.1^\circ \times 1.1^\circ$ of visual angle. There was a gap in the contour of each object, on the left or right side. The size of this gap was 0.6° , and it was always centred between the top and bottom of each shape (as illustrated in Figure 4.1). The possible stimulus colours were blue (CIE colour coordinates: .185/.188), cyan (.212/.347), or green (.262/.572). All colours were equiluminant (9.8 cd/m^2). Stimuli were presented at an eccentricity of 3.0° from central fixation against a black background. A central grey (.321/.352) fixation point ($0.2^\circ \times 0.2^\circ$) remained continuously present for the duration of each experimental block.

On each trial, two successive stimulus displays were each presented for 50 ms. Each stimulus display contained one target object (matching both the target shape and colour), and a distractor on opposite sides. One of the two distractors in each trial matched the target shape but had one of the two nontarget colours (shape-matching distractor). The distractor in the other display on the same trial matched the target colour but had one of the two nontarget shapes (colour-matching distractor). Nontarget colours and shapes were randomly selected on each trial. One target/distractor pair was presented on the horizontal meridian (left and right of fixation), and the other pair appeared on the vertical meridian (above and below fixation). In half of all trials, the horizontal stimulus pair was presented first (horizontal target first: H1 target). In the other half, the vertical target/distractor display preceded the horizontal display (horizontal target second: H2 target). These two display sequences were randomly intermixed in each block. The position of the two target objects in the two displays (left/right; top/bottom), as well as the order in which the shape-matching and colour-matching distractors appeared, were randomly and independently determined on each trial. There were two blocked SOA conditions. In SOA 10 blocks, the onset of the first display preceded the onset of the second display by 10 ms (i.e., there was a 40 ms overlap between these two displays). In SOA 100 blocks, the onset of the two consecutive displays was separated by 100

ms, and there was a 50 ms blank interval between the offset of the first display and the onset of the second display. The interval between the offset of the second display and the onset of the first display on the next trial was 1900 ms.

Each participant was assigned a specific target-defining shape/colour conjunction that remained constant throughout the experiment. Each of the three possible shapes (circle, square, and triangle) and colours (blue, green, and cyan) served as target-defining feature for four participants. Target colour and shape were selected independently, with the constraint that each of the nine possible colour-shape conjunctions served as target for at least one of the twelve participants (with three of these conjunctions each serving as target for two participants). Participants were instructed to find the two target objects in the two successively presented displays, and to report whether these objects had gaps on the same side (both left or right) or on different sides (one left, one right) by pressing one of two purpose-built vertically aligned response keys. The response-to-key mapping, as well as the hand-to-key mapping, was counterbalanced across participants. Trials requiring a “same” or “different” response were equiprobable and randomly intermixed in each block.

The experiment contained 12 blocks, with 64 trials per block, and 4 trials for each combination of display sequence (H1 target, H2 target), position of horizontal target (left, right), position of vertical target (top, bottom), and sequence of partially matching distractors (shape-matching followed by colour-matching distractor, or vice versa). Each SOA condition was run in 6 successive blocks, and the order of the SOA conditions was counterbalanced across participants. Each of the two SOA conditions was preceded by one practice block.

EEG recording and data analyses

The continuous EEG was DC-recorded from 27 scalp electrodes at standard positions of the extended 10/20 system, sampled at a rate of 500 Hz, and digitally low-pass filtered at 40 Hz. No other offline filters were applied. All channels were online referenced to the left earlobe and re-referenced offline to the average of both earlobes. Trials contaminated with artifacts (eye movements exceeding $\pm 30 \mu\text{V}$ in the HEOG channels; eye blinks exceeding $\pm 60 \mu\text{V}$ at Fpz; muscular movements exceeding $\pm 80 \mu\text{V}$ in all other channels), and trials with incorrect, anticipatory (faster than 200 ms), very slow (slower than 1500 ms), or missing responses were excluded from EEG analyses. This led to an exclusion of an average of 12.3% and 17.6% of all trials in the SOA 10 and SOA 100 conditions, respectively. For the remaining trials, EEG was segmented into epochs ranging from 100 ms prior to 500 ms after the onset of the first stimulus display, and was baseline corrected relative to the 100 ms interval prior to the onset of the first display. EEG was averaged separately for each of the eight combinations of SOA (10 ms, 100 ms), display sequence, and position of horizontal target.

N2pc components were quantified on the basis of ERP waveforms measured at lateral posterior electrodes PO7 and PO8. N2pc onset latencies were measured based on difference waveforms, computed by subtracting ipsilateral from contralateral ERPs at PO7 and PO8. Onset latencies were determined with a jackknife-based procedure (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). Twelve grand-average difference waves were computed for each experimental condition, each excluding one different participant from the original sample. N2pc onset latency was defined as the point in time when each subsample difference wave reached an absolute onset criterion of $-1 \mu\text{V}$.⁵ Differences in N2pc onset

⁵ A fixed onset criterion of $-1 \mu\text{V}$ was chosen to avoid distortion of N2pc onset latency estimates by differences in N2pc amplitude between experimental conditions. All N2pc onset latency analyses reported in this article were additionally run with a relative onset criterion of 50% (defined by the point in time when 50% of the N2pc peak amplitude is reached for each

latencies between H1 and H2 targets and between SOA conditions were assessed with repeated-measures ANOVAs and t -tests, with F - and t -values corrected according to the formulas described by Ulrich and Miller (2001) and Miller et al. (1998), respectively. The corrected statistical values are indicated with F_c and t_c , respectively. All t -tests were two-tailed and Bonferroni corrected where necessary. To measure effect sizes, Cohen's d (Cohen, 1988) was computed for all t -tests, and partial eta-squared (labelled η_p^2) was computed for all ANOVAs. In order to correct individual group means and standard deviations of jackknifed samples, the N2pc latency group means obtained through the jackknife procedure were fed into repeated-measures ANOVAs from which the error variance was corrected according to the formula described by Ulrich and Miller (2001). For this reason, effect sizes from N2pc latency analyses are reported as $\eta_p^2_c$.

N2pc mean amplitudes were computed within 100 ms time intervals. For H1 targets, a 200-300 ms time interval after the onset of the first display was employed for both SOA conditions. For H2 targets, time windows were adjusted relative to the SOA between the first and second display (210-310 ms after the onset of the first display for the SOA 10 condition; 300-400 ms for the SOA 100 condition).

4.2.3 Results

Behavioural performance

Reaction times (RTs) were measured relative to the onset of the second display on each trial. Anticipatory or exceedingly slow RTs (faster than 200 ms or slower than 1500 ms) were removed from analysis, resulting in the exclusion of less than 1% of all trials. A

subsample difference wave), as described by Miller et al. (1998). The results of these analyses confirmed those obtained with the fixed onset criterion.

repeated-measures ANOVA with the factors SOA (10 versus 100 ms) and display sequence (H1 versus H2 targets) was run separately for RTs and for error rates. RTs were faster in the SOA 10 than in the SOA 100 condition (682 ms versus 727 ms), but this difference was not significant, $F(1,11) = 4.06$, $p = .069$, $\eta_p^2 = .27$. There was also no main effect of display sequence on RTs (705 ms versus 704 ms for H1 and H2 targets, respectively), nor any interaction between these two factors, both $F(1,11) = .01$, $p = .916$, $\eta_p^2 = .00$. For error rates, a main effect of SOA was observed, $F(1,11) = 22.21$, $p < .001$, $\eta_p^2 = .67$, with more errors in the SOA 100 condition than in the SOA 10 condition (10.1% versus 4.4%). There was no effect of display sequence on error rates (7.1% and 7.4% for H1 and H2 targets, respectively) and no interaction between these two factors, both $F(1,11) < 1.11$, $p = .745$, $\eta_p^2 = .01$.

N2pc components

Figure 4.2 (left and middle panels) shows ERPs at posterior electrodes PO7/8 contralateral and ipsilateral to the side of the horizontal conjunction target for trials where this target appeared in the first display (H1 targets) or in the second display (H2 targets). The right panel of Figure 4.2 shows N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for H1 and H2 targets. ERPs are shown separately for the SOA 10 (top) and SOA 100 (bottom) condition. In both SOA conditions, clear N2pc components of similar size were elicited to both H1 and H2 targets. The onset latency differences of the N2pc components to H1 and H2 targets reflected the objective SOA between the two displays in the SOA 10 and SOA 100 conditions.

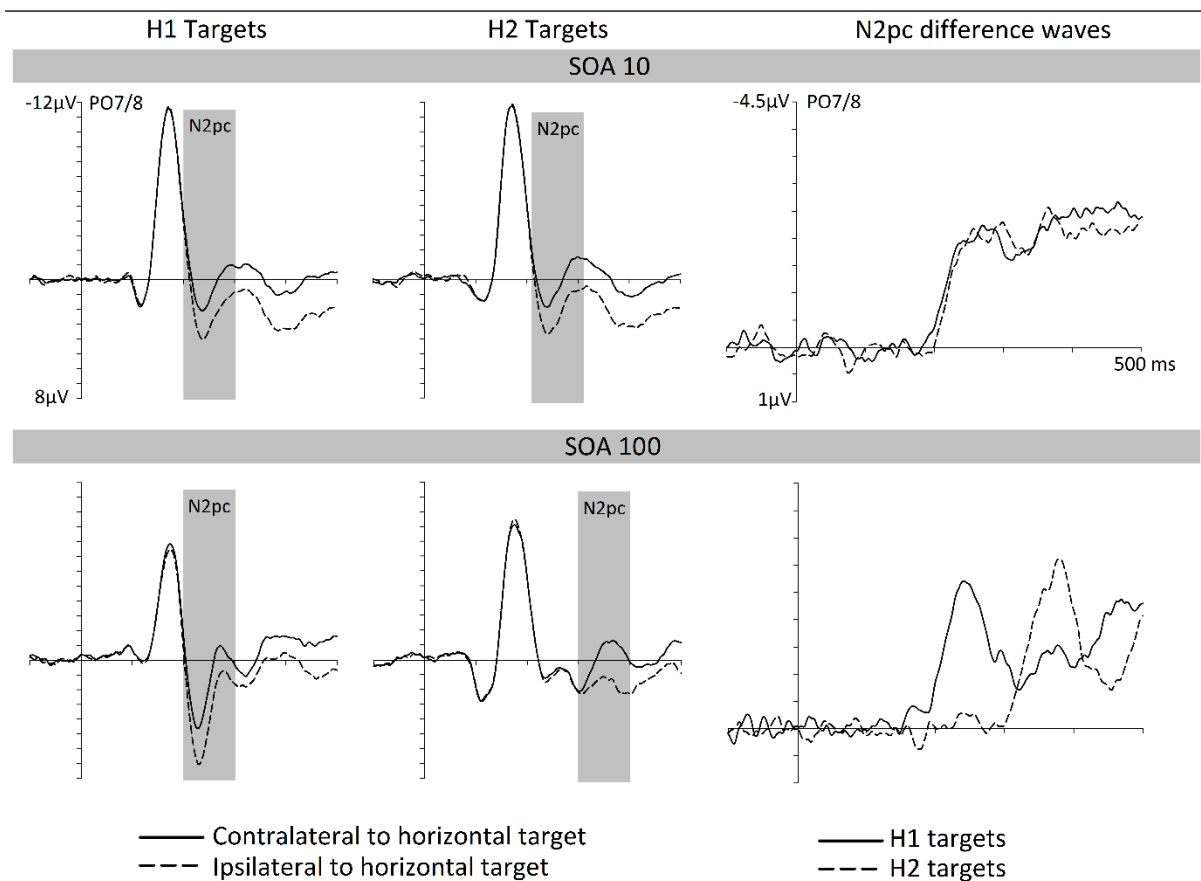


Figure 4.2: N2pc components elicited by target objects in the SOA 10 and SOA 100 conditions of Experiment 4. Left and middle panels: Grand-average ERP waveforms measured in the 500 ms interval after the onset of the first search display at posterior electrodes PO7/PO8 contralateral and ipsilateral to a horizontal target in the first display (H1 targets) or second display (H2 targets). Right panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for H1 and H2 targets, and both SOA conditions.

These observations were confirmed by analyses of N2pc mean amplitudes and onset latencies. In a repeated-measures ANOVA of N2pc mean amplitudes with the factors display sequence (H1 versus H2 targets), SOA (10 versus 100 ms), and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target), a main effect of laterality, $F(1,11) = 45.70, p < .001, \eta_p^2 = .81$, indicated that N2pc components were reliably elicited by horizontal target objects. There were no reliable effects of SOA, $F(1,11) = 1.11, p = .315, \eta_p^2$

= .09, or display sequence, $F(1,11) = 2.20$, $p = .183$, $\eta_p^2 = .16$, and no significant interactions between these two factors and laterality, both $F(1,11) < 1.32$, $p > .276$, $\eta_p^2 < .12$, indicating that N2pc amplitudes did not differ systematically between SOA conditions, or between H1 and H2 targets. Follow up t -tests comparing contra- with ipsilateral activity separately for H1 and H2 targets and both SOA conditions confirmed that all four N2pc components were reliably present, all $t(11) > 5.34$, $p < .001$, $d > .31$.

A repeated-measures ANOVA of N2pc onset latencies with the factors SOA and display sequence revealed a significant interaction between these two factors, $F_c(1,11) = 150.03$, $p < .001$, $\eta_p^2 = .93$, showing that N2pc latency differences between H1 and H2 targets were more pronounced in the SOA 100 condition. A paired t -test revealed that the N2pc to H2 targets emerged 121 ms later than the N2pc to H1 targets in this condition, (324 ms versus 203 ms after the onset of the first display), $t_c(11) = 17.56$, $p < .001$, $\eta_p^2 = .97$. In the SOA 10 condition, the N2pc onset latency difference between H1 and H2 targets (214 versus 219 ms) failed to reach significance, $t_c(11) = 1.29$, $p = .224$, $\eta_p^2 = .13$.

N2pc components to targets with colour-matching and shape-matching distractors

Although the N2pc results shown in Figure 4.2 suggest that two successively presented colour/shape targets can be selected rapidly and independently, they do not yet provide conclusive evidence for the rapid guidance of attention by colour/shape conjunctions. Target objects were accompanied either by a shape-matching or by a colour-matching distractor, and it remains theoretically possible that target selection was controlled exclusively by one of the two target-defining features, and thus operative only for one of the two displays on each trial. For example, a purely colour-based attentional guidance process would result in N2pc components only for displays with a horizontal target and a shape-

matching distractor on opposite sides, but not for displays with two target-colour objects (the target and a colour-matching distractor). The N2pc components shown in Figure 4.2 could reflect the average across these two types of displays. To rule out this possibility, we computed N2pc components separately for targets accompanied by colour-matching and shape-matching distractors, separately for H1 and H2 targets and both SOA conditions.

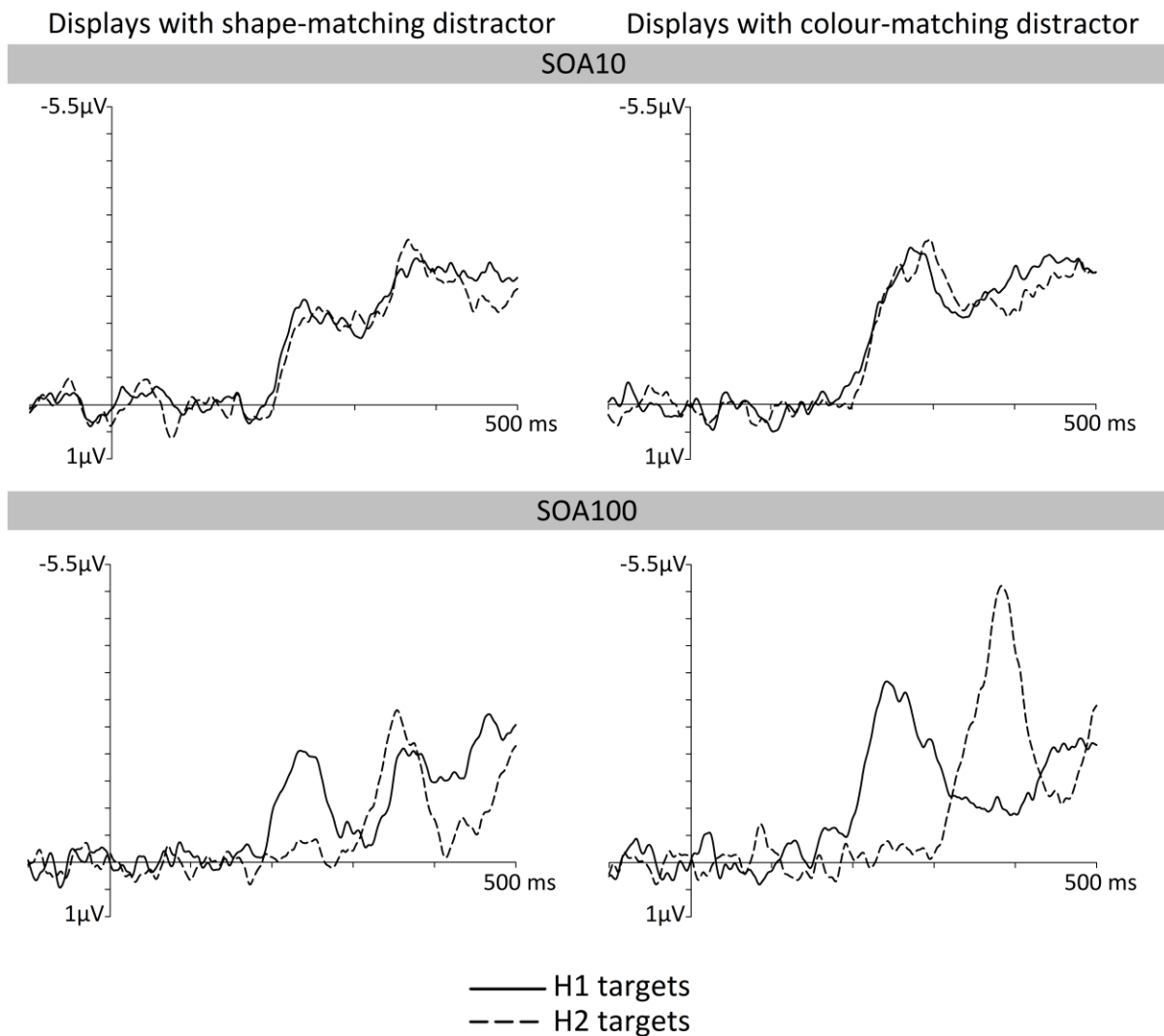


Figure 4.3: N2pc difference waveforms obtained by subtracting ERPs ipsilateral to the target from contralateral ERPs in Experiment 4, shown separately for H1 and H2 targets that were accompanied by a shape-matching distractor (left panels) or colour-matching distractor (right panels) in the SOA 10 condition and the SOA 100 condition.

As can be seen in the resulting N2pc difference waveforms shown in Figure 4.3, target N2pc components were not only present for horizontal displays that included shape-matching distractors but also for displays where targets and colour-matching distractors appeared on opposite sides. Paired t-tests comparing contralateral and ipsilateral ERPs in the N2pc time windows confirmed that reliable target N2pc components were present both when targets were accompanied by colour-matching or by shape-matching distractors, for each combination of SOA condition and display sequence, all $t(11) > 3.93$, $p < .01$, $d > .27$. N2pc components were larger for targets accompanied by colour-matching distractors than for those in displays with shape-matching distractors (see Figure 4.3). This was confirmed in a repeated-measures ANOVA of N2pc mean amplitudes with the factors SOA condition, display sequence, laterality, and the new additional factor distractor type (colour-match versus shape-match). This ANOVA revealed a significant interaction between distractor type and laterality, $F(1,11) = 11.93$, $p < .01$, $\eta_p^2 = .52$, reflecting the fact that targets triggered larger N2pcs when they appeared together with a colour-matching distractor than when they were accompanied by a shape-matching distractor.

4.2.4 Discussion

In Experiment 4, two targets defined by a conjunction of colour and shape appeared in two displays that were presented in rapid succession, with SOAs of 100 ms or 10 ms. The results obtained in this experiment provide no evidence that the allocation of attention to these two target objects operated in a serial fashion under these conditions. In fact, the temporal pattern of N2pc components to H1 and H2 targets was very similar to the results of previous studies where target selection could be based on a single feature such as colour or

shape (e.g., Eimer & Grubert, 2014a). As in these earlier studies, N2pc components of similar size were elicited by horizontal targets in the first and second display, and the onset latency difference between these two N2pc components approximately matched the objective SOA between the two displays. Critically, this was the case not only in the SOA 100 condition, where the interval between the two displays may have been long enough to accommodate serial attention shifts between the two targets, but also in the SOA 10 condition. Here, the N2pcs to H1 and H2 targets were identical in size and overlapped in time (see Figure 4.2, top panels). This observation is inconsistent with the hypothesis that the attentional selection of two conjunctively defined targets always requires serial shifts of attention, so that attention can only be allocated to the second target after it has been withdrawn from its original location. This serial selection scenario would also predict substantial performance costs for the SOA 10 relative to the SOA 100 condition. In fact, participants were more accurate with shorter SOAs, and there was also a tendency towards faster RTs in the SOA 10 condition. This pattern of behavioural results is most likely due to the fact that in the SOA 10 condition, a sensory representation of the first target was still available when a visual representation of the second target is generated, so that gap locations of both targets could be directly compared. In the SOA 100 condition, the sensory representation of the first target shape may have already faded when the percept of the second target was created, and a stable working memory representation of this shape was not yet available, resulting in performance costs (see Brockmole, Wang, & Irwin, 2002; Dalvit & Eimer, 2011, for behavioural and ERP studies of perceptual and memory-based comparison processes across successive displays and how they are affected by the SOA between these displays).

The fact that N2pcs to H1 and H2 targets were present regardless of whether targets were accompanied by shape-matching or by colour-matching distractors in the same display (see Figure 4.3) demonstrates that target selection was not only based on one of the two

target-defining features, and confirms that both colour and shape were involved in the parallel guidance of attention. The results of Experiment 4 thus provide clear evidence that attentional biases in favour of two target objects presented in rapid succession can be triggered independently and in parallel, even when these objects cannot be discriminated from distractors on the basis of a single visual feature, but are defined by a conjunction of colour and shape. This raises the important question of how these spatially selective processing biases were generated. One possibility is that they emerged as the result of separate search templates for the target colour and the target shape that operated independently and in parallel. In displays where a target was accompanied by a colour-matching distractor on the opposite side, shape-based attentional guidance would result in a lateralised spatial bias for the target location, resulting in a target N2pc. Colour-based guidance would result in a bilateral bias, and two N2pc components over opposite hemispheres that cancel each other out. If these two guidance processes operated in parallel, their net result would be an N2pc contralateral to the target. An analogous pattern can be predicted for displays where the target is presented together with a shape-matching distractor. In this case, the N2pc components observed in Experiment 4 would reflect the net spatial bias triggered by target objects due to the fact that they always possess both template-matching features, whereas the distractor in the same display only has one of these features. An alternative possibility is that attention was guided by a single target object template that represents both target-defining features in an integrated fashion (e.g., “blue circle”). In this case, target objects will attract attention but partially matching distractors will not, because they do not match the integrated target object template. The N2pc components measured in Experiment 4 would therefore exclusively reflect the spatial bias triggered by target objects. Because N2pc components reflect relative differences in attentional biases between hemispheres, these two possibilities cannot be distinguished on the basis of the N2pc results of Experiment 4, where targets and partially

matching distractors always appeared in the same display. To find out whether attentional allocation processes during search for colour/shape conjunction targets are controlled by separate feature templates for colour and shape or by an integrated object template, N2pc components need to be measured independently for targets and for colour-matching and shape-matching distractors. This was done in Experiment 5.

4.3 Experiment 5: Attentional Selection of Partially Target-matching Distractors

4.3.1 Introduction

As in Experiment 4, targets were defined by a specific colour/shape combination, and trials where a horizontal stimulus pair preceded or followed a vertical stimulus pair were randomly intermixed. The SOA between the two displays was always 10 ms. However, some displays now contained a colour-matching or shape-matching distractor with a nontarget object without target-matching features on the opposite side. These displays were either preceded or followed by another display that contained a target and a task-irrelevant nontarget object (see Figure 5.1). In addition to these one-target (1T) trials, there were also two-target (2T) trials with two successive displays that contained a target and a task-irrelevant nontarget object on opposite sides. Participants' task was to report the number of target objects. The temporal pattern of N2pc components to H1 and H2 targets was expected to be similar to the results observed in the SOA 10 condition of Experiment 4. The critical new question was whether horizontal shape-matching and colour-matching distractors would elicit N2pc components in 1T trials when they were preceded or followed by another display that included a vertical target. If attention was controlled by templates that represent targets as integrated objects, these partially matching distractors should not be able to attract attention and should therefore

not trigger any N2pcs. If the allocation of attention was guided in a strictly feature-based fashion by separate colour and shape templates, N2pc components should not only be triggered by targets but also by colour-matching and shape-matching distractors. If colour-based and shape-based guidance processes operated in an entirely independent non-interactive way, target N2pc components should reflect the additive effects of the spatial biases triggered by target colours and shapes, and should therefore be identical to the sum of the two N2pc components triggered by colour-matching and shape-matching distractors.

4.3.2 Methods

Participants

Thirteen participants were paid to take part in this experiment. One of them was excluded from analysis due to excessive eye movement activity. The remaining twelve participants were aged between 20 and 38 ($M = 29$, $SD = 5.39$). Nine were female; four were left-handed. All participants had normal or corrected-to-normal vision.

Stimuli and Procedure

As in Experiment 4, stimuli were coloured outline shapes, but no longer included any gaps. The possible stimulus colours were blue (CIE colour coordinates: .279/.265), purple (.365/.299), or red (.470/.340). All colours were equiluminant (11.5 cd/m²). Each participant was assigned a specific target shape/colour conjunction that remained constant throughout the experiment. In contrast to Experiment 4, each display now contained only one object with target-matching features (either the target or a partially matching distractor), which was always accompanied by a nontarget object without target-matching features on the opposite

side. The other main difference to Experiment 4 was that trials could include either one or two target objects (see Figure 5.1). In one-target trials, one of the two displays contained a target/nontarget pair, while the other contained a partially matching distractor/nontarget pair. In two-target trials, the two successive displays both contained a target/nontarget pair. There were also infrequent no-target catch trials, where both displays contained a partially matching distractor/nontarget pair. Participants' task was to report the number of targets presented in each trial (one or two), and to refrain from responding if no targets were detected.

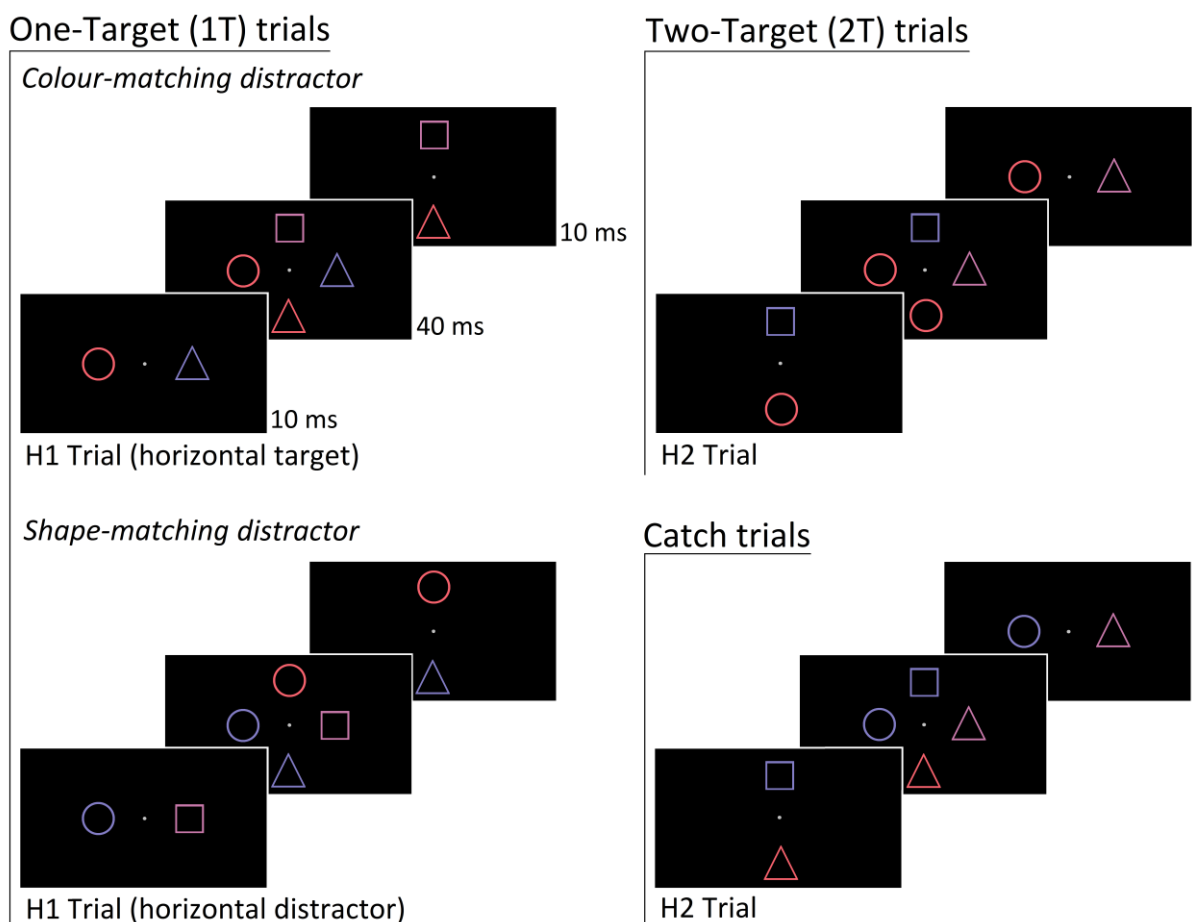


Figure 5.1: Schematic illustration of the search displays and the time course of events in one-target (1T) trials, two-target (2T) trials, and catch trials of Experiment 5. In the examples shown, the target is the red circle. Participant's task was to report the number of targets (one or two) and refrain from responding on catch trials. On 1T trials, one display contained the target and a task-irrelevant nontarget, and the other a colour-matching or shape-matching distractor with an irrelevant nontarget (shown

separately). Displays with a horizontal target or distractor preceded vertical displays (H1 trials) or vice versa (H2 trials).

Only the SOA 10 condition was tested in Experiment 5, which contained 24 blocks of 72 trials. In each block, there were 48 one-target (1T) trials, 16 two-target (2T) trials, and 8 catch trials, which were presented in a randomly intermixed fashion. Note that “one target” responses were three times as likely as “two target” responses. Display sequence (horizontal display first or second: H1 or H2 trials, with horizontal displays containing either a target or a partially matching distractor), and the temporal and spatial position of targets and partially matching distractors was randomly and independently determined on each trial. Each display was presented for 50 ms, and the interval between the offset of the second display and the onset of the first display on the next trial was 1500 ms. All other aspects of procedure and stimulus presentation were identical to Experiment 4.

EEG recording and data analyses

All aspects of EEG recording and data analysis were identical to Experiment 4. Rejection of trials contaminated with artifacts, very slow or anticipatory responses, or incorrect or missing responses led to an exclusion of an average of 13.4% of all trials (12.4% and 11.8% in 1T trials with a horizontal target or partially matching distractor, respectively, and 17.5% in 2T trials). N2pc components were computed separately for target objects and for colour-matching and shape-matching distractor objects on the horizontal midline, separately for H1 and H2 trials, and for 1T and 2T trials. The time windows used for N2pc mean amplitude analyses were the same as in the SOA 10 condition of Experiment 4, and jackknife-based N2pc latency analyses were also identical to these experiments.

4.3.3 Results

Behavioural performance

There were no anticipatory or very slow RTs in Experiment 5. A repeated-measures ANOVA with the factors trial type (1T versus 2T trials) and display sequence (H1 versus H2 targets) was run separately for RTs and for error rates. For RTs, there was a main effect of trial type, $F(1,11) = 59.87, p < .001, \eta_p^2 = .85$, indicating faster RTs in the more frequent 1T trials relative to the less frequent 2T trials (504 ms versus 567 ms). There was no effect of display sequence (536 ms for both H1 and H2 trials) and no interaction between both factors, both $F(1,11) < 1.05, p > .834, \eta_p^2 < .01$. For error rates on target-present trials, a main effect of trial type, $F(1,11) = 27.70, p < .001, \eta_p^2 = .72$, indicated that error rates were less frequent in 1T than in 2T trials (1.5% versus 9.0%). The main effect of display sequence (3.9% and 3.6% for H1 and H2 trials, respectively) only approached significance, $F(1,11) = 4.67, p = .054, \eta_p^2 = .30$, as did the interaction between both factors, $F(1,11) = 4.06, p = .069, \eta_p^2 = .27$. The False Alarm rate on target-absent catch trials was 3.6% where there was no target present.

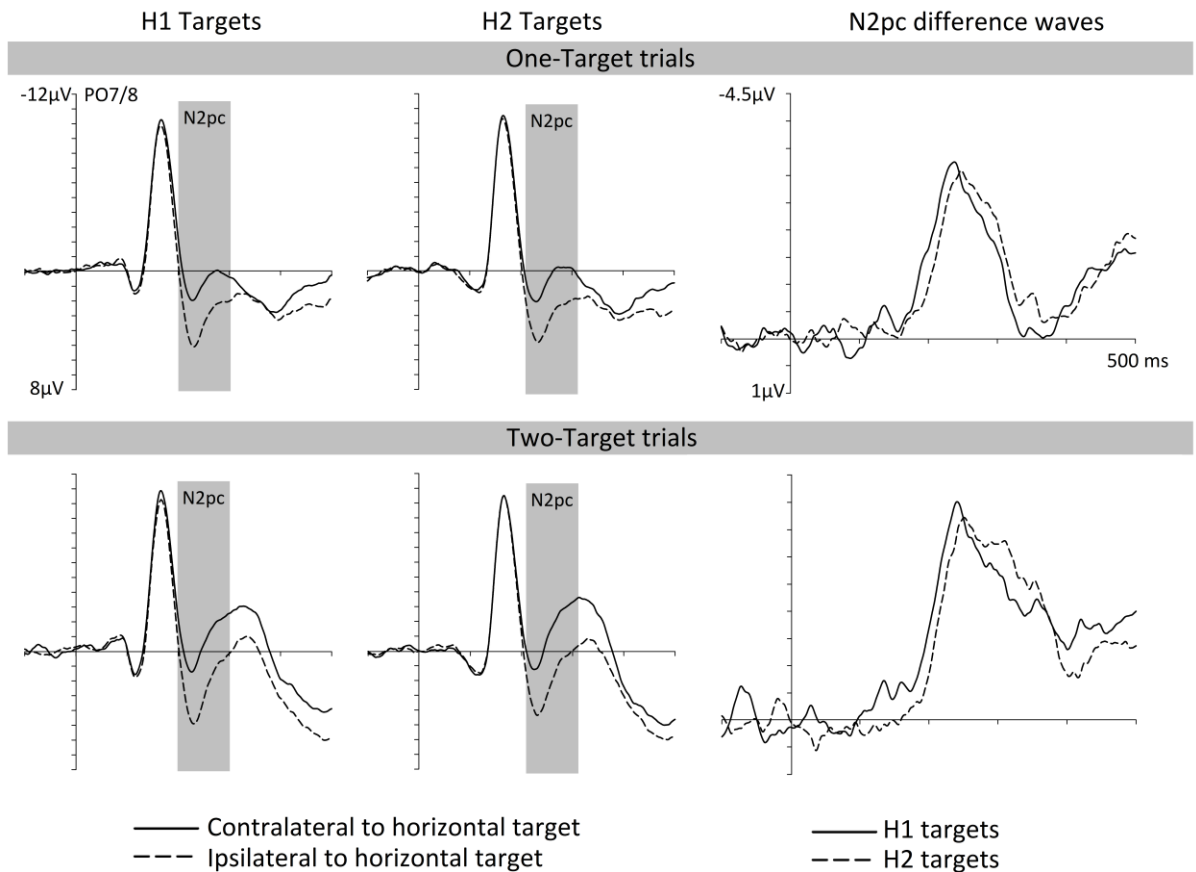


Figure 5.2: N2pc components elicited by target objects on one-target (1T) and two-target (2T) trials in Experiment 5. Left and middle panels: Grand-average ERP waveforms measured in the 500 ms interval after the onset of the first search display at posterior electrodes PO7/PO8 contralateral and ipsilateral to a horizontal target in the first display (H1 targets) or second display (H2 targets). Right panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for H1 and H2 targets, and for 1T and 2T trials.

N2pc components to targets

Figure 5.2 (left and middle panels) shows ERPs for target-horizontal trials in an identical fashion to Experiment 4. Clear N2pc components were elicited by H1 and H2 targets on 1T as well as 2T trials, and N2pc latencies to H1 and H2 targets reflected the objective 10 ms SOA between the two displays (as shown in the right panel of Figure 5.2

depicting difference waves obtained by subtracting ipsi- from contralateral ERPs). A repeated-measures ANOVA of N2pc mean amplitudes with the factors trial type (1T versus 2T), display sequence (H1 versus H2 target), and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target), revealed a main effect of laterality, $F(1,11) = 67.16, p < .001, \eta_p^2 = .86$, indicating that N2pc components were reliably elicited by horizontal target items. There was a significant interaction between trial type and laterality, $F(1,11) = 13.87, p < .01, \eta_p^2 = .56$, as N2pc components were generally larger on 2T than on 1T trials (as shown in Figure 5.2). None of the interactions involving the factor display sequence reached significance, all $F(1,11) < .20, p > .665, \eta_p^2 < .02$. Follow up *t*-tests comparing contra- with ipsilateral activity in response to H1 and H2 targets separately for 1T and 2T trials, confirmed that all four N2pc components were reliably present, all $t(11) > 6.86, p < .001, d > .55$. For N2pc onset latency values, a repeated-measures ANOVA with the factors trial type and display sequence revealed a main effect of display sequence, $F_c(1,11) = 20.71, p < .001, \eta_p^2_c = .65$, demonstrating that N2pc components to H2 targets were reliably delayed relative to the N2pcs to H1 targets by about 15 ms (201 ms versus 185 ms for 1T trials; 202 ms versus 188 ms for 2T trials).

N2pc components to partially matching distractors

Figure 5.3 shows ERPs measured on 1T trials that included a vertical target in one display and a horizontal colour-matching or shape-matching distractor in the other display. Clear N2pc components were elicited by both types of horizontal partially matching distractors in the first and second display (H1 and H2 trials). A repeated-measures ANOVA conducted on N2pc mean amplitudes with the factors distractor type (shape-match versus colour-match), display sequence (H1 versus H2 distractor) and laterality (electrode

contralateral versus ipsilateral to the side of the horizontal distractor), revealed a main effect of laterality, $F(1,11) = 52.86, p < .001, \eta_p^2 = .83$, indicating that N2pc components were reliably elicited in response to these partially matching distractors. There were no reliable interactions between laterality and display sequence, $F(1,11) = .00, p = .960, \eta_p^2 = .00$, or between laterality and distractor type, $F(1,11) = 1.50, p = .246, \eta_p^2 = .12$, suggesting that N2pc amplitudes did not differ between H1 and H2 distractors, or between colour- and shape-matching distractors. Follow up *t*-tests comparing contra- with ipsilateral activity separately for H1 and H2 trials and both types of partially matching distractors confirmed that all four N2pc components were reliably present, all $t(11) > 4.41, p < .01, d > .23$.

N2pc components to targets and partially matching distractors

Finally, we directly compared N2pc components to targets and to partially matching distractors. These analyses included N2pcs measured in response to colour-matching and shape-matching distractors in 1T trials, and target N2pc components observed in 2T trials, because these two types of trials both contained a target object in the other (vertical) display. N2pc components to targets were larger than N2pc components to partially matching distractors (as is evident when comparing Figures 5.2 and 5.3). Repeated-measures ANOVAs conducted separately for targets versus colour-matching or shape-matching distractors on H1 or H2 trials confirmed that target N2pc amplitudes were significantly larger than N2pc amplitudes to shape-matching or colour-matching distractors, all $F(1,11) > 23.89, p < .001, \eta_p^2 > .68$.

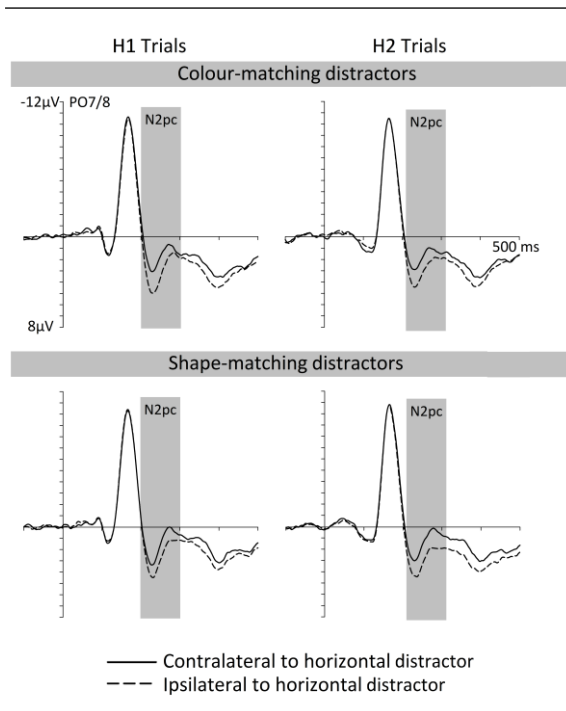


Figure 5.3: N2pc components elicited in Experiment 5 on 1T trials by horizontal colour-matching or shape-matching distractors. Grand-average ERP waveforms measured in the 500 ms interval after the onset of the first search display at posterior electrodes PO7/PO8 contralateral and ipsilateral to a horizontal partially matching distractor are shown separately for trials where the distractor appeared in the first display (H1 distractor) or second display (H2 distractor).

Do the N2pc components triggered by target objects simply reflect the additive contributions of the N2pc components to colour-matching and shape-matching distractors, or are target N2pc amplitudes larger than the sum of the two N2pcs to these two types of distractors? To answer this question, we averaged N2pc components across H1 and H2 trials (after aligning them temporally to the onset of the respective horizontal display, which was 10 ms later on H2 trials), separately for target objects on 2T trials and for colour-matching and shape-matching distractors on 1T trials. Next, N2pc components triggered by colour-matching and shape-matching distractors were summed, and compared to the N2pc elicited by target objects. The resulting N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs are shown in Figure 5.4. The summed N2pc response to colour- and shape-matching distractors was initially very similar to the target N2pc, up to approximately 230 ms after display onset. Beyond this point in time, the N2pc to target objects became larger than the summed N2pc to the two types of distractors (i.e., superadditive). We employed two procedures to formally test when the target N2pc became larger than the summed contribution of the N2pcs to colour- and shape-matching distractors.

First, the summed N2pc difference waveform for partially matching distractors was subtracted from the N2pc difference wave for targets, separately for each participant, followed by a jackknife-based analysis of these double subtraction waveforms with an onset criterion of $-0.5 \mu\text{V}$. This analysis showed that N2pc amplitudes to targets became larger than the summed N2pcs to partially matching distractors at 232 ms after display onset. In an independent second analysis, we conducted successive one-tailed paired t-tests comparing individual N2pc difference waves for targets and summed partially matching distractors for each consecutive 2 ms sampling point after display onset. A significant amplitude difference between these two waveforms had to remain present for at least five consecutive subsequent sampling points (corresponding to 10 ms) in order to be interpreted as marking the onset of a superadditive target N2pc component. This procedure yielded an onset estimate of 234 ms post-stimulus (with p values of .040, .029, .019, .014, and .014 in the 10 ms time period from 234 ms to 244 ms, respectively), which matched the result from the jackknife-based analysis almost perfectly.

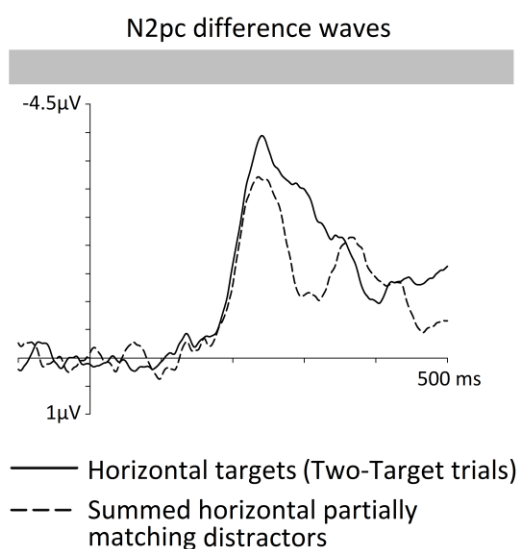


Figure 5.4: N2pc difference waveforms obtained in Experiment 5 by subtracting ipsilateral from contralateral ERPs. These difference waves were collapsed across H1 and H2 trials, after temporal alignment to the onset of the horizontal display on these trials. The solid line shows the N2pc component triggered by horizontal target objects on 2T trials. The dashed line shows the sum of the two N2pc components elicited by horizontal colour-matching and shape-

matching distractors on 1T trials. See text for details.

4.3.4 Discussion

The N2pc results obtained in Experiment 5 rule out the hypothesis that the attentional selection of targets defined by a conjunction of colour and shape is guided by templates that represent targets as fully integrated objects. If this was the case, colour-matching or shape-matching distractors should not have been able to attract attention and to trigger N2pc components. In fact, horizontal colour-matching and shape-matching distractors elicited clear N2pc components on 1T trials where they were preceded or followed by a vertical target in the other display (see Figure 5.3). The presence of N2pc components to partially matching distractors shows that the attentional processing biases triggered during colour/shape conjunction search are at least in part controlled by processes that operate in a feature-specific fashion, irrespective of the presence or absence of the other target attribute.

N2pc components to targets were larger than the N2pcs triggered by colour- and shape-matching distractors, in line with the possibility that target N2pcs reflect the additive effects of independently operating colour-based and shape-based guidance processes. Direct comparisons between the sum of the N2pcs to these two types of partially matching distractors to target N2pc amplitudes revealed that this was indeed the case for the early phase of the N2pc, up to around 230 ms after display onset (see Figure 5.4). During this phase, attentional processing biases were apparently generated in a local fashion by independent feature-specific guidance processes. Beyond this time point, the target N2pc was larger than the sum of the two N2pcs to partially matching distractors, suggesting that attentional guidance was no longer exclusively feature-based (see below for further discussion). Whether such object-based processing resulted in attentional enhancement of the conjunctive target, or suppression of the partially matching nontargets, is unclear on the basis of the current results, and would require direct comparisons with N2pc responses to single-feature targets in a feature search task.

In addition to the presence of N2pc components to colour- and shape-matching distractors, Experiment 5 also revealed a pattern of target N2pc components that was similar to the SOA 10 condition of Experiment 4. Temporally overlapping N2pc components of similar size were triggered by H1 and H2 targets, both on 1T and 2T trials (see Figure 5.2). The onset latency differences between N2pcs to H1 versus H2 targets (about 15 ms) closely matched the objective 10 ms between the two displays. In contrast to Experiment 4, this latency difference was significant, and target N2pc amplitudes were substantially larger in Experiment 5 (compare Figures 4.2 and 5.2). As discussed below, these differences are likely to reflect the fact that targets were accompanied in the same display by partially matching distractor objects in Experiment 4, but by objects without template-matching features in Experiment 5.

In line with the assumption that the two targets in the two successive displays were selected independently and in parallel, there was no evidence that the presence of a vertical target in the second display attenuated the N2pc to horizontal targets on 2T trials relative to 1T trials where only a single target was present. In fact, the opposite was the case, as target N2pc components were larger on 2T trials as compared to 1T trials (Figure 5.2). The factors responsible for this unexpected result are not clear. One possibility is that 1T trials were much more frequent than 2T trials, which may have resulted in an increased attentional bias towards targets when two target objects appeared unexpectedly in rapid succession. Another possibility that needs to be investigated in future experiments is that the near-simultaneous presentation of two identical target objects magnifies the attentional response to both of them relative to trials where only a single target is present.

4.4 General Discussion

The current study measured N2pc components to track the allocation of attention to two target objects in two displays that were presented in rapid succession. Previous studies using similar rapid sequential presentation procedures with feature-defined targets have shown that attention is allocated rapidly and in parallel to both target objects, with each selection process following its own independent time course (Eimer & Grubert, 2014a; Grubert & Eimer, 2015, 2016; Experiment 1 of this thesis). In contrast to these earlier experiments, target objects were now defined by a specific combination of colour and shape. According to Feature Integration Theory (e.g., Treisman & Gelade, 1980; Treisman, 1988), the identification of such targets is based on the integration of information across feature dimensions, which requires focal attention that can only be allocated serially to one object at a time. The Guided Search model (Wolfe, 2007) also assumes that attentional object selection processes during conjunction search operate in a sequential fashion. If this was the case, the temporal pattern of N2pc components elicited by the two target objects in the present study should be different to the pattern found previously when targets and nontargets could be distinguished on the basis of a single feature. In fact, the N2pc results obtained in Experiment 4 were very similar to results found in these earlier studies, in spite of the fact that targets were always accompanied by a colour-matching or shape-matching distractor in the same display, and could therefore not be selected on the basis of a unique target-defining feature. The observation that targets in the first and second display both elicited N2pc components of similar size, and the fact that these two components overlapped in time when the SOA between the two displays was 10 ms, shows that spatial biases for both target objects developed rapidly and independently, in line with the assumption that attention was allocated in parallel to both objects.

Experiment 5 investigated whether the parallel attentional processing biases for two conjunctively defined target objects revealed in Experiment 4 were the result of a single

integrated object template, or of independent feature-specific search templates for colour and shape. Horizontal colour-matching and shape-matching distractors that appeared together with a nontarget in the same display both elicited reliable N2pcs, demonstrating that they were able to attract attention. This observation rules out the possibility that attentional selectivity was entirely controlled by search templates that represent target features in an integrated object-based fashion. During the initial phase of the N2pc until about 230 ms after display onset, the sum of the two N2pc components to partially matching distractors was identical to the N2pc triggered by targets. During this time window, the attentional processing biases reflected by the N2pc were generated entirely independently by colour and shape templates, with target N2pcs reflecting the joint contribution of these feature-specific guidance processes.

If attentional selection processes are initially guided exclusively in a feature-specific fashion, thereby allowing partially matching distractors to attract attention and elicit N2pc components, as shown in Experiment 5, this implies that the target N2pc components observed in Experiment 4 do not exclusively reflect the attentional selection of these target objects, but instead the difference between the spatial biases elicited simultaneously in opposite hemispheres by targets and by colour-matching or shape-matching distractors in the same display. In Experiment 5, targets were always accompanied by objects without any target-matching features, and N2pc components to target objects will therefore reflect the pure spatial bias triggered by these objects. If this is correct, target N2pc components should be larger in Experiment 5 relative to Experiment 4. A comparison of N2pc components to H1 and H2 targets elicited in the SOA 10 conditions of Experiment 4 (Figure 4.2, top panels) and Experiment 5 (Figure 5.2, top panels) shows that this was indeed the case. A post-hoc analysis of target N2pc mean amplitudes in Experiment 4 (SOA 10 condition) and Experiment 5, with laterality and display sequence as within-participant factors, and

experiment as between-participant factor, confirmed this observation. There was a significant interaction between laterality and experiment, $F(1,22) = 7.89, p < .05, \eta_p^2 = .26$, reflecting the presence of attenuated N2pc components in Experiment 4 as compared to Experiment 5. This provides additional support for the hypothesis that rapid parallel feature-guided attentional biases were triggered concurrently in opposite hemispheres by targets and partially matching distractors in Experiment 4.

In Experiment 5, target N2pc amplitudes became superadditive (i.e., larger than the sum of the N2pcs to colour-matching and shape-matching distractors) beyond 230 ms. A similar temporal pattern of N2pc amplitudes was observed in several of our previous studies investigating visual search for conjunctively defined target objects. In these experiments, search displays could contain a target, a distractor that matched one but not the other target-defining feature, or both the target and a partially matching distractor. Targets were defined by a combination of colour and shape (Eimer & Grubert, 2014b), a combination of two colours (Berggren & Eimer, 2016), or a combination of colour and alphanumeric category (Nako, Grubert, & Eimer, 2016). In all of these tasks, target N2pc amplitudes initially equalled the sum of the N2pcs to the two partially matching distractors, and became superadditive at some point between 220 and 250 ms after search display onset. Interestingly, a very similar temporal pattern of additive, followed by superadditive ERP modulations in response to target-defining features and feature conjunctions, was found in a study by Anllo-Vento, Schoenfeld, & Hillyard (2004) for displays that contained only a single stimulus at fixation. These stimuli were vertical or horizontal bar gratings that were either orange or red, and participants had to attend to one specific colour/orientation combination. Stimuli with the attended orientation and attended colour both elicited a posterior selection negativity (SN), which is observed in non-search tasks where each display contains a single object for objects with attended features (e.g., Anllo-Vento, Luck, & Hillyard, 1998). Importantly, the SN

elicited by target objects that matched both the task-relevant bar orientation and colour was initially identical in amplitude to the sum of the two SN components triggered by the colour-matching and orientation-matching nontargets. Beyond 225 ms, SN amplitudes to targets became superadditive. This result was interpreted by Anllo-Vento et al. as demonstrating that at this point in time, attentional selection processes became sensitive to the presence of the target-defining feature conjunction. In contrast to the N2pc, which reflects a lateralised bias of visual processing elicited by task-relevant features or objects in the left or right visual field, the SN components reported by Anllo-Vento et al. were not lateralised, due to the fact that they were triggered in response to single objects at fixation. In spite of this difference, the observation that a superadditive attentional bias for conjunctively defined target objects emerges at almost exactly the same point in time for both components is intriguing, since it suggests that similar attentional selection processes may be operative in single-stimulus and multiple-stimulus visual displays. The onset of superadditive N2pc and SN components to conjunctively defined targets may mark the point in time where attentional biases are no longer generated in an entirely feature-specific fashion, but start to be affected by the joint presence of different target-defining features in the same object. The fact that this superadditivity was observed in the present Experiment 5 where the critical display was immediately preceded or followed within 10 ms by another display that contained a vertical target object suggests that such processing biases for feature conjunctions can be triggered in parallel for different objects in the visual field.

In Experiment 5, the N2pc to horizontal targets was compared to the sum of the two N2pc components to horizontal shape-matching and colour-matching distractors elicited on trials where the other display contained a vertical target object (see Figure 5.4). A potential problem with this approach is that by adding the N2pcs to partially matching distractors, any impact of the vertical target object on these N2pcs is also included twice in the resulting

summed waveforms. The observation that the target N2pc initially equalled the sum of the two N2pcs to partially matching distractors shows that up to about 230 ms post-stimulus, vertical targets in the other display had no impact on the attentional biases triggered by these distractors, in line with the assumption that these biases were triggered in a local feature-based fashion. However, the presence of vertical targets in the other display may have contributed to the reduction of summed N2pc amplitudes to these distractors beyond this point in time. Although this possibility cannot be ruled out entirely, it is important to note that previous N2pc studies of conjunction search (e.g., Eimer & Grubert, 2014b; Berggren & Eimer, 2016) found analogous sequences of additive followed by superadditive target N2pc components for displays where targets and partially matching nontargets appeared without a potentially competing target-matching object on the vertical midline. Furthermore, as described earlier, Anllo-Vento et al. (2004) found a nearly identical temporal sequence of additive followed by superadditive SN components for conjunctively defined target objects in single-stimulus displays. The similarity between these previous findings and the results of the current Experiment 5 suggests that competitive influences from vertical targets on N2pcs to partially matching distractors are unlikely to be the main cause of the superadditivity of target N2pcs observed beyond 230 ms post-stimulus.

What are the general implications of the current results for the nature of attentional mechanisms in conjunction search tasks? The current N2pc results demonstrate that attentional biases for target features and objects can be triggered in parallel and independently at different locations in the visual field. However, it could be argued that the presence of such spatially selective processing biases does not provide sufficient evidence to conclude that attentional selection operates in parallel during conjunction search. One central finding of the current study was that these biases were initially triggered independently and in parallel by target colours and target shapes, and contributed additively to the early phase of

the N2pc component in the present experiments. This is very much in line with previous research on feature-based attention in humans and non-human primates, which has demonstrated that currently task-relevant features trigger attentional modulations of visual processing in a spatially global fashion across the visual field (e.g., Martinez-Trujillo & Treue 2004; Saenz, Buracas, & Boynton, 2002; Serences & Boynton, 2007), even when attention and eye gaze are directed elsewhere (Bichot, Rossi, & Desimone, 2005). Visual processing modulations produced by feature-based attention can occur simultaneously at multiple locations in the visual field (Andersen, Hillyard, & Müller, 2008; Andersen, Müller, & Hillyard, 2015), as was the case for the parallel colour-based and shape-based attentional biases found in Experiment 5. It is often assumed that feature-based attention and attentional object selection are separate processes. For example, feature-based attention may highlight the locations of potentially task-relevant features during visual search, thereby providing guiding signals for a subsequent serial object selection stage (e.g., Bichot et al., 2005; Maunsell & Treue, 2006). Such suggestions are based on the traditional two-stage architecture of visual processing (e.g., Broadbent, 1958), which assumes a fundamental division between early parallel automatic processes (including spatially global feature-based attention) and later serial controlled processes, with attentional selection marking the transition between these two types of processing. If feature-based attention and attentional selection are separate processing stages, the presence of parallel feature-based attentional modulations for multiple objects cannot be used to draw conclusions about the nature of attentional object selection processes during conjunction search. An alternative is to reject the standard two-stage architecture and to describe attentional selection instead as a temporally extended process where visual processing biases for task-relevant features and objects (as reflected by N2pc components) develop continuously in real time. Such attentional biases can initially be generated in parallel at multiple locations, but may then become more selective,

due to competitive interactions between objects at different levels of the visual processing hierarchy (e.g., Desimone & Duncan, 1995; Duncan, 2006). Within this alternative conceptual framework, attentional selectivity refers to the presence of such visual processing biases at a particular time point, with spatially global effects of feature-based attention and subsequent biases that are sensitive to the presence of feature conjunctions reflecting different phases of selective attentional processing at different moments in time (see Eimer, 2014, 2015, for further discussion). In this context, the current results show that both types of biases can be elicited in parallel by multiple objects during conjunction search.

A final important conceptual issue concerns the role of display size for the efficiency of conjunction search. In the present study, each of the two successive displays only contained two objects on opposite sides, and participants had to select two out of these four objects as targets. As shown by the N2pc results for Experiment 4, attentional biases for conjunctively defined target objects were triggered rapidly and in parallel even though these targets were accompanied by a single partially matching distractor in each display. It is well known that the efficiency of conjunction search decreases as the number of partially target-matching distractor objects increases (e.g., Wolfe, 1998b). Because these distractors all have the potential to elicit feature-based attentional processing biases, adding more of them to the same display will reduce the net attentional bias towards the target, and therefore make target-distractor discriminations more difficult. According to a recent suggestion by Hulleman & Olivers (2017), the difficulty of these discriminations determines the size of the functional viewing field (FVF) – the area within which attentional selection processes operate in parallel during any given fixation period. When conjunction search becomes more difficult because more partially matching distractors are added, the size of each FVF decreases, resulting in more eye movements and longer search times. In the present study, where each display was presented for 50 ms and eye movements were not allowed, all objects had to be

processed within a single fixation and therefore all needed to be included within the same FVF. The time course of the attentional selection processes revealed by the temporal pattern of N2pc components therefore reflects the guidance of attention during conjunction search within a single fixation episode where the FVF included all display stimuli. Increasing the number of partially matching distractors in each of the two successively presented displays will decrease the size of the FVF, up to the point where it no longer includes both target objects. Under these conditions, the two targets may no longer be detectable within a single fixation episode, resulting in increased error rates and attenuated target N2pc components, which may specifically affect the N2pc to targets in the second display. These predictions will need to be assessed in future experiments.

In summary, the current study has demonstrated that two target objects defined by a conjunction of colour and shape and presented in rapid succession trigger parallel and independent attentional biases of visual processing. Initially, these biases are entirely feature-based, and are elicited separately for target-matching colours and shapes. During a subsequent phase, they become sensitive to the joint presence of target features in the same object. These findings show that the guidance of attentional object selection during conjunction search is based on spatially selective processing biases for objects with task-relevant features or feature combinations that emerge simultaneously and independently at different locations in the visual field.

When considering the current findings in the context of the attentional template, it is clear that precise conjunction representations are not possible; this is demonstrated by observable N2pc responses to partially matching distractors. Since these do not fully match the conjunctive target itself, the erroneous selection of these targets shows that they elicit a match with the representation(s) of the attentional template. In other words, features must be represented separately, without the possibility of combining feature information into a

conjunctive object representation in preparation for an upcoming search display. Despite this limitation of the attentional template's content, additional cognitive mechanisms are available to rapidly combine the responses across the retinotopic map that are elicited by these features, producing superadditive enhancements of visual processing of conjunctive targets. Thus, rapid parallel attentional selection of conjunctive targets is still made possible.

Chapter 5

When Attention is Necessarily Serial: Attention Shifts between Targets in Static Displays

The following experiments from this chapter have been accepted for publication in a peer-reviewed journal.

Experiments 7a & 7b:

Jenkins, M., Grubert, A., & Eimer, M. (in press-b). The speed of voluntary and priority-driven shifts of visual attention. *Journal of Experimental Psychology: Human Perception and Performance*.

5.1 Chapter Overview

This chapter explores scenarios in which attention must be allocated serially and sequentially between objects, rather than being allocated in parallel. Experiment 6 attempts to determine whether competition is a factor that necessitates serial attention shifts. In Experiments 7a and 7b, serial and sequential attention shifts are strictly necessitated by requiring the selection of a benchmark object before knowing the location of the target. The speed of priority-driven attention shifts, which are made on the basis of feature information, and voluntary attention shifts, which must be made on the basis of location and cannot be guided by the presence of stimulus properties, are directly compared.

5.2 Experiment 6: Can Serial Attention Shifts be induced by Competition Between Template-matching and Template-nonmatching Targets?

5.2.1 Introduction

When an observer searches for a known target object, the attentional selection of this object is facilitated by the use of an attentional template (see General Introduction chapter). While search for a single object can be easily explained by this top-down attentional control, there has been debate over the temporal dynamics of attentional selection of multiple task-relevant objects in the same display. As has been discussed throughout the previous chapters of this thesis, different models of visual search have argued either for the serial selection of objects that is limited to only one object at a time, or for parallel selection of multiple objects simultaneously.

The previous chapters of this thesis, along with a host of studies from our lab (e.g., Eimer & Grubert, 2014, Grubert & Eimer, 2015), have used the N2pc component to provide

strong evidence that attentional selection can take place in parallel. However, this does not imply that attention must always operate in this way. It is clear that serial shifts of attention can take place in tasks that require them. Horowitz, Wolfe, Alvarez, Cohen, and Kuzmova (2009) presented participants with rapidly changing displays containing objects at multiple locations. Participants were asked to move their attention in a specific sequential order between locations (e.g., clockwise), starting from a cued location. Crucially, the target object appeared in only one of these displays, at a location that corresponded to when this display was presented; for example, if the target appeared in the fourth display, it would appear in the fourth position clockwise from the cued location, requiring participants to shift their attention at each change in the display. Only when displays were changed with a speed of at least 250 ms were participants able to perform this task, suggesting that such voluntary movements of attention operate slowly. Further studies such as Sperling and Weichselgartner (1995) and Reeves and Sperling (1986) have used rapid serial visual presentation (RSVP) of characters in two separate streams, in which participants are asked to shift their attention from one stream to the next after encountering a cue. Results from these studies generally suggest that approximately 300 ms are required to perform such voluntary shifts of attention.

However, an important distinction can be made between such voluntary shifts of attention, where the focus of attention is endogenously moved to a location regardless of the visual properties of objects at these locations, and attention shifts that are guided by specific object features and can therefore be facilitated by attentional templates. At what speed do such priority-driven (template-guided) attention shifts take place? On the basis of behavioural evidence, serial shifts of attention should be able to operate at a rate of approximately 50 ms per item (e.g., Wolfe, 1998b), but the results of previous N2pc studies provide mixed answers. Woodman and Luck (2003) measured attention shifts between coloured objects in displays containing many grey distractors and two coloured objects, which shared the same

colour. One of the coloured objects was always nearer to fixation than the other, and participants were told that their target (as defined by its orientation) was one of these two coloured objects (Landolt squares). A sequential movement of attention was encouraged on the basis of the objects' distances from fixation: it was assumed that participants employed a strategy of attending to the near object first, and shifting attention to the further object if necessary. N2pc results indicated shift times of approximately 150 ms; though this is somewhat faster than behavioural measures of voluntary attention shifts (e.g., Horowitz, Wolfe, Alvarez, Cohen, & Kuzmova, 2009; Wolfe, Alvarez, & Horowitz, 2000), it is certainly slower than suggested by behavioural estimates of attention shifts (Wolfe, 1998b).

Grubert and Eimer (2016b) also used the N2pc to study priority-driven attention shifts; in their paradigm, four digits were presented on a single display at vertical and lateral locations. Two digits were grey, while the other two digits were coloured. More specifically, one digit always possessed a fixed colour that was known in advance to participants, while the other digit varied in colour randomly from trial to trial. Participants' task was to report whether the variable-colour digit was higher or lower in value than the fixed-colour digit. In this way, Grubert and Eimer assumed that a serial selection strategy was encouraged, as the task specification meant participants were likely to select the fixed-colour object first, before selecting the unknown variable-colour object for comparison (median split analyses confirmed the use of this strategy). The results of their study, as reflected by onset latencies of the N2pc responses to each coloured digit, revealed that priority-driven attention shifts could take place within just 60 ms. A further experiment attempted to maximise this shift speed by masking stimuli after 150 ms, but virtually identical shift times were found relative to their original experiment, indicating that 60 ms may represent a limit in the speed of priority-driven attention shifts. However, the nature of the task may also have created speed limits; because participants had to report a property of the variable-colour digit that was

relative to the fixed-colour digit (i.e., ‘higher’ or ‘lower’), it is likely that some identity processing of the fixed-colour digit took place before or concurrently to the selection of the variable-colour digit (see Moore & Wolfe, 2001; Wolfe, 2003; Wolfe, 2007, for models of concurrent processing of multiple objects that are selected serially), which presents two alternative accounts of the results. If the fixed-colour digit was identified before attention was deployed to the variable-colour digit, then the observed 60 ms N2pc onset delay between these two objects will also include the time taken to process the value of a digit. Alternatively, even if the processing of the fixed-colour digit’s identity can take place in parallel with the attentional selection of the variable-colour digit, such concurrent identity processing may still have slowed the speed of selection. A task which does not require processing of one object before shifting attention to the next would avoid this potential confound and may show that even faster priority-driven attention shifts are possible.

The goal of the current study was to determine whether rapid serial attentional selection mechanisms can result in serial attention shifts between objects that take place in less than 60 ms in static, rather than dynamic, visual displays. A similar task as in Grubert and Eimer (2016b) was employed to encourage sequential selection of two objects, but identity processing of the first relevant object was no longer required to correctly respond in each trial. Search displays contained four letters and digits. In half of all trials, one object possessed a fixed colour that was known in advance and remained the same across all trials, while the remaining three objects were grey (one-colour trials). The remaining half of trials also contained this fixed-colour object, along with a variable-colour object whose colour changed randomly across trials, in addition to two grey objects (two-colour trials). Participants’ task was to report the alphanumeric category of the fixed-colour target (whether it was a letter or a digit) when it was the only coloured object in the display, but to ignore this object and instead report the alphanumeric category of the variable-colour

object when this was also present. This meant that the presence of the variable-colour object negated the response-relevance of the fixed-colour object. As in Grubert and Eimer (2016b), the attentional selection of the fixed-colour object can be guided by a preparatory attentional template that represents its colour, thus triggering rapid deployment of attention to its location (Duncan & Humphreys, 1989). However, a shift of attention should be made to the variable-colour object as soon as it is detected, and this should also take place rapidly.

The N2pc component was employed as a marker of the attentional selection of each of the coloured objects, both in trials containing only the fixed-colour object and in trials containing both coloured objects. Crucially, to independently track the selection of each simultaneously present object (in trials where they were both present), one of these coloured objects was always presented on the horizontal midline while the other appeared on the vertical midline. Displays containing a lateral fixed-colour object (and vertical variable-colour object), and displays where this spatial arrangement was reversed, were equiprobable in randomly intermixed trials. The important question concerned the time-course of selection of each of these two objects: If a serial selection strategy is indeed used by participants on two-colour trials, N2pc components should emerge earlier for the fixed-colour object relative to the variable-colour object, and the time between these responses should reflect the time taken to shift attention between the objects. Furthermore, if shifts of attention in this task operate more rapidly than in Grubert and Eimer's (2016b) task, the N2pc in response to the variable-colour object should emerge less than 60 ms after that in response to the fixed-colour object.

However, there are alternative possibilities to be addressed. Firstly, attention may not operate in a serial fashion in this task; instead, multiple foci of attention may be allocated in parallel to both coloured objects on two-colour trials, which would lead to two N2pc responses that emerge at the same time. In this scenario, the ability to successfully perform

the task may require the disengagement of attention from the fixed-colour object at some point in time (see Desimone, 1998, for a model that accounts for such competitive interactions). If this takes place during the concurrent attentional object selection of both objects, then the N2pc response to the fixed-colour object may be reduced in amplitude, as the bias of spatial attention towards this object disappears. In addition, participants may instead use a strategy in which they initially search for the variable-colour object (which is always response-relevant), and subsequently search for the fixed-colour object if required. Here, there may be no N2pc response at all to the fixed-colour object in trials where the variable-colour object also appears, as well as a delayed response to the fixed-colour object in trials where it appears alone (relative to the N2pc to variable-colour objects on two-colour trials), as participants' strategy would cause them to attempt to search for the variable-colour object first. A similar form of 'reverse strategy' was seen in three participants from Grubert and Eimer's (2016b) study who each reported processing the variable-colour object first; for these participants, serial selection was observed but with the sequence of N2pc onset being reversed. Thus, it is entirely possible that participants adopt a reversed strategy in the current study whereby the variable-colour object is prioritised. Nonetheless, the fact that the fixed-colour object matches the observers' attentional template, combined with the fact that the presence of the variable-colour object in the upcoming trial is not known in advance, means it is likely that attention will be deployed first to the fixed-colour object even on trials when it is no longer response-relevant.

It is also important to address the possible influence of bottom-up stimulus salience signals on the attentional selection of objects in this task. When an object is not task-relevant but is salient (e.g., through unique differences between itself and other objects in the display, see Jonides, 1981; Folk, Remington, & Johnston, 1992), these can capture attention in a way that is not controlled by observers' intentions. It is possible that the variable-colour object

will initially attract attention in this way, as it does not match the attentional template of the observer but does differ from other two grey distractors in each display. It is possible, then, that an N2pc component in response to the variable-colour object is elicited purely on the basis of such bottom-up salience signals, and does not result from a shift in the cognitively-controlled allocation of attention. Alternatively, the initial bottom-up activation caused by the presence of this object may be combined with information about its task relevance to result in top-down enhancement of its attentional processing. To distinguish between these possible accounts, an additional experimental condition was tested (baseline condition) in which the same stimuli were used, but participants simply had to report the alphanumeric category of the fixed-colour object on all trials. If the variable-colour object attracts attention only on the basis of bottom-up salience, then an N2pc component should be observed in response to this object even when it is never task relevant. In addition, the amplitude of the N2pc response to the fixed-colour object can be compared in visually identical trials across these conditions, when the variable-colour object is either task-relevant or task-irrelevant. Any differences in N2pc amplitudes across these trials should reflect changes in the allocation of attention to the fixed-colour object as a result of the task-relevance of the variable-colour object.

5.2.2 Methods

Participants

Twelve participants were paid to take part in the experiment, and were aged between 20 and 40 years ($M = 30.25$ years, $SD = 6.13$). Eight of these participants were female, and three were left handed. All participants had normal or corrected-to-normal vision. The choice of this particular sample size ($n=12$) was based on a power analysis that employed the effect

size obtained from a previous N2pc experiment in our lab (Eimer & Grubert, 2014a), in which the same sample size was used to measure N2pc responses to colour-defined targets.⁶

Stimuli and procedure

Stimuli were presented on a 22-inch Samsung wide SyncMaster 2233 LCD monitor (resolution of 1280 x 1024 pixels, 100 Hz refresh rate; 16ms black-to-white-to-black response time as verified using a photodiode). Participants were seated in a dimly lit cabin and viewed the screen from an approximate distance of 100 cm. Stimulus presentation, timing, and response recollection were controlled by a LG Pentium PC operating under Windows XP, using the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.). Stimuli were letters (A, D, E, K, N or U) and digits (2, 4, 5, 6, 7, or 9). All stimuli were matched in height and width ($0.8^\circ \times 0.8^\circ$), and were either grey (.321/.352), red (.623/.337), green (.266/.564), blue (.194/.214), or magenta (.307/.180). All colours were equiluminant ($\sim 7.5 \text{ cd/m}^2$). Stimuli were presented at an eccentricity of 3.0° from central fixation, against a black background, and a central grey fixation point ($0.2^\circ \times 0.2^\circ$) remained continuously present throughout each experimental block. In each trial, a single stimulus display contained four objects (letters or digits), which appeared above, below, to the left, and to the right of central fixation (as illustrated in Figure 6.1).

⁶ To ensure a large enough sample size providing enough power to reliably exclude false rejection of the null hypothesis, power ($1-\beta$) was calculated using the G*Power program (Faul, Erdfelder, Lang, & Buchner, 2007), using the a priori option and the η_p^2 effect size (.74) of the SOA * Display sequence interaction of Experiment 1 in Eimer & Grubert (2014; $n=12$). Power analysis revealed a test power of .997 (with an effect size f determined according to Cohen, 1988, of 1.37) and suggested that a sample size of $n=6$ was sufficient to achieve the desired effect size of .74.

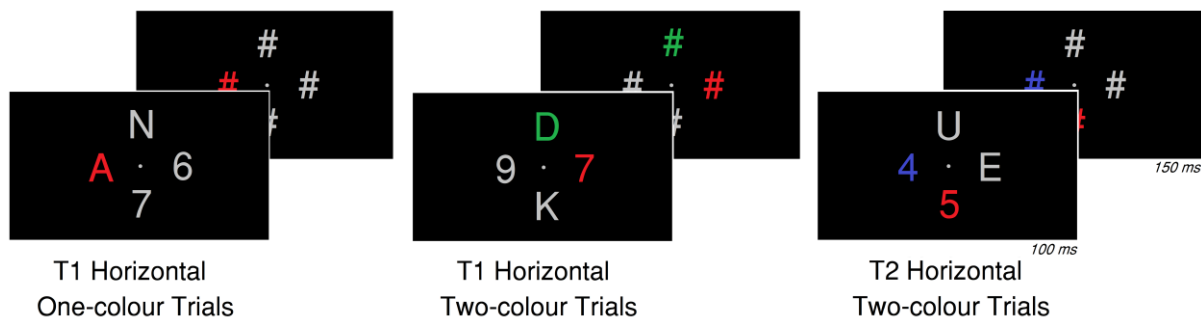


Figure 6.1: Schematic illustration of the search displays in Experiment 6. The left panel shows one-colour trials in which the fixed-colour object (T1, red in this example) appeared on the horizontal midline (trials where this object appeared on the vertical midline are not shown). In these trials, participants' task was to report the alphanumeric category (letter versus digit) of T1. The middle and right panels show randomly intermixed two-colour trials, separately for when T1 appeared on the horizontal midline (middle panel) and when the variable-colour object (T2, green and blue in this example) appeared on the horizontal midline (right panel). In these trials, participants had to report the alphanumeric category of T2. Every display was followed by a mask array, containing matching-colour hash marks at respective stimulus locations.

In all trials, one of the four objects (T1) was presented in a fixed specific colour, which varied across participants but remained the same throughout the experimental session. This object appeared equiprobably in each of the four possible locations. Each of the four colours served as the fixed T1 colour for three participants. In half of all trials, the three remaining objects were grey (one-colour trials). In the other half of trials, one of the three remaining objects (T2) was presented in one of the three remaining colours (selected randomly on each trial), while the other two objects were grey (two-colour trials). In these two-colour trials, one of the coloured target objects (T1 or T2) appeared on the horizontal

midline (to the left or right of fixation) and the other coloured object appeared on the vertical midline (above or below fixation). Two physically identical conditions were tested in a blocked fashion, in which participants' task varied. In the shift condition, participants' task was to report the alphanumeric category (letter versus digit) of T1 in one-colour trials, but to ignore T1 and report the alphanumeric category of T2 in two-colour trials, by pressing one of two purpose-built vertically aligned response keys. In the baseline condition, their task was simply to report the alphanumeric category of T1 on all trials. The response-to-key mapping, as well as the hand-to-key mapping, was counterbalanced across participants. Trials requiring a letter or digit response were equiprobable and randomly intermixed in each block.

In each trial, the stimulus display was presented for 100 ms, followed immediately by a mask display which remained on the screen for 150 ms. In this display, hash marks were presented in the same size, colour and location as the stimuli in the preceding stimulus display. The interval between the offset of the mask display and the onset of the stimulus display on the next trial was 1650 ms. Responses could be made immediately after offset of the stimulus display, resulting in a response duration of 1800 ms in each trial.

The experiment contained 16 blocks, consisting of 64 trials; the 32 one-colour trials consisted of 8 trials for each target position [left, right, top, bottom]; the 32 two-colour trials consisted of 4 trials for each combination of horizontal target [T1 horizontal, T2 horizontal], horizontal target position [left, right], and vertical target position [top, bottom]. Each task condition was run in 8 successive blocks, with the order of task conditions counterbalanced across participants. Each task condition was preceded by one practice block.

EEG recording and data analyses

The continuous EEG was DC-recorded from 27 scalp electrodes at standard positions of the extended 10/20 system, sampled at a rate of 500 Hz, and digitally low-pass filtered at 40 Hz. No other offline filters were applied. All channels were online referenced to the left earlobe and re-referenced offline to the average of both earlobes. Trials contaminated with artifacts (eye movements exceeding $\pm 30 \mu\text{V}$ in the HEOG channels; eye blinks exceeding $\pm 60 \mu\text{V}$ at Fpz; muscular movements exceeding $\pm 80 \mu\text{V}$ in all other channels), and trials with incorrect, anticipatory (faster than 200 ms), very slow (slower than 1500 ms), or missing responses were excluded from EEG analyses. This led to an exclusion of an average of 12.7% and 11.9% of all trials in the shift and baseline conditions, respectively. For the remaining trials, EEG was segmented into epochs ranging from 100 ms prior to 500 ms after the onset of the first stimulus display, and was baseline corrected relative to the 100 ms interval prior to the onset of the first display. EEG was averaged separately for each of the twelve combinations of task condition (shift or baseline), horizontal target (T1 horizontal in one colour-trials, T1 horizontal in two-colour trials, or T2 horizontal in two-colour trials), and location of horizontal target (left or right).

N2pc components were quantified on the basis of ERP waveforms measured at lateral posterior electrodes PO7 and PO8. N2pc mean amplitudes were computed within 100 ms post-stimulus time intervals, with a constant time window of 180-280 ms for all trials. N2pc onset latencies were measured on the basis of difference waveforms, computed by subtracting ipsilateral from contralateral ERPs at PO7 and PO8. Onset latencies were determined with a jackknife-based procedure (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). Twelve grand-average difference waves were computed for each experimental condition, each excluding one different participant from the original sample. N2pc onset latency was defined as the point in time when each subsample difference wave reached a relative onset

criterion of 50% (i.e., the point in time when 50% of the peak amplitude was reached in these difference waves), as described by Miller et al. (1998). Differences in N2pc onset latencies between H1 and H2 targets were assessed with repeated-measures ANOVAs and *t*-tests, with *F*- and *t*-values corrected according to the formulas described by Ulrich and Miller (2001) and Miller et al. (1998), respectively. The corrected statistical values are indicated with F_c and t_c , respectively. All *t*-tests were two-tailed and Bonferroni corrected where necessary. To measure effect sizes, Cohen's *d* (Cohen, 1988) was computed for all *t*-tests, and partial eta-squared (labelled η_p^2) was computed for all ANOVAs. As no standardised formula exists for correcting individual group means and standard deviations of jackknifed samples to calculate effect size measures such as Cohen's *d*, jackknifed group means of N2pc latency and peak amplitude values were fed into repeated-measures ANOVAs where the error variance can be corrected according to the formula described by Ulrich and Miller (2001) to calculate corrected partial eta-squared values for all *t*-tests on N2pc latency and peak amplitude measures (reported as $\eta_p^2_c$).

5.2.3 Results

Behavioural performance

Anticipatory or exceedingly slow reaction times (RTs; faster than 200 ms or slower than 1500 ms) were removed from analysis, resulting in the exclusion of less than 3.6% of all trials. A repeated-measures ANOVA with the factors task condition (shift versus baseline) and trial type (one-colour versus two-colour) on RTs revealed a main effect of task condition, $F(1,11) = 49.76, p < .001, \eta_p^2 = .82$, with faster RTs in the baseline condition (565 ms) relative to the shift condition (688 ms, mean difference 123 ms). A main effect of trial type was also observed, $F(1,11) = 50.86, p < .001, \eta_p^2 = .82$, revealing faster RTs in one-colour

trials (596 ms) relative to two-colour trials (657 ms, mean difference 61 ms). In addition to these main effects, the interaction was also found to be significant, $F(1,11) = 15.77, p < .01, \eta_p^2 = .59$. Follow-up paired t-tests revealed that although the effect of trial type was significant in the baseline condition, $t(11) = 3.65, p < .01, d = .36$ (552 ms and 579 ms in one-colour and two-colour trials, respectively, mean difference 27 ms), this difference was much larger in the shift condition, $t(11) = 6.19, p < .001, d = 1.01$ (641 ms and 736 ms in one-colour and two-colour trials, respectively, mean difference 95 ms). The same ANOVA was conducted on error rates, and revealed a main effect of task condition, $F(1,11) = 7.98, p < .05, \eta_p^2 = .42$, indicating higher error rates in the shift condition (4.26%) relative to the baseline condition (2.69%, mean difference 1.58%). An additional main effect of trial type, $F(1,11) = 6.50, p < .05, \eta_p^2 = .37$, suggested generally higher error rates in two-colour trials (4.26%) relative to one-colour trials (2.69%, mean difference 1.58%). No interaction between these factors was observed, $F(1,11) = 3.23, p = .10$.

N2pc components

The left and middle panels of Figure 6.2 show ERPs at posterior electrode sites PO7/8 contralateral and ipsilateral to the side of the horizontal coloured object, separately for trials where the fixed-colour target (T1) appeared horizontally as the only coloured object in the display (T1 horizontal one-colour trials), where this target appeared horizontally in addition to the variable-colour target (T2) appearing on the vertical midline (T1 horizontal two-colour trials), and where T2 appeared on the horizontal midline in addition to T1 appearing on the vertical midline (T2 horizontal two-colour trials). The right panel of Figure 6.2 shows N2pc difference waveforms computed by subtracting ipsilateral from contralateral ERPs in each of these trial types. ERPs are shown separately for the shift condition (top) and the baseline

condition (bottom). In the shift condition, N2pc components were clearly elicited to horizontal coloured object in each of the three trial types. In the baseline condition, N2pc responses were elicited for T1 horizontal trials (in both one-colour and two-colour trials), but not in response to T2 horizontal trials.

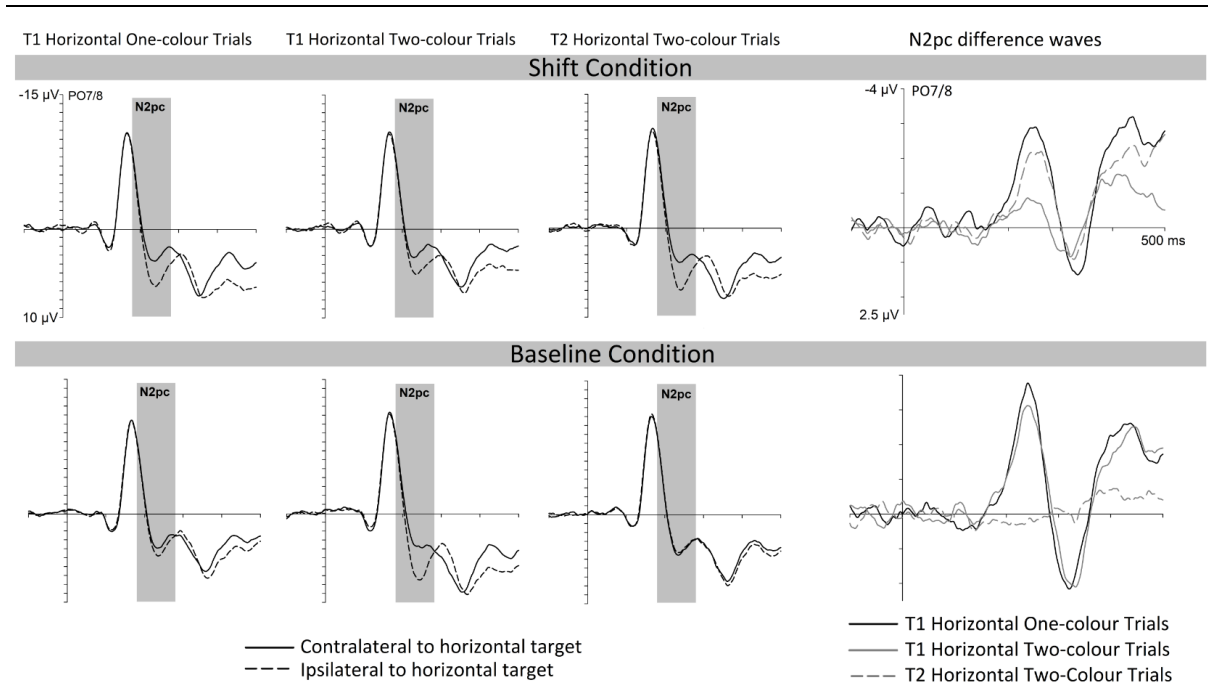


Figure 6.2: N2pc results in the Shift (top panels) and Baseline (bottom panels) conditions of Experiment 6. The three leftmost panels show grand-average ERP waveforms measured in the 500 ms interval after display onset at posterior electrodes PO7/PO8, contralateral and ipsilateral to horizontal T1 objects in one-colour trials (left panels), and to horizontal T1 objects and horizontal T2 objects in two-colour trials (middle and right panels, respectively). Time-windows used for measuring N2pc mean amplitudes are shown with grey bars. The rightmost panels show N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for the three target types and for each condition. Solid black lines in these difference waves represent T1-horizontal one-colour trials, solid grey lines represent T1-horizontal two-colour trials, and dashed grey lines represent T2-horizontal two-colour trials.

For the shift condition, a repeated-measures ANOVA was run on N2pc mean amplitudes using the factors target type (T1 horizontal one-colour, T1 horizontal two-colour, and T2 horizontal two-colour) and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target). A main effect of laterality was revealed by this ANOVA, $F(1,11) = 27.27, p < .001, \eta_p^2 = .72$, demonstrating that N2pc components were reliably present in response to horizontal coloured objects. An interaction between target type and laterality, $F(2,22) = 11.33, p < .001, \eta_p^2 = .51$, indicated differences in amplitude across the three target types. To investigate these differences, three additional t-tests were conducted on N2pc difference wave amplitude values to compare each pair of target types. T1 horizontal one-colour trials, where this object served as the target, produced significantly larger N2pc mean amplitudes ($-1.88 \mu\text{V}$) relative to T1 horizontal two-colour trials where this same object was not task-relevant ($-0.55 \mu\text{V}$, mean difference $1.33 \mu\text{V}$), $t(11) = 4.90, p < .001, d = 1.55$, but only produced marginally larger N2pc responses relative to T2 horizontal two-colour trials ($-1.35 \mu\text{V}$, mean difference $0.53 \mu\text{V}$), $t(11) = 2.16, p = .054, d = .45$. In two-colour trials, N2pc responses to horizontal T1 objects ($-0.55 \mu\text{V}$) were significantly smaller than those in response to horizontal T2 objects ($-1.35 \mu\text{V}$, mean difference $0.80 \mu\text{V}$), $t(11) = 2.49, p < .05, d = .84$. Finally, three follow-up t-tests comparing contra- with ipsilateral activity in response to the three target types confirmed that N2pc components were indeed reliably present in all conditions, all $t(11) > 3.73, p < .01, d > .12$.

For the baseline condition, the same ANOVAs were run. Firstly, the comparison between all three target types revealed a main effect of laterality, $F(1,11) = 29.98, p < .001, \eta_p^2 = .73$, confirming the general reliable presence of N2pc components across the target types. In addition, target type interacted with laterality, $F(2,22) = 56.04, p < .001, \eta_p^2 = .84$, revealing differences in N2pc amplitude across these target types. Follow-up t-tests comparing N2pc difference wave mean amplitudes for each pair of trial types revealed that

horizontal T1 objects in one-colour (-2.13 μV) and two-colour trials (-1.90 μV , mean difference 0.23 μV) were similar in amplitude, $t(11) = 1.33$, $p = .211$, $d = .22$, indicating no influence of the presence of a vertical variable-colour T2 object on N2pc amplitudes in response to the task-relevant T1 object. N2pc amplitudes in T1 horizontal one-colour trials were significantly larger than in T2 horizontal two-colour trials (0.22 μV , mean difference 2.34 μV), $t(11) = 8.16$, $p < .001$, $d = 2.55$. In two-colour trials, N2pc responses to the task-relevant T1 object were significantly larger than those to the task-irrelevant T2 object (mean difference 2.12 μV), $t(11) = 8.20$, $p < .001$, $d = 2.44$. The three follow-up t-tests comparing contra- and ipsilateral activity in response to each of the three target types revealed reliable N2pc components in response to the T1 object in both one-colour and two-colour trials, both $t(11) > 6.67$, $p < .001$, $d > .40$. However, there was no significant N2pc response to the task-irrelevant T2 object, $t(11) = 1.03$, $p = .326$, $d = .05$.

To directly compare N2pc mean amplitudes across these two task conditions, three repeated-measures ANOVAs were carried out separately for each target type, with the factors task condition (shift condition versus baseline condition) and laterality. Unsurprisingly, for T1 horizontal one-colour trials, there was no interaction between task condition and laterality, $F(1,11) = 1.71$, $p = .217$, $\eta_p^2 = .13$, suggesting no difference in N2pc response to the T1 object in one-colour trials across task conditions (-1.88 μV in the shift condition versus -2.13 μV in the baseline condition, mean difference 0.25 μV). For T1 horizontal two-colour trials, a significant interaction between task condition and laterality, $F(1,11) = 24.37$, $p < .001$, $\eta_p^2 = .69$, indicated larger N2pc amplitudes in the baseline condition, where T1 was task-relevant in these two-colour trials (-1.90 μV), relative to the shift condition, where this object was not task-relevant in these trials (-0.55 μV , mean difference 1.35 μV). Finally, for T2 horizontal two-colour trials, an interaction was observed between task condition and laterality, $F(1,11) = 30.68$, $p < .001$, $\eta_p^2 = .74$, demonstrating larger amplitude N2pc responses to the task-relevant

T2 object in the shift condition ($-1.35 \mu\text{V}$) compared with those in the baseline condition, when T2 was never task-relevant ($0.22 \mu\text{V}$, mean difference $1.57 \mu\text{V}$).

In the shift condition, clear N2pc responses were elicited to both T1 and T2 objects in two-colour trials, suggesting that attention was allocated to both of these two objects to some degree. However, in one-colour trials, attention was allocated only to one object. To determine whether there were any differences in the overall allocation of attention in one-colour versus two-colour trials, the N2pc responses to both T1 and T2 objects in two-colour trials were summed, with this new summed component compared with the N2pc response to T1 in one-colour trials. A repeated-measures ANOVA with the factors trial type (one-colour versus summed two-colour) and laterality revealed no interaction, $F(1,11) = .006$, $p = .942$, $\eta_p^2 = .00$, indicating no difference in the overall N2pc response in one-colour ($-1.88 \mu\text{V}$) and two-colour trials ($-1.90 \mu\text{V}$, mean difference $0.02 \mu\text{V}$).

In the shift condition, it is possible that the reduced amplitude of N2pc responses to horizontal T1 objects in two-colour trials relative to one-colour trials does not reflect consistently smaller N2pc responses to this object, but instead reflects an average of different trials where participants fully attended to T1 (resulting in an N2pc response with similar amplitude to those in one-colour trials) and trials where they fully ignored T1 (resulting in no N2pc response at all). To determine whether these different processes indeed took place in different trials, an RT-based median split analysis was conducted on N2pc mean amplitudes in the shift condition. For each participant, all trial conditions were split on the basis of their median RT and pooled into ‘fast’ trials (resulting in a RT lower than the median) and ‘slow’ trials (resulting in a RT higher than the median), with trials resulting in median RTs excluded from the analysis. These separate fast and slow trials were pooled across participants separately for each of the three target types (T1 horizontal one-colour trials, T1 horizontal two-colour trials, and T2 horizontal two-colour trials), and a repeated-measures ANOVA was

run separately for these target types, with the factors response time (fast, slow) and laterality. For all three target types, there was no interaction between these factors, all $F(1,11) < 2.38$, $p > .152$, $\eta_p^2 < .18$, suggesting no influence of response time on the selection of each object. In addition to these analyses, a further repeated-measures ANOVA comparing N2pc responses in one-colour trials and summed N2pc responses in two-colour trials was again carried out, separately for slow and fast trials, with the factors trial type (one-colour versus two-colour) and laterality. In both slow and fast trials, these ANOVAs revealed no interaction, both $F(1,11) < .83$, $p > .382$, $\eta_p^2 < .07$.

Finally, and critically, a one-way ANOVA was conducted for N2pc onset latency values in the shift condition, determined with a jackknife-based procedure (see Methods), using the factor target type (T1 horizontal one-colour, T1 horizontal two-colour, and T2 horizontal two-colour). This revealed no effect of target type, $F_c(2,22) = .33$, $p = .722$, $\eta_p^2 = .03$. If attention was shifted serially from T1 to T2 in two-colour trials, the N2pc response to T1 should emerge earlier than to T2. This was directly tested with a paired-samples t-test comparing N2pc onset latency in T1 horizontal and T2 horizontal two-colour trials. This t-test revealed no difference in N2pc onset latency between these trials, $t_c(11) = .65$, $p = .528$, $\eta_p^2 = .04$. In the baseline condition, a paired samples t-test compared N2pc onset latencies in the baseline condition to horizontal T1 objects in one-colour and two-colour trials. This revealed no difference in onset latency, $t_c(11) = 0.07$, $p = .943$, $\eta_p^2 = .00$. Comparisons of N2pc onset latencies across task conditions were carried out using paired samples t-tests, comparing T1 horizontal trials separately in one-colour and two-colour trials. In both trial types, N2pc onset latency did not significantly differ between task conditions, both $t_c(11) < .37$, $p > .722$, $\eta_p^2 < .02$.

5.2.4 Discussion

The current study aimed to determine rapid serial attentional mechanisms could be used to shift attention between two objects in less than 60 ms. If selection of each of these objects took place in a specific serial sequence, delays in N2pc onset latency would be predicted, with N2pc responses emerging earlier for fixed-colour objects (T1) relative to variable-colour objects (T2), and with the size of this delay reflecting the speed of shifting attention from one object to the next. However, the results of this study demonstrate that attention was in fact allocated in parallel to both T1 and T2 in trials where they both appeared. Instead of serially selecting these objects in a fixed sequence, participants appeared to have allocated their attention to both T1 and T2 simultaneously, as was shown by N2pc responses to each coloured object emerging at the same time. In addition, these N2pc responses were not delayed relative to the selection of a T1 when it was presented alone in one-colour trials. However, the substantially reduced amplitude of the N2pc response to fixed-colour objects in two-colour trials (when this object was made irrelevant by the presence of the variable-colour object) may suggest one of two possibilities: first, attention may have been rapidly disengaged from T1 in these two-colour trials. If this was the case, such disengagement must have taken place as a result of the detection of the presence of T2, as this was the factor that determined the response-relevance of the fixed-colour object. Another possibility is that the presence of T2 simply reduced the ability of T1 to attract attention, rather than facilitating active disengagement processes. From the current ERP waveforms obtained in this experiment, it is possible that active disengagement from T1 did occur. In any case, it can be concluded from this experiment that the accumulation of information about the variable-colour object that resulted from its attentional selection was able to concurrently influence the simultaneous attentional response to the fixed-colour object. In other words, while both selection processes were taking place in parallel, at some

point in time the detection of the variable-colour object triggered changes in the allocation of attention to the fixed-colour object. This process demonstrates the highly flexible parallel nature of cognitively controlled attention, even in scenarios where objects directly compete for the focus of attention.

Importantly, the possibility of bottom-up attentional capture by the variable-colour object was ruled out by the baseline condition. Here, no N2pc component at all was observed in response to the entirely task-irrelevant variable-colour object, suggesting that the allocation of attention to this object in the shift condition (when it was task-relevant) was purely facilitated by top-down attentional control. Notably, there was a small but significant delay in RTs when the task-irrelevant variable-colour object was present, indicating a small interference effect. This discrepancy between behavioural and ERP data may suggest that the presence of T2 was in fact detected (without necessitating focused attention) concurrently with the attentional selection of T1 in two-colour trials in the baseline condition; this early detection may have caused the reduction in the ability of T1 to attract attention in two-colour trials in the shift condition, thus accounting for such rapid influences of T2 presence on T1 selection in this task condition.

Another finding of interest was the fact that the N2pc response to T2 in two-colour trials was somewhat diminished relative to the response to T1 in one-colour trials (as shown by a trend towards a significant difference), despite the fact that both of these objects were response-relevant in these respective trials. One account of this result is that selection of the task-relevant target was affected by the presence of a competing object; however, an alternative possibility is that this difference reflects the ability of template-matching targets (in this case, the fixed-colour T1 object, whose colour was known in advance) to produce larger amplitude N2pc responses relative template-nonmatching targets (in this case, the variable-colour T2 object whose colour was not known in advance). To gain more insight

into the nature of the interplay between these competing objects, summed responses to both coloured objects in two-colour trials was compared with the response to the coloured object in one-colour trials. No difference was found between these N2pc responses, suggesting that the degree to which attention is allocated to the task-irrelevant fixed-colour object (as measured by N2pc amplitude) is inversely proportional to the degree of attentional selection of the task-relevant variable-colour object. In other words, there appears to be a direct relationship between the attentional selection of two concurrently competing objects. As previous studies from our lab (e.g., Grubert & Eimer, 2016a, Experiment 1 of this thesis) have shown that this is not the case when both objects are equally task-relevant, such an observation is likely to be a result of the competitive nature of the current study's task.

The original purpose of this experiment (as described in the Introduction) was to find new evidence for the speed of priority-driven attention shifts. However, there was no latency difference between T1 and T2 N2pc responses in two-colour trials, demonstrating that participants clearly did not select these objects in a serial fashion. This means that no new information was provided in this experiment about the speed of such serial shifts. It is entirely possible that serial shifts, as measured by N2pc responses, cannot take place in under 60 ms, but it may also be possible that certain search scenarios could elicit such rapid shifts. It is clear from the results of this study that distinguishing between tasks that require serial versus parallel attentional selection mechanisms can be difficult.

What can be gained from this study is further evidence for the powerful nature of parallel attentional processes. While previous studies from our lab have demonstrated that entirely independent selection of two relevant targets can take place concurrently, it is demonstrated here that integration of information across stimulus locations (i.e., about the presence versus absence of T2) can take place in order to alter the attentional bias at these locations. This may be linked to recent findings from our lab regarding conjunction search

(Experiment; Eimer & Grubert, 2014b). Here, when a target is defined by a conjunction of colour and shape (e.g., a red square), all objects possessing target features initially elicit an N2pc response, but within the time-window of this response (at approximately 250 ms post-stimulus), these separate feature dimensions were bound together at the locations of conjunctive targets to boost the attentional response to these targets relative to nontargets possessing only one relevant feature. Additional studies (e.g., Kiss, Grubert, & Eimer, 2013) also show supporting evidence for rapid disengagement of attention from potentially task-relevant objects, on the basis of new emerging information. In the current study, the information about the presence of the variable-colour object is made available to processes that can either rapidly withdraw attention from other locations, or attenuate attentional allocation processes towards these location, on the basis of such new information. The new evidence observed in the current study for such flexible and continuous processes, in which attentional modulations unfold in real time (see Eimer, 2014, for a review), lends further insight into the highly interconnected systems that are involved in visual search.

5.3 Experiments 7a & 7b: Priority-driven versus Voluntary Attention Shifts

5.3.1 Introduction

In many visual search tasks, the time required to find a target increases as a function of the number of display objects. Serial selection models interpret such search slopes as reflecting the speed with which attention moves between individual objects, which would yield shift times of approximately 50 ms per object (e.g., Wolfe, 1998b). Because movements of attention during visual search are believed to be under voluntary control, doubts have been raised as to whether such voluntary shifts can really be initiated this rapidly (e.g., Desimone

& Duncan, 1995). Endogenously controlled attention shifts are assumed to operate relatively slowly (e.g., Cheal & Lyon, 1991; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989), and certainly not at the fast pace postulated by serial selection accounts. However, it is important to note that in most visual search tasks, shifts of attention between objects are not exclusively controlled by endogenous mechanisms, but are also driven by the visual properties of these objects. When target-defining features are known, observers activate an internal representation of these features (“attentional template”; Duncan & Humphreys, 1992), and attention shifts are determined by how well particular objects match the search template. Such template-guided attention shifts have been described as “priority-driven” (Horowitz, Wolfe, Alvarez, Cohen, & Kuzmova, 2009), because they are neither fully voluntary nor entirely stimulus-driven. It remains possible that priority-driven attentional movements are indeed as fast as assumed by serial selection models, whereas fully voluntary attention shifts operate at a slower pace.

Behavioural evidence for differences in the speed of voluntary and priority-driven attention shifts comes from a series of elegant experiments by Horowitz et al. (2009; see also Wolfe, Alvarez, & Horowitz, 2000). To study voluntary attention shifts, observers were instructed to monitor a rapid sequence of brief circular displays containing letters, and to shift their attention sequentially between adjacent locations within successive displays (e.g., clockwise from the top) to detect target objects. Because a target was present only in one display at one particular position (e.g., at 3 o’clock in the fourth display), it could only be found if attention was focused at this position at the correct point in time. Observers were able to perform this task only when each display was presented for at least 250 ms, suggesting that voluntary attention shifts operate relatively slowly. Similar results were obtained with static circular displays containing letters and mirror-reversed letters (Horowitz et al., 2009, Exp. 4). Here, a cue signalled the starting point for focal attention, and observers

had to report the identity of the first mirror-reversed letter clockwise from the cue. Reaction times (RTs) increased as the number of objects between the cue and the target letter increased, with a slope of 200 ms per object. These findings suggest that fully voluntary shifts of attention operate at rates of about 200 – 250 ms per object. In contrast, the speed of priority-driven attention shifts was estimated to be 100 ms or even faster (Horowitz et al., 2009).

While these observations provide initial evidence for the speed differences between voluntary and priority-driven shifts of attention, it is difficult to draw firm conclusions about serial attentional selection processes on the basis of behavioural data alone (e.g., Townsend, 1990). To obtain more direct insights into the speed of voluntary and priority-driven attention shifts, additional on-line markers of attentional object selection are needed that can track such attention shifts continuously across time. In the current study, we employed the N2pc component of the event-related potential (ERP) to determine the speed with which attention moves between objects in the visual field.

A methodological challenge for investigating the speed of serial attention shifts is the necessity to ensure not only that participants move their attention sequentially between different target objects in the same display, but also that they select these objects in a constant order on each trial. Two previous N2pc studies have used different methods to encourage such constant serial selection strategies for priority-driven shifts of attention. Woodman & Luck (2003) presented search displays with two colour-defined target objects (Landolt squares) among multiple distractors. One target appeared close to fixation and the other at a more peripheral position (near versus far targets). On different trials, the near target appeared on the horizontal midline and the far target on the vertical midline, or vice versa. Participants had to report whether a gap in a specific position (e.g., at the top) was present in one of the two target objects. Woodman & Luck (2003) assumed that participants would consistently

allocate attention first to the near target before shifting it to the far target. In line with this prediction, N2pc components to horizontal near targets preceded the N2pc to horizontal far targets by about 150 ms, suggesting that it took about 150 ms to move attention between the two target locations. A different method for imposing serial attention shifts was employed in a recent study from our lab (Grubert & Eimer, 2016b). Search displays contained four digits (two on the horizontal and two on the vertical midline). One vertical and one horizontal digit was coloured (targets) and the other two were grey (distractors). Critically, one target appeared in a known colour that remained constant throughout the experiment (fixed-colour target), while the colour of the other target varied unpredictably across trials (variable-colour target). Participants were instructed to select the known fixed-colour target and to compare its value to the variable-colour target (e.g., “find the red digit and report whether the other coloured digit is bigger/smaller”). The N2pc to horizontal fixed-colour digits emerged 60 ms earlier than the N2pc to horizontal variable-colour digits, demonstrating that in this particular task, serial attention shifts were triggered even faster than in the study by Woodman & Luck (2003).

In these earlier N2pc studies of serial selection, target objects were defined by their colour. The attention shifts investigated in these studies were therefore priority-driven, because they could be controlled by colour-specific search templates. In contrast, the speed of fully voluntary shifts of attention has never been investigated with electrophysiological measures. Do attention movements that are under full voluntary control operate more slowly than priority-driven attention shifts, as suggested by previous behavioural evidence (Horowitz et al., 2009)? One goal of the two experiments reported here was to answer this question. Another goal was to compare the speed of priority-driven attention shifts when these shifts are controlled by different types of priority signals (spatial cues versus target features).

In both experiments, search displays contained four alphanumeric objects (two on the horizontal and two on the vertical midline; see Figure 7.1). One of them was the response-relevant target, and participants' task was to report its category (letter versus digit). Critically, which object was the target on any given trial was not known in advance, because this was determined by another object in the same display (the "benchmark"). Participants therefore had to first process this benchmark object (T1) before they could shift attention to the response-relevant target (T2). The benchmark object was defined by a known constant feature (shape in Experiment 7a, colour in Experiment 7b), to ensure that attention shifts to this object could be triggered rapidly and consistently in all trials. In Experiment 7a, the benchmark location was signalled by a unique shape (e.g., the only circle among three squares; Figure 7.1). There were two task conditions. In the priority-driven shift task, the response-relevant T2 was the object that matched the colour of the object at the benchmark location (e.g., "find the object within the circle and report the category of the other object in the same colour"). Here, attention shifts from T1 to T2 were priority-driven because they were determined by a colour match between T1 and T2. In the voluntary shift task, participants had to localize the T1 benchmark shape, and then move their attention in a pre-specified direction (either clockwise or anticlockwise relative to the benchmark, varied across blocks) towards the response-relevant T2 object (e.g., "report the category of the object that is located clockwise from the circle"). Here, attention shifts between T1 and T2 had to be initiated in a fully voluntary (endogenous) fashion, because there were no visual features associated with the status of T2 as the target object. In both tasks, T1 appeared on the horizontal midline and T2 on the vertical midline on 50% of all trials and vice versa on the other trials, so that N2pc components could be measured separately and independently to T1 and T2. Because the T1 benchmark had to be processed in order to determine the response-relevant T2 object in both tasks, N2pc components to horizontal T1 objects should always

precede N2pc components to horizontal T2 objects, reflecting serial attention shifts to T1 and then from T1 to T2. Critically, the onset delay between these two N2pc components should reflect the time required for attention to shift between T1 and T2. If fully voluntary shifts of attention are slower than priority-driven shifts (Horowitz et al., 2009), this should be reflected by longer T1/T2 N2pc onset latency differences in the voluntary shift task of Experiment 7a.

5.3.2 Experiment 7a: Feature-defined versus Location-defined Targets

5.3.2.1 Methods

Participants

Fifteen participants were paid to take part in Experiment 7a. Two participants were excluded from analysis due to low accuracy (with error rates higher than 30%), and another participant was excluded due to excessive eye movement activity (resulting in a loss of more than 50% of all data during artefact rejection). The remaining twelve participants were aged between 20 and 41 years ($M = 29$, $SD = 5.92$). Six were female and three were left-handed. All participants had normal or corrected-to-normal vision. To ensure a large enough sample size providing enough power to reliably exclude false rejection of the null hypothesis, power ($1-\beta$) was tested with the G*Power program (Faul, Erdfelder, Lang, & Buchner, 2007), using the a priori option and the η_p^2 effect size (.87) of Experiment 3 in Grubert & Eimer (2016b; $n=12$). Power analysis revealed a test power of .995 (with an effect size f determined according to Cohen, 1988, of 2.59) and suggested that a sample size of $n=6$ was sufficient to achieve the desired effect size of .87. The study was conducted in accordance with the Declaration of Helsinki, and was approved by the Psychology Ethics Committee, Birkbeck, University of London.

Stimuli and Procedure

Stimuli were presented on a 22-inch Samsung wide SyncMaster 2233 LCD monitor (resolution of 1280x1024 pixels, 100 Hz refresh rate; 16ms black-to-white-to-black response time, as verified with a photodiode). Participants were seated in a dimly illuminated cabin. The monitor was placed at a viewing distance of approximately 100 cm. Stimulus presentation, timing, and response collection were controlled by a LG Pentium PC running under Windows XP, using the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.).

Stimuli were coloured uppercase letters (A, D, E, K, N, or U) or digits (2, 4, 5, 6, 7, or 9), each covering $0.5^\circ \times 0.5^\circ$ of visual angle. They were surrounded by grey (CIE xyY colour coordinates: .321/.352) outline shapes (circles or squares; 0.2° line width), subtending $1.1^\circ \times 1.1^\circ$ of visual angle. All stimuli were presented at an eccentricity of 3.0° from central fixation (with respect to the centre of the letters/digits) against a black background. The four possible object colours were red (.623/.337), green (.266/.564), blue (.194/.214) and magenta (.307/.180). All colours were equiluminant ($\sim 7.6 \text{ cd/m}^2$). A central grey fixation point ($0.2^\circ \times 0.2^\circ$) remained continuously present throughout each experimental block. Each stimulus display contained four objects, of which two shared one colour and two shared another colour. Both colours were selected randomly from the four possible colours on each trial. One of these four objects was surrounded by the benchmark shape (e.g., circle), and the three other objects were each surrounded by the other shape (e.g., square; Figure 7.1). Circles served as benchmark shape for six participants, and squares were the benchmark shape for the other six participants. This benchmark shape remained constant for each participant throughout the experiment. On each trial, four different stimulus identities were selected

randomly from the twelve-item set of letters and digits. Stimulus displays were presented for 100 ms and the interval between the offset of the stimulus display in one trial and the onset of the stimulus display in the next trial was 1900 ms.

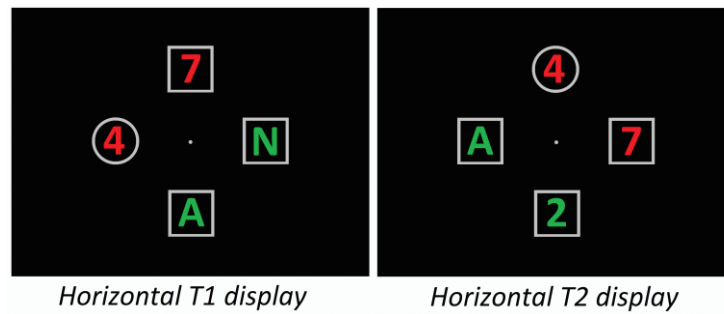


Figure 7.1: Schematic illustration of the search displays in Experiment 7a. Displays with T1 or T2 objects on the horizontal midline are shown in the left and right panels, respectively. T1 benchmark objects were defined by their unique shape (e.g., the circle among squares). In the priority-driven shift task, T2 was defined as the object that matched the colour of the item at the benchmark location (the red “7” in Figure 1). In the voluntary shift task, T2 was defined as the object at the position clockwise or anticlockwise from T1. Search displays were identical in both task conditions. Participants reported whether T2 was a letter or a digit.

Two task conditions were tested in Experiment 7a. In both tasks, the known shape marked the benchmark location (first target; T1). In the priority-driven shift task, participants had to report the alphanumeric category (letter or digit) of the item (second target; T2) that matched the colour of the object at the benchmark location (i.e., a digit “7” with respect to the red benchmark target T1 in Figure 7.1). In the voluntary shift task, observers had to report the alphanumeric category of the item that was one position clockwise or anticlockwise from the benchmark location (i.e., a letter “A” which is located anti-clockwise relative to the red benchmark object in Figure 7.1). Shift direction (clockwise or anticlockwise) remained

constant within each block, but alternated across experimental blocks. At the beginning of each block, participants were presented with an on-screen specification of the required shift direction for this block. On 50% of trials, T1 was presented on the horizontal midline (to the left or right of fixation), and T2 was presented on the vertical meridian (above or below fixation). On the other 50% of trials, T1 appeared on the vertical and T2 on the horizontal meridian. Trials where T2 was a letter or digit were equiprobable and randomly intermixed in each block. Responses were given by pressing one of two purpose-built vertically aligned response keys. The response-to-key mapping, as well as the hand-to-key mapping, was counterbalanced across participants.

Experiment 7a contained 24 blocks, with 32 trials per block. Each condition was run in 12 successive blocks, and was preceded by two practice blocks. In the priority-driven shift task, each block contained four trials for each combination of horizontal target [T1 horizontal, or T2 horizontal], position of horizontal target [left, or right] and position of vertical target [top, or bottom]. In the voluntary shift task, each block contained 8 trials for each combination of T1 position [left, right, top, or bottom]. The position of T2 relative to T1 [clockwise, or anticlockwise] was alternated block-wise, and the initial direction in the first block was counterbalanced across participants.

EEG Recording and Data Analyses

The continuous EEG was DC-recorded from 27 scalp electrodes at standard positions of the extended 10/20 system. EEG data were sampled at a rate of 500 Hz, with a digital low-pass filter of 40 Hz. No other offline filters were employed. All electrode impedances were kept below 5 k Ω . During recording, all channels were referenced to the left earlobe. They were then re-referenced offline to the average of both earlobes. Trials containing eye

movement artefacts (horizontal eye movements associated with EEG activity exceeding ± 30 μV in the HEOG channels; eye blinks associated with signals exceeding ± 60 μV at Fpz), artefacts due to muscular movements (activity exceeding ± 80 μV in any other channel), and trials with incorrect, anticipatory (faster than 200 ms), very slow (slower than 1800 ms), or missing responses were excluded from EEG analyses. After excluding trials based on these criteria, the rate of trials that were retained for analyses was 83.1% (ranging from 70.5% to 93.5% between participants) in the priority-driven shift task, and 85.7% (ranging from 70.0% to 94.5% between participants) in the voluntary shift task. EEG was segmented into epochs from 100 ms prior to 500 ms after the onset of each stimulus display, relative to a 100 ms pre-stimulus baseline. EEG was averaged separately for each of the eight combinations of shift task (priority-driven or voluntary), horizontal target (T1 or T2) and location of the horizontal target (left or right).

N2pc components were quantified on the basis of ERPs measured at lateral posterior electrodes PO7 and PO8. N2pc onset latencies were determined on the basis of difference waveforms (computed by subtracting ipsilateral from contralateral ERPs at PO7 and PO8) with a jackknife-based procedure (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). Twelve grand-average difference waves were computed for each task condition, with each difference wave excluding one different participant from the original sample. N2pc onset was defined as the point in time when a difference wave fell below a fixed onset criterion of $-0.5\mu\text{V}$ (starting at the maximum negative peak of each difference waveform and moving backwards in time). N2pc onset latency differences between trials with horizontal T1 and T2 objects were assessed with repeated-measures ANOVAs and paired t -tests. All F - and t -values were corrected according to the formulas described by Ulrich and Miller (2001) and Miller et al. (1998), respectively. The corrected statistical values are indicated with F_c and t_c , respectively. All t -tests were two-tailed and Bonferroni-corrected where necessary. To

confirm that N2pc components were reliably elicited both for T1 and T2 objects in both tasks, N2pc mean amplitudes measured at electrodes PO7/PO8 contralateral and ipsilateral to these objects were compared with two-tailed paired *t*-tests. These mean amplitudes were obtained within 100 ms time windows starting at the onset latency of the respective N2pc component, rounded to the nearest 10 ms. For T1 objects, these time windows were 210-310 ms and 230-330 ms post-stimulus in the priority-driven and voluntary shift tasks, respectively. For T2 objects, the corresponding latency windows were 260-360 ms and 350-450 ms, respectively.

To measure effect sizes, Cohen's *d* (Cohen, 1988) was computed for all *t*-tests, and partial eta-squared (labelled η_p^2) was determined for all ANOVAs. To correct individual group means and standard deviations of jackknifed samples, the jackknifed group means of N2pc latency values were fed into repeated-measures ANOVAs where the error variance was corrected according to the formula described by Ulrich and Miller (2001). Effect sizes for N2pc latency measures are therefore reported as η_p^2 .

5.3.2.2 Results

Behavioural Performance

Anticipatory or exceedingly slow RTs (faster than 200 ms or slower than 1800 ms) were removed from analysis, resulting in the exclusion of less than 0.9% of all trials. A repeated-measures ANOVA with the factors Task (priority-driven shift, voluntary shift) and Display Type (T1 horizontal/T2 vertical versus T1 vertical/T2 horizontal) revealed a main effect of Task on RTs on trials with correct responses, $F(1,11) = 6.28$, $p < .05$, $\eta_p^2 = .36$, as RTs in the priority-driven shift task were slower than in the voluntary shift task (987 ms versus 943 ms). There was no main effect of Display Type and no interaction between Task and Display Type, both $F(1,11) < .61$, $p > .450$, $\eta_p^2 < .06$. For error rates, there was also a

main effect of Task, $F(1,11) = 13.33, p < .01, \eta_p^2 = .55$, with higher error rates in the priority-driven shift task condition relative to the voluntary shift task (8.2% versus 6.3%), but no main effect of Display Type, $F(1,11) = 1.21, p = .295, \eta_p^2 = .10$, and no significant interaction between Task and Display Type, $F(1,11) = 3.91, p = .074, \eta_p^2 = .26$.

In both tasks, the alphanumeric category of T1 and T2 was the same (both letters or both digits) on half of all trials (congruent trials) and different on the other half (incongruent trials). To assess congruency effects on RTs, a repeated-measures ANOVA was conducted with the factors Task and Congruency (congruent, incongruent). A main effect of Congruency was obtained, $F(1,11) = 8.04, p < .05, \eta_p^2 = .42$, reflecting faster RTs on congruent relative to incongruent trials (953 ms versus 976 ms). There was no interaction between Congruency and Task, $F(1,11) = 0.11, p = .747, \eta_p^2 = .01$, indicating that similar congruency effects were present in the priority-driven and voluntary shift tasks.⁷

N2pc Components

Figure 7.2 (left and middle panels) shows ERPs at posterior electrodes PO7/PO8 contralateral and ipsilateral to the side of a horizontal benchmark object (T1) and a horizontal response-relevant object (T2), separately for the priority-driven shift task (top panels) and the

⁷ Because T2 was defined as the object that shared the colour of T1 in the priority-driven shift task, attention shifts in this task were always between two objects in the same colour. In the voluntary shift task, where T2 was defined by its clockwise/counterclockwise position relative to T1, attention shifts were equally likely to be required between same-colour and different-colour T1 and T2 objects. A paired *t*-test revealed that RTs on same-colour shift trials were faster than on different-colour shift trials in this task (930 ms versus 956 ms; $t(11) = 2.66, p < .05, d = .14$).

voluntary shift task (bottom panels). The right panels of Figure 7.2 show N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for horizontal T1 and T2 objects and both tasks. Solid N2pc components were elicited in response to both types of targets in both tasks. Importantly, the N2pc to T2 was delayed relative to the N2pc to T1, indicating that the benchmark object was indeed selected first, before attention was shifted to the response-relevant T2 object. The critical finding was that this T1/T2 N2pc onset difference was substantially longer in the voluntary shift task than in the priority-driven shift task.

These observations were confirmed by analyses of N2pc onset latencies and mean amplitudes. A repeated-measures ANOVA on N2pc onset latencies with the factors Task and Display Type (T1 horizontal versus T2 horizontal) revealed a main effect of Display Type, $F_c(1,11) = 22.93, p < .001, \eta_p^2 = .68$, confirming that the N2pc to horizontal T2 objects was delayed relative to the N2pc to horizontal T1 objects. Additionally, an interaction between Task and Display Type was observed, $F_c(1,11) = 8.14, p < .05, \eta_p^2 = .43$, reflecting the fact that this T1/T2 N2pc delay was larger in the voluntary shift task. Follow-up *t*-tests comparing N2pc onset latencies in response to T1 and T2 revealed that in the priority-driven shift task, the N2pc to horizontal T2 objects was delayed by 47 ms relative to the N2pc to horizontal T1 objects (259 ms versus 212 ms; $t_c(11) = 2.30, p < .05, \eta_p^2 = .33$). In the voluntary shift task, this T1/T2 N2pc onset difference was 128 ms (354 ms versus 227 ms; $t_c(11) = 5.07, p < .001, \eta_p^2 = .69$). When N2pc onset latencies were compared across both tasks, no significant difference was found for horizontal T1 objects, $t_c(11) = .59, p = .565, \eta_p^2 = .03$, while the N2pc to horizontal T2 objects emerged reliably later in the voluntary shift task as compared to the priority-driven shift task (354 ms versus 259 ms; $t_c(11) = 7.18, p < .001, \eta_p^2 = .82$).

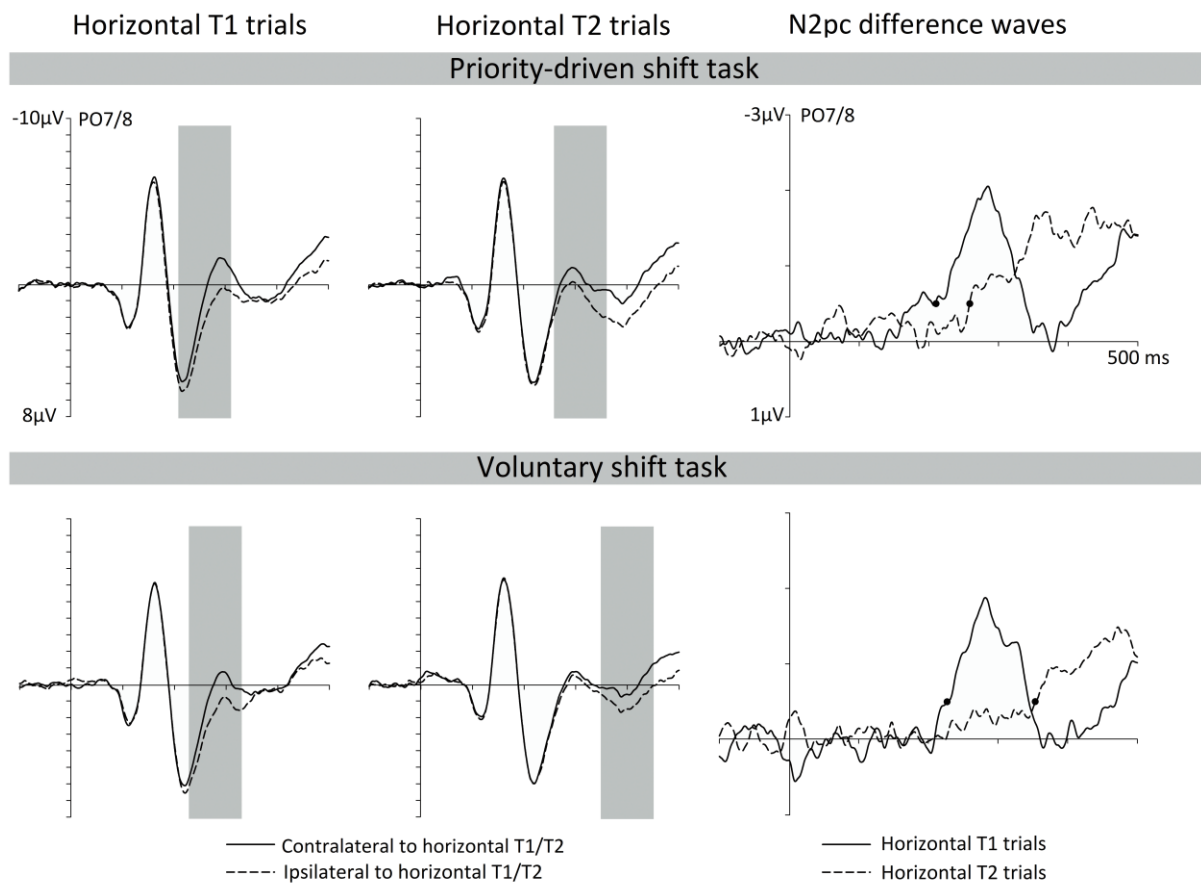


Figure 7.2: N2pc results in the priority-driven and voluntary shift tasks of Experiment 7a. The left and middle panels show grand-average ERP waveforms measured in the 500 ms interval after search display onset at posterior electrodes PO7/PO8 contralateral and ipsilateral to a horizontal T1 or T2 object. ERPs are shown separately for displays where T1 appeared on the horizontal midline and displays where T2 was presented horizontally. The right panels show N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for horizontal T1 and horizontal T2 trials and both shift tasks. Circles mark the point in time when N2pc difference waves reached an absolute onset criterion value of $-0.5 \mu\text{V}$, and shaded areas indicate N2pc time windows.

To confirm that N2pc components were reliably elicited by horizontal T1 and T2 objects in both tasks, a repeated-measures ANOVA of N2pc mean amplitudes (obtained within different post-stimulus latencies for T1 and T2 objects; see Methods section) was run

with the factors Task, Display Type and Laterality (electrode contralateral, versus ipsilateral to the side of the horizontal target). A main effect of Laterality, $F(1,11) = 22.12, p < .001, \eta_p^2 = .67$, confirmed that N2pc components were reliably elicited by horizontal target items. There was no interaction between Task and Laterality, $F(1,11) = .03, p = .863, \eta_p^2 = 0$, showing that N2pc components of similar size were elicited in both tasks. An interaction between Display Type and Laterality, $F(1,11) = 7.01, p < .05, \eta_p^2 = .39$, was due to the fact that N2pc components to T1 benchmark objects were generally larger than N2pcs to response-relevant T2 objects (see Figure 7.2). There was no three-way interaction between Task, Display Type, and Laterality, $F(1,11) = .07, p = .793, \eta_p^2 = 0$.

5.3.2.3 Discussion

The N2pc results of Experiment 7a were in line with previous suggestions based on behavioural results that purely voluntary attention shifts are slower than priority-driven shifts (Horowitz et al., 2009). Reliable N2pc components were elicited both in response to lateral benchmark items (T1) as well as to lateral response-relevant targets (T2). The N2pc to T1 objects preceded the N2pc triggered by T2 objects in both shift tasks. This demonstrates that participants first attended to the benchmark before shifting attention to the response-relevant T2 objects, both when these objects were indicated by the colour of the benchmark (priority-driven shifts) or its location (clockwise or anticlockwise voluntary shifts). Critically, the onset difference between N2pc components to T1 and T2 objects was larger in the voluntary shift task (128 ms) than in the priority-driven shift task (47 ms). The rapid speed of priority-driven shifts of attention indicated by the N2pc results of Experiment 7a is consistent with the findings of an earlier study (Grubert & Eimer, 2016b) that found N2pc onset latency differences of about 60 ms between a known fixed-colour target and an unpredictable

variable-colour target. Critically, the speed of fully voluntary attention shifts was tracked for the first time with ERP markers in Experiment 7a. The observation that the N2pc to T2 objects emerged 128 ms later than the N2pc to T1 benchmark objects in the voluntary shift task suggests that although fully endogenous attention shifts that cannot be guided by visual signals are slower than priority-driven shifts, they are still elicited relatively rapidly, and faster than suggested by the behavioural results reported by Horowitz et al. (2009). To test the possibility that the slower shift times in the voluntary as compared to the priority-driven shift task were caused by the fact that participants had to change shift direction from clockwise to anticlockwise and back across successive blocks in the voluntary task, we ran an additional N2pc analysis for this task, excluding the first six trials from each block. The temporal pattern of N2pc components was virtually identical to the pattern observed when all trials were included, which makes it unlikely that the requirement to change shift direction in each block was responsible for the delayed shift speed in the voluntary task.

There was one puzzling inconsistency between the behavioural and N2pc results observed in Experiment 7a. While the temporal pattern of N2pc components demonstrated faster attention shifts towards response-relevant T2 objects in the priority-driven shift task, target RTs were faster in the voluntary task. This RT delay in the priority-driven shift task may have been due to the fact that while T2 objects were defined by their colour, response selection was based on the shape-related categorization of these objects as letters or digits. This need to shift from colour to shape processing may have slowed response selection in the priority-driven task relative to the voluntary task, where T2 objects were defined by their spatial relationship to the benchmark shape, and no shift between relevant feature dimensions was needed. One goal of Experiment 7b was to assess this hypothesis.

5.3.3 *Experiment 7b: Guiding Voluntary Attention with Shape Cues*

5.3.3.1 Introduction

In the priority-driven shift task of Experiment 7a, movements of attention were guided by the presence of a benchmark-matching colour at the target location of an attention shift. In this case, priority-driven attention was “pulled” by a particular target-defining feature. There is another type of priority-driven attention where target locations for an attention shift are defined by visual signals at a different location, such as spatially informative cues. In this case, attention is “pushed” towards a new location by the visual properties of a cue at a currently attended position. A classic example is the spatial cueing paradigm developed by Posner and colleagues (e.g., Posner, Snyder, & Davidson, 1980; Posner, 1980), where informative arrow cues signal the location where expected target objects are likely to appear. Behavioural studies have suggested that attention shifts triggered by arrow cues are relatively slow, and take about 250-300 ms to be completed (e.g., Müller & Rabbitt, 1989; Cheal & Lyon, 1991; see also Müller, Teder-Sälejärvi, & Hillyard, 1998, for electrophysiological evidence). Although such cued attention shifts are usually described as “endogenous”, they are controlled by visual attributes of the cue (e.g., arrow direction). For this reason, and analogous to template-guided shifts of attention, attention shifts in response to spatial cues are also priority-driven. The aim of Experiment 7b was to employ N2pc components to determine the speed of such priority-driven shifts of attention that are triggered by spatial cues, and to compare it to the speed of fully voluntary attention shifts. Procedures were similar to Experiment 7a. T1 benchmark objects were now defined by colour, and there were two shift tasks (see Figure 7.3). In the priority-driven task, the response-relevant T2 object

was signalled by the arrow cue at the benchmark location. In the voluntary task, T2 was the object that was located clockwise or anticlockwise relative to the colour-defined benchmark.

5.3.3.2 Methods

Participants

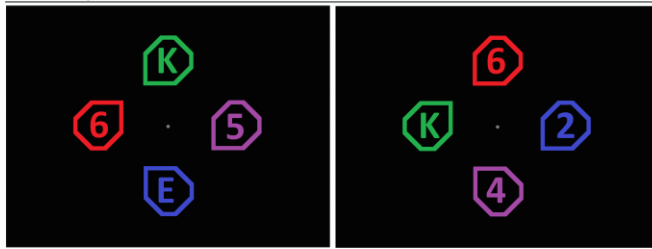
Thirteen participants were paid to take part in Experiment 7b. One participant was excluded from analysis due to excessive eye movement activity (leading to a loss of more than 50% of all trials during artefact rejection). The remaining twelve participants were aged between 24 and 42 years ($M = 31$, $SD = 5.37$). Five were female and three were left-handed. All participants had normal or corrected-to-normal vision.

Stimuli and Procedure

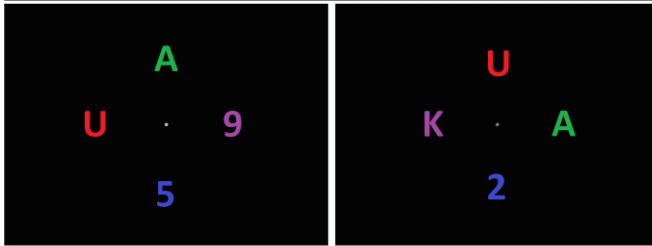
These were analogous to Experiment 7a with the following exception. The four alphanumeric objects in each display now appeared in four different colours (red, green, magenta and blue, Figure 7.3). Colour coordinates and luminance were the same as in Experiment 7a. Displays again contained one benchmark object (T1), one second response-relevant object (T2), and two nontargets. One of these target objects always appeared on the vertical meridian and one on the horizontal meridian, as in Experiment 7a. Importantly, T1 was now defined by its colour, which remained constant for each participant, and was counterbalanced across participants (each of the four colours defined the benchmark object for three participants). Two task conditions were tested. In the priority-driven shift task, each of the four letters or digits ($0.5^\circ \times 0.5^\circ$) was surrounded by matching-colour outline arrow shapes (0.2° line width; sized $1.1^\circ \times 1.1^\circ$ of visual angle, Figure 7.3, top panel). Each arrow

was tilted by 45° with respect to the horizontal so that it pointed to one of its two adjacent objects (e.g., the arrow surrounding the right-sided stimulus would either point to the top or bottom stimulus; see Figure 7.3, top panel). Participants' task was to locate the arrow in the benchmark colour (T1), and then to direct attention to the object (T2) specified by the direction of this arrow and report its alphanumeric category (e.g., the letter "K" signalled by the red benchmark arrow in Figure 7.3). In the voluntary shift task, the four letters and digits were presented without arrow shapes. Observers had to localize the coloured benchmark object (T1) and to report the category of the object (T2) at the clockwise or anticlockwise location relative to this object (e.g., the letter "A", located clockwise relative to the red benchmark object, in Figure 7.3, bottom panel). All other methodological and procedural aspects of the stimulus presentation, response collection and trial balancing were identical to Experiment 7a.

Priority-driven shift task



Voluntary shift task



Horizontal T1 display

Horizontal T2 display

Figure 7.3: Schematic illustration of the search displays in Experiment 7b.

Displays with T1 or T2 objects on the horizontal midline are shown in the left and right panels, respectively. In the priority-driven shift task (top panels), T1 was defined by its colour and T2 was signalled by the direction of the arrow shape at the benchmark location (e.g., the

“K” indicated by red benchmark arrows). In the voluntary shift task (bottom panels), T1 was again defined by its colour, and T2 by its location relative to T1 (clockwise or anticlockwise). In both tasks, participants reported whether T2 was a letter or a digit.

EEG Recording and Data Analyses

All aspects of EEG recording and data analyses were identical to Experiment 7a. After artefact rejection and exclusion of anticipatory, slow, or incorrect responses, the proportion of retained trials was 85.7% (ranging from 71.6% to 96.9% between participants) in the priority-driven shift task, and 85.6% (ranging from 70.6% to 96.8% between participants) in the voluntary shift task. N2pc mean amplitudes were measured within the 100 ms time window starting at the onset latency of the respective wave form. The time windows for the N2pc mean amplitude analyses (defined again as the 100 ms time window following N2pc onset for a particular trial condition) were 180-280 ms and 190-290 ms post-stimulus for horizontal T1 trials in the priority-driven and voluntary shift tasks, respectively. For horizontal T2 trials, the respective time windows were 290-390 ms and 360-460 ms.

5.3.3.3 Results

Behavioural Performance

Anticipatory or exceedingly slow RTs (faster than 200 ms or slower than 1800 ms) were removed from analysis, resulting in the exclusion of less than 0.5% of all trials. A repeated-measures ANOVA with the factors Task (priority-driven versus voluntary shift) and Display Type (T1 horizontal, T2 horizontal) revealed a main effect of Task on RTs on trials with correct responses, $F(1,11) = 12.73, p < .01, \eta_p^2 = .54$, with faster RTs in the priority-driven relative to the voluntary shift task (863 ms versus 910 ms). There was no main effect of Display Type, $F(1,11) = 2.61, p = .192, \eta_p^2 = .19$, and no interaction between Task and Display Type, $F(1,11) = 1.24, p = .290, \eta_p^2 = .10$. For error rates, there was no significant difference between the priority-driven and voluntary shift tasks (8.2% versus 7.1%; $F(1,11) = 3.36, p = .094, \eta_p^2 = .23$), no main effect of Display Type, and no interaction between Task and Display Type, both $F(1,11) < .17, p > .694, \eta_p^2 < .02$.

As in Experiment 7a, the assessment of T1-T2 congruency effects on RTs revealed a main effect of Congruency, $F(1,11) = 19.85, p < .001, \eta_p^2 = .64$, with faster RTs on congruent relative to incongruent trials (845 ms versus 886 ms). There was again no interaction between Task and Congruency, $F(1,11) = .08, p = .782, \eta_p^2 = .01$.

N2pc Components

Figure 7.4 shows ERPs at posterior electrodes PO7/PO8 contralateral and ipsilateral to the side of horizontal benchmark T1 objects and horizontal response-relevant T2 objects in the priority-driven and voluntary shift tasks, together with the corresponding contralateral-

ipsilateral N2pc difference waveforms. As in Experiment 7a, the N2pc to T1 objects emerged earlier than the N2pc to T2 objects, and this T1/T2 N2pc latency difference was larger in the voluntary shift task.

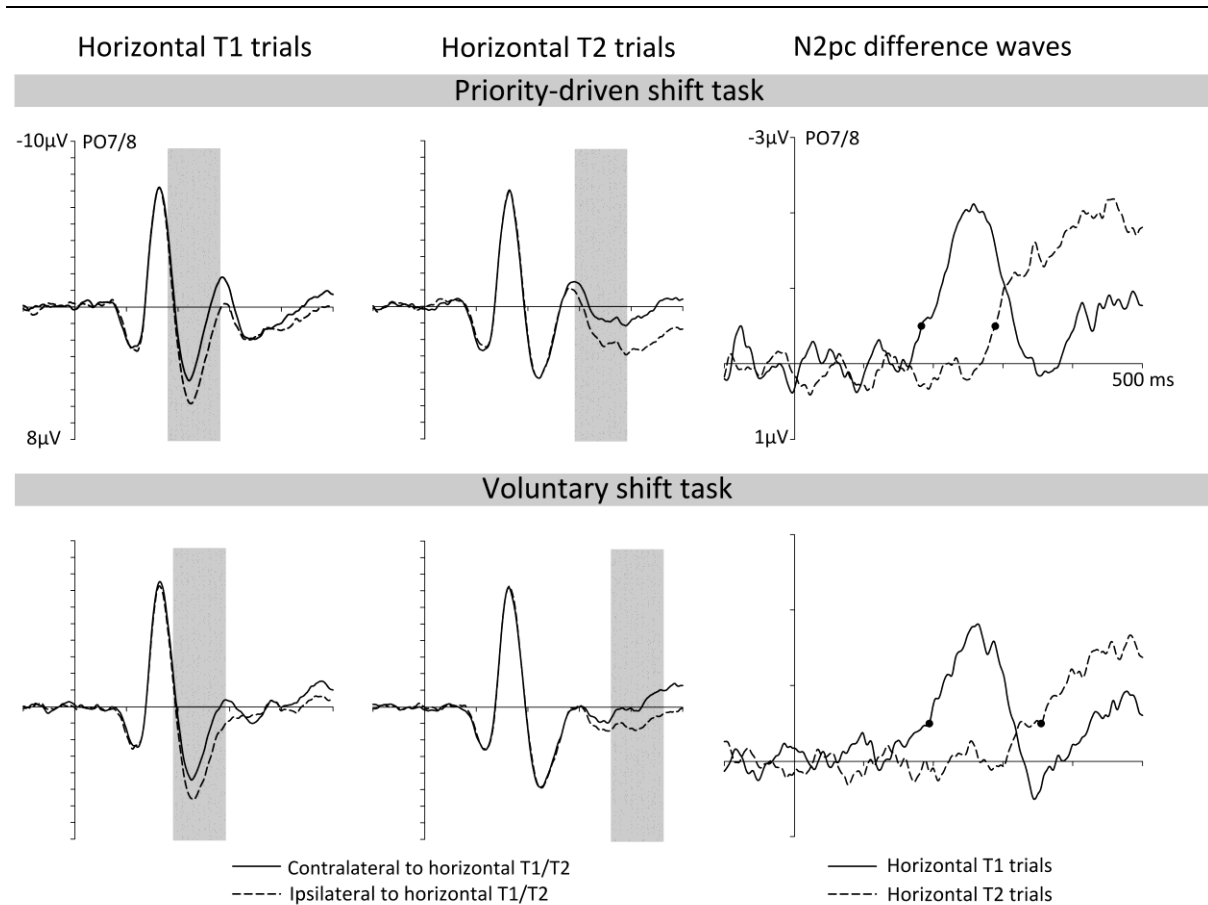


Figure 7.4: N2pc results in the priority-driven and voluntary shift tasks of Experiment 7b. Grand-average ERP waveforms (left and middle panels) measured in the 500 ms interval after display onset at electrodes PO7/PO8 contralateral and ipsilateral to T1/T2 and the corresponding ipsilateral-contralateral N2pc difference waveforms (right panels) are shown separately for displays with horizontal T1 and horizontal T2 objects and separately for both shift tasks. Circles mark the point in time when N2pc difference waves reached an absolute onset criterion value of $-0.5 \mu\text{V}$, and shaded areas indicate N2pc time windows.

A repeated-measures ANOVA on N2pc onset latencies with the factors Task and Display Type (horizontal T1 versus horizontal T2) revealed a main effect of Display Type, $F_c(1,11) = 1605.02, p < .001, \eta_p^2 = .99$, confirming that N2pc components to horizontal T2 objects emerged later than N2pcs to horizontal T1 objects. A significant Task x Display Type interaction, $F_c(1,11) = 24.02, p < .001, \eta_p^2 = .69$, showed that this T1/T2 delay was more pronounced in the voluntary shift task. For the priority-driven shift task with arrow cues, the N2pc to horizontal T2 objects was delayed by 106 ms relative to the N2pc to horizontal T1 benchmark objects (289 ms versus 183 ms; $t_c(11) = 15.98, p < .001, \eta_p^2 = .96$). For the voluntary shift task, this delay was 163 ms (356 ms versus 194 ms; $t_c(11) = 24.27, p < .001, \eta_p^2 = .98$). As in Experiment 7a, the N2pc to horizontal T1 benchmark objects did not differ reliably between the two tasks, $t_c(11) = 1.76, p = .105, \eta_p^2 = .22$. In contrast, the N2pc to horizontal T2 objects emerged significantly later in the voluntary shift task relative to the priority-driven shift task (356 ms versus 289 ms; $t_c(11) = 6.72, p < .001, \eta_p^2 = .80$).

The analysis of N2pc mean amplitudes with the factors Task, Display Type and Laterality (electrode contralateral versus ipsilateral to the side of the horizontal target) confirmed the presence of reliable N2pc components in Experiment 7b (main effect of Laterality: $F(1,11) = 95.25, p < .001, \eta_p^2 = .90$). There was no interaction between Task and Laterality, $F(1,11) = .87, p = .372, \eta_p^2 = .07$, and also no Display Type x Laterality interaction, $F(1,11) = 1.29, p = .28, \eta_p^2 = .10$, indicating that N2pc amplitudes were not reliably different for horizontal benchmark (T1) and response-relevant (T2) targets.

Analyses of N2pc Onset Latencies across Experiments 7a and 7b

To obtain further insights into speed differences between fully voluntary attention shifts and different types of priority-driven shifts, additional N2pc latency analyses were

conducted across the two experiments. For the N2pc to horizontal benchmark objects (T1), a 2-way mixed-design ANOVA with the within-subjects factor Task (priority-driven versus voluntary shift) and the between-subjects factor Selection Attribute (shape in Experiment 7a versus colour in Experiment 7b) obtained no main effect of Task, $F_c(1,22) = 1.02$, $p = .496$, $\eta_p^2 = .04$, confirming that the speed with which attention was allocated to the benchmark item did not differ between priority-driven and voluntary shift tasks. The effect of Selection Attribute approached significance, $F_c(1,22) = 3.34$, $p = .081$, $\eta_p^2 = .13$, as N2pcs to colour-defined benchmark objects in Experiment 7b tended to emerge earlier than N2pc components to the shape-defined benchmark objects in Experiment 7a (196 ms versus 219 ms). For the N2pc to T2 objects, there were no onset latency differences between the voluntary shift tasks of Experiments 7a and 7b, $F_c(1,22) = .02$, $p = .894$, $\eta_p^2 = 0$. However, there was a difference in N2pc onset latencies to T2 objects between the two types of priority-driven attention shifts examined in Experiments 7a and 7b. When the location of T2 was signalled by its colour match with the benchmark object (Experiment 7a), the N2pc emerged earlier than when it was indicated by an arrow at the benchmark location (Experiment 7b; 259 ms versus 289 ms; $F_c(1,22) = 14.16$, $p < .01$, $\eta_p^2 = .39$). To confirm that priority-driven shifts of attention were faster when they were controlled by target colour than by arrow cues, N2pc onset latencies to horizontal T1 objects were subtracted from onset latencies to T2 objects, and the resulting difference values were compared across these two types of priority-driven selection tasks. Shift times were indeed reliably faster for the colour-guided shifts in Experiment 7a relative to the arrow-guided shifts in Experiment 7b (47 ms versus 106 ms), $F_c(1,22) = 7.64$, $p < .05$, $\eta_p^2 = .26$). An analogous comparison between the two voluntary shift tasks of Experiments 7a and 7b found that shift times were not significantly different (128 ms versus 163 ms; $F_c(1,22) = 1.74$, $p = .200$, $\eta_p^2 = .07$).

5.3.3.4 Discussion

The results of Experiment 7b demonstrate that priority-driven shifts are faster than fully voluntary shifts of attention even when priority-driven attention is not “pulled” towards target-matching features, as in Experiment 7a, but is “pushed” towards target locations signalled by spatial cues. In the voluntary shift task, the N2pc to T2 objects was delayed by 163 ms relative to the onset of N2pc components triggered by T1 objects. This T1/T2 N2pc onset difference did not differ reliably from the (numerically smaller) difference observed in the voluntary shift task of Experiment 7a. Together, these results strongly suggest that fully voluntary shifts of attention between visual objects can be elicited within less than 200 ms. For priority-driven shifts triggered by arrow cues, the N2pc to T2 targets emerged 106 ms later than the N2pc to the T1 benchmark cues. This shows that cued shifts of attention are triggered faster than fully voluntary attention shifts, and also more rapidly than was suggested by previous behavioural studies (e.g., Cheal & Lyon, 1991). On the other hand, these cue-triggered attention shifts appear to operate at a slower pace than the feature-guided shifts investigated in Experiment 7a.

While target RTs were unexpectedly faster in the voluntary task relative to the priority-driven shift task in Experiment 7a, RTs were faster in the priority-driven task of Experiment 7b, consistent with the N2pc evidence for more rapid attention shifts in this task. This supports the hypothesis that the RT costs found for the priority-driven task in Experiment 7a was due to the fact that different dimensions (colour versus shape) were relevant to find T2 and to select the correct response. No such shift between selection criteria was required in the priority-driven task of Experiment 7b, where T2 was signalled by the shape of the benchmark arrow.

5.4 General Discussion

The goal of the current study was to measure the speed of serial attention shifts between visual objects, and to find out whether fully voluntary shifts of attention are slower than priority-driven shifts that can be guided by visual features. We employed a novel task design where observers first had to localise and/or identify a benchmark (T1) object, in order to determine which other object in the search display (T2) was the response-relevant target. N2pc components in response to T1 objects preceded N2pc components to T2 objects in all task conditions. This shows that as intended, attention was first directed to T1 before a second attention shift towards T2 was initiated. Critically, the onset latency difference between these two N2pc components could therefore be used to determine the speed of these serial attention shifts from T1 to T2.

In the voluntary shift tasks of Experiments 7a or 7b, the benchmark object (T1) was defined by its shape or its colour, and participants had to move their attention either clockwise or anticlockwise from the benchmark to another response-relevant object (T2). In these tasks, the initial allocation of attention to T1 objects was priority-driven, as it was guided by the known shape or colour of the benchmark object. In contrast, because the location of T2 was not signalled by any visual features in the search displays, shifts of attention from T1 to T2 had to be exclusively based on endogenous (voluntary) control processes. The N2pc to T2 objects emerged 128 ms (Experiment 7a) and 163 ms (Experiment 7b) later than the N2pc to T1 objects in these voluntary shift tasks. These findings provide new objective estimates for the speed of fully voluntary attention movements. The shift times suggested by this temporal pattern of N2pc components are faster than the shift rates of 200 – 250 ms per object that were inferred by Horowitz et al. (2009) on the basis of behavioural measures. This discrepancy may be primarily due to differences in attentional task demands. In the experiments by Horowitz et al. (2009), participants had to execute multiple serial

attention shifts on each trial, and each attended object had to be identified as target or nontarget before attention could move to the next location. In the voluntary shift tasks of the present study, only one voluntary movement of attention (from T1 to T2) was required, and the T1 benchmark item had to be localised, but not fully identified. Even though the identity of T1 was irrelevant, there were still behavioural congruency effects in these voluntary shift tasks (i.e., faster RTs on trials where the alphanumeric category of T2 items matched the category of the object at the benchmark location), suggesting that the category of T1 benchmark objects was in fact discriminated. The size of these congruency effects did not differ between the voluntary and priority-driven shift tasks, which further suggests that T1 category was processed in a task-independent automatic fashion (see also Egeth, Jonides, & Wall, 1972; Duncan, 1980, for similar conclusions). Overall, the N2pc results obtained in the voluntary shift tasks provide novel electrophysiological insights into the pace of fully voluntary shifts of attention. They show that the “clock speed of free will” (Horowitz et al., 2009) in the control of spatial attention can be measured objectively. Voluntary shift of attention from a currently attended location to a new object can be initiated within approximately 150 ms.

The other main finding from the present study was that priority-driven shifts of attention are faster than purely voluntary shifts, confirming previous suggestions based on behavioural results (Horowitz et al., 2009). In the priority-driven shift task of Experiment 7a, where T2 matched the colour of the object at the T1 benchmark location, the T1/T2 N2pc onset latency difference was 47 ms. The fast pace of colour-guided shifts observed in Experiment 7a is also consistent with the results of our recent N2pc study (Grubert & Eimer, 2016b), where the N2pc elicited by known fixed-colour target preceded the N2pc to a variable-colour target by 60 ms. It is notable that in an earlier N2pc investigation of colour-guided serial attention shifts (Woodman & Luck, 2003), considerably longer shift times (100

– 150 ms) were observed. In this study, a difficult perceptual discrimination of the shape of Landolt squares was required at each attended location, which may have delayed attention shifts to a new target location. It is important to note that priority-driven attention shifts are not entirely stimulus-driven, but subject to top-down strategic control. For this reason, the speed of such shifts is unlikely to be constant, but will instead be affected by the demands of a specific selection task (see also Grubert & Eimer, 2016b, for evidence that priority-driven attention shifts operate more slowly when temporal task demands are relaxed). More generally, the finding that priority-driven shifts of attention to new target objects that are guided by target-defining stimulus features can be triggered within approximately 50 ms is important for serial models of visual search. These models have used search slopes to infer the speed of such attention shifts (e.g., Treisman & Gelade, 1980; Wolfe, 2007), and assume that priority-based attention can move between objects at rates of about 50 ms or even faster (Wolfe, 1998b). The temporal pattern of N2pc components observed during priority-driven attention shifts in the current Experiment 7a and in our previous study (Grubert & Eimer, 2016b) provides electrophysiological evidence that attention can indeed move at the relatively fast speed postulated by these serial models.

In the priority-driven shift task of Experiment 7b, arrow cues at the benchmark location signalled the location of the response-relevant T2 object. Here, priority-driven attention was not pulled by a particular target feature, but pushed towards a target by a feature (arrow direction) at another currently attended location. The T1/T2 N2pc onset delay measured in this task (106 ms) was longer than the delay found for colour-guided attention shifts in Experiment 7a, but shorter than the delay observed during fully voluntary attention shifts. This suggests that shifts of spatial attention in response to arrow cues can be triggered about 100 ms after the onset of such cues, which is substantially faster than previous estimates based on behavioural results (e.g., Cheal & Lyon, 1991; Müller & Rabbitt, 1989;

Nakayama & Mackeben, 1989). It is difficult to directly compare the time course of cued attention shifts reflected by the N2pc results of Experiment 7b with these behavioural spatial cueing studies. In these earlier studies, spatial cues were presented prior to search displays whereas cues and targets appeared simultaneously in Experiment 7b. The onset of N2pc components reflects an early phase of attentional selectivity (i.e., the emergence of a spatially selective processing bias in ventral visual areas; see Eimer, 2014, 2015, for further discussion), whereas behavioural spatial cueing effects may be generated at later stages of attentional processing. The fact that colour-guided attention shifts investigated in Experiment 7a were faster than the attention shifts elicited by spatial cues measured in Experiment 7b is interesting, because it suggests that feature signals at target locations for an attention movement are more effective in controlling the focus of attention than spatially informative signals at previously attended locations. It is possible that identifying the colour of the benchmark object in Experiment 7a was faster than discriminating the direction of the benchmark arrow in Experiment 7b, and that attention shifts towards T2 could therefore be triggered earlier.⁸ Priority-driven attention shifts elicited by spatial cues and shifts that are guided by target-matching features are necessarily associated with different types of sensory signals which differ in their processing demands, and this factor may be largely responsible for differences in speed between these two types of priority-driven shifts.

⁸ It is also conceivable that once the colour of the object at the benchmark location was detected in Experiment 7a, attention was immediately shifted to the only other colour-matching item in the display (the T2 object), and that the fast shift times observed in this priority-driven task were a direct result of this colour match. However, this interpretation is not in line with the fact that very similar shift speeds were observed in our previous N2pc study of priority-driven attention shifts (Grubert & Eimer, 2016b) where the two target items in each display differed in colour.

Because the speed of attention shifts between different objects is modulated by the amount of processing required by these objects, the N2pc onset delay between T1 and T2 objects measured in the current study will be affected by how deeply T1 had to be processed in order to determine the response-relevant T2 object. In this context, the observation that purely voluntary shifts were slower than priority-driven shifts in both experiments is particularly remarkable, because T1 processing demands were actually higher in the priority-driven tasks. When performing the voluntary tasks, localising the benchmark object was sufficient to initiate the required clockwise or anticlockwise shift of attention towards the T2 object. In the priority-driven tasks, benchmark objects not only had to be localised, but their colour or shape also had to be discriminated in order to identify T2. In spite of the fact that an additional T1 processing step was required in the priority-driven shift tasks, N2pc components to T2 targets still emerged earlier than in the voluntary tasks, demonstrating that attention shifts were triggered more rapidly. This further underlines the fact that fully voluntary movements of attention are slower than attention shifts that are guided by visual features. When the time demands associated with T1 processing are taken into account, the true speed of priority-driven attention shifts may even be faster than suggested by the T1/T2 N2pc onset differences observed in the current study, and differences between the speed of voluntary and priority-driven shifts may even be larger.

In summary, the current study has provided new electrophysiological insights into the speed of priority-driven shifts of attention, and is the first to report on-line measures of purely voluntary movements of attention between different visual objects. We have shown that fully endogenous attention shifts that cannot be guided by visual signals are generally slower than shifts of attention that are controlled by target-matching visual features or by spatial cues. Purely voluntary attention shifts can be initiated within about 150 ms, feature-guided shifts are much faster (~50 ms), and attention shifts in response to spatial cues require about 100

ms. The speed of these three different types of attention shifts is unlikely to be completely fixed, but will vary to some degree as a function of the attentional processing demands of a particular task. The current results also demonstrate that ERP-based measures such as the N2pc component can be useful tools to uncover the temporal dynamics of attentional object selection mechanisms.

Chapter 6
Effects of Target Distance on Voluntary
Attention Shifts

6.1 Chapter Overview

While Chapter 5 demonstrated clear qualitative differences between priority-driven and voluntary attention shifts, questions were introduced regarding the nature of voluntary attention shifts. In particular, Chapter 6 sets out to uncover whether voluntary attention operates in a qualitatively different manner than priority-driven attention, by determining whether distance influences the speed of these shifts. Experiment 8a revealed that no distance effects were present for priority-driven shifts; Experiment 8b produced conflicting results whereby RTs supported an effect of distance but N2pc onset latencies did not. Finally, Experiment 8c accounted for this discrepancy and revealed that voluntary attention moves in a continuous fashion across the retinotopic map.

6.2 *Experiments 8a, 8b & 8c: Colour-guided versus Voluntary Attention Shifts*

6.2.1 Introduction

The debate about whether attention can be allocated serially (e.g., Wolfe, 1994, 2007; Treisman & Gelade, 1980) or in parallel (Desimone & Duncan, 1995) is one that concerns the nature of attentional responses to multiple different objects. For this reason, conclusions that shed light on the debate can be hard to achieve on the basis of behavioural data alone (see Townsend, 1990), as individual attentional responses to each object are difficult to distinguish from each other. In these multi-target scenarios, the N2pc component is useful because it can continuously track the time-course of attentional responses to specific objects; the previous chapters of this thesis demonstrate its benefits (see also Eimer & Grubert, 2014a; Grubert & Eimer, 2015).

While these experiments demonstrate flexible, rapid and parallel attentional mechanisms in search for multiple objects, some tasks require serial and sequential shifts of the focus of attention. In these scenarios, the question arises as to how quickly attention can be shifted between objects when it must be deployed sequentially. A behavioural measure of the speed of serial attention shifts comes from search slopes of visual search tasks, which measure the time required to find a target as a function of the number of objects in a search display. These search slopes are assumed to reflect the speed of moving the focus of attention between each object, and tend to yield shift times of approximately 50 ms (e.g., Wolfe, 1998b). However, this behavioural evidence is indirect, and the speed of attention shifts is likely to vary depending on the information that is available to guide them. While attention can be guided towards objects on the basis of relevant stimulus properties, such as those possessing a specific colour (priority-driven attention shifts, see Horowitz et al., 2009), it can also be re-oriented from one location to another endogenously and without influence by stimulus properties (voluntary attention shifts). It is possible that the rapid speed of attention shifts inferred from search slopes in behavioural experiments apply only to priority-driven attention shifts, while voluntary attention shifts may operate much more slowly (e.g., Cheal & Lyon, 1991; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989).

A direct behavioural comparison between priority-driven and voluntary attention shifts was made in a series of experiments by Horowitz et al. (2009; see also Wolfe, Alvarez, & Horowitz, 2000). Participants were presented with multiple rapid and brief displays containing circular arrays of letters, and were asked to shift their attention sequentially between adjacent locations with each successive display from a specified starting point and in a specified direction (e.g., clockwise from the top). The target was presented only at one location during one corresponding display (e.g., 4 o'clock in the fifth display), so that attention had to be focused at this position at the correct time. Thus, the task required

participants to endogenously shift their attention at a specified pace. Note that because these attention shifts were not dependent on the presence of any stimulus properties, but instead were made to a specific location, they are considered to be purely voluntary attention shifts. Participants were successful in this task only when each display was presented for at least 250 ms, indicating a slow speed for voluntary attention shifts. In another experiment by Horowitz et al. (2009), a static circular array was presented, and participants were asked to report the first mirror-reversed letter in a specified direction from the starting point (signalled by a cue). As the distance between this cue and the target increased along the circle, reaction times also increased linearly, with a slope of around 200 ms per object. This suggests that fully voluntary attention shifts between objects in static displays (where even the onset or change in a display cannot be used to mediate the speed of attention shifts) operate at rates no faster than 200 ms. Priority-driven shifts were encouraged in another experiment by Horowitz et al. (2009) where the stimuli remained the same on each frame. Here, the detection of the target stimulus was not based on purely voluntary shifts of attention, and instead relied on priority-driven shifts that were guided by the known features of the target object. The speed of these shifts was estimated at or slightly below 100 ms per shift.

While Horowitz et al. (2009) provided strong evidence for differences in the speed of voluntary and priority-driven attention shifts, these experiments were only able to indirectly determine their speed on the basis of reaction times, which measure the time taken for all processing to occur, from stimulus onset until response (and in this case across multiple stimulus displays). With the use of EEG, however, the attentional selection of individual objects can be directly tracked in real time to provide a more direct and pure measure of the speed of attention shifts. This was done in a recent study from our lab (Experiments 7a & 7b of this thesis), in a series of tasks that required sequential shifts of attention between a benchmark object and a target object. In providing the first electrophysiological measure of

the speed of fully voluntary shifts of attention, these experiments suggested that voluntary attention shifts can be made somewhat more quickly than previous behavioural studies have estimated. Crucially, however, this study also confirmed a clear difference of as much as 100 ms in the speed of these two types of attention shift, with voluntary, endogenous attention operating more slowly than priority-driven attention shifts.

Such a striking difference in speed warrants further investigation into differences between voluntary and priority-driven attention shifts. What are the qualitative differences in the way these attentional processes operate that lead to these speed differences? To begin answering this question, it is important to consider the information available to guide attention in these scenarios. By definition, voluntary attention shifts must be made without the guidance of any feature signals; the re-orienting of attention to a new location must be triggered endogenously through a conscious act of free will. Priority-driven attention shifts, on the other hand can be guided by specific feature signals that are relevant to the task at hand. For example, if an observer determines that the colour red is task-relevant, the presence of this colour at any location in the visual field will attract attention. The rapid parallel attentional allocation processes observed in previous studies from our lab (e.g., Eimer & Grubert, 2014a) are controlled by the attentional template, or task set (e.g., Folk & Remington, 1998; Olivers, Peters, Houtkamp, & Roelfsema, 2011; Wolfe & Horowitz, 2004; Duncan & Humphreys, 1989). An attentional template is an internal representation of a task-relevant feature that is thought to be held in visual working memory, and facilitates the visual processing of target objects that possess this feature (e.g., Eimer, 2014, 2015; Desimone & Duncan, 1995). Importantly, the guidance of attention by an attentional template is thought to operate initially in a spatially global fashion (Eimer, 2014), in that all instances of a template-matching feature across the retinotopic map will trigger an attentional modulation of visual activity, before attentional processing starts to become focused on one or several target

objects. In the context of serial attention shifts, priority-driven shifts should benefit from the use of these spatially global mechanisms that mark the location of the target object for an upcoming attention shift. In contrast, voluntary attention shifts cannot employ these mechanisms, and this may explain why voluntary attention shifts operate more slowly.

If no spatially global modulations of task-relevant features are available during voluntary shifts of attention, how does the focus of voluntary attention move from one target location to another in these circumstances? Priority-driven serial attention shifts may operate in a spatially discrete fashion from one object with target-matching features to another target location, irrespective of whether other non-matching distractor objects are present between the first and second attended target. Attention emerges at the location of the second target as a direct result of increased visual activity at this location (as measured by the lateralised N2pc component), which is in turn modulated by some form of integration between feed-forward stimulus signals and recurrent feedback loops (Luck & Vogel, 2013; Kravitz et al., 2013) elicited by the attentional template. When attention is voluntarily shifted from one target object to another, and such feature-based attentional guidance mechanisms are not available, an alternative possibility is that these shifts operate in a continuous fashion across the retinotopic map, so that intermediate distractor objects may also receive a transient attentional facilitation. In short, the discrete-continuous dichotomy may reflect a fundamental qualitative difference between priority-driven and voluntary attention shifts.

The concept of analogue movements of the attentional focus is not new. From as early as 1980, the metaphor of an attentional ‘spotlight’ (Posner, 1980) has been used to describe a focused region of enhanced processing within the retinotopic map. Studies of visual attention have often assumed that the focus of attention is necessarily spatially restricted in this way, with all information inside the spotlight being processed and all information outside it being completely ignored. This assumption has led to many debates over whether one or several

spotlights could exist simultaneously in the visual field (e.g., McMains & Somers, 2004), whether these spotlights could be varied in size or shape (e.g., Müller & Hübner, 2002), and whether a unitary spotlight moves in discrete steps (e.g., Sperling & Weichselgartner, 1995) or in a continuous fashion (e.g., Shulman, Remington, & McLean, 1979; Tsal, 1983). While it is now clear that attention is not always restricted to a small spotlight region of visual space (for example in the case of spatially global feature-based attention, e.g. Treue & Trujillo, 1999), the question whether attention moves discretely or continuously is still relevant in the context of voluntary attention, which may be spatially restricted in this way. The most obvious manipulation in a task that aims to understand whether attention is shifted continuously or discretely is to vary the distance between two locations or objects. Clear hypotheses can be generated from experiments with this manipulation: if attention does indeed move continuously, larger distances will correspond to longer delays in the attentional selection of the second object, whereas a discrete change in the spatial focus of attention should not be mediated by distance.

Behavioural studies, which measure reaction times as a function of distance between two objects, have produced conflicting results (e.g., Shulman et al., 1979; Kwak, Dagenbach, & Egeth, 1991; Tsal, 1983; LaBerge, 1983; LaBerge & Brown, 1989; Eriksen & Murphy, 1987; Remington & Pierce, 1984; Sagi & Julesz, 1985). For example, Kwak, Dagenbach & Egeth (1991) provided evidence for time-independent shifts of the focus of attention, by presenting two letters to be discriminated by observers in a same/different judgement task. These letters appeared at some point along the periphery of an imaginary circle, and their distance was varied from trial to trial. Reaction times did not increase when the targets were further in distance from one another, despite the fact that they were processed in serial. The conclusions considered on the basis of these results were that serial attention shifts between targets may not involve analogue movements through the visual field. Alternatively,

however, Tsal (1983) put forward the claim that attention moves at a fixed velocity that can be computed. In his task, participant simply had to report whether the object that appeared after a pre-cue in a previous display was an 'O' or an 'X'. Again, SOAs between pre-cue and target were manipulated, but in this study, reaction times reached asymptote later for objects presented further from fixation. In fact, Tsal estimated that the focus of attention travelled at a velocity of about 8 ms per degree of visual angle. Many similar studies have used similar paradigms and relied on reaction time measures to gain insight into the qualitative nature of attention shifts, but their results have often led to many different interpretations. On the basis of these behavioural studies, the question of whether voluntary attention is shifted discretely or continuously is still open. However, measuring the N2pc in these types of tasks may provide a more clear and precise estimate of differences in the point in time when an object is selected.

The question whether the time-course of voluntary and priority-driven attention shifts (as measured by the N2pc component) are mediated by the distance between two objects was addressed in three experiments in the current study, all of which included a circular array of stimuli with an easy to detect benchmark and a target that appeared at different positions relative to the benchmark object. In all experiments, the target's position was dependent on the position of the benchmark and attention had to be shifted in a specified direction (clockwise and anticlockwise) relative to the benchmark. The critical variable was the distance between the benchmark and the target. These two objects could either be adjacent to each other, or be separated by one or more intermediate distractor objects. In Experiment 8a, these shifts were at least in part priority-driven, because the target was defined by a specific feature ("find the next coloured item clockwise/counterclockwise from the benchmark"). In Experiment 8b, a similar task was used except that attention shifts were now purely voluntary attention shifts. Target location relative to the benchmark was specified by a number cue

presented at the start of each trial (“find the target 1/2/3 positions clockwise/counterclockwise from the benchmark”). In these two experiments, the benchmark was presented on the vertical midline and the target horizontally, or vice versa, to measure N2pc components independently to benchmark and target items. In Experiment 8c, both benchmark and target objects were lateralised, and N2pc polarity shifts were measured to clarify whether voluntary attention shifts operate in a continuous or discrete fashion.

6.2.2 Experiment 8a: Colour-guided Attention Shifts

6.2.2.1 Methods

Participants

Twelve participants were paid to take part in the experiment, and were aged between 25 and 42 years ($M = 31.42$ years, $SD = 5.30$). Six of these participants were female, and four were left handed. All participants had normal or corrected-to-normal vision.

Stimuli and procedure

Stimuli were presented on a 22-inch Samsung wide SyncMaster 2233 LCD monitor (resolution of 1280 x 1024 pixels, 100 Hz refresh rate; 16ms black-to-white-to-black response time, verified using a photodiode). Participants were seated in a dimly lit cabin and viewed the screen from an approximate distance of 100 cm. Stimulus presentation, timing, and response collection were controlled by a LG Pentium PC operating under Windows XP, using the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.). Stimuli were letters (A, D, E, K, N or U), digits (2, 4, 5, 6, 7, or 9), and a circle (line

width 0.2°). All stimuli were matched in height and width (0.8° x 0.8°), and were either grey (CIE colour coordinates: .321/.352), red (.623/.337), green (.266/.564), blue (.194/.214), or magenta (.307/.180). All colours were equiluminant (~7.6 cd/m²). Stimuli were presented at an eccentricity of 3.0° from central fixation, against a black background, and a central grey fixation point (0.2° x 0.2°) remained continuously present throughout each experimental block.

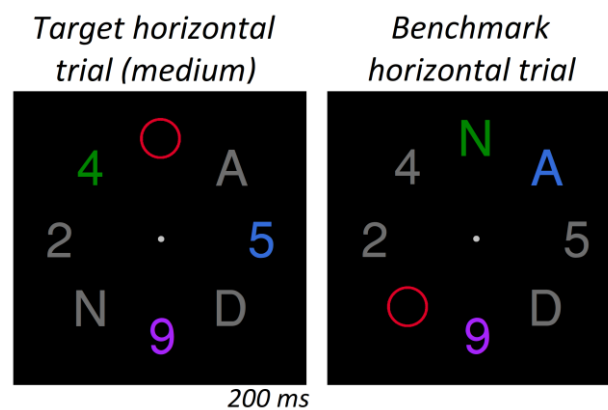


Figure 8.1: Schematic illustration of the search displays and the time course of events in Experiment 8a. All displays shown in this figure are from clockwise blocks. The left panel depicts trials in which the target appeared at one of the six horizontal locations and the benchmark appeared on the vertical midline (top or bottom). The right panel depicts trials in which this benchmark/target arrangement was reversed. A single stimulus display was presented, containing a coloured benchmark (circle), three coloured letters and digits, and four grey letters and digits; participants' task was to report the alphanumeric category (letter/digit) of the first coloured object in the specified direction (clockwise/anticlockwise) from the benchmark (a blue '5' in the left panel, and a green 'N' in the right panel).

Each trial contained an array of eight objects positioned along an imaginary circle centred at fixation (as illustrated in Figure 8.1, top-left panel). One object was a circle and served as the benchmark, whose colour was fixed and known in advance, while another object was a letter or digit and served as the target, whose colour varied across trials and was not known in advance. The target was defined as the first coloured object either clockwise or anticlockwise along the circle from the benchmark (the direction was alternated across experimental blocks). Participants' task was to report the alphanumeric category (letter versus digit) of the target by pressing one of two purpose-built vertically aligned response keys.

Critically, the number of positions between the benchmark and the target was manipulated; in near trials, the target was in one of the positions adjacent to the benchmark; in medium and far trials, the target was two or three positions along the circle from the benchmark, respectively (with one or two intermediate objects, respectively). In three quarters of all trials, this benchmark appeared equiprobably directly above or below fixation, and the target appeared at any of the six lateral positions (at 45°, 90°, 135°, 215°, 255°, or 295° clockwise from directly above fixation; target-horizontal trials). In the remaining randomly intermixed trials, the benchmark appeared equiprobably in one of the six lateral locations while the target appeared above or below fixation (benchmark-horizontal trials). Two of the six remaining letters and digits in each display possessed a unique colour which varied from trial to trial. One of these coloured nontargets appeared in the position directly opposite the vertical target/benchmark, while the other appeared randomly in one of the three lateral locations on the opposite side to the horizontal target/benchmark. This meant that each trial contained a coloured object in the left, right, top, and bottom of the display. The remaining four nontarget objects were grey and filled the remaining positions along the imaginary circle. All letters and digits were randomly selected with no repetitions of identity

in any single trial. The specific arrangement of the laterally presented benchmark/target (i.e., which of the three lateral locations that it appeared in) was dependent on the trial type (near, medium, or far, determining the distance of the target from the benchmark), and on the blocked task instruction (determining the direction of the target from the benchmark, either clockwise or anticlockwise). The three trial types were randomly intermixed in each block, and the direction of the target from the benchmark was alternated in each successive block; clear instructions of this direction were given before every block, and the direction in the first block was counterbalanced across participants.

In target-horizontal trials, the three trial types varied the position of the lateral target, in benchmark-horizontal trials, the position of the lateral benchmark was varied in the same way. In this way, either the target or the benchmark appeared vertically, while the other appeared laterally, and the target was always in the specified direction from the benchmark at a distance of either one, two, or three spaces. The response-to-key mapping, as well as the hand-to-key mapping, was counterbalanced across participants. Trials requiring a letter or digit response (and thus the identity of the target itself) were equiprobable and randomly intermixed in each block.

In each trial, the stimulus display was presented for 200 ms. The interval between the offset of the stimulus display and the onset of the stimulus display on the next trial was 1800 ms. Responses were recorded immediately after onset of the stimulus display, until the onset of the stimulus display in the next trial. The experiment contained 8 blocks consisting of 48 trials. Each block contained 12 benchmark-horizontal trials, with one trial for each combination of target identity [letter, digit], side of horizontal benchmark [left, right], and trial type [near-target, medium-target, far-target]. The remaining 36 target-horizontal trials consisted of three trials for each combination of target identity, horizontal target [left, right], and trial type. Thus, trials consisting of a benchmark and horizontal target were three times as

likely to appear as trials consisting of a horizontal benchmark and vertical target. However, each computed N2pc component consisted of the same number of trials, as three N2pc components were computed in target-horizontal trials, separated as a function of benchmark-target distance (near, medium and far), while only one N2pc component was computed in benchmark-horizontal trials, collapsed across benchmark-target distance.

EEG recording and data analyses

The continuous EEG was DC-recorded from 27 scalp electrodes at standard positions of the extended 10/20 system, sampled at a rate of 500 Hz, and digitally low-pass filtered at 40 Hz. No other offline filters were applied. All channels were online referenced to the left earlobe and re-referenced offline to the average of both earlobes. Trials contaminated with artefacts (eye movements exceeding $\pm 30 \mu\text{V}$ in the HEOG channels; eye blinks exceeding $\pm 60 \mu\text{V}$ at Fpz; muscular movements exceeding $\pm 80 \mu\text{V}$ in all other channels), and trials with incorrect, anticipatory (faster than 200 ms) or missing responses were excluded from EEG analyses. This led to an exclusion of an average of 15.4% of all trials. For the remaining trials, EEG was segmented into epochs ranging from 100 ms prior to 500 ms after the onset of the stimulus display, and was baseline corrected relative to the 100 ms interval prior to the onset of the display. For benchmark-horizontal trials, EEG was averaged separately for each location of horizontal benchmark (left or right). For target-horizontal trials, EEG was averaged separately for each of the six combinations of horizontal target (left or right) and trial type (near-target, medium-target, far-target).

N2pc components were quantified on the basis of ERP waveforms measured at lateral posterior electrodes PO7 and PO8. N2pc onset latencies were measured on the basis of difference waveforms, computed by subtracting ipsilateral from contralateral ERPs at PO7

and PO8. Onset latencies were determined with a jackknife-based procedure (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). Twelve grand-average difference waves were computed for each experimental condition, each excluding one different participant from the original sample. N2pc onset latency was defined as the point in time when each subsample difference wave reached a fixed onset criterion of $-0.5 \mu\text{V}$. Differences in N2pc onset latencies between trial types were assessed with repeated-measures ANOVAs and t -tests, with F - and t -values corrected according to the formulas described by Ulrich and Miller (2001) and Miller et al. (1998), respectively. The corrected statistical values are indicated with F_c and t_c , respectively. All t -tests were two-tailed and Bonferroni corrected where necessary. To measure effect sizes, Cohen's d (Cohen, 1988) was computed for all t -tests, and partial eta-squared (labelled η_p^2) was computed for all ANOVAs. Jackknifed group means of N2pc latency and peak amplitude values were fed into repeated-measures ANOVAs where the error variance can be corrected according to the formula described by Ulrich and Miller (2001) to calculate corrected partial eta-squared values for all t -tests on N2pc latency and peak amplitude measures (reported as η_p^{2c}).

N2pc mean amplitudes were computed within 100 ms post-stimulus time intervals, starting at the point in time when each waveform reached $-0.5 \mu\text{V}$ in amplitude, and extending 100 ms after this point. This time-window was 194-294 ms for benchmark-horizontal trials. For near-target, medium-target, and far-target horizontal trials, these time-windows were 315-415 ms, 314-414 ms, and 357-457 ms, respectively.

6.2.2.2 Results

Behavioural performance

Anticipatory reaction times (RTs; faster than 200 ms) were removed from analysis, resulting in the exclusion of less than 0.1% of all trials. A one-way ANOVA was run on RTs with the factor trial type (near-target, medium-target, and far-target trials), revealing a main effect, $F(2,22) = 18.20, p < .001, \eta_p^2 = .62$. To examine this more closely, three follow-up paired-samples t-tests were carried out for each of the three combinations of pairs of trial type (near versus medium, near versus far, and medium versus far). RTs were significantly slower in far-target trials (907 ms) than in both other trial types (870 ms and 875 ms for near-target and medium-target trials, respectively), both $t(11) > 3.25, p < .01, d > .28$. However, near-target and medium-target RTs did not differ, $t(11) = 1.06, p = .311, d = .05$.

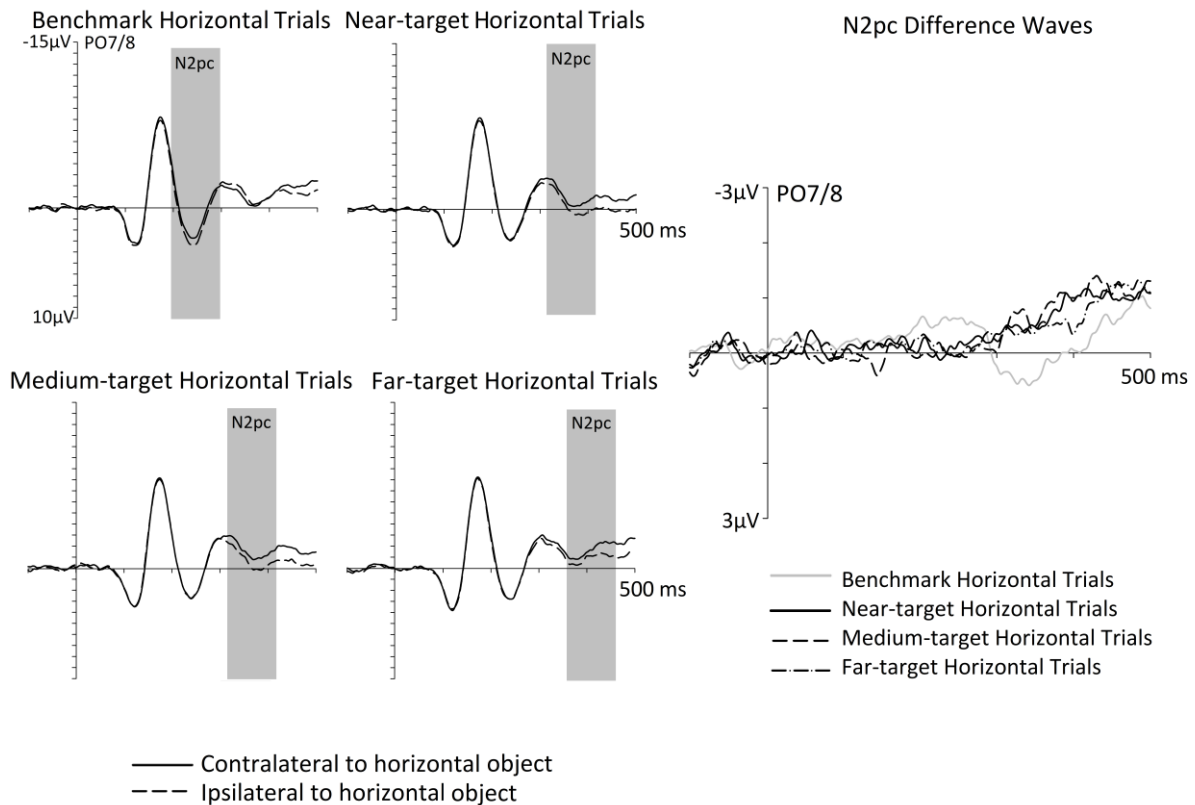
For error rates, the same ANOVA was conducted. This revealed only a trend towards a main effect of trial type, $F(2,22) = 4.19, p = .054, \eta_p^2 = .28$, due to more errors on far-target trials. Error rates were 6.60%, 6.80%, and 8.25%, in near-target, medium-target and far-target trials, respectively (mean error rate 7.22%).

N2pc components

The left and middle panels of Figure 8.2 show ERPs at posterior electrode sites PO7/8 contralateral and ipsilateral to the side of the horizontal target, separately for benchmark-horizontal trials (pooled across trial type), near-target horizontal trials, medium-target horizontal trials, and far-target horizontal trials. The right panel of Figure 8.2 shows N2pc difference waveforms computed by subtracting ipsilateral from contralateral ERPs in each of these trial types. In both task conditions, N2pc components were clearly elicited in response to each of the three lateralised targets as well as to the lateralised benchmark. Importantly, N2pcs were delayed in target-horizontal as compared to benchmark-horizontal trials.

A repeated-measures ANOVA was run on N2pc mean amplitudes using the factors trial type (benchmark-horizontal, near-target horizontal, medium-target horizontal, far-target horizontal) and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target or benchmark). This ANOVA revealed a main effect of laterality, $F(1,11) = 44.02$, $p < .001$, $\eta_p^2 = .80$, demonstrating reliably present N2pc responses to horizontal benchmark and target objects. Laterality did not interact with trial type, $F(3,33) = .78$, $p = .517$, $\eta_p^2 = .07$. Paired-samples t-tests compared contra- and ipsilateral activity, separately in response to each of the four trial types. All four of these t-tests reached significance, all $t(11) > 2.39$, $p < .05$, $d > .11$.

Figure 8.2: N2pc components elicited by the four trial types of Experiment 8a. Left and middle panels: Grand-average ERP waveforms measured in the 500 ms interval after the onset of the search display at posterior electrode PO7/PO8 contralateral and ipsilateral to the horizontal benchmark, or the horizontal target when it was one, two, or three spaces from the benchmark. Right panel: N2pc



difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for the four trial types. Grey bars indicate N2pc time-windows used for analysis.

For N2pc onset latency values, determined with a jackknife-based procedure (see Methods), a one-way ANOVA was run with the factor target distance to compare N2pc onset latency in target-horizontal trials. Even though N2pcs appeared to emerge later in far-target trials (see Figure 8.2), no main effect of target distance was observed, $F_c(1,11) = 1.61$, $p = .223$, $\eta_p^2 = .13$. Paired-samples t-tests were conducted to compare the benchmark-horizontal N2pc onset latency separately with each of the three target-horizontal trial types (near-target, medium-target, and far-target). The onset latency of the N2pc in benchmark-horizontal trials (194 ms) was significantly earlier compared with those in near-target trials (315 ms, mean difference 120 ms), medium-target trials (314 ms, mean difference 120 ms), and far-target trials (357 ms, mean difference 163 ms), all $t_c(11) > 5.24$, $p < .001$, $\eta_p^2 > .71$.

6.2.2.3 Discussion

The results of Experiment 8a confirmed the findings from Experiments 7a & 7b of this thesis by revealing a considerable delay in target selection relative to benchmark selection, indicating a serial shift of attention between these two objects that took an average of 130 ms to complete. It is important to acknowledge that in this experiment, the shifts of attention were at least partially voluntarily controlled; although the presence of colour was able to guide participants' attention towards the correct target in a priority-driven fashion, this information alone was insufficient, as other irrelevant objects also possessed colours. To complete the task, participants had to also use information about the direction of the shift, which may explain why the observed shift times are more similar to the voluntary conditions, rather than the priority-driven conditions, of Experiments 7a & 7b of this thesis. Thus, it is likely that two general cognitive tasks were required to select the target in this experiment; one task involved localising the potentially relevant objects on the basis of their location (by combining information about the location of the benchmark in each trial with the information about the direction of the shift as determined by the task instruction in each block), and the other involved detection of a salient coloured object among grey objects within this localised region. It is difficult to determine the order in which these two processes occur, or whether they take place in parallel, but both would be required in order to select the target.

The primary goal of this experiment was to determine if these attention shifts were mediated by distance between the benchmark and the target. No such effect was found on N2pc onset latency, suggesting that the speed of selecting the target was not influenced by distance in this particular task, although there was a tendency for delayed selection specifically in far trials. Given the cognitive tasks described above that are likely required

here, such a finding is unsurprising: The task of localising the target region on the basis of a given direction (“clockwise” or “anticlockwise”) should not be affected by differences in distance between benchmark and target, and the task of detecting a coloured object within this region is likely to be based on spatially global mechanisms (see Eimer, 2014). Although there was a general effect of distance on RTs, this was driven by slower responses in trials where the target was in the furthest position from the benchmark, and did not demonstrate a linear distance effect, which would be expected if these attention shifts were mediated by distance. This observation may alternatively be caused by an influence of crossing the horizontal midline (from top to bottom, or vice versa) in only far trials, and not in near or medium trials.

The fact that no effect of benchmark-target distance on N2pc onset latency was observed suggests that larger distances between two objects do not increase the time taken for attention to shift between them when some form of priority information (in the case of Experiment 8a, the presence of a colour among grey objects) is available to guide such a shift. However, voluntary shifts of attention (e.g., Experiments 7a & 7b of this thesis), where attention is endogenously re-oriented to a location regardless of the properties of the object at that location, are thought to operate in a different fashion; as spatially-global mechanisms cannot be available to guide attention, it is possible that object locations play a more prominent role in the speed of these attention shifts. Experiment 8b tested this prediction using similar procedures as in Experiment 8a. However, targets were now defined only by their location relative to the benchmark (which was cued before the onset of each display), and possessed no feature that distinguished them from the other nontarget objects in the display. Thus, no stimulus-based mechanisms could be employed to detect the target, and attention had to be voluntarily allocated to a specific location. As in Experiment 8a, the distance between benchmark and target was manipulated (one, two, or three locations). If the

N2pc to target objects was delayed the when distance between benchmark and target was increased, this would suggest that purely voluntary shifts of attention do not operate in a discrete fashion, but are affected by the spatial distance between two attended locations and/or the number of intermediate distractor objects between them.

6.2.3 *Experiment 8b: Voluntary Attention Shifts*

6.2.3.1 Methods

Participants

The same participants as in Experiment 8a were tested in Experiment 8b, but in a different session on a separate day.

Stimuli and procedure

The presentation of the stimulus display was identical to the Experiment 8a, apart from the fact that now only the benchmark possessed a colour and all other objects were grey (see Figure 8.3). In addition, a cue display preceded the stimulus display in which a grey digit ('1', '2', or '3') replaced the fixation point for 150 ms. A blank display containing only the fixation point subsequently appeared for 100 ms, before the stimulus display was presented. The digit that appeared in the cue display was dependent on the trial type (near-target, medium-target or far-target trials). Participants' task was to report the alphanumeric category (letter or digit) of the object that was the cued number of positions from the benchmark object, as cued by the value in the cue display (for example, if the cue display contained a '2', participants had to report the category of the object two positions clockwise

or anticlockwise from the benchmark). All other aspects of stimulus presentation and procedure were identical to Experiment 8a.

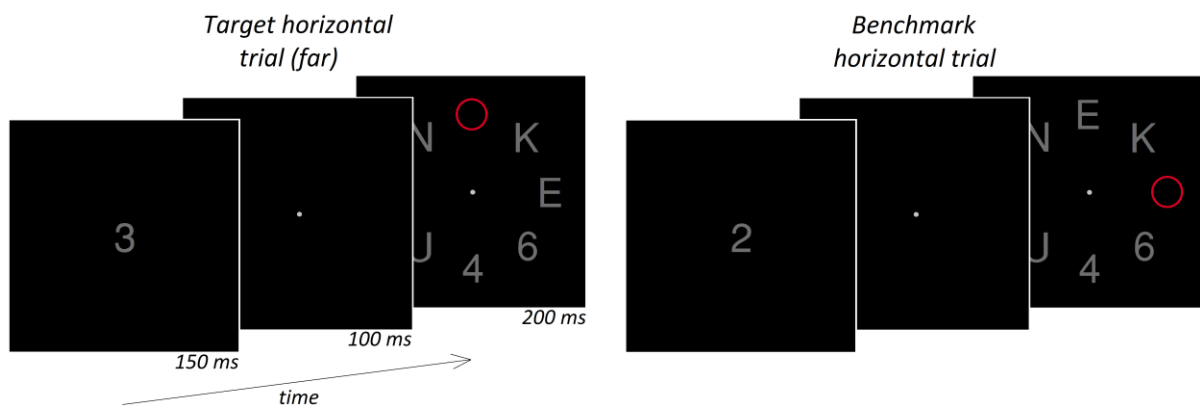


Figure 8.3: Schematic illustration of the search displays and the time course of events in Experiment 8b. All displays shown in this figure are from clockwise blocks. The left panels depict trials in which the target appeared at one of the six horizontal locations and the benchmark appeared on the vertical midline (top or bottom). The right panels depict trials in which this benchmark/target arrangement was reversed. A stimulus display contained eight objects, all of which were grey apart from the benchmark; this display was preceded by a number cue ('1', '2', or '3'), indicating the number of spaces between the benchmark and target (a '6' in the left panel, and a '4' in the right panel).

EEG recording and data analyses

All aspects of EEG recording and analysis were identical to Experiment 8a. Exclusion of trials contaminated with artefacts and incorrect, anticipatory, and missing responses led to an exclusion of an average of 15.9% of all trials. Mean amplitude time-windows were 215-315 ms for benchmark-horizontal trials, and 291-391 ms, 296-396 ms, and 284-384 ms for near-target, medium-target, and far-target horizontal trials, respectively.

6.2.3.2 Results

Behavioural performance

Exclusion of anticipatory RTs resulted in the removal of less than 0.4% of trials. A one-way ANOVA was run on the remaining trials, separately for RTs and error rates, with the factor trial type (near-target, medium-target, far-target). For RTs, a main effect of trial type was observed, $F(2,22) = 153.78, p < .001, \eta_p^2 = .93$. Follow-up paired-samples t-tests confirmed a linear effect of distance; RTs in near-target trials (823 ms) were significantly faster than those in medium-target trials (927 ms, mean difference 103 ms), and those in far-target trials (1002 ms, mean difference 179 ms), both $t(11) > 9.49, p < .001, d > 1.36$. In addition, RTs in medium-target trials and far-target trials differed significantly (mean difference 76 ms), $t(11) = 9.48, p < .001, d = 1.08$.

For error rates, a main effect of trial type was also revealed, $F(2,22) = 20.92, p < .001, \eta_p^2 = .66$. Follow-up paired-samples t-tests again revealed a linear effect of distance; error rates in near-target trials (6.47%) were lower than those in medium-target trials (10.37%, mean difference 3.90%), and in far-target trials (13.60%, mean difference 7.13%), both $t(11) > 3.67, p < .01, d > .67$. Comparing error rates in medium-target and far-target trials further revealed a significant difference (mean difference 3.23%), $t(11) = 3.34, p < .01, d = .44$.

N2pc components

Figure 8.4 shows ERP components and N2pc difference waves in the same format as Figure 8.2. Again, N2pc components were clearly elicited in all trial types, with N2pc onset emerging later for target-horizontal trials relative to benchmark-horizontal trials.

For N2pc mean amplitudes, a repeated-measures ANOVA with the factors trial type (benchmark-horizontal, near-target horizontal, medium-target horizontal, and far-target horizontal) and laterality (electrode contralateral versus ipsilateral to the side of the horizontal

target or benchmark) was conducted to compare the amplitude of N2pc components across all trial types. A main effect of laterality, $F(1,11) = 91.30, p < .001, \eta_p^2 = .89$, confirmed the reliable presence of N2pc components, but was not accompanied by an interaction, $F(3,33) = .76, p = .523, \eta_p^2 = .06$. Paired-samples t-tests compared contra- and ipsilateral activity separately in response to each of the four trial types. All four of these t-tests reached significance, all $t(11) > 3.99, p < .01, d > .33$.

N2pc onset latencies were determined using the same methods and onset criterion as Experiment 8a. Paired-samples t-tests were conducted to compare N2pc onset latencies in benchmark-horizontal trials separately with those in near-target, medium-target, and far-target trials. All three t-tests reached significance, all $t_c(11) > 2.91, p < .05, \eta_p^2_c > .43$, demonstrating earlier N2pc onset in benchmark-horizontal trials (215 ms) relative to near-target (291 ms, mean difference 76 ms), medium-target (296 ms, mean difference 81 ms), and far-target trials (284 ms, mean difference 69 ms). Critically, the analysis of N2pc onset latencies across target-horizontal trials with the factor target distance revealed no effect of target distance, $F_c(2,22) = .39, p = .683, \eta_p^2_c = .03$, suggesting that the N2pc elicited by horizontal targets was not affected by their distance from the benchmark.

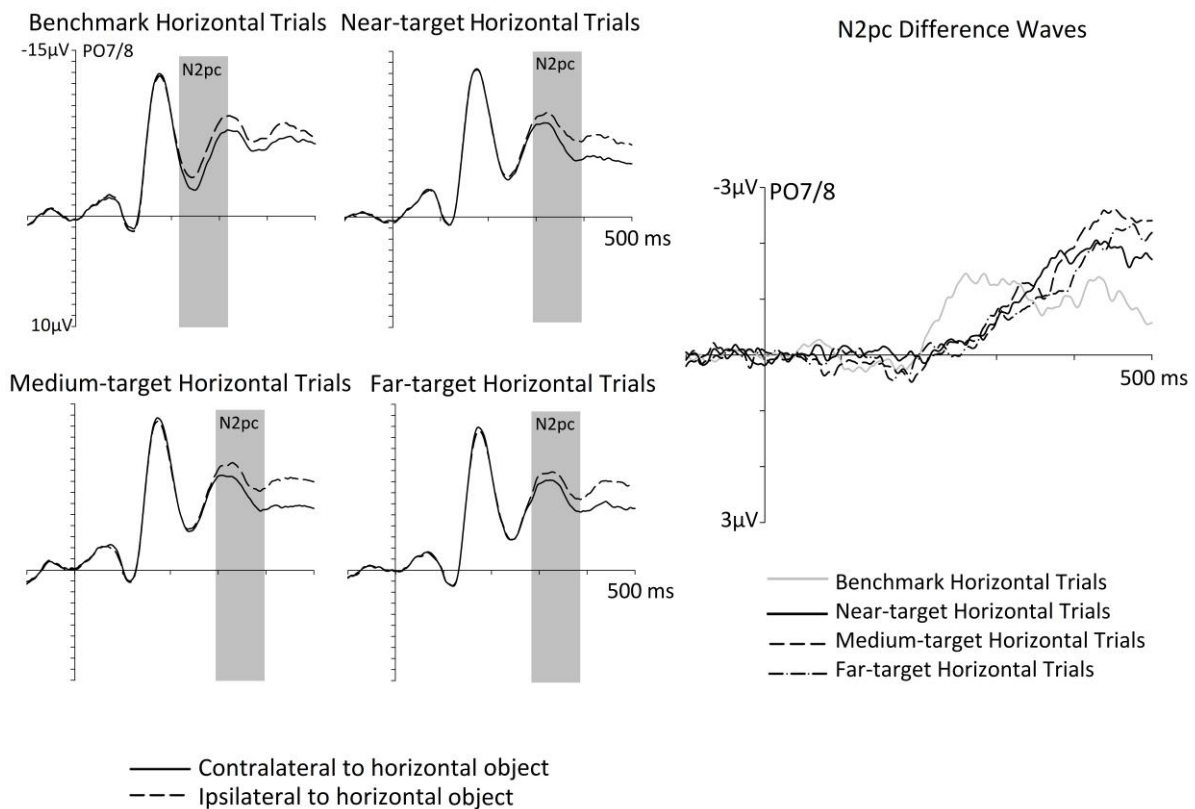


Figure 8.4: N2pc components elicited by the four trial types of Experiment 8b, shown in an identical fashion to Figure 8.2. Left and middle panels: Grand-average ERP waveforms measured in the 500 ms interval after the onset of the search display at posterior electrode PO7/PO8 contralateral and ipsilateral to the horizontal benchmark, or the horizontal target when it was one, two, or three spaces from the benchmark. Right panel: N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for the four trial types. Grey bars indicate N2pc time-windows used for analysis.

6.2.3.3 Discussion

In addition to demonstrating serial shifts of attention between the benchmark and the target in all trials, Experiment 8b now also revealed a linear behavioural distance effect on both RTs

and error rates, in line with results from previous behavioural studies (e.g., Tsal, 1983; Shulman et al., 1979). Whether this effect was due to the increasing distance of the target from the benchmark, or the increasing number of intermediate grey objects between these two objects, is difficult to distinguish from this experiment alone. Nonetheless, the presence of a linear behavioural distance effect in the current experiment, along with a lack of such an effect in Experiment 8a, implies that voluntary attention shifts operate in a continuous fashion and are in this respect qualitatively different from priority-driven shifts.

Despite this behavioural distance effect, no accompanying effect of N2pc onset latency was found. N2pc onset latencies did not differ between near, medium, and far targets, suggesting that voluntary shifts operate in a discrete fashion. There are several possible explanations for such a discrepancy between behavioural and ERP measures. On the one hand, it is possible that the behavioural distance effect observed in Experiment 8b does not reflect continuous attention shifts. For example, it is possible that the selection of the target did indeed take place at the same time after selection of the benchmark, regardless of the distance between these objects, and the observed behavioural effects were a result of interference by intermediate distractors occurring at a post-selection stage. Another explanation for these behavioural effects is that they simply represent some degree of decreased fidelity in identification as a result of shifting attention further from its initial focus. Alternatively, it is possible that the N2pc components measured in Experiment 8b do not accurately reflect the time course of voluntary attention shifts. The observed N2pc onset latencies in response to targets may not reflect the actual point in time when these targets are selected. Because the N2pc is a lateralised bias in the processing of the hemifield contralateral to the side of the visual field in which the target appears, it is logical to assume that the emergence of this bias reflects the successful attentional selection of a target on this side. However, this argument assumes that such a bias emerges only at the target's location,

and this is not necessarily the case. It is possible that in the absence of feature-based attentional guidance processes, voluntary attention shifts towards a location may involve spatially continuous movements of the focus of attention, in such a way that it moves across the retinotopic map towards the intended location. If this is the case, then the corresponding N2pc response will emerge as this attentional shift from the benchmark to the target crosses the midline, rather than emerging at the point of target selection. Such a possibility may also account for the fact that average N2pc delays between benchmark-horizontal and target-horizontal trials were substantially shorter in Experiment 8b (about 75 ms) than in Experiment 8a (about 134 ms).

Applying this assumption to Experiment 8b, this means that on trials where the benchmark appears on the vertical midline and the target appears laterally, the N2pc emerges as soon as the voluntary shift of attention is initiated and the focus of attention begins to move continuously towards the target location. If this was the case, no effect of benchmark-target distance on N2pc onset latencies would be observed, as the time taken to simply initiate a voluntary attention shift may not be mediated by the distance of the shift. The continuous shift of attention, and any corresponding delays in the selection of targets at further distances, may only be reflected in the RTs and error rates, as found in Experiment 8b.

Experiment 8c aimed to determine whether the lack of a distance effect of N2pc onset latency in Experiment 8b was due to the fact that these N2pc components to lateralised targets measuring the initiation of a voluntary attention shift (i.e, the point in time where attentional processing started the become lateralised), rather than the voluntary selection of a target. To do this, Experiment 8c employed a new methodological technique to capture such continuous movements of voluntary attention across the visual field. In this experiment, both the benchmark and target objects were presented laterally, either on the same side of the

visual field or on opposite sides, with no objects on the vertical midline. Benchmark-target distance was now kept constant at three spaces (with two objects positioned at intermediate locations). The critical manipulation on these opposite-side trials concerned the distance between the benchmark and the vertical midline. In these trials, there a reversal in the polarity of lateralised activity should be observed at some point in time, as attention is initially allocated to the benchmark on one side of the display, and then to the target on the other side of the display. Crucially, if voluntary attention shifts operate in a spatially continuous fashion across the retinotopic map, this polarity reversal should emerge later on trials where the benchmark is further from the midline (i.e., two rather than one intermediate item before the midline along an imaginary circle). Alternatively, if voluntary attention shifts do not operate in this continuous fashion, and the N2pc response simply reflects the emergence of enhanced visual activity at the target location, no difference in the latency of polarity reversal should be seen as a result of varying distance between the benchmark and the vertical midline.

6.2.4 Experiment 8c: Using Polarity Reversals to Track Continuous Voluntary Movements of Attention

6.2.4.1 Methods

Participants

Sixteen new participants were paid to take part in this experiment. Four of these participants were excluded from analysis due to low accuracy (with more than 30% of trials producing incorrect responses). The remaining twelve participants were aged between 23 and 43 years ($M = 31.08$ years, $SD = 6.45$). Five of these participants were female, and one was left handed. All participants had normal or corrected-to-normal vision.

Stimuli and procedure

Stimuli were presented in eight lateralised locations, each of which differed by 45° along an imaginary circle, with no stimuli appearing on the vertical midline (see Figure 8.5). Stimulus locations on each trial were 22.5°, 67.5°, 112.5°, 157.5°, 202.5°, 247.5°, 292.5°, and 337.5° clockwise from directly above the fixation point. All stimuli possessed one of the four colours used in the Experiments 8a and 8b; the benchmark object uniquely possessed a colour that was fixed across the entire experimental session and varied only across participants. Two colours were randomly selected from the three remaining colours, and each of these colours were given to three of the remaining seven objects. The final remaining object was given the remaining colour.

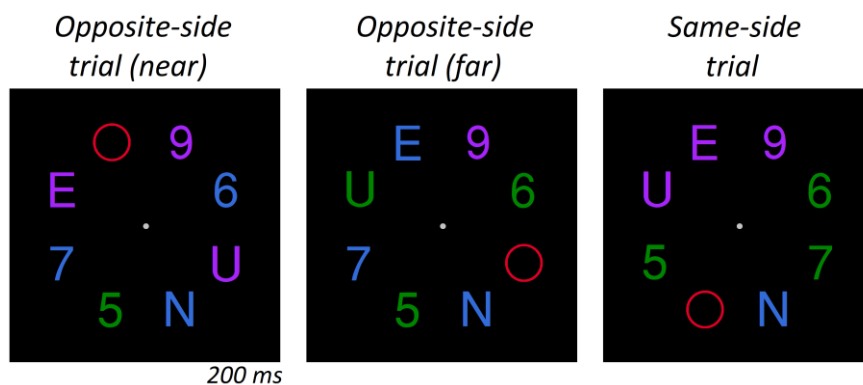


Figure 8.5: Schematic illustration of the search displays in Experiment 8c. All displays shown in this figure are from clockwise blocks. Participants' task was to report the object that was 3 spaces in the specified direction (clockwise/anticlockwise) from the benchmark. The left panel depicts trials in which the benchmark appeared directly adjacent to the vertical midline (near trials); the target is a magenta 'U'. The middle panel depicts trials in which the benchmark appeared further from the midline, with one intermediate object (far trials); the target is a blue '7'. The right panels depict trials in which both the benchmark and the target (a magenta 'E') appeared in the same visual hemifield (same-side trials).

The experiment consisted of 12 blocks of 64 trials. As in Experiments 8a and 8b, the direction of the target from the benchmark was varied in separate, alternating blocks. In 32 trials in each block, the benchmark and the target appeared on the same side of the stimulus display (same-side trials). These consisted of 8 trials for each combination of side of benchmark and target [left, right] and target identity [letter, digit]. In the remaining 32 trials, the benchmark and the target appeared on opposite sides of the stimulus display (opposite-side trials). These consisted of 4 trials for each combination of side of benchmark [left, right], target identity [letter, digit] and distance from benchmark to vertical midline [near (adjacent to midline), far (one object between benchmark and midline)]. All other aspects of stimulus presentation were identical to Experiment 8a.

EEG recording and data analyses

Artefact rejection and exclusion of incorrect, anticipatory, and missing responses led to a removal of an average of 25.7% of all trials. EEG was averaged separately for each combination of side of benchmark (left or right) and distance between benchmark and vertical midline (near, far, or same-side). Because EEG responses in opposite-side trials were split between near and far trials, a random subset of 50% of same-side trials was chosen for EEG analysis for each participant, to ensure that signal-to-noise ratio was equivalent in all three trial types. This randomisation was done before EEG recording by flagging half of trials where the benchmark and target appeared on the left, and half of trials where they appeared on the right, and analysing only these flagged same-side trials. Mean amplitude time-windows were determined using the same criteria as Experiments 8a and 8b. For benchmark objects, these time-windows were 230-330 ms for same-side trials, 212-312 ms for near trials,

and 205-305 for far trials. For target objects in opposite-side trials, these time-windows were 358-458 ms for near trials and 398-498 ms for far trials. No target N2pc mean amplitude analysis was conducted for same-side trials in response to targets, as lateralised activity did not reverse polarity on these trials, and no objective onset-defined time window could therefore be determined. N2pc onset latency for opposite-side targets was defined as the point in time when each subsample difference wave reached a fixed onset criterion that was determined as 50% of the pooled amplitude of these N2pc responses across the two opposite-side trial types (near and far); this onset latency value was 0.7 μ V. For benchmarks, the same procedure was used with the average of all three trial types (near, far, and same-side); this value was -0.5 μ V. For opposite-side trials, in addition to this method for determining onset latency, a relative onset criterion determined as 50% of the peak positive amplitude of each waveform was also calculated. All other aspects of EEG recording and data analysis were identical to Experiment 8a.

6.2.4.2 Results

Behavioural performance

Exclusion of anticipatory RTs resulted in the removal of less than 0.4% of trials. For RTs, a one-way ANOVA was run with the factor trial type (near, far, same-side). This revealed a main effect of trial type, $F(2,22) = 11.47$, $p < .001$, $\eta_p^2 = .51$. Follow-up paired-samples t-tests conducted separately for each pairing of trial type showed faster responses times for same-side trials (1006 ms) relative to both near trials (1093 ms, mean difference 87 ms) and far trials (1067 ms, mean difference 61 ms), both $t(11) > 4.24$, $p < .01$, $d > .75$, demonstrating faster responses when the benchmark and target appeared on the same side of the display. Near trials and far trials did not produce significantly different RTs, $t(11) = 1.20$,

$p = .257$, $d = .29$. The same ANOVA was conducted for error rates, which also found a main effect of trial type, $F(2,22) = 3.73$, $p < .05$, $\eta_p^2 = .25$. The follow-up paired-sample t-tests for error rates revealed significantly fewer errors in same-side trials (14.07%) relative to far trials (19.40%, mean difference 5.33%), $t(11) = 3.21$, $p < .01$, $d = .60$, and a tendency in the same direction relative to near trials (20.43%, mean difference 6.37%), $t(11) = 2.10$, $p = .060$, $d = .64$. Finally, no difference in error rates between near and far trials was observed, $t(11) = .40$, $p = .700$, $d = .11$.

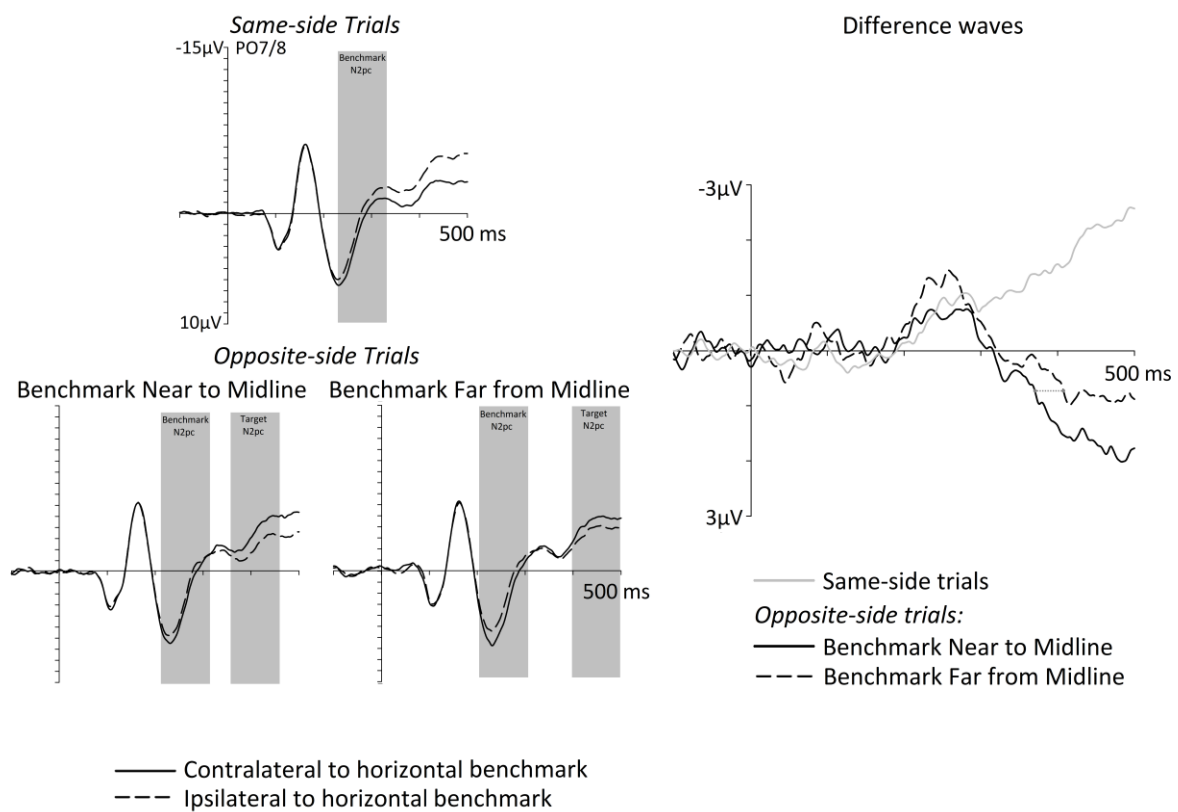


Figure 8.6: N2pc components elicited by the three trial types of Experiment 8c. Left panels: Grand-average ERP waveforms measured in the 500 ms interval after the onset of the search display at posterior electrode PO7/PO8 contralateral and ipsilateral to the horizontal benchmark, in same-side trials, and in opposite-side trials when the benchmark was near or far from the vertical midline. Right panel: Difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, separately for the three trial types. Grey bars indicate benchmark and target time-windows used for analysis. The dotted grey line shows the fixed onset criterion of $0.7 \mu\text{V}$ used to determine onset latency.

N2pc components

Figure 8.6 shows ERP components and difference waves in the same format as Figures 8.2 and 8.4. In same-side trials, clear lateralised activity was elicited to the side of the display containing both the benchmark and the target. In opposite-side trials, lateralised activity was first elicited to the side of the display containing the benchmark, followed by a reversal of polarity, reflecting a shift of lateralised activity to the side of the display containing the target.

Mean amplitudes in opposite-side trials were analysed in response to benchmark and target objects, using a repeated-measures ANOVA with the factors object type (benchmark versus target), trial type (near, far), and laterality (electrode contralateral versus ipsilateral to the side of the horizontal target or benchmark); the averaged mean amplitude values in response to target objects in these opposite-side trials were multiplied by -1 to ensure that comparisons did not take into account the opposite polarity of benchmark and target lateralised activity. A main effect of laterality, $F(1,11) = 22.97, p < .001, \eta_p^2 = .68$, confirmed the reliable presence of lateralised activity. Laterality did not interact with trial type, $F(2,22) = .01, p = .932, \eta_p^2 = .00$, or with object type, $F(1,11) = 4.08, p = .068, \eta_p^2 = .27$, but a three-way interaction was observed, $F(2,22) = 5.13, p < .05, \eta_p^2 = .32$. Paired-samples t-tests comparing contra- versus ipsilateral activity separately for each of the four combinations of trial type (near, far) and object type (benchmark, target) revealed reliably elicited lateralised activity in these trials, $t(11) > 2.39, p < .05, d > .17$. In addition, the same t-test for benchmarks in same-side trials also reached significance, $t(11) = 8.60, p < .001, d = .21$.

To analyse the onset latency of lateralised ERP activity, a one-way ANOVA was first conducted to compare this activity in response to benchmark objects with the factor trial type (near, far, same-side). This ANOVA found no main effect, $F_c(2,22) = .82, p = .453, \eta_p^2_c =$

.07, suggesting no influence of the spatial arrangement of benchmarks and targets on the speed of selection of the benchmark. For opposite-side trials only, a repeated-measures ANOVA was run with the factors trial type (near versus far) and object (benchmark, target). This revealed a main effect of object, $F_c(1,11) = 93.15$, $p < .001$, $\eta_p^2 = .89$, indicating significant delays in lateralised responses to targets (388 ms) relative to benchmarks (208 ms, mean difference 179 ms). To address the critical question whether the emergence of reversed-polarity lateralised activity on opposite-side trials was affected by the distance between the benchmark and the midline, a paired-samples t-test was carried out to specifically compare onset latencies of target-lateralised activity on near versus far opposite-side trials. This comparison revealed a significant latency difference, $t_c(11) = 2.50$, $p < .05$, $\eta_p^2 = .36$, with an earlier onset latency for near trials (368 ms) as compared to far trials (407 ms, mean difference 39 ms). However, it is important to note that when using the alternative relative onset latency criterion, the same t-test did not reveal a significant latency difference, $t_c(11) = .93$, $p = .372$.

6.2.4.3 Discussion

The results of Experiment 8c suggest that voluntary attention operates in a continuous fashion and is shifted across the retinotopic map from one location to the next. This was demonstrated by delayed polarity reversals of lateralised activity when only the position of the benchmark relative to the vertical midline was increased. Since benchmark-target distance was kept constant in this experiment, the difference in polarity reversal cannot be due to the distance of the shift itself; instead, it must reflect the point in time when the focus of voluntary attention reaches and crosses the vertical midline. This strongly supports the notion of continuous, analogue, movements of attention when it must be endogenously re-oriented to

a location, as opposed to spatially global, priority-driven modulations of attention that emerge in response to target properties regardless of their location, in line with previous behavioural evidence (e.g., Shulman et al., 1979; Tsal, 1983).

It is important to note that response times were faster in same-side trials relative to opposite-side trials, despite the fact that the distance between the benchmark and the target never changed. One explanation for this finding is that this may represent some cost of moving the focus of attention across the vertical midline (Rizzolatti et al., 1987; Tassinari et al., 1987), but it is unclear whether this cost is found in the speed of attention or in a later cognitive process such as identification. The current experiment was unable to measure the actual speed of shifting attention between the benchmark and the target and same-side trials, and therefore could not provide any evidence for or against faster selection of objects in the same visual hemifield.

6.3 General Discussion

The three experiments presented in this study show that there is not only a quantitative difference in the speed of priority-driven and voluntary shifts of attention, but that there is a qualitative difference in the mechanisms of these shifts. In particular, because priority-driven attention shifts can be guided by spatially global mechanisms, they are not mediated by distance, while voluntary attention shifts do not have access to these mechanisms (since no target property is available to guide attention towards it), and as such they operate in a way that appears to be influenced by distance. Another important finding was that due to the qualitative differences between these attention shifts, tracking them in real time requires different methods of measurement. When the enhancement of visual activity emerges at a specific location as a result of priority signals at that location, as is the case in priority-driven

attention shifts, this reflects the point in time that the object is selected and is marked by the onset of the N2pc component to the side of the visual hemifield that contains this object. When the focus of voluntary attention is shifted continuously from one object to another, the emergence of lateralised N2pc activity simply reflects the point in time when the focus of attention moves from one visual hemifield to another. For this reason, capturing differences in the time course of voluntary attention shifts requires manipulating the position of the vertical midline relative to the region of the shift. This provides an explanation for the lack of a distance effect on N2pc onset latency in Experiment 8b (despite an accompanying effect on RTs), along with the presence of an N2pc onset delay as a result of larger distances between the benchmark and the vertical midline in Experiment 8c.

A further important feature of Experiment 8c is that since distance between the benchmark and the target was not manipulated, the observed distance effect in this experiment cannot be due to any confounding factors, such as increased number of intermediate objects positioned between the benchmark and the target. While this lends further support to the idea that voluntary attention shifts do not operate entirely discretely, it does not account for the possibility that this movement is affected by the presence of such intermediate objects. In particular, it is possible that during a voluntary attention shift, intermediate objects fall under the ‘spotlight’ of attention and slow the speed of the shift, or even enter working memory or consciousness, in effect becoming unintentionally selected (see Sperling & Weichselgartner, 1995, for a description of varying hypotheses regarding the acquisition of intermediate information during continuous attention shifts). The delay in attentional selection of about 40 ms seen in Experiment 8c may result from distance per se, but alternatively may reflect a slowing voluntary movements of attention by the intermediate object that appears between the benchmark and the vertical midline. In fact, it is possible that rather than moving in a truly continuous fashion, attentional processing in this task involved

discretely selecting each subsequent object (as was necessitated in Horowitz et al., 2009) until reaching the correct number of objects (i.e., reaching the third object from the benchmark). However, in Experiment 8c this numerical relationship between the benchmark and the target was only specified once at the very beginning of the experiment, and it is likely that participants quickly learned the spatial, angular relationship between these objects (i.e., 135 degrees along the circle) rather than relying on a counting strategy that may slow the speed of attention. Further experiments are required to confirm whether voluntary attention truly can move in a purely continuous fashion through space, or whether it necessarily involves discrete steps across intermediate targets. However, evidence for purely continuous movements of voluntary attention would not imply that this is entirely unaffected by the presence of intermediate distractors, and this would also need to be investigated in more detail.

The question of the speed of voluntary attention has been difficult to answer, particularly in behavioural studies, because it is difficult to tease apart the time taken to perform non-attentional tasks such as object processing. In Horowitz et al. (2009), for example, it is likely that participants were, at least to some extent, processing each object that they attended to confirm whether it was the target or not, which would cause inflated estimates of the speed of attention shifts between each object. In addition, because this task necessitated multiple sequential shifts of attention, it is possible that each shift required some time to initiate before the focus of attention actually moved. In Experiments 8b and 8c of the current study, while the processing of the benchmark was minimised (as it only had to be localised and not identified in any way), the observed shift time as measured by the delay in selection of the benchmark and the target will also reflect such initiation processes. However, this can be isolated from actual voluntary attention shifts by examining the results of Experiment 8b, which is considered here to measure the time taken for voluntary attention to

begin moving from the vertical midline into one side of the visual hemifield (in other words measuring the initiation of a voluntary attention shift). Delays of at least 75 ms were observed between benchmark selection and lateralised N2pc activity in this experiment, suggesting that voluntary attention shifts require this amount of time before movements of the attentional focus actually take place. In Experiment 8c, this initiation time is controlled for, as the different trial types simply measure N2pc polarity reversals at different points in the same attention shift, and suggest that the speed of continuously moving voluntary attention is about 40 ms per space along the circle. When the information from these two experiments is combined, it provides an estimate of about 200 ms for voluntary attention to reach the target in Experiment 8c.

This study has provided novel electrophysiological evidence to demonstrate both quantitative and qualitative differences between priority-driven attention shifts and voluntary attention shifts. When attention can be shifted towards a target on the basis of its properties (such as colour), such feature-guided shifts operate in a discrete fashion independently of the spatial distance between two sequentially attended objects. When no target properties can guide the shifting of attention, so that these shifts have to be initiated endogenously, they are affected by spatial distance. While more experiments are required to understand the true nature of these voluntary attention shifts, the current study provides electrophysiological measures and procedures for studying them, and points to the idea that the voluntary movement of the attentional focus is continuous, rather than fully discrete, in nature.

Chapter 7

General Discussion

7.1 Chapter Overview

This thesis has aimed to improve the cognitive and neuroscientific understanding of attentional control and its impact on the allocation of attention, specifically in scenarios where multiple objects must be attended. In doing so, two broad lines of research have been presented, both of which investigate important aspects of attentional control mechanisms. The first line of research, presented in Chapters 2-4, examined the rapid and parallel allocation of attention to target objects when these objects are defined by different types of attributes. The results of these studies have provided new insights into the content of attentional templates, and also into the flexible nature of attentional deployments that are guided by such templates. The second line of research, presented in Chapters 5 and 6, investigated shifts of attention in tasks designed to ensure that attentional deployments to different target objects had to be performed in a sequential fashion. These studies have employed N2pc components to measure the speed of these attention shifts, and also to find out whether there are qualitative differences between different types of serial attention shift.

This final chapter will summarize the key findings from each of the experiments reported in this thesis, and will critically evaluate the evidence provided by these experiments and its implications for models of attentional control. Finally, the results reported in the previous empirical chapters will be considered together in an effort to establish an overarching view of attentional control within a cognitive and neuroscientific framework.

7.2 Rapid Parallel Attentional Allocation

By presenting two target objects in rapid succession, and by varying their vertical and horizontal positions as well as the SOA between these targets across different experimental trials, it is possible to independently track N2pc responses to each of these task-relevant

objects in tasks where they must both be attended as quickly as possible. This general experimental paradigm, in which two targets either had to be compared in same/different judgements, or the number of targets (one or two) had to be reported, was employed across Chapters 2-4. By using this paradigm, the experiments in these chapters were able to assess, with high temporal precision, the time course of attentional allocation processes for each target, and to determine the nature of attentional deployments, with particular regard to whether these deployments could operate in parallel or had to be elicited in a serial fashion. Critically, across these experiments, the type of information that defined the targets was manipulated, in order to assess how these rapid attentional allocation processes operate when they had to be guided by different types of target templates. These experiments have provided new insights about the content of attentional templates and their ability to guide attention rapidly and efficiently to multiple target objects. Perhaps the most striking finding from this line of research was that attentional templates appear to be able to represent high-level categorical information in tasks where targets and nontarget objects could not be distinguished on the basis of elementary visual attributes, and that these category templates facilitate fast and flexible parallel attentional deployments that were very similar to the processes observed when targets were defined by visual features.

Does the temporal pattern of N2pc results from the experiments in Chapters 2-4 provide truly conclusive evidence for rapid and parallel attentional selection mechanisms? The claim of serial selection models (Treisman & Gelade, 1980; Wolfe, 1994, 2007) that the focus of attention can be deployed to only one object at any given moment in time leads to clear predictions for the time course of N2pc components in the experimental paradigm employed in these experiments. When two targets are presented in unpredictable locations in rapid succession (particularly in the case of the SOA10 conditions), any serial account of attention would predict that the focus of attention must be withdrawn from the location of the

first target before being deployed to the subsequent location of the second target. The advantage of N2pc-based rapid sequential target presentation paradigm used in this thesis is that different variants of such a serial selection account can be addressed. If there was a limit to the speed of serial attention shifts between two task-relevant objects, very short SOA times should disrupt the deployment of attention to the second target object, resulting in delays in selection, or no selection at all (especially if the second target is presented very briefly). However, even if serial attention shifts can operate much faster than is commonly assumed, the fact that only one location can be attended at any time would imply that in these short SOA conditions the focus of attention will be very rapidly withdrawn from the first target. While the behavioural results from these tasks do not, on their own, rule out the possibility of extremely rapid serial re-orienting of the attentional focus from one target to the next, the accompanying N2pc results strongly reject any hypotheses made on the basis of serial attention models. In particular, the fact that the two N2pc components corresponding to the selection of each of target overlapped in time, did not differ in size, as well as the fact that the N2pc to the second target was not delayed, demonstrate that two parallel and independent attentional selection processes can take place extremely rapidly.

However, these interpretations make specific assumptions about the neural basis of the N2pc component. It has been assumed in this thesis that the N2pc reflects the neural enhancement of retinotopically organised neurons in extrastriate ventral visual cortex (Hopf et al., 2000), and that the onset of the N2pc therefore is a marker for the point in time when attention is first allocated to a particular object or feature at a specific location in visual space (Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999). When combined with the findings of Chapters 2-4, this interpretation of N2pc onsets may be consistent with the possibility that the focus of attention did indeed rapidly and serially shift between objects, especially since the targets did not appear simultaneously and thus the selection of the two

targets did not actually take place simultaneously. The critical question, then, is whether the full temporal extent of the N2pc (typically between 200 and 300 ms after target onset) reflects the time interval when attention is allocated to a specific location, or whether the N2pc is simply maintained as a result of the deployment of attention to this location, no matter how brief. Advocates of a serial selection account could argue that “selection” is exclusively reflected by the onset of an N2pc component, and that the temporal overlap of multiple non-simultaneous N2pc components does not necessarily imply the parallel selection of multiple objects. However, there is evidence from other N2pc studies that demonstrate that de-allocation of attention from an object or location is reflected in a rapid attenuation of N2pc amplitudes (e.g., Ansorge et al., 2011; Cosman et al., 2016). This evidence shows that the withdrawal of attention from one location is reflected by a reduction of N2pc amplitudes, which was not seen in any of the experiments from Chapters 2-4. In addition, Grubert and Eimer (2016a) recently found a very similar temporal pattern of N2pc components as was observed in the present thesis in a task where two target objects were presented simultaneously in the same display, supporting the interpretation that these objects do not compete for attentional allocation and are selected truly independently. These observations from earlier studies provide additional support for the interpretation of the N2pc results found in the current thesis, and these results provide strong support for the claim that the focus of attention can be deployed both rapidly and in parallel to multiple objects, in separate and independent selection processes for each object. The experiments presented in Chapters 2-4 aimed to determine whether the type of attribute that distinguishes targets from distractors affects the time course and qualitative nature of these attentional allocation mechanisms.

7.2.1 Feature-defined Targets

By producing almost identical electrophysiological results to those of Eimer and Grubert (2014) and Grubert and Eimer (2015) obtained in experiments where participants searched for targets defined by colour, Experiment 1 showed that rapid parallel attentional selection of objects is not solely driven by the guiding power of colour information. The fact that two rapidly elicited N2pc components were observed to two sequentially presented shape-defined target objects, which heavily overlapped in time and were not different in amplitude, with delays between them matching the objective SOA delay in each SOA condition, demonstrates that rapid parallel selection of shape-defined targets is possible. In addition, the fact that four SOA conditions were tested (10, 20, 50, and 100 ms) provides supporting evidence that the selection of each shape-defined target took place independently. Since the N2pc delays closely matched the SOA delays in every SOA condition, it is unlikely that the length of these delays had any impact on the qualitative nature of parallel attentional selection processes, and therefore unlikely that the mechanisms of target selection operated differently when the longer SOA exceeded the N2pc time window and allowed for two temporally distinct N2pc components to be elicited. In Experiment 1, no obvious qualitative distinction between target selection mechanisms was observed as the SOA delays gradually increased, and no evidence was found to dispute the claim that in all SOA conditions, N2pc responses were elicited independently and in parallel for both targets.

Theoretically, perhaps the most important contributions of this experiment are its implications for the types of attentional templates that can facilitate rapid parallel target selection processes. As explained in the introduction section of Experiment 1, the processing of shape information is very different to that of colours; while colours can be distinguished as early as the lateral geniculate nucleus (LGN), the extraction of shape-related information is more gradual, with the complexity of information processing increasing as visual input

travels through the visual system (Cheal & Lyon, 1992; Hubel & Wiesel, 1962, 1968; Lamme et al., 1992; Kanizsa, 1979; von der Heydt & Peterhans, 1989; Desimone & Schein, 1987).

This distributed processing reflects a clear contrast from basic colour-based processing, and may have implications for the way in which attentional templates can mediate the selection of colour-defined versus shape-defined targets. In line with this, it is interesting to note that delays between the N2pc to the two targets in shorter SOA conditions of Experiment 1 did not differ significantly. This is likely to be a result of temporal smearing from trial to trial, which may result from the more gradual processing of shape information. Nonetheless, the fact that parallel and independent N2pc components were observed in response to rapidly presented shape-defined targets strongly suggests that attentional templates can successfully prepare the brain for multiple upcoming shape targets that appear at unpredictable locations. More generally, these results show that attentional templates can rapidly modulate processing in different feature-specific visual brain regions of varying complexity.

An important limitation in the design of Experiment 1 was that the target and nontarget shapes were relatively simple: Circles, squares and triangles are easily visually distinguishable from one another, and it is unlikely that the processing of such basic shapes is similar (particularly in terms of complexity) to the processing of more complex real-world shapes. Thus, the results of this experiment do not imply that *any* shape template can guide attention rapidly and in parallel. While it is important to show that it is possible for at least some shape-defined objects to be represented in the attentional template, Experiment 1 itself does not rule out the possibility that these guiding shape representations are restricted to basic visual form attributes. This point was addressed in Experiment 3b (discussed in the next section): When specific line-drawings of real-world objects are defined as targets, these can also be held as visual representations in working memory, and these templates facilitate the rapid parallel attentional selection of more complex shape-defined targets.

7.2.2 Category-defined Targets

Experiment 2 revealed N2pc results that were qualitatively very similar to Experiment 1. N2pc responses to targets defined by their alphanumeric category, and whose visual appearance was therefore not known in advance still overlapped in time, despite the fact that these targets now changed unpredictably in each display. Similar results were also seen in Experiment 3a where objects were defined by semantic (rather than alphanumeric) category. In both experiments, no featural visual information could be used to distinguish targets from distractors, and only information about category membership (whether an object was a digit versus a letter in Experiment 2, and whether it was a clothing object versus a kitchen object in Experiment 3a) was available to guide attention to the targets. This fact allows the conclusion to be made that the attentional template is able to represent category information under conditions where targets are not defined by shared visual properties, in a way that guides attentional selection in a qualitatively similar fashion as with visual features.

Despite the similarity of N2pc results obtained in the experiments of this chapter to the results found in Experiment 1, there were several differences in the pattern of N2pc components that may suggest a reduction in the efficiency of attentional selection when guided by category templates rather than feature templates. Firstly, these N2pc components were generally smaller in amplitude; for targets defined by alphanumeric category (in Experiment 2), mean N2pc amplitudes were approximately $-1.24 \mu\text{V}$, and those in response to the real-world objects defined by semantic category (in Experiment 3a) were approximately $-1.36 \mu\text{V}$. In contrast, mean N2pc amplitudes in response to shape-defined targets (in Experiment 1) and specific real-world visual objects (Experiment 3b) were approximately $-2.17 \mu\text{V}$ and $-1.77 \mu\text{V}$, respectively. Differences in N2pc amplitude may reflect differences in attentional allocation processes, depending on the tasks and paradigms in which they are found. It is unclear whether smaller N2pc amplitudes seen in category

search are due to reductions in the strength of visual-attentional biases on any given trial, or the absence of such biases on a subset of all trials. In any case, if the reduction of N2pc amplitudes reflects a reduced efficiency of attentional allocation, this may also result in impaired behavioural performance. At least in the case of alphanumeric category search, this was not the case. Another explanation for the reduction in N2pc amplitudes is that they are a result of temporal smearing. According to this assumption, N2pc responses on any given trial would be no different in amplitude when elicited by feature or category targets, but the time at which they emerge will vary slightly, with more between-trial variability for category-defined targets. Averaging across these ERP responses will produce a waveform that is smeared across the horizontal time axis and reduced across the vertical amplitude axis, thereby giving an impression of smaller-amplitude responses. Why would temporal variability be larger for category search relative to feature search? It is possible that since category information is available at a later stage of visual processing (Nako et al., 2015, Zeki, 2015), the time between initial visual input and processing of category is not only delayed but also more varied. In line with this assumption, if the attentional selection of category-defined targets is mediated by an enhanced activation of higher-level categorical brain regions in response to information that matches the current attentional template, the timing of this selection should be directly influenced by the timing of this categorical processing. This would account not only for the reduced N2pc amplitudes, but also for the general delay in N2pc onsets that was found in Chapter 2. Critically, this does not rule out the possibility of rapid parallel attentional selection of category-defined objects. If these delays and amplitude reductions are indeed caused by template-guided enhancements of target-defining information in the visual field that occurs later and is more temporally varied, there is no reason to assume that such enhancements cannot still take place independently for multiple targets defined by category information. The results of Chapter 3 therefore support the claim

that attentional selection operates in a way that is qualitatively similar in feature-guided and category-guided search, despite being slightly slower and less temporally precise. If this was correct, it implies that there are no fundamental qualitative differences in the guiding power of category-based and feature-based attentional templates.

7.2.3 Conjunctively Defined Targets

Chapter 4 addressed a long-standing issue in the field of visual attention (the mechanisms of conjunction search), with particular regard to the time course of attentional selection of multiple objects. As discussed in this chapter, the attentional selection of targets defined by a conjunction of features from different feature dimensions is thought to operate differently than search for single features (Treisman & Gelade, 1980, Treisman & Gormican, 1988). The results of Chapters 2 and 3 demonstrated the power and flexibility of template-guided attentional selection and the ability of these templates to represent high-level information. However, but they did not provide any insight into whether these representations are restricted to a single target-defining attributes, or whether multiple such attributes can be represented together, and whether these attributes are combined to form an integrated object representation. Answering this question would be important in particular for real-world visual search scenarios, where objects may often not be distinguishable from others on the basis of one feature alone, and therefore can only be found when specific conjunctions of features (such as shape and colour) are taken into account.

Chapter 4 addressed this question firstly by determining whether rapid parallel selection of conjunctively-defined targets was possible (Experiment 4). In this experiment, targets defined by a specific combination of shape and colour were accompanied in the same display by partially matching nontargets which possessed one of the two task-relevant

features. By demonstrating qualitatively similar patterns of N2pc components in this task relative to feature and category search (Chapters 2 and 3), this experiment showed that such selection mechanisms were indeed activated. What is the nature of the attentional templates that facilitate these selection processes? There are two possibilities. The first is that the attentional template represents conjunctions of features as single integrated objects, thereby enabling efficient selection of multiple conjunctive targets in much the same way as in search for features and categories. While behavioural investigations into this question have tended to suggest that this is not the case (Treisman & Gelade, 1980; Nakayama & Silverman, 1986), the fact that conjunctive targets in Experiment 4 were selected in parallel appeared to support the possibility of preparatory integrated target templates. To address this issue directly, Experiment 5 examined whether attentional modulations of visual processing would also be triggered by partially matching nontargets. Because such nontargets would not match an integrated target object template, they should not be able to attract attention if attentional control was exclusively based on such a template. In contrast, because they would match one of two feature templates, they should retain an ability to attract attention if individual feature templates were active. The fact that N2pc responses were elicited by these partially matching nontargets rules out the possibility that targets were only represented by an integrated object template.

The second possible explanation for successful conjunction search in Experiments 4 and 5 is that the separate target-defining features were represented independently and simultaneously in multiple feature-specific attentional templates. The fact that all target-matching features across both feature dimensions (e.g., all red objects and all circles) were initially able to attract attention (as reflected by reliable N2pc components to such distractor objects) supports the notion that both of these features were represented independently in attentional templates. In other words, although attentional templates appeared unable to

represent bound conjunctions of features, they were able to represent these separate features simultaneously. This is an important observation, because it has implications for the cognitive and neural basis of attentional control. Can multiple attentional templates be activated to guide attention to different features? This question has been under much scrutiny in recent years (e.g., Olivers et al., 2011), and a host of evidence supporting both sides of the debate have surfaced. For example, search performance is known to be worse when searching for two possible targets defined by different features, rather than one (e.g., Huang & Pashler, 2007; Menneer et al., 2007), and ERP evidence suggests that multiple-target search is less efficient than single-target search (e.g., Grubert & Eimer, 2013). However, this alone does not imply that multiple attentional templates cannot be activated simultaneously, only that their guiding power is reduced. In contrast, Grubert and Eimer (2015) observed N2pc components elicited in response to two differently coloured targets among other coloured nontargets in rapidly presented displays. Critically, the possibility of participants switching between two single colour templates was ruled out by ensuring that even after the first target appeared, the second target could possess either of the two colours. While small delays in N2pc onset were observed, the results of this study demonstrate that two attentional templates can be simultaneously active by revealing overlapping and equal-amplitude N2pc components to both consecutive targets defined by two different colours.

The hypothesis that target-defining features are represented simultaneously and independently during conjunction search cannot fully explain how attentional control processes eventually distinguish between conjunctively defined target objects and partially matching nontargets. Successful target selection in these tasks clearly requires, at some point in time, attentional processing that is sensitive to the presence of both features in a single object. In other words, the integration of information across these different feature dimensions (e.g., red and circle) into single objects (e.g., red circles) must take place. The

results of Experiment 5 suggest that this integration takes place very rapidly. Target N2pc amplitudes were initially identical to the sum of the N2pc responses to individual features, there was a specific point in time during the course of the N2pc component at which these independent feature-based ERP responses could not fully account for the lateralised activity in response to conjunctive targets. In other words, the spatially selective processing of target objects was enhanced relative to the processing of separate task-relevant features, reflecting a transition from feature-based attention that operates in a spatially global fashion, to object-based attention that is sensitive to the locations of features and the simultaneous conjunctive presence of these features at target locations (see also Kiss, Grubert, & Eimer, 2013; Eimer & Grubert, 2014b). A critical additional observation of Experiment 5 was that these processes of integrating feature information across multiple attentional templates can take place rapidly and in parallel for multiple conjunctive targets. By employing the N2pc component as a continuous marker for the attentional selection both of targets and of partially-matching nontargets, these results suggest that feature integration processes may take place in parallel rather than serially, as is generally assumed (e.g. Treisman & Gelade, 1980). Crucially, these N2pc findings reveal the flexible and continuous nature of attentional control, and that transitions between different stages of attentional selection can take place seamlessly and independently at multiple locations in the visual field (see Eimer, 2014, for a review).

7.3 Serial Shifts of Attention

While Chapters 2-4 provided insights into the flexibility and power of attentional templates in guiding attention in parallel to multiple targets, Chapters 5 and 6 addressed scenarios in which the focus of attention must move sequentially from one location to another. It is clear from the results of Chapters 2-4 that when two targets are presented and have to be detected

as rapidly as possible, attentional control mechanisms are able to facilitate extremely rapid selection of these targets. However, not all search tasks require rapid selection of two equally relevant objects. There are many task contexts where the focus of attention needs to be moved between objects in a specific sequence. Can attentional templates be used to rapidly re-orient the focus of attention within static stimulus displays by changes in the enhancements of feature information across time? When there is no feature information available to guide such serial attention shifts, what other attentional control processes are available to facilitate changes in the focus of attention?

Experiment 6 aimed to determine whether the attentional selection of two objects can still take place in parallel when these objects compete for attention, by devising a task in which the presence of an occasional variable-colour object made another known-colour object task-irrelevant. Here, it was found that both objects were indeed attended in parallel in displays where they were both simultaneously presented. The comparison of N2pc components in response to each object suggested that competition between them was resolved rapidly, with attention then focused on the task-relevant variable-colour object. The proposed rapid disengagement of attention from the now-irrelevant object had to be based on information received in parallel about the presence of the task-relevant object, and the results of Experiment 6 showed that this type of attentional adjustment was activated continuously and seamlessly. Ultimately, this experiment demonstrated a situation where two competing objects initially trigger parallel attentional biases before this competition is resolved in favour of the current target. In this task, there was no clear evidence for the serial selection of objects, that is, the sequential allocation of attention first to one object and then to another.

Nonetheless, there are still many real-world scenarios that necessitate such serial shifts of attention. Knowing where to attend, or what to attend to, is often dependent on the processing of visual information at other locations in the visual field, and thus requires that

this location is attentionally processed before attention can be shifted from one location to another. For example, an observer in a busy airport may need to know the departure time of their flight; doing so may require attending to a sign that directs their attention to the display that contains the information they seek. In this example, a stimulus at one location provides information about where attention must be directed next. As explained in Chapter 5, one crucial difference in the type of information that guides these strictly serial shifts of attention is whether it consists of location information (e.g., ‘attend to the left’) or of feature information (e.g., ‘attend to the yellow object’).

Chapters 5 and 6 both employed experimental paradigms in which the attentional selection of the target was dependent on the processing of another known object, thus necessitating serial, sequential attention shifts between these two objects, and allowing the measurement of N2pc responses to each object. To do this, a benchmark object was presented at a random location in each visual display, and this benchmark was defined by a known feature (for example, a square). This benchmark also possessed information about either a featural property of the target object or its location. In Chapter 5, the speed of priority-driven attention shifts (made on the basis of feature information) and voluntary attention shifts (made in the absence of such feature information) was directly compared. Chapter 6 investigated the influence of the spatial distance between two sequentially attended objects on voluntary attention shifts.

7.3.1 Differences Between Priority-driven and Voluntary Attention

Experiment 7a was conducted to directly compare priority-driven and voluntary attention shifts, in task conditions that were physically identical. For this reason, differences in N2pc results can be interpreted as reflecting attentional differences rather than differences in

physical stimulation. The different attentional demands of these two task conditions caused substantial differences in the time between selection of the known benchmark object and the target, indicating that voluntary attention shifts are much slower than priority-driven attention shifts. These findings support earlier behavioural evidence for such differences (see Horowitz et al., 2009), but critically provide the first direct electrophysiological comparison of these two forms of attentional control.

Despite the fact that the two task conditions in Experiment 7a were physically identical, differences in the speed of voluntary versus priority-driven attention shifts may be caused by a number of factors that need to be dissociated. By subtracting the onset latency of the N2pc to the benchmark from the N2pc onset to targets, any differences in benchmark selection speed can be ruled out; therefore, the differences in N2pc delays across these two task conditions must be due to processes occurring after benchmark selection. Does the re-orienting of attention from the benchmark to the target occur immediately after selection of the benchmark? The answer to this question is almost certainly no, since some form of processing of the benchmark must take place. However, the amount of processing required by the benchmark may differ across the two tasks, and thus contribute to the measurement of the speed of attention shifts. In the voluntary shift task, participants had to localise the benchmark and combine this with their prior knowledge of the relative location of the target (i.e., clockwise or anticlockwise). Once this was done, the focus of attention could be voluntarily re-oriented towards the target's location, regardless of the target's properties. In contrast, the priority-driven shift task required participants to detect the benchmark on the basis of its shape, and then process the colour of this benchmark before being able to select the target. While it was not possible to measure the time course of these processes, or disentangle them from the time course of subsequent attention shifts, it is obvious that the benchmark processing required in the priority-driven shift task was probably more time-

demanding than in the voluntary shift tasks (see Donders, 1868, for an account of the speed of such mental processes). This would suggest that the disparity in the speed of selection between these two task conditions may in fact be larger than the N2pc results suggest, reinforcing the claim that there is a clear quantitative difference in the speed of these two types of attention shifts.

The priority-driven shifts in Experiment 7a could be initiated once information from the benchmark about the target-defining feature was processed. Due to the fact that these priority-driven shifts relied on feature information, it is possible that an attentional template was activated once this information had become available, and was then involved in facilitating these shifts. Thus, the delay in selection of benchmark and target may largely be a result of the time taken to activate or update the attentional template to represent the target's feature once it became known. This raises an interesting question which as yet has not been tested: Can an attentional template alter the neuronal enhancement of feature information in order to influence the allocation of attention in a display that is already present? If the attentional template is involved in this task, then it would suggest that this process is indeed possible, but further research is needed to understand how this takes place. When set up in advance, attentional templates facilitate the selection of targets in around 200 ms, but this time likely reflects many early visual feedforward processes that must take place before enhancements in visual processing emerge as a result of attentional control. Future N2pc studies should investigate the speed with which the template can be changed during the continuous presentation of static displays (when these early visual processes have already taken place), and the speed with which they can alter the selective processing of stimuli and locations in the visual field.

To further examine the nature of the quantitative differences between priority-driven attention shifts and voluntary attention shifts, and to determine which factors influence the

observed speed differences between these shifts, Experiment 7b introduced a new comparison. In both task conditions of this experiment, the target was defined only by its location and held no task-relevant features. However, in the priority-driven shift condition, arrow cues were placed at the location of the benchmark in order to facilitate shifts of attention to the target. Thus, while feature information was not available (and thus the attentional template could not be employed), stimulus information at the benchmark location directly cued the location of the target. In the voluntary shift task, this direction was based only on pre-defined instructions. Again, priority-driven shifts were faster than voluntary driven shifts, but this difference was smaller than in Experiment 7a, as priority-driven shifts were now slower. This suggests that the process of ‘pushing’ the focus of attention to a location is slower than the process of ‘pulling’ attention to a specific feature-defined object. It also suggests that the faster speed of priority-driven shifts of Experiment 7a was not simply a result of the presence of stimulus information in guiding the shift, but may also have been the result of the availability of an attentional template in facilitating this guidance. If this is correct, it would also highlight the speed with which the attentional template can operate. As soon as it is set up, it appears to rapidly facilitate the attentional selection of objects that match its representation. Taken together, the two experiments in this chapter suggest that attention shifts guided by visual features can operate more rapidly than those made purely voluntarily.

7.3.2 The Qualitative Nature of Voluntary Attention Shifts

The large speed differences between priority-driven and voluntary attention shifts raise the question whether these processes operate in a qualitatively different fashion. As discussed in Chapter 6, it is intuitive to assume that there are such differences, as the availability of visual

features in priority-driven shifts allows the operation of attentional control mechanisms (templates) that operate on the basis of these features. On the other hand, when no such feature information is available (as in the case of voluntary attention shifts), it is clear that these control mechanisms are unable to operate in the same way. The question of how these voluntary attentional control processes operate was investigated in Chapter 6.

The primary focus of Chapter 6 was determining whether the time taken to voluntarily shift attention between two objects was related to the distance in the visual field between these objects. This was examined because it has implications for the fundamental way in which the focus of attention is changed; an effect of distance on shift times would provide support for the notion that these shifts operate in a continuous fashion across the retinotopic map. Why might voluntary attention move continuously through space, while priority-driven attention does not? When attention is shifted to a particular feature, as was the case in the priority-driven shift tasks of Experiment 7a and Experiment 8a, it is likely that this shift requires the use of the attentional template in order to locate this feature, since the location of the target is unknown. Thus, these shifts are likely to rely on spatially global attentional control mechanisms which are unlikely to be influenced by the location of objects. As has repeatedly been observed throughout this thesis, all objects possessing target-matching properties are selected in parallel within cortical retinotopic maps.

This was suggested by the results of Experiment 8a, where the target was defined as the first coloured object among grey objects in a specified direction. It is important to acknowledge that the shifts of attention in this task relied on a combination of location-based and feature-based attentional control, since participants had to first determine the relevant region of the visual field on the basis of the specified direction (clockwise or anticlockwise) before detecting the coloured object that could appear anywhere within that region. The control of such shifts therefore does not entirely reflect the operation of spatially global

mechanisms. However, the critical comparison was between the selection of near, medium, and far targets, averaged across each specified direction, allowing the isolation of distance effects on feature-based attention. No such distance effects were observed either for RTs or for N2pc onset latency delays between benchmarks and targets, suggesting that priority-driven attention shifts are made on the basis of spatially global processes that detect the presence of task-relevant objects at any location within the visual field. Interestingly, this experiment also revealed that this spatially global control process can be restricted to specific regions of the visual field by combining feature and location information. The interplay between these two different attentional mechanisms is as yet poorly understood and certainly requires more focused research to reveal its mechanisms and constraints.

The most important task condition in Chapter 6 was the purely voluntary attention shift task in Experiment 8b, where shifts could not be based on any visual target-defining information. Here, participants could only rely on the direction information given at the start of each block and the distance information given at the start of each trial (by cues indicating the number of positions between the benchmark and the target), ensuring that the guidance of selection on the basis of spatially global feature-based mechanisms (attentional templates) was impossible. Though it was predicted that an effect of distance would be observed in this task, such an effect was only seen in RTs (which revealed a linear increase as distance increased), but not in N2pc delays. Although some previous behavioural studies have supported the notion that voluntary attention shifts are not mediated by distance (e.g., Remington & Pierce, 1984), it was this discrepancy between the behavioural and electrophysiological data in Experiment 8b that motivated an alternative interpretation of what the N2pc component reflects during voluntary attention shifts. Rather than marking the point in time at which the target is selected, the lateralisation of ERP activity observed in Experiment 8b might instead reflect the point in time at which the focus of attention began to

move away from the vertical benchmark and into the horizontal region of the visual field. According to this interpretation, no N2pc effect of benchmark-target distance was observed in Experiment 8b because increasing the distance of the horizontal target from the vertical benchmark did not influence the time at which attention began to move from the benchmark.

To assess this interpretation directly, Experiment 8c employed a novel technique where all objects were lateralised and the distance between the benchmark and target remained the same throughout the task, but the position of these objects relative to the vertical midline was systematically manipulated. If the N2pc component does indeed reflect the movement of the focus of voluntary attention into one hemifield, then a reversal in the polarity of lateralised ERP activity should be seen in trials where the benchmark and target are on opposite hemifields, and the onset of this reversal should reflect the point in time when voluntary attention passes over the vertical midline. In addition, if voluntary attention does move continuously through the retinotopic map, this polarity reversal should take place later when the benchmark is further away from the vertical midline. This was indeed the case, as shown in Experiment 8c, providing the first electrophysiological evidence for continuous movements of voluntary attention, and highlighting the importance of ERP measures in tracking such continuous movements. The fact that differences in the latency of polarity reversals were observed even when the shift of attention travelled the same distance provides particularly strong support for the claim that attention shifts made voluntarily move through space rather than simply emerging at the target location.

Overall, Chapter 6 provided novel N2pc evidence to demonstrate clear and fundamental qualitative differences between priority-driven and voluntary attention shifts. When made on the basis of visual features, priority-driven attention shifts operate using spatially global mechanisms based on attentional templates, and the speed of these shifts does not differ as a function of the spatial location of target objects in the visual field. Conversely,

voluntary movements of attention to specific locations, which are made in the absence of any visual feature information, must rely on different attentional control processes that are unable to operate in a spatially global fashion and instead move continuously through the retinotopic map.

7.4 Bridging Cognitive and Neuroscientific Interpretations of Attentional Control

The aim of this section is to consider the attentional mechanisms that may account for the results obtained in this thesis, present a more integrated perspective of these processes in the context of an attentional control system, and propose a basic neural account of how attentional control operates within the brain.

The central feature of attentional control discussed in this thesis is the attentional template. It has been shown in Chapters 2-4 that this template allows for extremely rapid and efficient selection of multiple targets defined by a particular property, by enhancing the processing of visual information that matches these properties. The fact that this can take place in parallel suggests that this information is represented in a preparatory fashion, and directly influences the activity of neurons that respond to the task-relevant information. While Chapters 2-4 demonstrated some limits in the way that different types of attentional templates affect visual processing, it is not entirely clear how these representations are able to influence the processing of visual signals in a way that discriminates between objects on the basis of, for example, semantic category. What is clear is that the attentional template must have access to and/or be located in high-level brain regions that are involved in such discriminations. If not, there would be no way to select such complex objects rapidly and in parallel, and any allocation of attention to targets would have to operate in a much slower and serial fashion. In short, guidance by high-level object properties could not be possible if the

brain regions that are sensitive to these properties could not communicate with the attentional template in advance of incoming visual information. Importantly, these brain regions appear to include those that do not rely on visual information, as more abstract target-defining properties can be distinguished and rapidly selected.

The proposal put forward in this thesis is that the attentional template is an actively maintained working memory representation that is able to directly influence the baseline activity (see Chelazzi et al., 1998) of visual neurons that can distinguish between targets and distractors in the visual field. In the example of colour search, the attentional template is able to influence the activity of neurons in low-level visual areas that are sensitive to differences in colour; in the example of shape search, it is able to influence the activity of neurons at a later stage in visual processing that are sensitive to whichever properties are required to distinguish a particular target shape from nontarget shapes (see Hubel & Wiesel, 1962; 1968; Lamme et al., 1992; Desimone & Schein, 1987). When searching for objects defined by category, the attentional template may modulate activity in category-sensitive prefrontal regions (e.g., Freedman et al., 2001; Miller, Nieder, et al., 2003). If this is the case, then the point in time when incoming visual information receives preferential attentional processing will emerge later in each of these respective cases, as the complexity of target-defining information increases. Distinguishing objects on the basis of their semantic category occurs later than a discrimination based on colour, because the initial processing of category information takes place later in the visual system. However, as soon as this takes place, enhancements of visual processing in the corresponding regions of the retinotopic map will emerge, as these regions have already been modulated in advance by the attentional template. This may explain why attentional processing biases for more complex objects appear to be generally delayed and less temporally precise, but are still triggered rapidly and in parallel in response to multiple target objects. Thus, the key claim of this thesis is that any information

that can be represented by the attentional template is able to guide selective attention rapidly and in parallel.

In addition, this thesis also sheds some light on the ability of the attentional template to change rapidly during the presentation of a visual display. In Chapter 5, priority-driven attention shifts were likely made as a direct result of changes in the information represented in the template. For example, in Experiment 7a, once the benchmark was detected and its colour was processed, this colour could be represented in the attentional template. In this task, it is conceivable that the observed N2pc delays of 47 ms reflects the short time taken to update the content of the attentional template, indicating that it can change flexibly and rapidly. This is far from certain, but warrants further investigation into the temporally flexible nature of the attentional template and the speed with which these representations can change and alter the focus of attention in static stimulus displays.

When no attentional template exists or is able to guide search, attention shifts have to operate in a fully voluntary endogenous fashion, involving different mechanisms of attentional control, as shown in Chapters 5 and 6. In particular, these shifts of attention appear to take place in a continuous fashion through the retinotopic map, from one location to another. Two important questions are raised from these findings: Firstly, what are the implications of a continuously moving focus of attention? In particular, are objects at intermediate locations also temporarily attended during such voluntary shifts? This was not tested in Chapter 6, but previous behavioural research appears to suggest that this might be the case (Shulman, Remington, & McLean, 1979). To investigate this possibility, further experiments are required to track the speed of voluntary attention shifts when intermediate objects are present or absent. Secondly, what is the neural basis of continuous voluntary movements of attention? The N2pc results of Experiment 8c suggest that, within the retinotopically organised visual cortex, enhancements of visual processing (which reflect

lateralised ERP activity) emerge at gradually and continuously changing locations, in a fashion that corresponds to a specific path along the retinotopic map. However, the attentional control processes that govern such “analogue” movements are generally unknown, particularly in humans (but see Roelfsema, Lamme, & Spekreijse, 1998, for evidence of continuous modulations of V1 neural firing rates across the retinotopic map in primates), and the findings of this thesis cannot provide any more direct insight into these processes. More refined cognitive models of the operation of voluntary attention are needed in order to understand their neural basis. Future research that may begin to approach this question is briefly discussed in the next section.

What are the implications of the findings of this thesis in the context of competing theories of visual search? A major claim put forward here is that the attentional template can facilitate rapid and parallel search for multiple targets; such a claim reflects a fundamental contrast with theories that expect serial attentional selection even when task-relevant attributes are known in advance. As discussed throughout the chapters of this thesis, many of such theories, including Guided Search (Wolfe, 1998; 2004) and Feature Integration Theory (Treisman & Gelade, 1980), put forward the notion that the process of attentional selection must itself operate strictly serially. There is no doubt that these theories are fundamentally incompatible with the findings demonstrated in this thesis.

Why is there such a strong contrast between these accounts of visual attention? One possible reason is the use of ERPs in this thesis to directly track attentional selection, as opposed to relying only on behavioural measures. While the N2pc component has been employed as a marker for attentional selection for several decades (Eimer, 1996; Luck & Hillyard, 1994), it is only with the use of specific methodological techniques that clear conclusions have been made about the exact temporal dynamics of attentional selection in multi-target scenarios: the method of placing one of two targets on the vertical midline (e.g.,

Woodman, & Luck, 1999) has allowed for the ‘pure’ observation of independent attentional responses when multiple such responses are present, but only in paradigms where two rapidly presented targets are equally task-relevant can this ERP technique allow for observations of rapid and parallel N2pc responses that heavily overlap in time. Therefore, it may be that the rapid and parallel allocation of attention to multiple targets is difficult to observe except under these specific conditions.

An alternative possibility is that such rapid and flexible attentional processing is indeed only possible under specific task conditions; another difference between the experiments of this thesis and those of competing theories is the simplicity of the stimulus displays. Here, only four objects were presented in each trial, usually with two targets and two nontargets. In many visual search studies, arrays consist of many more stimuli, and the ratio of nontargets to targets is much higher (e.g., Duncan, Ward, & Shapiro, 1994). Though this thesis does not provide any evidence that rapid parallel attentional mechanisms are robust in the face of increasingly complex tasks or dense stimulus arrays, it is important to note that the results presented here demonstrate simply that rapid and parallel attentional selection is, at the very least, possible under all of these scenarios. In particular, this thesis demonstrates that the attentional template is able to represent targets defined by visual and categorical attributes and use this information to facilitate rapid and parallel attentional deployments to multiple such targets, regardless of whether or not this function breaks down in the case of more dense displays or complex tasks.

7.5 Future Directions

During the discussion of the chapters and experiments in this thesis, a number of areas have been identified which require further investigation. In this final section, these areas will be

explored in more detail, and the most crucial requirements of future experiments addressing these issues will be described.

In general, the results from Chapters 2-4 regarding rapid parallel attentional selection are robust and reliable, in that the same qualitative pattern of results is found across the different experiments for different target-defining attributes. The range of N2pc results provided here have allowed for the beginnings of a neural interpretation of the mechanisms of feature-guided attentional control, as described in the previous section. However, it is not certain that the conclusions gained from these findings can be generalised to all tasks that involve search for feature-defined target objects. In particular, all of the experiments in these chapters employed paradigms containing just four items in each trial. Methodologically, this is justified because it allows a tightly controlled measurement of biases in attentional processing towards targets (on one side of the display) relative to distractors (on the opposite side), while also allowing for independent tracking of N2pc responses to two targets. Including more distractors in these paradigms would be theoretically useful. The previously postulated cognitive and neural mechanisms of spatially global feature-guided attentional selection, as facilitated by the attentional template, may imply that there is no capacity limit to the number of target-defining features that can trigger concurrent attentional biases. When nontarget objects with target-matching features are present in the same display, as is often the case in conjunction search tasks (Experiments 4 and 5), the allocation of attention to them appears to be initially guided by separate information from individual features, before a processing bias for conjunctively defined target objects emerges. Such target-selective biases may be less easy to detect when more matching nontargets are present, because they would each trigger independent feature-selective modulations of visual processing. Future N2pc studies need to determine whether rapid parallel attentional selection processes during

conjunction search are still operative when display set size and the number of partially matching nontargets are increased.

The results of Chapters 5-6 have provided new ERP evidence to support the notion of continuous movements of voluntary attention. Several questions following these findings should be addressed. Firstly, it is unclear whether intermediate items receive enhanced processing in the same way as targets during the movement of voluntary attention. Developing new designs to specifically measure N2pc responses to these intermediate items could offer new insights into this possibility. Methodologically, it may also be possible to measure multiple voluntary attention shifts in single static displays. In an experimental paradigm where a benchmark object provides information about the location of another object, which itself provides information about a third object (and so on), multiple shifts of attention that must take place in a specific sequence are necessitated. The N2pc may be used to track each of these shifts and their respective time demands. Using polarity reversals as in Experiment 8c, it may also be possible to measure every point in time when attention crosses the vertical midline. Because such voluntary attention shifts are not locked to the onset of any particular stimulus, they are likely to vary in their time course across trials, which may make it challenging to provide meaningful ERP data that track these shifts. Another interesting question concerns the interplay between priority-driven and voluntary attention shifts (as in Experiment 8a). While these two types of attentional control appear to operate in a qualitatively different fashion, it is unclear whether and how these two processes can work together to aid in the guidance of attention. As suggested by the results of Experiment 8b, these processes may operate serially; first, participants localise a region of relevance (on the basis of the position of the benchmark and the specified direction of the shift), and then detect the presence of a salient stimulus (coloured among grey) within that region. It would be informative to investigate more generally whether and how spatially selective attentional

control processes (that may be linked to voluntary attention) interact with spatially global mechanisms that rely on stimulus features. Clearly, many other avenues can be explored to determine the nature of voluntary attention shifts, and the questions put forward here reflect the early stage of ERP research into this topic. Chapter 6 has provided a useful starting point to begin answering these questions.

7.6 Final Remarks

In summary, this thesis has investigated the mechanisms of attentional control in scenarios where multiple objects are presented, by tracking on a continuous basis the emergence of attentional processing biases for one or more of these objects. Using the N2pc component, it was shown that attentional templates can represent a varied set of target-defining object properties that is not limited to basic visual features. Once activated, target templates can facilitate the rapid, parallel and independent selection of multiple target objects that match one or all of these properties. In addition, this thesis has provided novel electrophysiological measurements of processes that control serial shifts of attention, revealing qualitative differences between priority-driven and voluntary attentional control mechanisms.

Ultimately, this thesis demonstrates the powerful and flexible nature of attentional control processes in guiding the focus of attention to task-relevant information, and highlights the utility of ERP measures in understanding the nature of attentional control.

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