Temporal activation parameters of attentional templates for visual search

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Temporal activation parameters of attentional templates for visual search

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Abstract

Visual search is guided by attentional templates that are maintained in visual working memory (VWM) and are activated during search preparation. However, it remains unclear how VWM capacity and strategic control affect the formation and activation of multiple attentional templates. This thesis presents six electrophysiological experiments to investigate the temporal and organisational properties of template co-activation. Experiments 1-2 (Chapter 2) examined template activation patterns in fully predictable two-colour search and found evidence for strategic template switching. Importantly, colour switch costs were due to delays in activating the relevant colour template rather than interference from a previously used template. Experiments 3-4 (Chapter 3) increased VWM load and measured template activation patterns in three-colour versus one-colour search. Results showed that three colour templates were activated in parallel when search targets varied unpredictably, but task performance was nevertheless reduced in the three- as compared to the one-colour search. Consequently, when participants were given the opportunity to reduce VWM load by making the colour sequence fully predictable, they chose to switch between templates rather than activate them in parallel. Experiments 5-6 (Chapter 4) widened the scope by studying the content and attentional guidance in conjunction search when target were defined by features from two different dimensions (colour and shape). The experiments revealed that attentional templates contained separate features rather than integrated object representations and that guidance was feature-based accordingly. Overall, these experiments demonstrated that three and possibly even four feature templates can be activated simultaneously in preparation for search. However, such template co-activation leads to mutual inhibition reducing template activation levels and search efficiency. This research contributes significantly to our understanding of the temporal and organisational parameters of memory-guided attention.

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Declaration

The author confirms that none of the material presented in this thesis has been submitted elsewhere for any other qualification and is the author's own work unless referenced otherwise.

Published and Submitted Work

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Statement of Copyright

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Chapter 1 General Introduction

One of the key human skills is the ability to focus on information relevant to our behaviour. For instance, when searching for our car in a crowded car park, directing attention towards specific visual information is crucial. In visual search, prior knowledge about the properties of target features, such as colour, shape, or size, allows us to guide our attention in a goal-directed manner towards potential targets among distractors. This prior knowledge is maintained and processed in visual working memory (VWM), supporting our ability to mentally process visual information even when it is no longer visible (Luck & Vogel, 2013). VWM is known to have a limited capacity of three to four items (Cowan, 2001; Luck & Vogel, 1997), but does the ability to maintain multiple target representations in VWM also mean that we can use all of these representations for attentional guidance at the same time? And what exactly is the content of such attention guiding memory representations when a target object is defined by multiple features? This distinction between memory maintenance and guidance is crucial, as it challenges our understanding of how VWM effectively interacts with attention when multiple target features are task relevant. Overall, the activation of multiple target representations within VWM and subsequent attentional guidance, has been the central topic of my research over the past three years and forms the basis of this thesis.

1.1 Memory-guided attention

In daily life, we human beings are constantly exposed to a vast amount of sensory information. For instance, when attempting to locate a specific car in a crowded car park, the amount of visual data received by our eyes far surpasses the processing capacity of our brain's visual system. Despite this influx of information, we are typically able to execute complex visual searches without the need to meticulously examine each individual car in the scene. This ability to selectively attend to relevant details (e.g., a white car) while ignoring irrelevant information (e.g., a red car) is a vital cognitive function that enables us to manage the inherent processing limitations of the brain's visual system (Moore & Zirnsak, 2017).

Although attention can sometimes be captured automatically by salient stimuli in a stimulus-driven, 'bottom-up' manner (see Egeth & Yantis, 1997, for a review), it is the goal-directed, top-down control that enables individuals to selectively focus on information that aligns with their current goals and intentions (Awh et al., 2012) and to ignore salient stimuli that are not relevant to those goals (Rock et al., 1992; Simons & Chabris, 1999). Central to this top-down control is the employment of attentional templates—mental representations of target features that are maintained in VWM (e.g., Carlisle et al., 2011; Desimone & Duncan, 1995; Duncan & Humphreys, 1992; Eimer, 2014; Olivers et al., 2011). Attentional templates, acting like search templates, are activated prior to search during the preparation stage, distinguish targets from task-irrelevant distractors (Duncan & Humphreys, 1989) and effectively guide the subsequent search process and influence selection by biasing incoming sensory representations to prioritise objects that match the template (Wolfe, 2021). Serences et al. (2005) observed neural responses in the visual cortex biased towards search items that matched the templates in VWM. In their fMRI study, participants were instructed to identify target-coloured letters in a central stream whilst ignoring flanking distractor streams. The researchers found that target-coloured distractors in the periphery impaired target detection and elicited increased activation in corresponding regions of visual cortex, indicating attentional capture. Additionally, target-coloured distractors produced heightened responses in the temporoparietal junction and ventral frontal cortex, areas implicated in coordinating top-down attentional control settings with stimulus-driven attentional capture. These findings suggest that these regions play a crucial role in filtering visual input for features specified by current attentional control settings, signalling the need to shift attention to stimuli possessing target-defining features even when they appear in task-irrelevant locations.

Given that VWM templates result in attentional shifts to the search items matching the template, some researchers have proposed an automatic memory-based attentional capture account, where a template-matching object will always automatically capture attention, even if this object is irrelevant to our current goal (e.g., Downing, 2000; Olivers et al., 2006; Soto et al., 2005). One influential study supporting this account was conducted by Soto et al. (2005). In their experiment, participants were asked to remember a coloured shape and then search for a tilted target line segment amongst distractors with vertical lines. The researchers found that when one of the distractor objects matched colour, shape, or both colour and shape of the item held in VWM, it captured attention and slowed down the search process, even though it was irrelevant to the search task. This occurred despite participants being explicitly instructed to ignore the working memory item during the search. Further evidence comes from Olivers et al. (2006), who asked participants to detect whether a target in a diamond shape was an 'N' or 'M', while holding a feature (either a colour or a shape) in working memory. The researchers observed that when a distractor matching the memorised feature appeared in the search display, it impaired target detection, as shown by longer reaction times (RTs). This occurred even when participants knew that the memory-matching item was irrelevant to their task and that they had to focus on target identification, suggesting an automatic, rather than strategic, allocation of attention.

The automatic capture of attention by memory-matching distractors can not only be measured by means of terminal RTs at the end of a trial, but also in the modulation of oculomotor behaviour, indicating that the content of VWM directly influences the spatiotemporal dynamics of attention. For example, in a study by Soto et al. (2006), participants were first asked to memorise a coloured shape (e.g., a red square). They then performed a visual search task where they had to locate a tilted target line among vertical line distractors. Crucially, these lines were presented within coloured shapes, one of which occasionally matched the item held in memory. Using an eye-tracking device, the researchers found that even when participants were explicitly instructed to ignore the memory-matching item, their saccades (eye movements) to the target curved towards the distractor that matched the memorised shape. This was even the case in trials in which participants successfully moved their eyes directly to the target, suggesting an automatic influence of VWM on eye movement planning that participants could not fully suppress. The study also revealed that participants were more likely to make erroneous saccades towards the memory-matching distractor, especially when it was near the target. These findings demonstrate a robust and involuntary effect of VWM content on attention allocation, as reflected in oculomotor behaviour. Other studies have corroborated and extended these results. For instance, Hollingworth and Luck (2009) showed that the first saccade in a visual search task often lands between the target and a distractor object, and when this distractor object had the VWM-colour, the second saccade to correct the focus onto the target was impaired. Olivers et al. (2006) also observed more eye movements towards distractors matching the content of VWM as compared to other non-matching distractors. Together, these studies support the idea that active representations in VWM serve as attentional templates, guiding attention in a content-based manner even when such guidance is detrimental to the current task.

However, this automaticity is not universally observed. Woodman and Luck, (2007) conducted a series of experiments using similar paradigms and found contradictory results. In a dual task, participants performed both a memory and a visual search task. They were asked to memorise the colour of a square (e.g., red) at the beginning of each trial and then, at the end of the trial, determine if the colour of the memorised object had changed. Between the memory and test display, however, they had to quickly identify a target object (e.g., a square with a gap at the top or bottom) in a visual search task. On some trials, one of the distractors in the search task matched the memory colour. Contrary to previous findings, Woodman and Luck, (2007) observed that, even when distractors matched the memorised colour, there was no evidence of automatic attentional capture, suggesting that attentional selection is not automatically biased by VWM contents. In fact, in some conditions, participants were faster at finding the target when a memory-matching distractor was present. The researchers proposed that participants could strategically use the memory-matching item to guide attention away from it, thereby facilitating search for the target. This suggests a more flexible relationship between VWM and attention than previously believed. Similarly, Carlisle & Woodman (2011) provided evidence for this flexible regulation by asking participants to search for a target whilst holding a colour in memory, which sometimes appeared as a distractor during the search. When memory-matching distractors were infrequent (20% of trials), they captured attention and slowed search times. However, when these distractors were frequent (80% of trials), participants learnt to strategically avoid them, resulting in faster searches. This study demonstrated that whilst VWM contents can automatically influence attention, this effect can be modulated by task demands and learning, highlighting the dynamic interplay between automatic and strategic processes in attentional guidance. More recently, van Loon et al. (2017) provided further evidence to show that participants could strategically control which items in VWM guided attention, by examining participants’ eye movements. Participants were required to remember two coloured disks and search for them sequentially. The experiment introduced four probe conditions: one where both the current and the prospective colour were presented (both condition), one where the current colour was presented with an irrelevant colour (current condition), one where the prospective colour was paired with an irrelevant colour (prospective condition), and one where two irrelevant colours were presented in the probe display before the search. The results showed that significantly more saccades were directed towards probes with the current search colour compared to irrelevant probes, as indicated by an above-chance-level saccade probability in the current and both probe conditions. Saccade amplitudes were larger for probes with the current search colour compared to irrelevant colours and slightly larger still than for prospective items in the both condition. In the prospective condition, the probe with the prospective colour did not attract larger saccades compared to irrelevant colour probes. The saccadic rate analysis revealed that more saccades and micro saccades were directed towards the VWM-colour matching side of the probe display, particularly within a time window of approximately 150 to 250 ms after probe presentation. These findings suggest that the current search template exerts a strong influence on saccadic behaviour, while the prospective template has a lesser impact. These findings from the literature collectively point to a more dynamic interaction between VWM and attention, where cognitive control processes play a crucial role in determining which memory representations influence attentional deployment.

Another key factor that cannot be ignored when discussing attentional guidance from VWM is inter-trial priming, i.e., whether the search target is repeated across trials or varies from trial to trial. Studies supporting VWM-based attentional capture often employed designs in which the search target remained constant across consecutive trials (Olivers et al., 2006; Soto et al., 2005). In contrast, studies that failed to observe automatic memory biases typically used designs where the search target changed from trial to trial (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006). This distinction in target presentation may fundamentally alter how information is prioritised within VWM and, consequently, how it influences attention deployment (Olivers et al., 2011). For instance, Downing and Dodds (2004) found that memory-matching distractors did not capture attention when participants were actively maintaining a search template for a different object. Houtkamp and Roelfsema (2006) demonstrated that when participants had to search for a new target on each trial, memory-matching distractors had no effect on search performance. To further disentangle the effects target repetition across trials, Carlisle et al. (2011) presented participants with a search task (e.g., for a red square) with the critical manipulation being that the target definition remained the same for seven trials in a row. They found that with increasing number of target repetitions (e.g., trials 5-7 vs trials 1-2), the Contralateral Delay Activity (CDA), an electrophysiological marker of VWM maintenance, decreased in amplitude. This decrease suggests a transfer of the target template from VWM to long-term memory, a process termed "template learning" which potentially enhances the automatic capture of attention by memory-matching items, as long-term memory assumes the role of guidance.

Altogether, more research is needed to further investigate memory-guided attention, particularly in the context of task-specific demands. Rather than isolating the processes of VWM maintenance and attentional guidance, studies should consider the dynamic nature of VWM, in other words, the dynamic allocation of cognitive resources. This adaptive mechanism raises important questions about the limitations of VWM and how the cognitive system manages these constraints. The subsequent section reviews VWM capacity, discussing how this fundamental constraint influences the interplay between memory and attention, and shapes cognitive performance across diverse tasks.

1.2 Capacity limits of template-guided visual search

It has been suggested that human VWM can typically hold three to four items at a time (e.g., Cowan, 2001; Luck & Vogel, 1997; Vogel et al., 2001). Since attentional templates are target representations held in VWM, it is reasonable to assume that the capacity limitations of VWM translate to the number of attentional templates that can be simultaneously activated, i.e., it can be assumed that three to four attentional templates can be concurrently activated during visual search. This means that template-guided attention for multiple possible target objects should be as efficient as search for one target object (Grubert et al., 2016). However, some researchers have claimed that the number of objects that can be maintained in VWM is reduced when resources related to attention (e.g., visual search) are concurrently being occupied. They have suggested that only one attentional template in VWM can be activated at a time and effectively guide attention towards the target (e.g., Dombrowe et al., 2011; Houtkamp & Roelfsema, 2006; McElree, 2001; Oberauer & Bialkova, 2009; Olivers et al., 2011). For example, in Houtkamp and Roelfsema (2006), participants were tasked with remembering two items and searching for them sequentially in a visual search task. The first object was the immediate search target, while the second was a "memory item" to be searched for later. On some trials, the memory item appeared as a distractor during the first search. Eye movements and RTs were measured to assess attentional capture. The researchers found that crucially the presence of the irrelevant memory item did not interfere with search performance when the first target was present in the first search. Even in the target absent trials, the irrelevant memory item only caused slight interference. These findings strongly support the notion that only one item can serve as an active attention-guiding memory representation at any given time. The results suggest that when the target is absent, the irrelevant memory item competes for the status of the active representation, leading to a slight performance decrement. But when the target is present, the target template is the sole active representation, delegating the irrelevant item to a dormant state where it no longer interferes with the search process. This study not only demonstrated the limited capacity of memory-guided attention but also highlighted the restrictive nature of the interaction between VWM and attentional guidance in visual search tasks. In a later study of Houtkamp and Roelfsema (2009), the authors conducted consecutive search tasks and found that even when participants knew the two potential targets in the two searches in advance, they could not prepare both templates simultaneously. Performance suffered equally whether the second target was cued before or after the first search, with a RT cost of 200-300 ms when switching targets. Together, these studies strongly support the notion that while multiple items can be maintained in VWM, only one can be in the active state that directly guides attention at any given moment.

Building upon these empirical findings, Olivers et al. (2011) proposed a theoretical framework that distinguishes between two states of VWM representations (see Figure 1). The first is an active state, where a single item directly interacts with perception and guides attention. The second is an accessory state, in which multiple items can be maintained simultaneously but in a passive fashion, i.e., they have limited influence on attentional processes. According to this model, although multiple representations can be maintained in VWM, only one of these representations can be in the active state at any given time to interact with sensory processing and bias attentional selection. The authors posited that items can flexibly switch between these states, albeit with a time cost, which explains the performance costs observed in task-switching paradigms. This framework elegantly accounts for the seemingly contradictory findings in the field, reconciling studies that suggest a multi-item capacity in VWM with those indicating a single-item limit in attentional guidance. The model also has important implications for understanding individual differences in template maintenance and switching abilities, as well as practical applications in designing visual search tasks and interfaces.

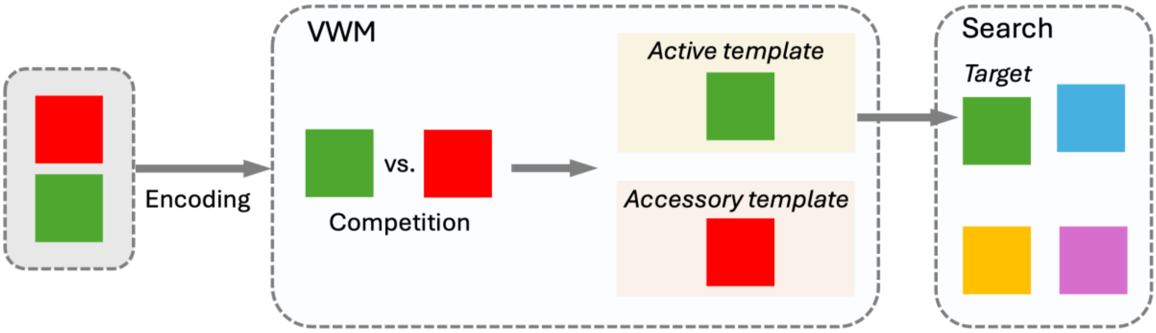

Figure 1 Schematic illustration of the single template activation framework of Olivers et al. (2011).

Instead of using one target and one task-irrelevant items in each task like in the studies of Houtkamp and Roelfsema (2006, 2009), van Moorselaar et al. (2014) further investigated the single template activation theory by examining how multiple task-irrelevant items in VWM affect attentional capture. Participants performed a visual search task, looking for a diamond target among circle distractors while simultaneously holding a varying number of task-irrelevant colours in VWM. During the search, a coloured singleton distractor appeared that either matched or did not match a colour held in VWM. When only one colour was held in VWM, the researchers observed memory-driven capture i.e., RTs were slower and error rates higher when the distractor matched the memorised colour. Crucially, this memory-driven capture effect disappeared when participants held more than one colour in VWM. These findings support the notion that only one representation in VWM can actively guide attentional selection at a time.

The single template account was further discussed by a series of subsequent studies (Ort et al., 2017, 2018, 2019), which demonstrated serial template switch costs and limits to attentional selection in search tasks in which multiple target representations were task relevant. In their 2017 study, Ort et al. employed a novel paradigm in which participants searched for two colour-defined targets simultaneously. In the free choice condition both targets were presented simultaneously and participants had the flexibility to choose which target to focus on. In the no choice condition, only one of the two possible targets as presented so that participants did not have a choice to switch freely between the two templates but simply had to find the target that was present. Crucially, they found that, only under the no choice condition, RTs were significantly slower on trials where the target colour switched compared to those when it repeated, even though both colours were known in advance. This switch cost, averaging about 250-300 milliseconds, suggests that participants could not maintain two active search templates concurrently and instead had to switch between them. In a follow-up study (2018), they replicated these findings in multiple-target search within and across feature dimensions. Using a similar paradigm, Ort and colleagues instructed participants to simultaneously search for two potential targets defined by two colours, two shapes, or one colour and one shape. There were still one free choice and one no choice condition. The results demonstrated that regardless of how target features were defined, whether they were from the same or different dimensions, switch costs existed when there was no free choice and only one target was available to be chosen in the search display. In their 2019 work, Ort et al. extended these findings to more complex scenarios where the number of target colours participants had to prepare for (one or two templates) and the number of unique target colours actually presented in the search displays (one or two features) were manipulated. All search displays always contained two targets. They found relatively small costs in behavioural and electrophysiological measures when the two targets were shown in the same colour, irrespective of whether participants just activated a single colour template or two templates for two different colours. However, when participants had to activate two different target colour templates and also search for two targets that actually had two different colours, the search costs were substantially larger than in the same colour conditions. The researchers interpreted these findings as evidence that limitations in multiple-target search stem primarily from engaging multiple templates in selection rather than preparing multiple templates. They proposed a limited parallel model where multiple templates can be activated simultaneously but compete through mutual suppression when being engaged in selecting targets, resulting in slower and weaker target selection. In other words, observers can prepare for multiple targets with little cost but will face significant limitations when selecting those targets. Collectively, these studies have painted a picture that multiple target search comes with costs, but the magnitude of this cost differs depending on the processing stage. Attentional selection appears to be strongly limited, while the preparation of multiple attentional templates, i.e., the activation of multiple target representation in VWM in anticipation of a search is possible with relatively small costs (Ort & Olivers, 2020).

Other studies, focusing on template relevance, also delivered evidence for the idea that multiple templates can be activated simultaneously and guide attention in parallel. Hollingworth & Beck (2016), for instance, used a paradigm similar to van Moorselaar et al.'s (2014) and showed that when two memory-matching colours appeared as distractors in the search array, they produced a larger capture effect than a single memory-matching distractor, suggesting that both memorised colours were actively guiding attention. The rationale behind this design is that, to make both colour representations equally relevant, they both need to be shown in the search display (in the form of two distractors). Along similar lines, Beck et al. (2012) presented observers with high-density search arrays with multiple targets and distractors. Participants had to search for all objects that either matched a single target colour (e.g., red), or one of two relevant colours (e.g., red or green). In two-colour trials, participants frequently switched between differently coloured targets without any evidence of switch costs, i.e., search was comparable whether successive targets had the same or different colours. The lack of switch costs led the authors to conclude that it was possible to simultaneously maintain two attentional templates, both of which guided attention in a comparable fashion when both target colours were equally relevant for the task at hand. This account of simultaneous activation of multiple attentional templates has received further support from subsequent studies, including work by Grubert et al. (2016) and Grubert and Eimer (2018, 2020), strengthening the evidence for the flexibility of attentional guidance by VWM.

Taken together, previous studies have yielded inconsistent findings on the question of whether multiple attentional templates can be activated simultaneously in VWM and effectively guide attentional selection. Two essential factors in these previous studies need to be considered. One is directly measuring attention selection, whereas the other is including other feature dimensions. For example, Hollingworth and Beck (2016) and van Moorselaar et al. (2014) did not directly measure attentional selection guided by multiple templates. Rather, they inferred the activation level of multiple templates in VWM by measuring interference effects produced by template-matching distractors. This design might lead to motivational suppression of representations in VWM (inhibiting distracting information rather than enhancing relevant information) and impaired performance in attentional selection in return (Carlisle & Woodman, 2011). By focusing on distractor interference rather than target facilitation, they seem to have confounded task relevance in VWM with response-irrelevance in the actual search displays. Furthermore, most of the studies reported above have used colour as the task-relevant feature dimension, but other feature dimensions were found to have various levels of complexity and relevance for guidance during search (Wolfe & Horowitz, 2004). To decide whether attentional processes can be tuned to multiple target objects simultaneously, it is crucial to take such other feature dimensions into consideration.

Even though Ort et al. (2019) established the simultaneous maintenance of one colour and one shape, their results could potentially be explained by the relatively easy maintenance of colour and shape separately in VWM (Ort & Olivers, 2020). Therefore, it is critical to study multiple features from the same dimension, but not colour due to its typically very salient characteristics (Lee et al., 2018). Another perspective is that, although costs between one and two templates have been found to be relatively small, it is unclear if the costs will increase dramatically with more templates being added. Therefore, Chapters 2 and 3 in this thesis will examine whether more than one template in VWM can be maintained and activated to guide subsequent selection processes during search preparation. These chapters will also explore the possibilities of strategically allocating cognitive resources during memory-guided attention under two distinct conditions: 1) VWM capacity limits have not been reached (two templates), and 2) VWM capacity is close to its limit (three templates).

1.3 Temporal dynamics of template activation in preparation

Visual search has been conceptualised as comprising four key stages, namely preparation, guidance, selection, and recognition (Eimer, 2014). The first stage, preparation, involves the activation of attentional templates. These templates are VWM representations of target-defining features that guide attention during the subsequent search process (Chelazzi et al., 1998; Desimone & Duncan, 1995; Olivers et al., 2011). The preparatory stage is crucial for efficient guidance and selection in the subsequent stages of search. In the guidance stage, attention is allocated based on template-matching features. Objects in the visual field that share characteristics with the activated template receive priority processing (Wolfe & Horowitz, 2004). This prioritisation helps to efficiently direct attention towards potential targets. The selection stage involves the focused processing of potential target objects. Attention is directed to specific locations or objects that closely match the search template, which is then analysed in detail. During the recognition stage entails the selected objects is classified as target or non-target (Wolfe, 2021). Target recognition will determine whether the search will be terminated or continue. While this general framework has been widely accepted, the specific temporal dynamics of these processes, particularly the activation of attentional templates during the preparatory phase, have been challenging to study in humans. Recent research has begun to address this gap, providing new insights into how and when search templates are activated prior to the onset of visual search (e.g., Grubert & Eimer, 2018, 2020, 2023).

Investigating the temporal dynamics of attentional template activation and rapid attentional shifts during visual search requires precise temporal measurements. The electroencephalography (EEG) technique, particularly the N2-posterior-contralateral (N2pc) component, is widely used for this purpose. The N2pc component of event-related potential (ERP) serves as an electrophysiological marker of attentional selection (Eimer, 1996; Luck &

Hillyard, 1994). It typically emerges 200-300 ms after stimulus onset as an enhanced negativity at posterior electrodes contralateral to the attended visual field. The high temporal resolution of ERPs allows researchers to track the rapid allocation of attention to potential target objects with millisecond precision (Eimer & Kiss, 2008; Woodman & Luck, 1999). This N2pc component has been widely employed in research studying the time course of attentional deployment during visual search tasks. The latency of the N2pc provides information about how quickly attention is deployed; and its amplitude can indicate the strength of the attentional focus (Luck & Kappenman, 2012). This makes the N2pc particularly useful for investigating when attentional templates are activated during the preparation stage and the subsequent selection of search targets.

To assess the temporal activation of attentional templates during visual search preparation, Grubert and Eimer (2018) developed a novel paradigm combining a visual search task with rapid serial probe presentation, allowing for precise temporal tracking of attentional processes prior and during search. Each search display contained six differently coloured bars, one of them matched a predefined target colour. Participants were instructed to find the colour target and discriminate its orientation (vertical or horizontal). A search display was presented every 1600 ms. Between the search display, series of task-irrelevant colour singleton probes were presented every 200 ms. Half of the probe displays contained a target-colour singleton, whilst the other half contained a distractor-colour singletons. Target and distractor-colour probes were presented randomly. N2pc components were measured in response to the target- and distractor-colour probes and the targets in the search displays.

The rationale of the paradigm was that template-matching probes would capture attention and elicit N2pc components only when the attentional template was active at the point in time a probe was presented. The results revealed that probes presented early in the search preparation period did not elicit any N2pcs, whereas probes presented from about

1,000 ms before the search display succeeded in eliciting N2pcs. These probe-elicited N2pc components increased in amplitude until they were largest for the probes that immediately preceded the search displays. These findings suggest that search templates became active approximately 1,000 ms before the arrival of the target and were deactivated immediately after each search episode. Search templates are therefore not activated continuously but are transiently activated in preparation for each new search episode. The timing of this activation pattern was found to be influenced by temporal expectations regarding the onset of the search display. When the interval between search displays was shortened or increased, template activation started earlier or later, respectively. Both Chapters 2 and 3 will report new research adapting this paradigm to further investigate the temporal activation parameters of attentional templates during search preparation.

1.4 Contents of conjunction templates

Research has shown that attentional templates hold information of target features, such as specific colours or shapes, which are maintained in VWM and activated before a search task begins (Chelazzi et al., 1998; Grubert & Eimer, 2018). Once activated, these templates help directing attention automatically to any object in the visual field that matches the template's information (Desimone & Duncan, 1995; Folk et al., 1992; Grubert & Eimer, 2016b; Wolfe, 2021). However, it remains unclear what these templates contain exactly. A critical question is whether they by default include just single features, like a colour and a shape separately (e.g., white and circle as separate features), or if they can also include a conjunction of features, like white and circle, to represent a complete object during searches that require finding items with multiple characteristics, such as a large white car.

As attentional templates are the information of targets maintained in VWM, it seems logical to assume that the content of templates depends on how information is stored in VWM. An influential study by Luck and Vogel (1997), using a change detection paradigm with arrays of coloured bars in varying orientations showed that the change detection performance was not impaired in a condition where participants had to remember a combination of colour and orientation, compared to conditions where they only remembered a single feature, i.e., colour or orientation. These results indicate that the colour and orientation information in the conjunction condition must have been integrated into holistic object representations to keep the memory load comparable with the single feature conditions. Hence, Luck and Vogel proposed that VWM capacity is limited by the number of distinct objects encoded into memory, rather than the number of features within each object. Supporting this perspective, later studies also provided evidence that remembering several features of one object is easier than remembering the same features spread across multiple objects, a phenomenon known as the "object-based benefit" (e.g., Ngiam et al., 2024; Olson

& Jiang, 2002; Vogel et al., 2001). Nevertheless, this enhanced performance does not inherently suggest the storage of integrated object-based representations. It is plausible that there is a cognitive cost associated with representing additional objects, which explains the advantage of encoding information from a smaller number of objects containing multiple features. However, the memory representations themselves might still be composed of non-integrated collections of features (see Brady et al., 2011, for a review; Fougnie et al., 2013; Wang et al., 2017; Wheeler & Treisman, 2002). Wheeler and Treisman (2002) designed feature and binding tasks with feature conjunctions (colour, location, and shape) to investigate how features are stored and bound in VWM. In the feature tasks, participants were shown displays with coloured shapes at various locations and had to detect changes in a single feature, while the other features remained constant or were made irrelevant. For example, in the colour task, shapes could move to new locations, but participants were only asked to detect colour changes; in the location task condition, colours or shapes could change, but participants only had to detect location changes. In the binding task, the combinations of the features were changed. For example, two coloured shapes could swap locations, or two shapes could swap colours. For each task, there were two types of test displays. One type presented all objects (whole-display), whereas the other type presented one object only (single-probe display). Their findings indicated that detecting changes in feature conjunctions was much more difficult than change detection in single features in the whole-display stimuli, but not in the single-probe stimuli. This suggests that, while feature conjunctions were encoded and stored as effectively as individual features in VWM, they were more vulnerable to interference from whole-display test images. The researchers proposed that VWM can access information from separate features, each with its own capacity limit, as well as from separate objects containing integrated features. However, forming and maintaining these integrated representations requires extra attentional resources. During detection of feature combinations in whole-displays, each probe object demands selective attention and diverts focal attention from items stored in VWM. Conversely, with single-probe presentations, feature binding occurs automatically, allowing attention to remain focused on the memorised items. The authors attributed the superior performance in detecting feature changes over conjunction changes to the presence of additional memory traces of unbound features. Overall, this study proposed that features are stored in parallel, while bindings require additional attentional resources to maintain, challenging the view that visual information is automatically stored as integrated object representations and highlighting the fragility of feature bindings in memory. This idea was also supported by a later study (Fougnie et al., 2013), which suggested that participants recalled features more efficiently when these features were grouped in fewer objects. However, they also noted that memory for individual features remained largely independent. The authors proposed that the better changed detection performance of integrated object representations was due to reduced representational noise with fewer numbers of objects rather than the integration of features.

Very recently, Ngiam et al. (2024) tested the VWM contents again in four experiments by employing whole-report tasks, where participants recall features from arrays of six items, including both single-feature and multi-feature objects (colour-orientation or colour-shape conjunctions). Participants were tasked with reporting both features of multi-feature objects. Across all experiments, accurate recall was limited to the first three or four reported objects, irrespective of them being single-feature or multi-feature. It was therefore suggested that VWM capacity is fundamentally object-based. Furthermore, this study also found similar results to those of Fougnie et al. (2013) in that more features were recalled in the conjunction condition (multiple features were combined into single objects) than in the single-feature conditions, even though fewer full conjunctions were reported (that is, both features were correctly reported in a conjunction) than single-feature items. When the number of features in an object increased, the performance declined slightly. Altogether, this study proposed that VWM has a capacity limit of three for object representations, a number similar to the capacity limit of single features, despite that not all features in an object representation are being correctly reported.

While the debate on whether VWM contents are primarily feature-based or object-based continues, it is crucial to consider how these representations influence attentional processes in conjunction search. An important question is whether attentional templates operate at a feature- or conjunction-based level when guiding attention. Modern theories of visual search posit that the initial visual processing occurs at the feature level. For example, Guided Search 6.0 (Wolfe, 2021) assumes a feature-based "priority map" as a central mechanism of attentional guidance during search. This map integrates information from multiple feature dimensions (e.g., colour, shape, orientation and size) and guides attention to locations that have the highest bottom-up salience or contain a template-matching feature. The features at the attended location are then forwarded to higher cognitive processes where they are bound together to determine whether the attended object is the sought-for target. This model has been supported by empirical findings from behavioural, eye-tracking, computational modelling, and electrophysiological data, showing that early visual selection relies on individual features (e.g., Adamian et al., 2020; Andersen et al., 2015; Bahle et al., 2020; S. I. Becker et al., 2020; Berggren & Eimer, 2018; Chapman & Störmer, 2021; Dent, 2023; Eimer & Grubert, 2014; Rutishauser & Koch, 2007; Williams & Reingold, 2001). For example, an EEG study by Eimer and Grubert (2014) had participants search for targets defined by a colour-shape conjunction (e.g., a blue square). There were two conditions, namely a no-competition condition and a competition condition. In the no-competition condition, a search display contained either the target or a partially matching distractor (matching either colour or shape) among nontargets. In the competition condition, both the target and the partially matching distractor were presented together. The study revealed that early attentional selection is guided by feature-specific signals, with attention being allocated independently and in parallel to any objects with target-matching features. Around 250 ms post-stimulus, attentional processing transitions to an object-based stage, integrating information across feature dimensions. Interestingly, even in the competition condition, partially matching nontargets elicited the N2pc component, suggesting parallel allocation of attention to features. Jenkins et al. (2017) also provided evidence that attention was initially guided independently by feature-specific processes operating in parallel, rather than by integrated object representations, with reliable N2pc components elicited by partially matching distractors. Similar to Eimer and Grubert (2014), they also observed that, beyond 230 ms after display onset, the N2pc evoked by targets became super-additive, indicating that attentional selection processes had begun to integrate the features of the targets. Overall, these findings demonstrated that attentional selection during conjunction search can occur rapidly and in parallel, with initial biases being feature-specific before becoming sensitive to feature conjunctions, challenging the traditional view that such selection operates serially. The results from these two empirical studies are consistent with Guided Search 6.0 (Wolfe, 2021) which posits that, in visual search, a 'guiding template' (containing a target's features) biases attention to the potential locations, while a separate 'target template' (holding the expected features of the target) enables verification of a potential match. At the comparison stage, the integration of features will likely happen. That might be shown as a super-additive N2pc component in the empirical data.

Taken as a whole, these discrepancies among VWM models and attentional guidance theories have raised intriguing questions about the nature of attentional templates, which are believed to be part of VWM. To date, it remained unclear why these templates would not be capable of holding integrated target representations when guiding attention. Therefore, Chapter 4 will directly compare conjunction search with single-feature search (one-colour and one-shape search) under low and high memory load conditions.

1.5 Thesis outline and aims

This thesis aims to better understand the temporal dynamics of attentional template activation during visual search. It focuses on the capacity limits of visual search involving single-feature and conjunction templates during task preparation and target selection, and whether potential template co-activation is under strategic control, i.e., whether participants activate multiple templates simultaneously by default or choose to strategically activate a single template in line with specific task demands. Additionally, this thesis examines the organisational properties of features in conjunction search, i.e., whether attentional templates contain separate single features or integrated object representations during conjunction search. The empirical work of this thesis comprises six EEG studies, which are divided into three chapters. The first two experimental chapters, Chapters 2 and 3, explore the activation of attentional templates during search preparation when multiple target colours are presented randomly or in a fully predictable manner. The final experimental chapter, Chapter 4, addresses how multiple features from different dimensions are combined to form a conjunction template and whether multiple conjunction templates can be simultaneously activated to guide attention. The main body of this thesis is outlined below:

Chapter 2: This chapter presents two EEG experiments examining the mechanisms involved in switching between target templates during visual search tasks. Previous research by Grubert and Eimer (2020), using a rapid serial probe presentation (RSPP) paradigm where participants searched for one of two colour-defined target objects that changed predictably every trial (i.e., in a pattern of ABAB), found that multiple target colour templates could be activated simultaneously, even though only one was relevant for the next search episode. The coactivation of both templates in this experiment was unexpected, as strategic control should have been possible, i.e., the temporarily irrelevant target colour template could have been deactivated in alternate trials. However, the short alternating sequence may have made template switching not worthwhile. To further explore the strategic control in template activation, the current study employed an alternating-runs procedure. In Experiment 1, the target identity changed every second trial (i.e., AABB), whilst Experiment 2 used four-trial runs (i.e., AAAABBBB). These longer sequences were chosen to identify potential strategic control in template activation that might not have been observable in the shorter ABAB design. They also allowed examination of the activation of both target colour templates separately for target switch and target repeat trials. Using a similar RSPP paradigm and measuring N2pc components to probes presented during search preparation, we tracked the real-time activation of target colour templates prior to search displays. The results of both experiments revealed significant behavioural switch costs on switch trials compared to repeat trials. Crucially, the electrophysiological data showed a delay in the activation of the relevant target colour template on switch trials. Interestingly, the study found no evidence of task-set inertia, as there were no N2pc responses to probes matching the previously relevant but currently irrelevant target colour. These findings demonstrate that the activation of target templates can be strategic and that switch costs in search tasks arise from delays in activating the correct target template rather than interference from previous templates.

Chapter 3: This chapter expands the multiple template account by introducing a third target template to examine the capacity limitations and template activation processes during search preparation for three colours in two new EEG experiments. The three-colour search allowed us to measure template activation at the VWM capacity limit. These experiments build on previous experiments in which Grubert and Eimer found simultaneous template activation in random (2023) and predictable (2020) two-colour search. However, search for two colours will very likely not have challenged the working memory capacity of most of the participants. Therefore, co-activating two colour templates might have been less costly than switching between them. The current study investigated how increasing the number of potential target colours affects template activation processes. It might be that introducing an additional target colour reveals the true capacity limitations in preparatory target template activation, potentially leading to more selective, single-colour template activation. Experiment 1 used a predictable ABCABC sequence and revealed reliable N2pc components only for probes that matched the upcoming target colour. Probes that matched the other target colours that were relevant on previous trials did not elicit any N2pcs. This suggests that only a single template was activated in the three-colour search. To explore whether this was a strategic decision or a true capacity limit, Experiment 2 introduced a task with randomised target colours. Now, all probes that contained a target colour elicited N2pcs, demonstrating that three target colour templates can be activated in parallel. However, the N2pcs that were triggered in response to the search targets showed a different pattern. In comparison to a single-colour search, the target N2pc in the three-colour task was significantly attenuated and delayed. These multiple-template search costs are due to inhibitory interactions among the simultaneously active search templates. Overall, the findings demonstrate that while three target templates can be activated in parallel, multiple-template search and target selection is subject to capacity limitations.

Chapter 4: This chapter expands the investigation of multiple template activation from single feature (colour, as examined in Chapters 2 and 3) to more complex conjunction templates, which incorporate features from multiple dimensions, such as colour and shape. The primary objective was to determine whether attentional templates can accommodate integrated object representations, and if these integrated representations can effectively guide attention when chunking in VWM is advantageous for reducing memory load. Experiment 1 served as a prerequisite to the conjunction task, directly comparing the efficiency of colour and shape templates in guiding attention. Experiment 2 consisted of three tasks: a colour task, a shape task, and a conjunction task, each with two load conditions. In the conjunction task, each target was paired with a distractor matching either its colour or shape. This design allowed testing whether conjunction search is guided by combined feature templates (in which case partially matching distractors should be ignored) or by individual feature templates (where partially matching distractors would be attended to, triggering N2pc). The three tasks had identical cue displays to compare the CDA components. The results showed substantially increased load effects in the target N2pcs of the conjunction task compared to the single-feature tasks (pooled colour and shape tasks). The target-elicited N2pc components were significantly delayed when the target and the partially matching distractor were in opposite hemifields compared to the same hemifield. This indicates that distractors matching either the target colour or shape captured attention, a notion consistent with the idea of independent parallel selection guided by separate feature templates for colour and shape. The CDA amplitudes, measured in response to the cue displays, were twice as large in the conjunction task as compared to the single feature conditions in terms of load effect, suggesting that conjunction search is feature-based, because the load effect in the single-feature tasks was caused by one additional template (one in the low-load trials, two in the high-load trials), yet that in the conjunction task was caused by two additional features (two in the low-load search, four in the high-load search). In conclusion, these results indicate that single features rather than integrated object representations were activated prior to search and held active during attentional guidance.

Chapter 2 Target switch costs in visual search arise during the preparatory activation of target templates

2.1 Introduction

The ability to change cognitive task settings and behavioural responses when this is required by a change in circumstances is a central function of human cognitive control (e.g., Shallice & Cooper, 2011). The evolution of cognitive control mechanisms has enabled humans to interact with the external world flexibly and adaptively, in ways that sets us apart from all other animals. In the lab, this remarkable ability is often studied by investigating how humans prepare to perform a specific task, and how they reconfigure a particular task set when their goals change. The task switch paradigm (D. A. Allport et al., 1994; Jersild, 1927) has become a popular tool to explore the mechanisms involved in activating specific task sets and changing them when needed. In a typical task-switching experiment, participants are instructed to perform one of two possible tasks. On any given trial, the task either repeats or switches relative to the previous trial. The crucial finding in such experiments is that response times (RTs) are slower and errors often more frequent on switch trials as compared to repeat trials ("switch costs"; see Kiesel et al., 2010; Monsell, 2003; Vandierendonck et al., 2010, for review). The mechanisms that produce such switch costs have been investigated extensively because it is assumed that these costs reflect the operation of domain-general cognitive control processes that are involved in the selection and coordination of many different types of tasks. One widely used procedure to study task switches is the alternating-runs paradigm, where participants perform two tasks in a constant order (e.g., AABBAABB, see Rogers & Monsell, 1995). The comparison of trials where a task is repeated and trials where it changed revealed substantial behavioural switch costs, in spite of the fact that task switches were fully predictable. Such costs are assumed to reflect the time demands of preparatory endogenous task-set reconfiguration processes (e.g., Meiran et al., 2000; Monsell et al., 2000). The observation that these costs become smaller but remain reliably present even when participants are given several seconds to prepare for each task (Rogers & Monsell, 1995) suggests that task switching cannot be fully completed on the basis of purely endogenous preparation mechanisms, but also includes a stimulus-driven component. To fully establish a task set, a new task has to be performed at least once (see also Rubinstein et al., 2001). In line with this hypothesis, experiments with longer alternating runs (e.g., AAAABBBB in Monsell et al., 2003) have found performance costs only for the first trial after a switch, but not on subsequent trials of the same run. It has also been suggested that such costs may emerge more passively, as a result of the persistence of a previously active task set (task-set inertia; e.g., Allport & Wylie, 1999). Any persisting irrelevant task set activation may interfere with the operation of a new task set, and thus produce switch costs that are unrelated to the preparatory activation of the other task (see Kiesel et al., 2010, for further discussion). Active endogenous task-set reconfiguration and passive task-set inertia are not mutually exclusive; it is possible that both contribute to empirically observed switch costs (Monsell, 2003; see also Imburgio & Orr, 2021).

Most previous investigations of the processes involved in switching between task sets used procedures where tasks were defined in terms of the rules that associate particular stimuli and responses (e.g., categorising digits with respect to their magnitude or parity, or categorising words in terms of their meaning or colour). However, there are many different types of task sets, which raises the question how task switching operates in such different contexts. For example, an important function of cognitive control is the guidance of selective attention in line with current intentions, which requires task sets that specify the relevance of particular objects or object features in a given context (e.g., Folk et al., 1992). For example, in visual search tasks, where multiple stimuli are present in a single display, targets are defined by one or more attributes that distinguish them from distractors. Such target-defining features are usually known in advance and are assumed to be represented as attentional templates (e.g., Duncan & Humphreys, 1992). Such templates can be activated prior to the onset of a search display, in order to guide attention to objects with target-matching features and facilitate the detection of search targets. Target templates are a particular type of task set that specifies object attributes that are relevant for current search goals, rather than mappings between stimuli and responses, as investigated in most previous task switching experiments (see Rushworth et al., 2002, for a study where both types of task settings were combined). Thus, the question arises whether switching between target templates also induces behavioural switch costs, and which mechanisms are responsible for such costs.

Several previous visual search studies have used tasks where participants had to find one of several possible target objects, and these studies have typically revealed performance costs on trials where the identity of the target changed relative to target repetition trials (e.g., Christie et al., 2015, Experiment 2; Dombrowe et al., 2011; Grubert & Eimer, 2013; Juola et al., 2004; Olivers & Meeter, 2006). It remains unknown which mechanisms are responsible for these target switch costs, and at which stage they are generated (see Ort & Olivers, 2020, for discussion). Because target identity changed unpredictably across trials in most of these previous studies, participants could not strategically activate a particular target template while preparing for the next search episode. However, in tasks where the identity of an upcoming search target is predictable, target switch costs may be produced by processes that take place during the search preparation period, analogous to the processes investigated in standard task switching experiments. They could be the result of less efficient endogenous template activation prior to target switch versus repeat trials. Such template switch costs would be analogous to the endogenous task-set reconfiguration processes postulated in the task switching literature (e.g., Monsell et al., 2000). But target switch costs could also be produced by the persistence of a previously active target template (i.e., task-set inertia; e.g., Allport & Wylie, 1999) interfering with the activation of the currently relevant template.

To investigate these possibilities, search tasks have to be employed where target switch and target repeat trials are fully predictable. The goal of the present study was to use such tasks in order to obtain new insights into preparatory target template activation and reconfiguration processes in visual search. To track target template activation processes in real time, we employed a rapid serial probe presentation (RSPP) paradigm that we used in several previous studies (Grubert & Eimer, 2018, 2020, 2023). In these experiments, participants searched for targets defined by a specific constant colour. Search displays were preceded by a series of irrelevant probe displays that appeared in rapid succession throughout the interval between successive search displays. Some of these probe displays included a colour singleton item that matched the current target colour. These colour probes will capture attention only when a corresponding target colour template is active, but not at other times. To track the time course of target template activation by measuring probe-induced attentional capture, we recorded event-related potentials (ERPs) and computed N2pc components separately for each successive probe presented between two search displays. The N2pc is a negativity at posterior scalp electrodes triggered contralateral to attended objects in multi-stimulus displays. It usually emerges about 200ms after stimulus onset, is generated in ventral extrastriate visual areas (Hopf et al., 2000), and reflects the rapid allocation of attention to candidate target objects (e.g., Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999; see Eimer, 2014, for a review). In our previous RSPP experiments, target colour probes triggered N2pc components from about 1000ms prior to the onset of the next search display, indicating that a corresponding colour template was active during this period. Manipulating the predictable interval between two search displays changed the temporal pattern of probe N2pcs (Grubert & Eimer, 2018). They were triggered earlier when this interval was short than when it was longer, demonstrating that target template activation processes are sensitive to temporal expectations about search display onset. Importantly, no probe N2pcs were elicited by colour singleton probes that did not match the current target colour.

In one previous experiment (Grubert & Eimer, 2020), we employed this probe procedure in a task where observers searched for one of two colour-defined targets. Target identity swapped on each trial (ABAB) and probes matching either of these two colours were randomly intermixed. Here, N2pcs emerged for both target colour probes during search preparation, indicating that both colour templates were active concurrently, even though only one of them was relevant for the next search episode. The co-activation of both templates in this experiment might have been a strategic choice, as target colour changed on every trial (see also Grubert et al., 2017). Alternatively, it could have been the result of task-set inertia, that is, the persistence of the target colour template that was relevant on the preceding trial, analogous to the persistence of previously relevant stimulus-response mappings postulated by Allport and Wylie (1999).

The ABAB design employed in this previous experiment (Grubert & Eimer, 2020) did not allow to compare and contrast target template activation processes prior to target switch and target repeat trials. In the current study, we therefore used an alternating-runs procedure analogous to Rogers and Monsell (1995). As before, search displays included one of two possible colour-defined targets, but target identity now either repeated or switched across successive trials, in a fully predictable fashion. This allowed participants to activate a corresponding target colour template in a preparatory fashion prior to the presentation of each search display. In Experiment 1, the target identity changed every second trial (i.e., AABB), so that target colour repetitions and switches occurred on half of all trials. Colour singleton probe displays were presented every 200ms in the interval between two search displays, and each singleton probe was equally likely to match either of the two possible target colours (see Figure 2 for illustration).

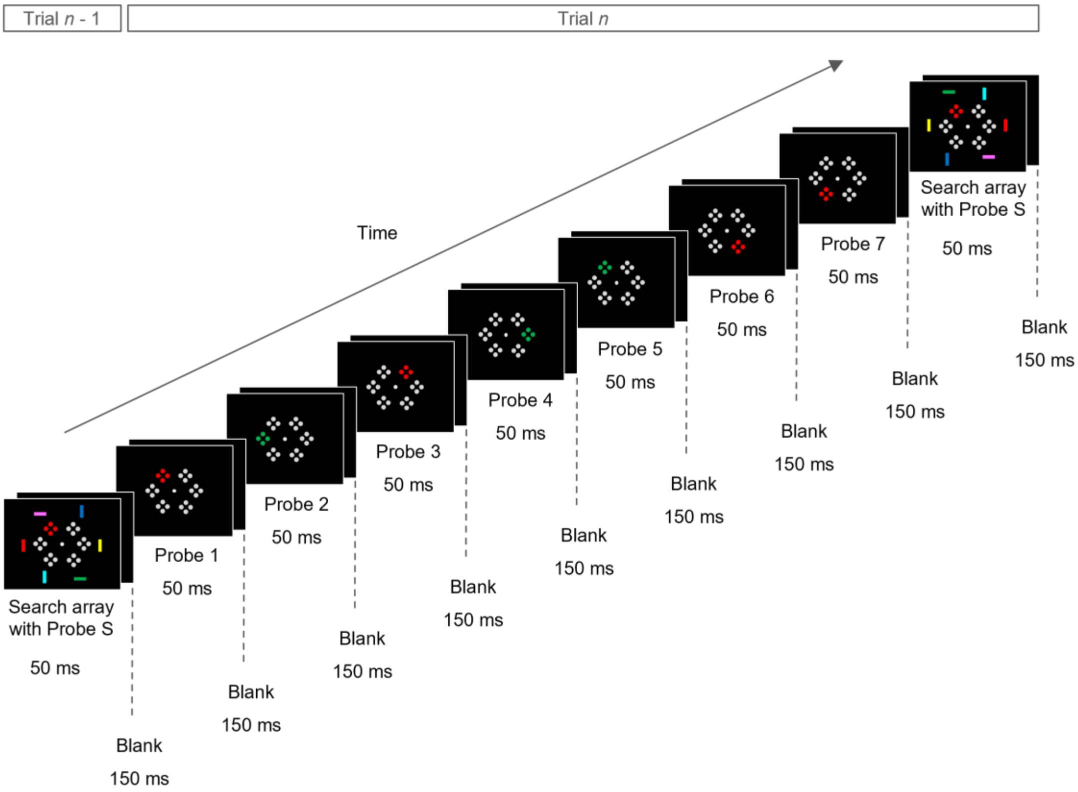

Figure 2 Schematic illustration of the stimuli and presentation times in Experiment 1 and 2. Search displays contained two colour-defined target bars (e.g., red, green) and four nontarget bars in four different nontarget colours (e.g., blue, yellow, pick, cyan). Importantly, only one of the two target colour bars was response relevant in each trial. In Experiment 1, the colour of the response relevant target changed after every second trial (e.g., red in trials 1-2, green in trials 3-4, red in trials 5-6, etc.), while it changed after every fourth trial in Experiment 2 (e.g., red in trials 1-4, green in trials 5-8, red in trials 8-12, etc.). Probe displays contained a colour singleton that randomly matched one of the two possible target colours amongst five grey items. Probe displays were presented every 200ms in the interval between two search displays (probes 1-7) and simultaneously with a search display (probe S). The items in the probe and search arrays were arranged on imaginary circles at an eccentricity of 0.5° and 1.4° from central fixation, respectively.

With this AABB design, we could measure behavioural template switch costs for search performance, and also track the activation of both target colour templates, separately for target switch and target repeat trials. Analogous to the findings by Rogers and Monsell (1995), we expected RTs to be slower and error rates higher on switch relative to repeat trials. The critical new question was whether target template activation processes observed during the preparation for the upcoming search episode would also differ between these two types of trials, as reflected by systematic differences in the pattern of probe N2pc components. If there are switch costs for the activation of the colour template that is relevant for the next search display, this should be indicated by a delay in the emergence of N2pc components triggered by the corresponding colour singleton probes on switch as compared to repeat trials, and/or an attenuation of N2pc amplitudes on switch trials. Furthermore, the presence of task-set inertia should be reflected by the presence of N2pcs in response to singleton probes that match the currently irrelevant target colour, indicating the persistent activation of the corresponding target template. Such an effect should be primarily or even exclusively observed prior to target switch trials.

2.2 Experiment 1

2.2.1 Methods

2.2.1.1 Participants

Twenty-two paid participants were tested in Experiment 1. The experiment was approved by the Ethics Committee of the Psychology Department at Durham University and was conducted in accordance with the Declaration of Helsinki. Participants gave informed written consent prior to testing. Four participants were excluded from analysis due to excessive eye movement artefacts (>40% of trials were lost during artefact rejection). The remaining 18 participants were between 19 and 47 years of age (mean=30.5, SD=8.6). Fourteen participants were female and four were male. All participants were right-handed and had normal or corrected-to-normal vision and normal colour vision (tested with the Ishihara colour vision test; Ishihara, 1972). The sample size of 18 was calculated by means of an a priori power analysis using MorePower 6.0.1 (Campbell & Thompson, 2012) to detect an interaction in a 2×2×7×2 factorial repeated measures ANOVA (within-subjects) with an assumed alpha of .05, power of .85, and a large effect size of 0.80[1].

2.2.1.2 Stimuli and procedures

Participants were sat in a dimly lit and sound attenuated Faraday cage with a 90cm viewing distance from the monitor. Stimuli were presented on a 22-inch MSI Optix G272 LCD monitor with a 100-Hz refresh rate and a resolution of 1920×1080 pixels. PsychoPy (psychophysics software in Python; Peirce et al., 2019) was used on an LG Pentium PC running under Windows 10 to control stimulus presentation, timing, and response collection. Figure 2 illustrates the time course of stimulus events. All stimuli were presented on a black background with a constant central grey fixation point (CIE x/y colour coordinates: .327/.348; 0.2°×0.2° of visual angle). Each block contained 12 trials with eight stimulus displays that were presented in a continuous serial presentation stream. Each stimulus display was presented for 50ms and followed by a 150ms blank (200ms stimulus onset asynchrony; SOA). The first seven displays in each trial each contained a probe display (probes 1 to 7), the eighth displays contained both the response-relevant search display and a probe display (probe S[earch][2]).

Search arrays were presented at an eccentricity of 1.4° from central fixation and contained six vertically (0.2°×0.6°) or horizontally (0.6°×0.2°) oriented bars at the 1, 3, 5, 7, 9, and 11 o'clock positions of an imaginary circular clock face. The orientations of the six bars were selected independently and randomly in each search display. Each bar had a different colour which was randomly allocated from the set of red (.610/.321), green

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[1] *A large effect size was expected to replicate partial eta squared values (η_p^2) of .14, which we measured in a previous RSPP experiment in which participants searched for two alternating target colours (3-way interaction between Laterality*Probe type*Probe number in Experiment 1 of Grubert & Eimer, 2020; p.1531).).*

[2] *In our previous work (e.g., Grubert & Eimer, 2018), probes that were presented together with the search displays (probe S) never triggered reliable N2pc components. However, these probes were still included in the present experiments to maintain a temporally consistent visual pattern of probe presentations throughout each block.*

(.273/.624), blue (.172/.181), yellow (.435/.490), cyan (.222/.313), and pink (.483/.246). All colours were equiluminant (~11.9cd/m^2). Each participant was assigned two of these colours as possible target colours. Each of the six possible target colour pairs (red/green, red/blue, red/yellow, green/blue, green/yellow, blue/yellow) was assigned to three participants. The other two colours (cyan and pink) served as nontarget colours only. Participants' task was to report the orientation (vertical/horizontal) of the target colour bar in each trial by pressing the up/down arrow keys on a standard keyboard. Critically, the response-relevant target colour switched after every second trial (e.g., red in trials 1 and 2, green in trials 3 and 4, red in trials 5 and 6, etc.). Since search displays always contained both target colours participants had to keep track of the target colour sequence. There were no cues indicating the upcoming target colours during a block, but participants received a reminder about the target colour sequence and the first relevant target colour in the first trial of the new block in the block breaks. The target colour sequence (e.g., red/green or green/red) was randomised between participants but remained the same for each participant during the whole experiment. The locations of the two target colour bars were determined randomly and independently of each other in each trial. The response-to-key mapping (vertical/horizontal response on arrow up/down key) and the hand-to-key mapping (left/right hand on arrow up/down key) was counterbalanced across participants but was kept constant for each participant for the duration of the whole experiment.

Probe displays that were presented prior to search (probes 1-7) or together with search (probe S) contained six items composed of four closely aligned dots, two on the vertical, and two on the horizontal axis (0.1°×0.1° for each dot, 0.25°×0.25° for each four-dot probe item). The probe items were also presented at the 1, 3, 5, 7, 9, and 11 o'clock positions of an imaginary circular clock face, but closer to fixation (at an eccentricity of 0.5°) than the search bars. One of the probe items was a colour singleton that randomly matched one of the two possible target colours among five uniformly grey probe items. These grey probes were always equal in luminance to the colour singleton probe (~11.9cd/m^2). Probe singletons that matched the colour of the upcoming search target were *relevant target colour probes*, and probes that did not match this colour but instead the other possible target colour that was relevant before the last colour switch were *irrelevant target colour probes*. The probe singleton locations were selected randomly and independently in each probe display, with the following two restrictions: Successive singleton probes were equally likely to appear on same or opposite display sides, but immediate repetitions of the exact probe location (on the imaginary clock face) were not allowed. As a result, each probe display was equally likely to be preceded and followed by probe displays that contained a colour singleton on the same or the opposite side. This was done to ensure that lateralised responses to any particular probe singleton would remain unaffected by any lateralised response triggered by singletons in temporally adjacent probe displays. Participants were informed that probe displays were task-irrelevant and should be ignored.

Experiment 1 contained 70 blocks of twelve trials each. Blocks were short to minimize the presence of blinks within each block. In each block, the twelfth search display was followed by seven additional probe displays to keep stimulus conditions during the post-target response interval identical across all trials in a block. Each block thus contained twelve search displays and 91 probe displays (13 for each of the seven probes). The first trial in each block was excluded from all analyses, because it could not be classified as a target colour repetition or switch trial. Each block therefore included six repetition and five switch trials. Before the experiment proper, participants practised the task until they felt comfortable with it (usually after two to four blocks). These data were not recorded.

2.2.1.3 EEG recording and data analyses

EEG was DC-recorded from 25 scalp sites (standard positions of the extended 10/20 system), sampled at 500Hz, and digitally low-pass filtered at 40Hz (no other filters were applied after data acquisition). Impedances were kept below 5kΩ. The left earlobe served as online reference during data acquisition, but all channels were re-referenced offline to linked earlobes. The EEG was segmented into 500ms time windows including a 100ms pre-stimulus baseline and a 400ms ERP time window following the onset of a particular stimulus display (probes 1 to 7, search display). Data from the first and last seven probe displays in each block, and from trials with anticipatory (<200ms), very slow (>1500ms), missing or incorrect responses were excluded from analysis. So were segments that contained eye movements (±30µV in the bipolar HEOG channel), blinks (±60µV at Fpz), and muscular movements (±80µV in all channels). Artefact rejection resulted in an exclusion of 8.4% of all segments (SD=6.6%; ranging between 2.1% and 25.6% across participants). The remaining segments were averaged separately for each probe display (probes 1-7) in which the probes were in the left versus right hemifield. Separate averages were computed for relevant and irrelevant target colour probes in target colour repetition versus switch trials. In addition, averages were also computed for search displays with a target in the left or right hemifield.

N2pc components to probes were quantified based on ERP mean amplitudes obtained at lateral posterior electrodes PO7 and PO8, contralateral and ipsilateral to the side of a probe, within an 80ms time window starting at 190ms after the respective probe display onset. As in our previous work using analogous rapid serial probe presentation procedures (Grubert & Eimer, 2018), the start of this time window was determined by measuring the point in time (rounded to the nearest 10) when the ascending flank of the averaged probe N2pc (pooled across all relevant target colour probes in Experiment 1) reached 50% of the peak amplitude (at -0.10µV). N2pc components to target bars in the search displays were computed within the same 190-270ms post-stimulus time window for consistency. Target N2pc onset latencies were substantiated by means of jackknife-based procedures (Miller et al., 1998). Eighteen grand-average difference waves (contralateral minus ipsilateral ERPs at PO7/8) were computed separately for targets in colour repetition versus switch trials, each excluding one different participant from the original sample. N2pc onset latencies were defined as the point in time when each subsample difference wave reached an absolute onset criterion of -0.8µV (50% of the peak amplitude of the pooled target N2pc in Experiment 1; see Grubert & Eimer, 2018, 2020, 2023, for identical procedures). All *t*-tests on jack-knifed N2pc onset latencies were power-corrected as suggested by Miller et al., (1998) and are denoted with t_c. Generally, all *t*-tests reported are two-tailed and Bonferroni and Greenhouse-Geisser corrected were necessary. Effect sizes are reported in terms of Cohen's *d* (Cohen, 1988), with a confidence interval of 95%, for *t*-tests, and partial eta squared (η_p^2) for *F*-tests and power corrected t_c-tests.

2.2.2 Results

2.2.2.1 Behavioural results

Trials with anticipatory (<200ms) or exceedingly slow (>1500ms) reaction times (RTs) were excluded from analysis (0.7% of all trials). Typical target colour switch costs were observed both in RTs and error rates (see Figure 3, top panel). Mean RTs were 54ms faster in target colour repetition (629ms) as compared to switch trials (683ms), $t(17)=5.8, p<.001, d=.67$, and error rates were 4.4% lower (6.5% vs 10.8%), respectively, $t(17)=6.1, p<.001, d=.95$.

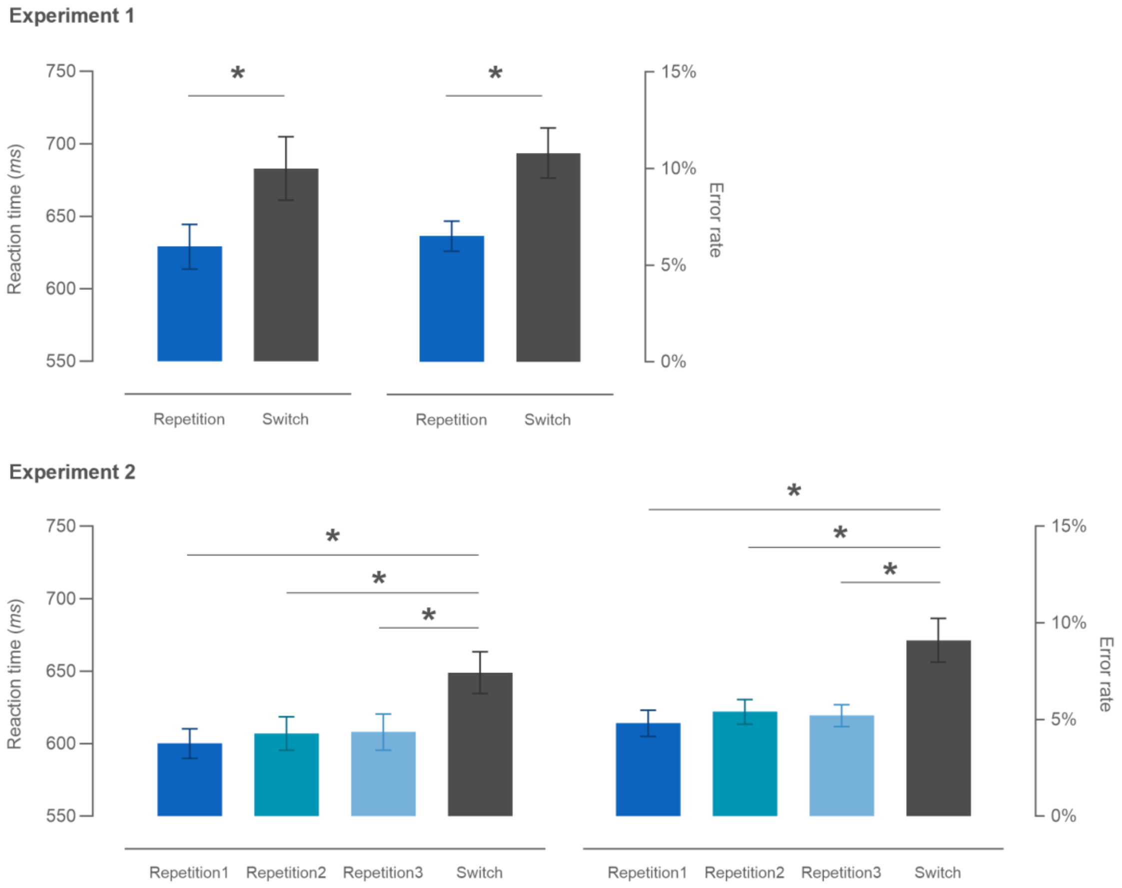

Figure 3 Reaction times (measured in milliseconds; left axes) and error rates (percentage of all trials; right axes) measured in colour repetition versus switch trials of Experiment 1 (top panel) and 1st, 2nd, and 3rd colour repetition trials versus switch trials in Experiment 2 (bottom panel). Statistically reliable differences are marked by asterisks.

2.2.2.2 N2pc components for probe displays

To measure the time course of template activation prior to search, N2pcs elicited by probes that matched the relevant (upcoming) or the irrelevant (previous) target colour were extracted by computing ERPs at posterior sites PO7/8, contralateral and ipsilateral to the side of a probe, separately for each of the seven successive probes in a trial (probes 1-7) in target colour repetition versus switch trials. For illustration, these ERPs are shown in Figure 4 for relevant target colour probes 1-7 in colour repetition trials. ERPs for all other types of probes are included in the Supplementary Materials. The time course of the successive probe N2pcs is easier to see in Figures 5 and 6 which show probe N2pc difference waves (obtained by subtracting ipsi- from contralateral ERPs at PO7/8) in a temporally continuous fashion, separately for relevant (Figure 5) and irrelevant (Figure 6) target colour probes in colour repetition (top panels) and switch trials (bottom panels), respectively. Note that N2pc components were extracted individually for each probe (probes 1-7) and that Figures 5 and 6 were compiled to show these probe N2pcs in a successive fashion for illustration purposes only. Each figure starts with the activity triggered in response to probe 1 (100ms prior to 350ms after onset of probe 1) which was the first probe presented directly after a previous search display. For the subsequent probes (probes 2-7), 200ms intervals (150ms to 350ms after onset of each respective probe) are shown sequentially with interpolated data points between adjacent intervals. The onset of each probe is marked with a vertical line, and the N2pc time window for each probe (190-270ms post-stimulus) is shaded in grey. As probes were presented every 200ms, each individual probe was therefore presented within the N2pc time interval of its immediately preceding probe.

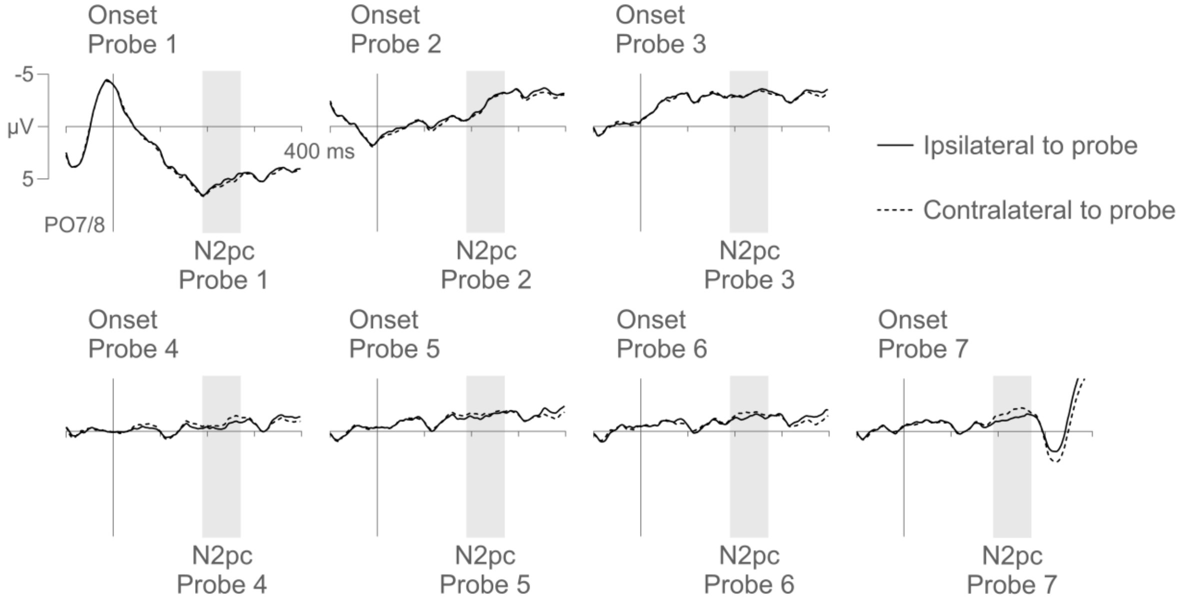

Figure 4 Grand-averaged ERPs elicited by relevant target colour probes in colour repetition trials of Experiment 1 at electrodes PO7/8 contralateral and ipsilateral to colour singleton probes in each of the seven probe displays presented between consecutive search displays. Probe 1 is the first probe to follow the previous search display

and probe 7 is the probe to immediately precede the next search display. Shaded areas mark N2pc time windows (190-270ms after onset of each individual probe).

In line with our previous RSPP findings (Grubert & Eimer, 2018; 2020; 2023), Figure 5 (top panel) shows that relevant target colour probes triggered N2pc components at intermediate and late stages during the search preparation period. These N2pcs were largest for probe 7, just before the next search display. Probes that were presented earlier in the trial did not trigger any N2pcs. Importantly, this pattern looked fundamentally different when relevant target colour probes were presented in colour switch trials (Figure 5, bottom panel). Here, only probe 7, which immediately preceded the search display, triggered an N2pc, whereas no clear N2pc was present for any of the preceding probes. Furthermore, irrelevant target colour probes (Figure 6) never triggered any N2pcs, neither in colour repetition (top panel) nor switch trials (bottom panel).

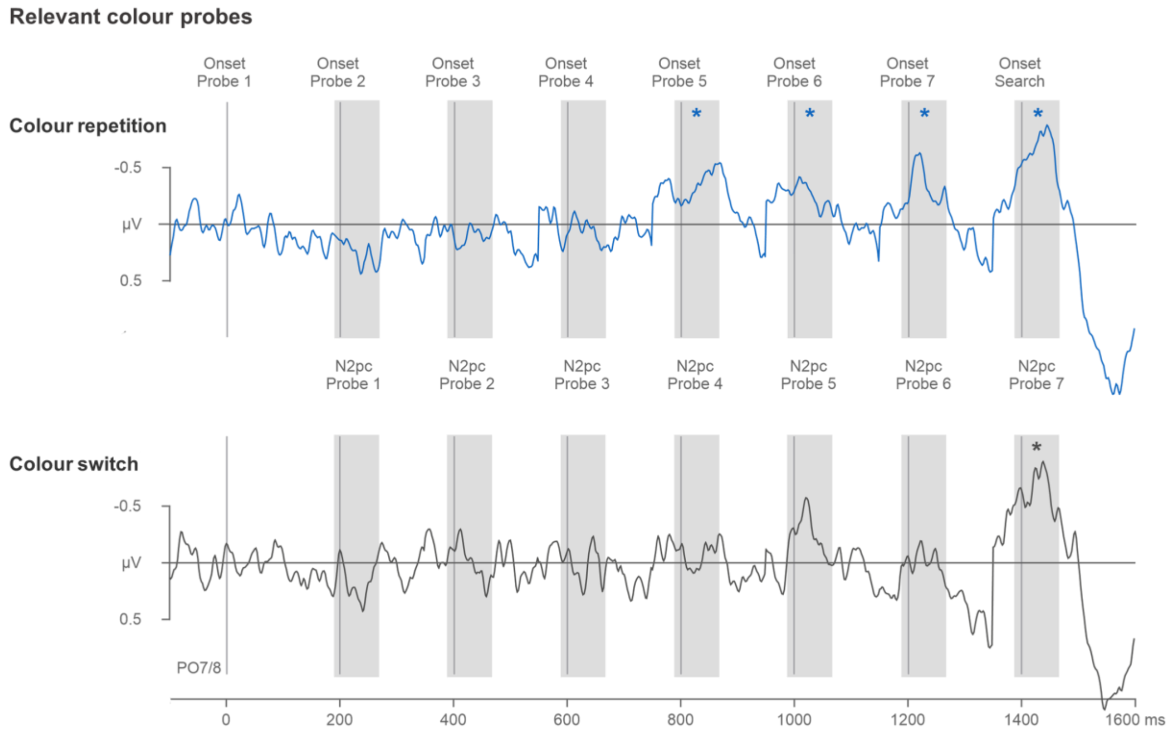

Figure 5 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for relevant target colour probes in colour repetition (top panel) and switch trials (bottom panels) of Experiment 1.

Difference waves for the seven probes presented between search displays (probes 1-7) are shown in a temporally continuous fashion in 200ms segments (150-350ms) after onset of each probe. N2pc components were extracted individually for each probe, the successive presentation of the probe N2pcs is for illustration purposes only. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe). Note that the onset of each probe coincides within the N2pc window for the preceding probe. Statistically reliable probe N2pcs are marked by asterisks.

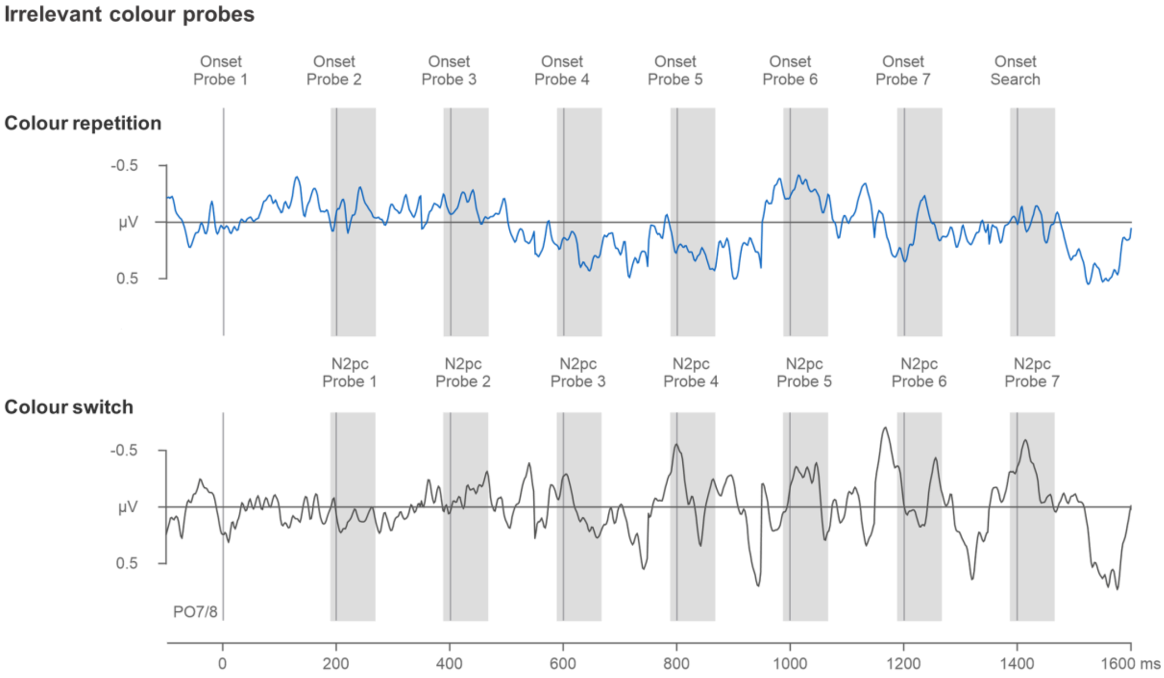

Figure 6 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for irrelevant target colour probes in colour repetition (top panel) and switch trials (bottom panels) of Experiment 1. Difference waves triggered by individual probes are shown in the same continuous fashion as in Figure 5. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe). None of these probes triggered reliable N2pcs.

Statistical analyses confirmed these informal observations. ERP mean amplitudes measured at PO7/8 in the 190-270ms post probe time windows were fed into a repeated-measures omnibus ANOVA with the factors Trial Type (colour repetition versus switch), Probe Colour (relevant versus irrelevant target colour probe), Probe Number (Probe 1, 2, 3, 4, 5, 6, 7), and Laterality (electrode contralateral versus ipsilateral to the hemifield of a probe). The main effect of Laterality just failed to reach significance, $F(1,17)=3.6$, $p=.076$, $\eta_p^2=.17$, but there was interaction between Laterality and Probe Number, $F(6,102)=7.0$, $p<.001$, $\eta_p^2=.29$, confirming that N2pc amplitudes differed between probes at different temporal positions. Laterality did interact with Trial Type and Probe Colour, $F(1,17)=5.0, p=.039, \eta_p^2=.23$, and there was also a significant four-way interaction, $F(7,98)=2.3, p=.034, \eta_p^2=.14$. This suggests that the temporal pattern of probe N2pcs differed between relevant and irrelevant target colour probes, and that this was further modulated by whether these probes were presented in colour repetition or switch trials.

To assess differences between colour repetition and switch trials more directly, two follow-up ANOVAs were conducted separately for relevant and irrelevant target colour probes, with the factors Trial Type (colour repetition versus switch), Probe Number (Probe 1-7), and Laterality (contralateral versus ipsilateral activity). For relevant target colour probes, there was a main effect of Laterality, $F(1,17)=5.2, p=.036, \eta_p^2=.23$, and an interaction between Laterality and Probe Number, $F(6,102)=10.6, p<.001, \eta_p^2=.40$, confirming that probe N2pc amplitudes differed across the preparation period. Importantly, there was also a significant three-way interaction, $F(6,102)=2.3, p=.043, \eta_p^2=.12$, indicating that the temporal pattern of probe N2pcs differed between target colour repetition versus switch trials. This was confirmed by follow-up ANOVAs comparing ipsi-and contralateral activity in colour repetition versus switch trials separately for each individual probe location. For probes 1, 2, and 3, there was no reliable contralateral negativity, all $F(1,17)<1, p>.452, \eta_p^2<.03$, and no interactions involving the factor Laterality, all $F(1,17)<1.1, p>.327, \eta_p^2<.06$, confirming that these early relevant target colour probes did not trigger N2pcs, regardless of whether they were presented in colour repetition or swich trials. In contrast, Laterality did interact with Trial Type for relevant target colour probes 4, 5, and 6, all $F(1,17)>5.2, p<.037, \eta_p^2>.23$. These probes produced reliable N2pc components only in colour repetition trials (-0.34µV, -0.25µV, and -0.33µV, respectively), all $t(17)>2.5, p<.021, d>.27$, but not in colour switch trials, all $t(17)<1, p>.471, d<.01$. Finally, for probe 7, there was a main effect of Laterality, $F(1,17)=20.4, p<.001, \eta_p^2>.55$, but no interaction with Trial Type, $F(1,17)<1, p=.969$,

$\eta_p{}^2<.01$. These probes triggered reliable N2pc components, both $t(17)>4.2$, $p=.001$, $d>.58$, which were virtually identical in size (-0.63µV), $t(17)<1$, $p>.969$, $d<.01$, irrespective of whether they were presented in colour repetition or switch trials.

The ANOVA for irrelevant target colour probes did not produce any reliable main effects or interactions involving the factor Laterality, all $F(1,17)<2.0$, $p>.084$, $\eta_p{}^2<.10$, confirming that none of these probes triggered an N2pc, regardless of whether they were presented in colour repetition or switch trials.

2.2.2.3 N2pc components in the search displays

N2pcs elicited by search targets in colour repetition versus switch trials were measured at PO7/8 in the 190-270ms time window after search display onset. These ERPs, together with the respective N2pc difference waves, are shown in Figure 7 (top panel). A repeated-measures ANOVA with the factors Trial Type (colour repetition versus switch) and Laterality (contralateral versus ipsilateral activity) revealed a main effect of Laterality, $F(1,17)=41.4$, $p<.001$, $\eta_p{}^2=.71$, and a significant interaction, $F(1,17)=12.9$, $p=.002$, $\eta_p{}^2=.43$, demonstrating that reliable target N2pcs were triggered both in repeat and switch trials, both $t(17)>4.6$, $p<.001$, $d>.24$, but that N2pc amplitudes were larger in colour repetition trials (-1.2µV versus -0.8µV, respectively). Matching the behavioural RT pattern, the N2pc also emerged earlier in colour repetition as compared to colour switch trials (204ms versus 231ms), $t_c(17)=2.9$, $p=.012$, $\eta_p{}^2=.42$[3].

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[3] *The same jack-knifed onset latency analysis was also conducted with a relative onset criterion (50% of each subsample's peak amplitude, as recommended by Kiesel et al., 2008). Results were identical: Target N2pcs were faster in colour repetition (206ms) than switch trials (228ms), $t_c(17)=2.3$, $p=.040$, $\eta_p{}^2=.31$.*

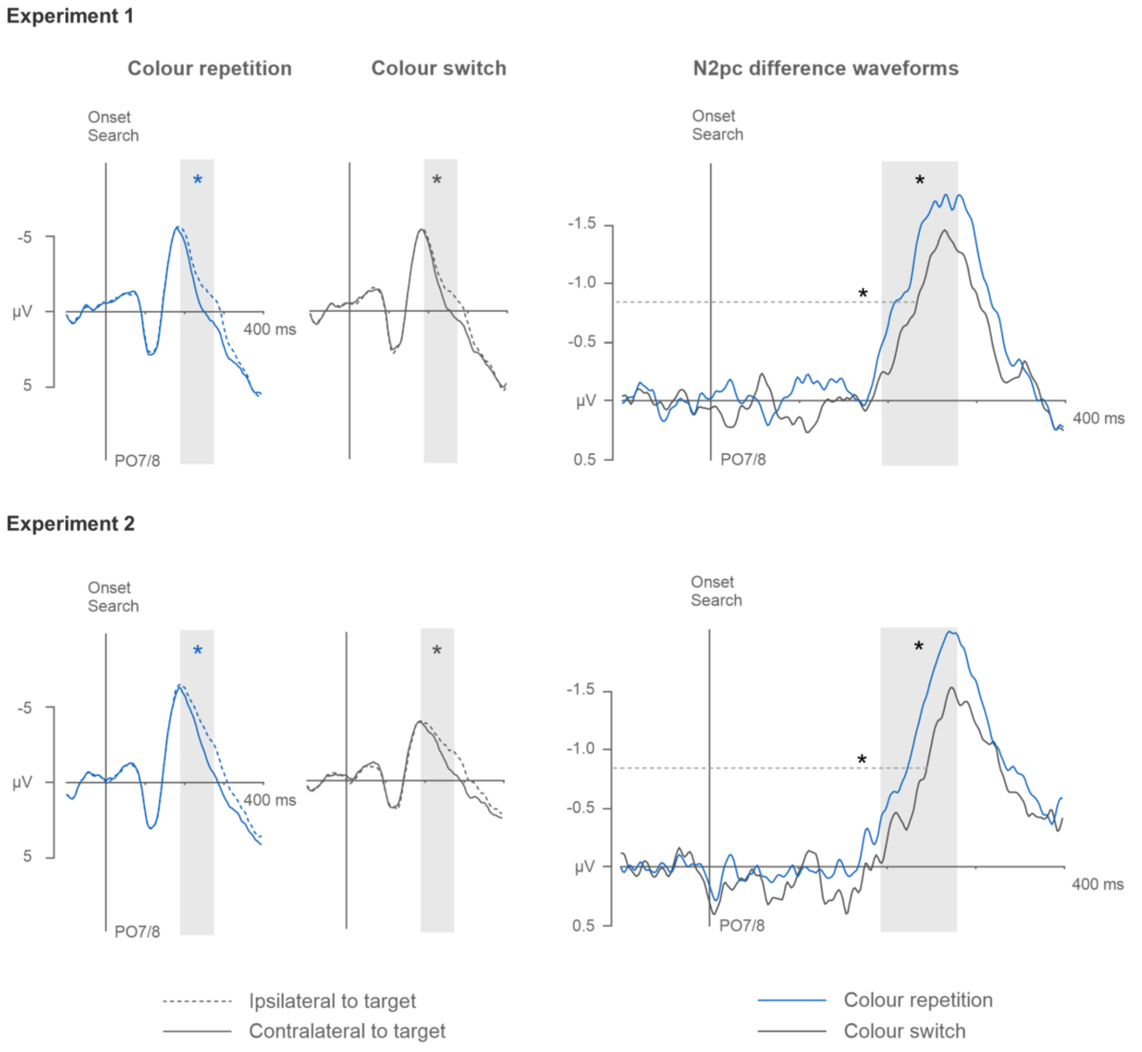

Figure 7 Grand-averaged ERPs elicited in the search displays in colour repetition and switch trials of Experiment 1 (top panel) and Experiment 2 (bottom panel) at electrodes PO7/8 contralateral and ipsilateral to the response-relevant target (left panels), together with the corresponding contralateral-ipsilateral N2pc difference waveforms (right panel). In Experiment 2, to equate the signal-to-noise ratio between the two trial types, only 1st colour repetition trials were included in the target N2pc analyses. Shaded areas indicate N2pc time windows (190-270ms after search display onset). Asterisks in the ipsi/contralateral panels (left) indicate significant N2pcs. Asterisks in the difference wave panels (right) represent significant differences in mean amplitudes and onset latencies (measured at -0.8µV, as indicated by the dashed horizontal lines).

2.2.3 Discussion of Experiment 1

As expected, search performance was impaired on target switch as compared to target repeat trials, with slower RTs and higher error rates. The presence of such target switch costs is analogous to the costs observed for predictable changes of stimulus-response mappings (e.g., Rogers & Monsell, 1995). They also mirror the target switch costs observed in previous visual search tasks (e.g., Grubert & Eimer, 2013; Olivers & Meeter, 2006), and demonstrate that such costs occur even when a change of target identity is fully predictable. Notably, these behavioural costs were accompanied by corresponding modulations of N2pc components triggered by search targets on switch versus repeat trials. These N2pcs were smaller and emerged significantly later on switch trials, indicating that the allocation of attention to target objects was slower and less efficient on these trials.

The critical new finding of Experiment 1 concerned the temporal pattern of probe N2pc components observed prior to switch or repeat trials, which revealed clear switch-induced costs for the preparatory activation of target colour templates. On target repeat trials, this template was active from about 800ms prior to search display onset, as reflected by the presence of reliable N2pc components to singleton probes that matched this target colour from probe 4 onwards. On target switch trials, the activation of the template for the new target colour was considerably delayed. Here, a reliable N2pc was only present for the target colour probe that immediately preceded the search display, but not for any earlier probe. This difference suggests that the need to change a colour-specific target template across successive trials delays the point in time at which this template is activated during search preparation.

This delay could in principle be caused by task-set inertia on switch trials, as the continued persistence of the previously relevant target template may interfere with the activation of a new template. However, the N2pc results of Experiment 1 provide no evidence for this hypothesis. Any continued activation of the target template for the currently irrelevant target colour should have been reflected by reliable N2pc components triggered by the corresponding colour singleton probe during the preparation period, in particular on switch trials. However, N2pcs for irrelevant target colour probes were entirely absent, not only on repeat but also on switch trials. Thus, there was no evidence that any task-set inertia across successive trials might have contributed to the observed switch costs.

The absence of any N2pcs for irrelevant target colour probes may seem surprising, given that our previous experiment which employed an ABAB design (Grubert & Eimer, 2020) observed clear N2pcs for probes that matched either the preceding or the upcoming target colour, indicating that both colour templates (including the template that was not relevant for the next search episode) were activated in parallel. Given this apparent discrepancy (which will be further considered in the General Discussion), it is important that the results of Experiment 1 are replicated before any firm conclusions about the factors responsible for search target switch costs can be drawn.

One goal of Experiment 2 was to provide such a replication. The other goal was to investigate the impact of the number of task repetitions on the activation of target templates and the possible emergence of task-set inertia. The task setup and experimental logic were the same as in Experiment 1, except that the length of each alternating run with the same search target colour was increased from two to four (i.e., AAAABBBB). As noted before, Monsell et al. (2003) employed an analogous manipulation and found behavioural switch costs only for the first trial after a switch, suggesting that task sets are fully established after a new task has been performed once. In Experiment 2, we investigated whether this also applies to switches between templates for target features.

To confirm the main results of Experiment 1, we first compared N2pc components triggered by relevant target colour probes on switch trials and on first colour repetition trials that immediately followed the target colour switch. The central question was whether the delay of preparatory target template activation on switch trials (as reflected by the later emergence of probe N2pcs) found in Experiment 1 would also be observed in Experiment 2.

The four-trial alternating runs procedure in Experiment 2 made it possible to investigate whether task-set inertia in target template activation might emerge when the previous template remained continuously relevant across multiple trials. If this was the case, evidence for inertia (i.e., reliable probe N2pcs for irrelevant target colour probes) might be observed for target switch trials in Experiment 2, as these trials where always preceded by four (as compared to two) trials where this colour was relevant. Furthermore, increasing the number of target colour repetitions might also differentially affect the activation of target colour templates across successive repeat trials. To test this, we compared the temporal pattern of target colour probe N2pcs elicited prior to the first, second, and third colour repetition of a particular search target.

2.3 Experiment 2

2.3.1 Methods

2.3.1.1 Participants

Nineteen new participants were paid to participate in Experiment 2. All participant procedures were identical to Experiment 1. One participant was excluded due to excessive eye movement activity (>40% trials lost during artefact rejection). The remaining 18 participants were between 18 and 47 years of age (mean=27.5, SD=7.5). Fourteen participants were female and four were male. One participant was left-handed, the remaining 17 participants were right-handed. All participants had normal or corrected-to-normal vision and normal colour vision (as tested with Ishihara, 1972).

2.3.1.2 Stimuli and procedures

All experimental procedures were identical to Experiment 1 with the following exceptions: Each block now contained 16 trials and the response-relevant target colour switched after every fourth trial (e.g., red in trials 1-4, green in trials 5-8, red in trials 8-12, green in trials 13-16). Search displays contained both the relevant and irrelevant target colour bar together with four differently coloured nontarget bars of the colour set, as described in Experiment 1. As in Experiment 1, probes 1-7 and probes S were randomly shown in either of the two target colours and were either relevant target colour probes (that matched the upcoming target colour) or irrelevant target colour probes (that matched the previous target colour that was relevant before the last colour switch). Experiment 2 contained 64 blocks of 16 trials each. The sixteenth search display was followed by seven additional probe displays for constant response conditions, so that each block contained 16 search displays and 135 probe displays (17 for probes 1 to 7, and 16 for probe S).

2.3.1.3 EEG recording and data analyses

All EEG procedures were identical to Experiment 1. During artefact rejection, 3.3% of all segments were excluded from analysis in Experiment 2 (SD=2.3%; ranging between 0.9% and 9.4% across participants). Averaged ERP waveforms were computed for probes 1-7 in the left or right hemifield, separately for relevant and irrelevant target colour probes. Separate averages were computed for colour switch trials (i.e., the first trial with a new target colour after four successive trials with the other target colour), and for the 1st, 2nd, and 3rd colour repetition trial before a target colour switch. Apart from allowing the assessment of possible effects of successive target colour repetitions on target template activation, this also kept the signal-to-noise ratio equivalent across all types of trials. All data analysis procedures were identical to Experiment 1. In addition, Bayesian statistics (Rouder et al., 2009) were used in JASP to evaluate empirical evidence in favour of the null hypothesis. Substantial evidence for the null hypothesis is marked by Bayes factors (BF_{01}) > 3 (Jeffreys, 1961), indicating that the empirical data are more than three times more likely under the null hypothesis as compared to the alternative hypothesis.

2.3.2 Results

2.3.2.1 Behavioural results

After exclusion of all trials with anticipatory or slow responses (0.6% of all trials), RTs in correct trials and error rates were subjected to two repeated measures ANOVAs with the factor trial type (1st colour repetition, 2nd colour repetition, 3rd colour repetition, versus colour switch). Both ANOVAs revealed main effects, both $F(3,51)>14.8$, $p<.001$, $\eta_p^2>.46$, indicating that RTs and error rates differed between these four types of trials. As can be seen in Figure 3 (bottom panel), RTs were slower and errors more frequent in colour switch trials (RT: 649ms; error rate: 9.1%) relative to trials where the target colour was repeated for the first, second or third time (RTs: 600ms, 607ms, and 608ms; error rates: 4.8%, 5.4%, and 5.2%). Follow-up t-tests confirmed that the corresponding RT and error rate differences were significant, all $t(17)>4.0$, $p<.007$, $d=.95$. In contrast, there were no further benefits for performance when the same target colour was repeated for the second or third time. RTs and error rates were numerically even higher for these trials relative to 1st colour repetition trials, but these differences were not reliable, all $t(17)<2.2$, $p>.222$, $d<.15$.

2.3.2.2 N2pc components for probe displays

Figure 8 shows probe N2pc difference waves (obtained by subtracting ipsi- from contralateral ERPs at PO7/8) in the same temporally continuous fashion as in Figures 5 and 6. The top and middle panel show N2pcs in response to relevant target colour probes in 1st target colour repetition and switch trials, respectively. The temporal pattern of probe N2pcs in these two types of trials was identical to the results observed in Experiment 1, with clear N2pcs emerging from probe 4 onwards on repetition trials, but only for probe 7 on switch trials. For relevant target colour probes 1-3, there was no main effect or interactions involving the factor Laterality, all $F(1,17)<1$, $p>.361$, $\eta_p^2<.05$, demonstrating that these early probes did not trigger any N2pcs. An ANOVA conducted for probes 4-6 produced a main effect of Laterality, $F(1,17)=7.2$, $p=.016$, $\eta_p^2=.30$, but importantly, also a significant interaction between Trial Type and Laterality, $F(1,17)=6.1$, $p=.024$, $\eta_p^2=.27$. Follow-up comparisons confirmed that relevant target colour probes 4, 5, and 6 produced reliable N2pcs in 1st colour repetition trials (-0.3μV, -0.3μV, and -0.5μV, respectively), all $t(17)>2.2$, $p<.041$, $d>.10$, but not in colour switch trials, all *t*(17)<1, *p*>.418, *d*<.01. In contrast, and as in Experiment 1, relevant target colour probes 7 triggered reliable N2pcs both in colour repetition (-0.6µV) and switch trials (-0.5µV), both *t*(17)>2.7, *p*>.014, *d*>.32, which did not differ from each other, *t*(17)<1, *p*>.375, *d*<.01.

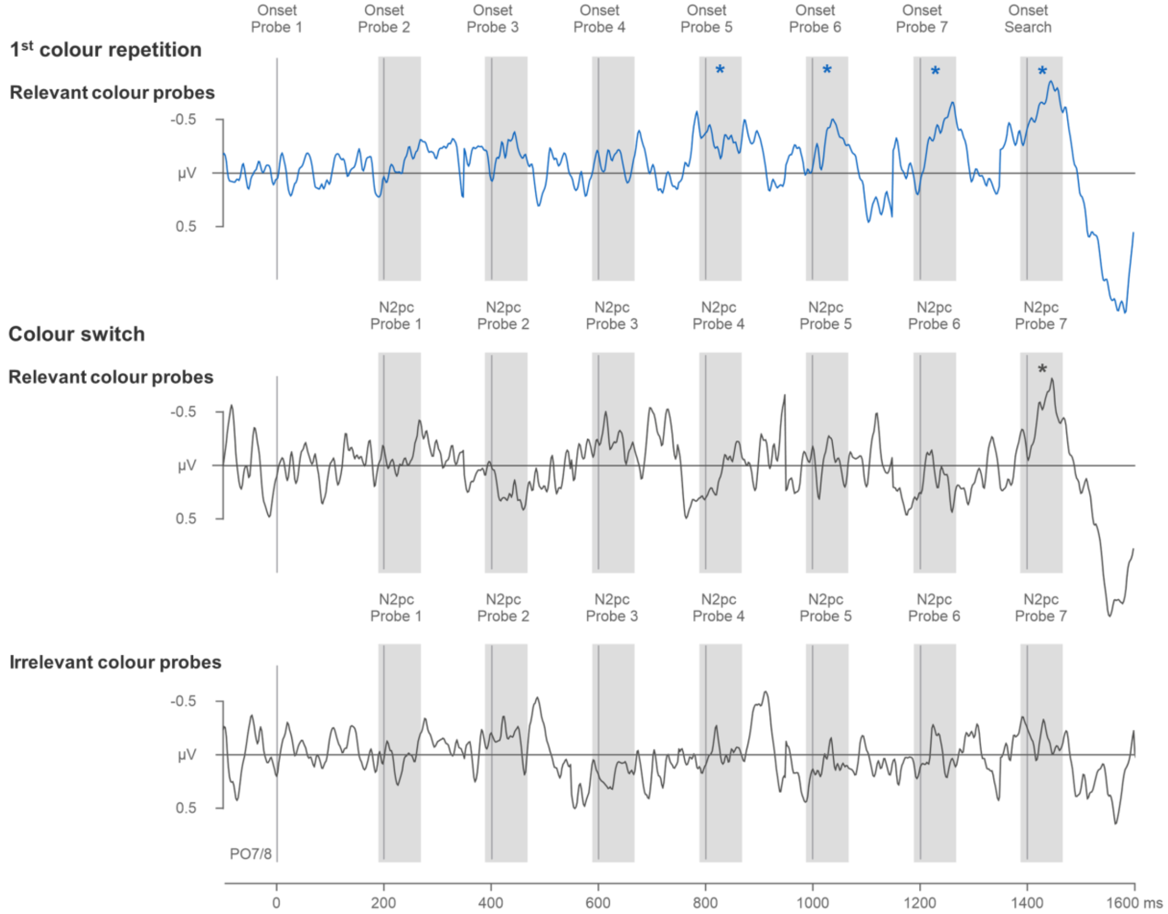

Figure 8 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for relevant target colour probes in 1st colour repetition trials (top panel) and in switch trials (middle panel), and for irrelevant target colour probes in switch trials (bottom panel) of Experiment 2. Difference waves triggered by individual probes are shown in the same continuous fashion as in Figure 5 and 6. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe). Statistically reliable probe N2pcs are marked by asterisks.

To assess the existence of target template inertia effects on switch trials after the same colour template had been involved in search preparation and target selection in four successive trials, we analysed N2pcs to irrelevant target colour probes on these trials (as shown in Figure 8, bottom panel). A repeated-measures ANOVA with the factors Probe Number (1-7) and Laterality, did not produce a main effect of Laterality, $F(1,17)<1$, $p=.944$, $\eta_p^2<.01$, and also no interaction involving the factor Laterality, $F(6,102)<1$, $p=.746$, $\eta_p^2=.03$. In other words, there was no evidence for any residual activation of the corresponding colour template, even though this template had been activated in the four preceding trials[4]. Further support for the null hypothesis was provided by the corresponding Bayes factors for both the main effect, $BF_{01}=4.9$, and interaction, $BF_{01}=20.0$.

Finally, we also analysed possible effects of successive target colour repetitions on the activation of the corresponding relevant colour template. ERPs in response to relevant target colour probes in 1st, 2nd, and 3rd colour repetition trials were analysed in a repeated-measures ANOVA with the factors Trial Type (1st, 2nd, 3rd colour repetition), Probe Number (probe 1-7), and Laterality. Both the main effect of Laterality, $F(1,17)=5.4$, $p=.033$, $\eta_p^2=.24$, and the interaction between Probe Number and Laterality reached significance, $F(6,102)=4.3$, $p=.001$, $\eta_p^2=.20$, reflecting the absence of N2pcs for early probes (see above). However, and importantly, Trial Type did not interact with Probe Number and Laterality, $F(1,17)<1$, $p=.965$, $\eta_p^2=.02$, $BF_{01}=172.2$, demonstrating that successive repetitions of the same target colour did not affect the temporal pattern probe N2pcs during search preparation. The continuous N2pc difference waves in response to relevant target colour probes on 2nd and 3rd colour repetition trials are included in the Supplementary Materials.

2.3.2.3 N2pc components in the search displays

Target N2pcs in colour repetition versus switch trials are shown in Figure 7 (bottom panel). To equate the signal-to-noise ratio between the two trial types, only 1st colour

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[4] *As would be expected, there were also no N2pcs for irrelevant target colour probes on 1st, 2nd, and 3rd target colour repetition trials, i.e., no increased contralaterality at PO7/8 and no interactions involving the factor laterality, all $F<1$, $p>.336$, $\eta_p^2<.06$. The corresponding continuous probe N2pc difference waveforms for these trials are included in the Supplementary Materials, for completeness.*

repetition trials were included in the target N2pc analyses. A repeated-measures ANOVA with the factors Trial Type (1st colour repetition versus switch) and Laterality (contralateral versus ipsilateral activity) revealed a main effect of Laterality, $F(1,17)=32.93$, $p<.001$, $\eta_p^2=.66$, and a significant interaction, $F(1,17)=12.2$, $p=.003$, $\eta_p^2=.42$. Substantial N2pcs were triggered both in colour repetition and switch trials, both $t(17)>4.1$, $p<.002$, $d>.33$, but N2pcs triggered in colour repetition than switch trials were larger (-1.1µV versus -0.6µV, respectively). N2pcs in colour repetition as compared to switch trials were also triggered earlier (218ms versus 245ms), $t_c(17)=4.1$, $p=.001$, $\eta_p^2=.59$[5].

2.3.3 Discussion of Experiment 2

The results of Experiment 2 were clear-cut. First, and most importantly, the pattern of probe N2pc components observed on target colour switch and repetition trials fully confirmed the results of Experiment 1. Again, probe N2pcs were reliably present on switch trials only for the probe display that immediately preceded the search display. In contrast, they emerged from probe 4 onwards on the first repeat trial following a target switch. Behaviourally, there were again clear behavioural performance costs on target switch relative to target repeat trials, and these costs were again mirrored by smaller and delayed target N2pc components on switch trials. Notably, there were no further performance improvements for the second and third repetition of a given target colour relative to its first repetition. This is in line with the results found by Monsell et al. (2003) for successive repetitions of S-R mappings, and suggests that analogous to such mappings, target templates are also fully activated after they have been used once to guide target selection. Further support for this conclusion comes from the comparison of probe N2pcs on successive target colour repetition trials in Experiment 2,

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[5] *The same latency analysis with a relative 50% onset criterion also revealed faster target N2pcs in colour repetition (228ms) than switch trials (242ms), $t_c(17)=2.4$, $p=.028$, $\eta_p^2=.34$."*

which found no difference in preparatory template activation prior to the first, second, and third repetition of a particular target.

Finally, Experiment 2 obtained no evidence for any task-set inertia effects for target template activation processes on switch trials. Even though the previous target colour had been relevant on four successive trials, there was no indication that the corresponding colour template was partially activated on switch trials. Analogous to Experiment 1, there were no N2pc components in response to irrelevant target colour probes at any point during the preparation period, indicating that these probes failed to attract attention throughout this interval.

2.4 General Discussion

The goal of the present study was to provide new insights into the mechanisms involved in switching target templates in visual search. In tasks where observers search for one of several possible target objects, performance may be impaired on trials where the identity of the target changes relative to target repeat trials, even when the identity of the next target is fully predictable. Such search target switch costs might be similar to the behavioural task switch costs observed in many previous experiments (e.g., Monsell, 2003), in that they are produced, at least in part, by processes that operate during the preparation for an upcoming task. Preparatory target template activation processes might differ between target switch and target repeat trials, and this could result in performance costs, analogous to the task-set reconfiguration mechanisms investigated in previous research on task switching (e.g., Rogers & Monsell, 1995).

To compare and contrast preparatory target template activation processes on target switch and repeat trials, we employed the alternating runs procedure introduced by Rogers and Monsell (1995). Participants searched for targets that were defined by one of two possible colours, which changed predictably on every second trial (Experiment 1) or every fourth trial (Experiment 2). To track target template activation in real time, N2pc components were recorded in response to brief probe displays which appeared in rapid succession between search displays, and contained a colour singleton item that either matched the upcoming target colour or the other currently irrelevant colour.

Similar to our previous studies that employed analogous RSPP procedures (Grubert & Eimer, 2018; 2020; 2023), probes that matched the fully predictable upcoming target colour triggered N2pc components when they appeared during the 800ms interval prior to the arrival of the next search display. This temporal pattern was observed prior to target colour repetition trials. It demonstrates that these probes attracted attention, and that a corresponding colour-specific target template was active at the moment when they were presented. This is in line with previous experiments where observers always searched for a single colour-defined target (e.g., Grubert & Eimer, 2018) and shows that target templates are activated in a transient fashion during the preparation for each new search episode. The critical new finding of the present study was that the emergence of probe N2pc components was strongly delayed prior to target colour switch trials. Here, an N2pc was only observed for the final probe display that appeared 200ms prior to search display onset, but not in response to any of the preceding probes. This temporal dissociation in the pattern of probe N2pcs between target colour switch and repetition trials was observed in Experiment 1, and was replicated in Experiment 2, where the length of alternating runs was increased from two to four trials.

The marked difference in the temporal pattern of target colour probe N2pcs elicited prior to the onset of the next search display on target colour switch versus repetition trials strongly suggests that target templates are activated at a later point in time during the preparation for a target switch trial relative to a target repeat trial. The delayed emergence of target colour probe N2pcs on colour switch trials might reflect the time demands of target template reconfiguration processes, analogous to the task-set reconfiguration processes studied by Rogers and Monsell (1995). There were also clear behavioural target switch costs in both experiments, for RTs as well as error rates (see also Grubert & Eimer, 2013; Olivers & Meeter, 2006, for similar observations), in spite of the fact that the identity of the next target was fully predictable on all trials, and sufficient time was available between search displays to activate a corresponding target colour template. The delay of N2pc components to target colour probes on switch as compared to repetition trials observed in both experiments (about 600ms) was considerably larger than the switch costs for RTs (about 50ms) and target N2pc onset latencies (25-30ms). This delay was also larger than the template switch times estimated by Dombrowe et al. (2011) in an eye tracking study on the basis of saccade accuracy and latency on target colour switch versus repetition trials (about 250ms). These differences suggest that task switching has substantially stronger effects on the time course of preparatory search template activation than on the timing of subsequent attentional guidance and target selection processes.

In spite of differences in their magnitude, it is plausible to assume that behavioural target colour switch costs are at least in part the result of temporal template switch costs (i.e., delayed activation of target templates on switch trials) during the search preparation period. Alternatively, both these costs could also have been produced by a form of task-set inertia (e.g., Allport & Wylie, 1999), that is, a competition between the currently relevant target colour template and the residual activation of the previously relevant colour template. Such template inertia effects will be reflected by the presence of N2pc components to singleton probes that match the irrelevant target colour. These N2pcs should have been observed specifically on target switch trials, indicating that the corresponding colour template remained partially activated on these trials. However, no evidence for the presence of any target template inertia was found in either experiment. Singleton probes that matched the currently irrelevant target colour did not trigger N2pc components on switch trials at any point during the preparation interval. This was the case in Experiment 1 for switch trials that followed two repetitions of the other target colour, and in Experiment 2 after four repetitions of the other target colour. These observations strongly suggest that target template activation processes were colour-selective throughout, without any residual template inertia on target switch trials[6]. Thus, the presence of performance costs and the delay of target colour probe N2pcs on these trials cannot be attributed to any residual activation of previously relevant colour templates. In other words, search templates were switched off rapidly and fully during the preparation period of switch trials (see also Grubert et al., 2017; Olivers & Eimer, 2011 for additional electrophysiological and behavioural evidence for a fast de-activation of target templates that are no longer relevant).

The complete absence of N2pc components to irrelevant target colour probes in the current study may seem surprising, given that a previous study (Grubert & Eimer, 2020) obtained clear evidence for the parallel activation of two colour templates during search preparation. In this earlier study, two target colours alternated across successive trials, and probes that matched the previous or the upcoming target colour both triggered reliable N2pcs during the preparation period. In contrast to this study, where all trials were effectively target switch trials, the current experiments used an alternating runs procedure with predictable target switch and repeat trials. This difference may have resulted in observers adopting different search preparation strategies. Both target templates may have been activated concurrently when target colours swapped between consecutive trials, whereas only the relevant target colour template may be activated during search preparation when search targets always repeat at least once. It is interesting to note that observers chose to activate only the current target template in the current study, even though this single-template strategy

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[6] *The absence of any N2pcs to singleton probes that matched the currently irrelevant target colour also demonstrates that probe N2pc components were not associated with any salience-driven exogenous attentional capture triggered by colour singletons in probe displays (see also Grubert & Eimer, 2018, 2023, for further demonstrations that distractor-colour singleton probes do not trigger N2pcs).*

resulted in sizeable behavioural costs on target switch trials. It is possible that maintaining a single template is less demanding than the co-activation of two templates, and/or that any performance costs on switch trials are compensated for by substantial benefits on target colour repetition trials. The availability of different target template activation strategies, the factors that determine which strategy will be adopted in a particular task context, and the behavioural consequences of these choices, need to be investigated systematically in future research.

A crucial question posed by the present results concerns the relationship between the target template switch costs observed during the preparation for search and the target switch costs found for search performance. The temporal pattern of relevant target colour probe N2pcs observed in both experiments shows that preparatory target templates are activated earlier on colour repetition as compared to switch trials. However, these templates appeared to have been activated equally strongly on colour repetition and switch trials immediately prior to the presentation of the next search display, as reflected by the absence of any amplitude differences of the N2pc to probe 7. If target templates were equally active on all trials at the moment a search display was presented, it would be reasonable to assume that there should be no systematic difference in their ability to guide attention towards target locations. In fact, the pattern of target N2pc components suggested that this was not the case, and that search guidance was more effective on repeat trials. In both experiments, target N2pcs were smaller and emerged significantly later on colour switch as compared to repetition trials, indicative of target switch costs at the level of template-guided attentional target selection. These observations suggest that the quality of search guidance may not be exclusively determined by the activation state of a target template when the search display is presented but is also affected by the temporal profile of template activation processes.

Guidance appears to be more effective when the relevant target colour template has been activated earlier.

It should also be noted that the preparation for search does not just involve the activation of templates for target-defining features such as colour, but also the activation of templates for response-relevant features (e.g., target orientation, as in the present study). Observers are only fully prepared for an upcoming search task when both a template for the guidance of search and a template for target discrimination and response selection are activated (see Wolfe, 2023, for a similar distinction between guiding and target templates). Preparatory guidance templates may generally be activated prior to target templates because they are required for the guidance of attention at an early stage of the upcoming search process. If this is the case, the delayed activation of guidance templates observed in the current study on switch trials may be accompanied by an even later activation of target templates. This could result in costs for target identification and response selection on switch relative to repeat trials. In short, switch-related delays of preparatory target template activation processes could affect both the guidance of attention and the subsequent processing of target objects, and behavioural target switch costs could be generated at either or both of these stages.

In summary, the current study obtained new insights into the mechanisms involved in the preparatory activation of search target templates and the switch between templates across successive trials. Using on-line electrophysiological markers of target template activation, we demonstrated strong temporal template switch costs during search preparation, reflected by considerable delays in the activation of target colour templates on switch trials. In contrast, there was no evidence that any target template inertia on switch trials could have contributed to the target switch costs observed for search performance. We suggest that the delay in the activation of target templates on switch trials can adversely affect early attentional guidance mechanisms as well as subsequent target identification and response selection processes.

2.5 Supplementary Materials

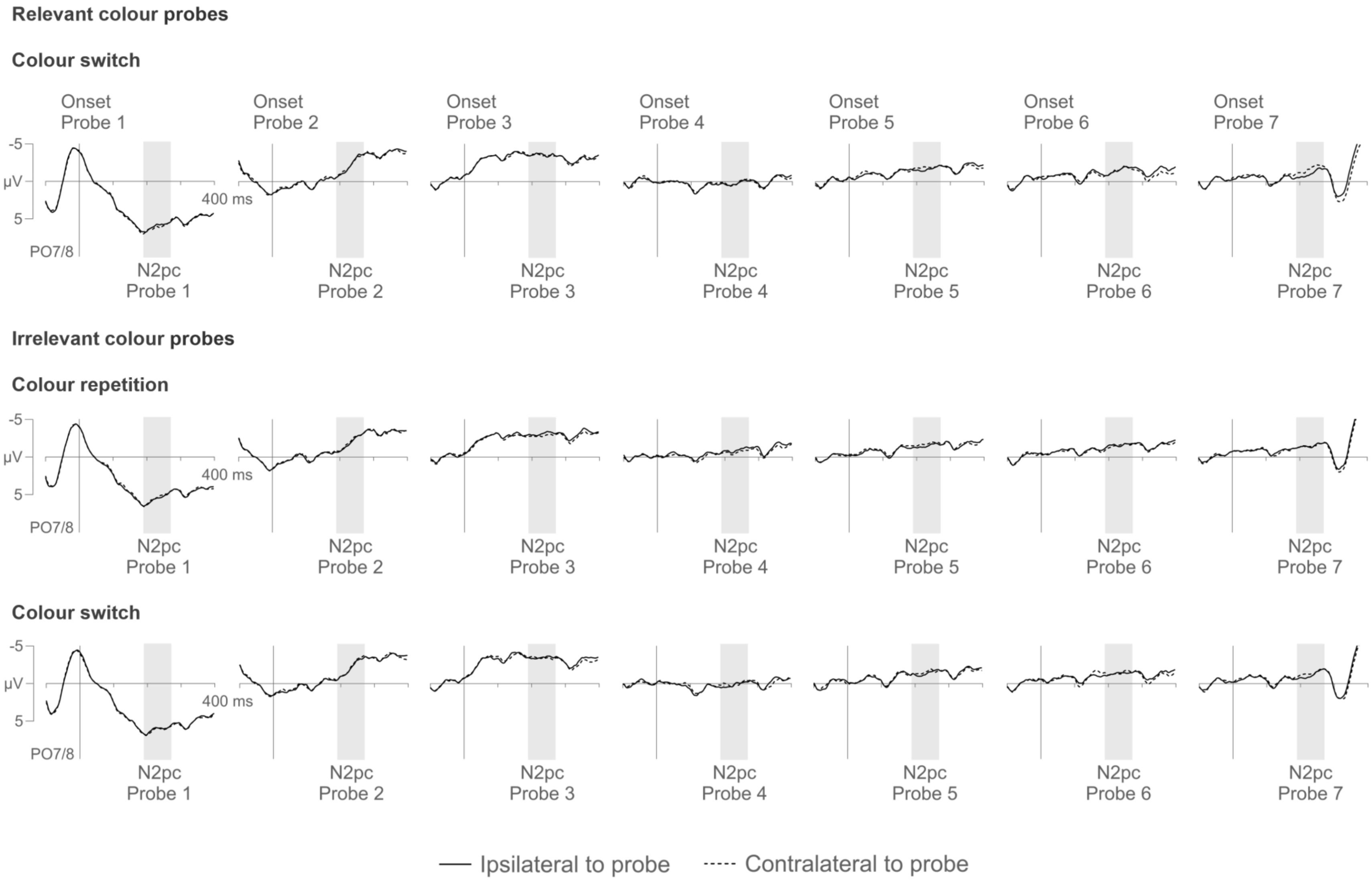


Figure 9 Grand-averaged ERPs elicited in Experiment 1 at electrodes PO7/8 contralateral and ipsilateral to each of the seven colour singleton probes presented between consecutive search displays. ERPs are shown separately for relevant target colour probes in colour switch trials (top panel; see Fig.3 for the corresponding ERPs in colour repetition trials) and for irrelevant target colour probes in colour repetition and switch trials (bottom panels). N2pc time windows are indicated by shaded areas (190-270ms after onset of each individual probe).

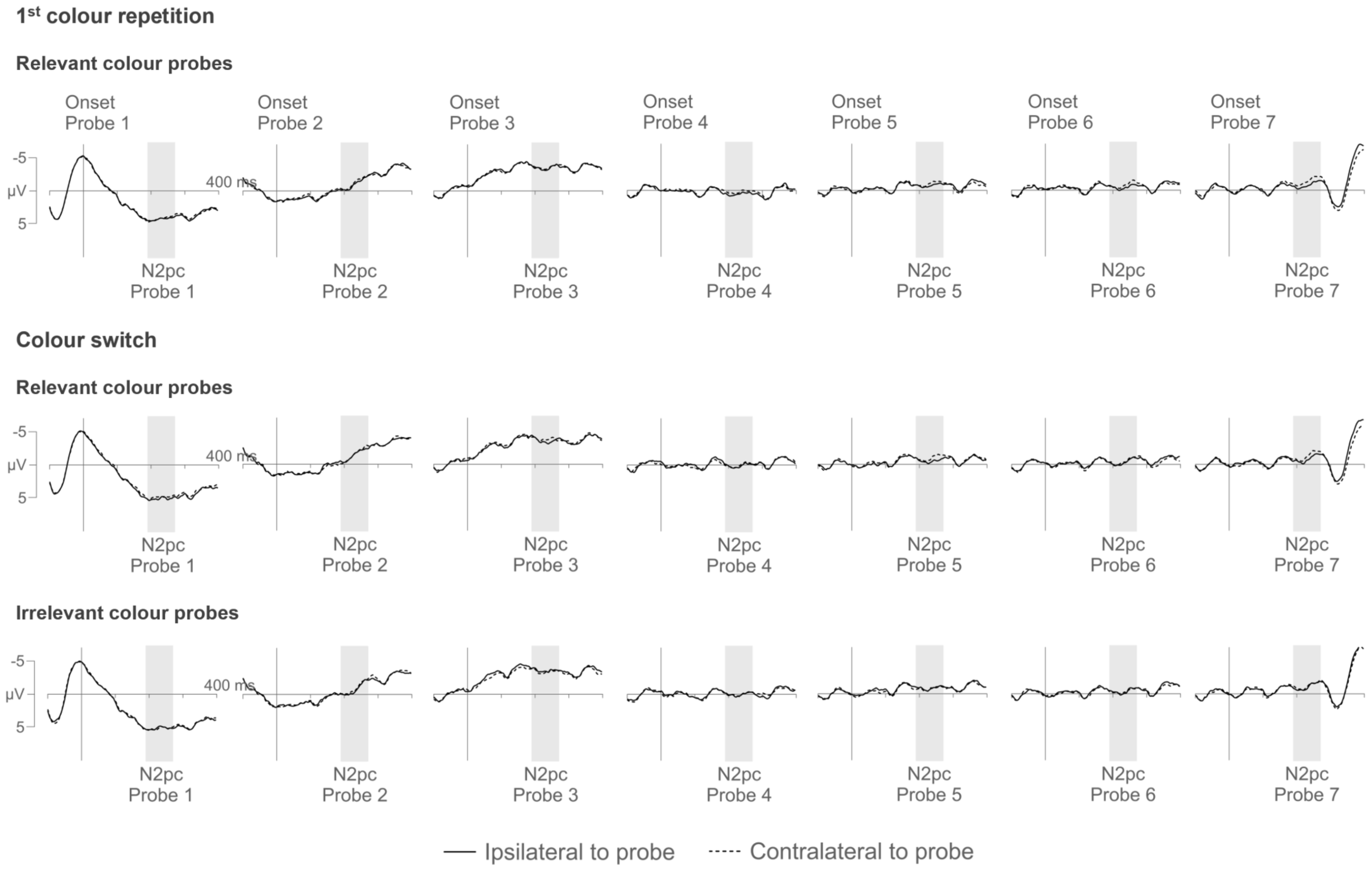

1st colour repetition
Relevant colour probes
Onset Probe 1
Onset Probe 2
Onset Probe 3
Onset Probe 4
Onset Probe 5
Onset Probe 6
Onset Probe 7
-5
μV
5
400 ms
N2pc Probe 1
N2pc Probe 2
N2pc Probe 3
N2pc Probe 4
N2pc Probe 5
N2pc Probe 6
N2pc Probe 7
Colour switch
Relevant colour probes
-5
μV
5
400 ms
N2pc Probe 1
N2pc Probe 2
N2pc Probe 3
N2pc Probe 4
N2pc Probe 5
N2pc Probe 6
N2pc Probe 7
Irrelevant colour probes
-5
μV
5
400 ms
N2pc Probe 1
N2pc Probe 2
N2pc Probe 3
N2pc Probe 4
N2pc Probe 5
N2pc Probe 6
N2pc Probe 7
Ipsilateral to probe
Contralateral to probe

Figure 10 Grand-averaged ERPs elicited in Experiment 2 at electrodes PO7/8 contralateral and ipsilateral to each of the seven colour singleton probes presented between consecutive search displays. ERPs are shown separately for relevant target colour probes in 1st colour switch trials (top panel) and for relevant and irrelevant target colour probes in colour switch trials (bottom panels). N2pc time windows are indicated by shaded areas (190-270ms after onset of each individual probe).

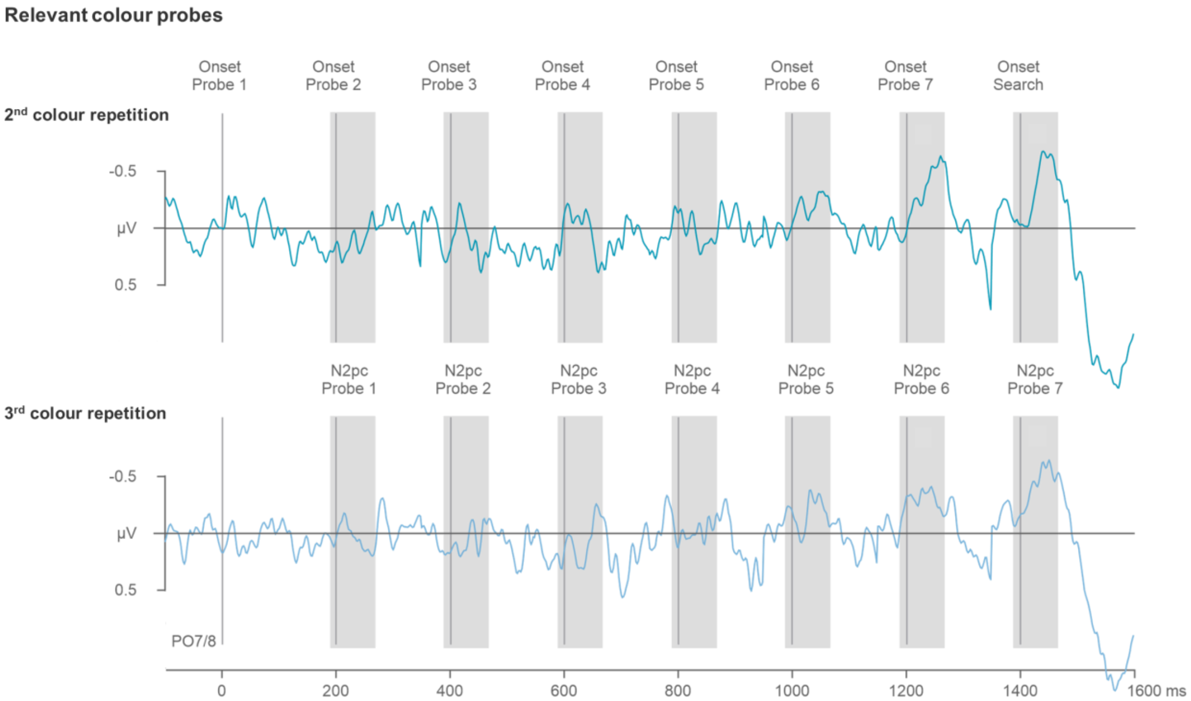


Figure 11 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for relevant target colour probes in 2nd (top panel) and 3rd colour repetition trials (bottom panel) of Experiment 2 (the corresponding difference waves for 1st colour repetition trails can be seen in Fig.7). Difference waves triggered by individual probes are shown in the same continuous fashion as in Figure 5 and 6. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe). Statistically reliable probe N2pcs are marked by asterisks.

Figure 12 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for irrelevant target colour probes in all types of colour repetition trials of Experiment 2. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe).

Chapter 3 The capacity limitations of multiple-template visual search during task preparation and target selection

3.1 Introduction

In visual search, knowledge about the properties of target features enables observers to guide their attention in a goal-directed fashion. Representations of target properties (attentional templates) bias visual processing in favour of objects with template-matching features, so that these objects are more likely to be detected, attended, and identified than non-matching distractors. Because target templates are assumed to be held in visual working memory (Carlisle et al., 2011; Eimer, 2014; Olivers et al., 2011), it should in principle be possible to activate multiple target templates simultaneously, until working memory capacity (typically 3-4 items; e.g., Cowan, 2001) is exceeded. Employing multiple templates in parallel would be particularly useful in tasks where observers search for one of several possible target objects.

The capacity of template-guided visual search, and the nature of any capacity limitations in this domain, has recently become the object of intense study (see Ort & Olivers, 2020, for a review). While it has been argued that only a single attentional template can be maintained at any given time (e.g., Houtkamp & Roelfsema, 2009; Olivers et al., 2011), there is now strong behavioural and electrophysiological evidence for multiple target template activation (e.g., Beck et al., 2012; Berggren & Eimer, 2019; Grubert et al., 2016; Grubert & Eimer, 2016a, 2023; Irons et al., 2012; Kerzel & Grubert, 2022; K. S. Moore & Weissman, 2010; Ort et al., 2019). While it seems clear that at least two target templates can be maintained simultaneously, multiple-target search is typically less efficient than search for a single constant target object (see Ort & Olivers, 2020, for a summary). These costs indicate that some capacity limitations arise when several attentional templates are activated at the same time.

Because attentional templates for known target features are activated in a preparatory fashion, insights into possible capacity limitations of template activation can be obtained by investigating these processes prior to the start of a particular search episode. We have recently developed a new method that employs EEG markers to track the activation states of target templates in real time during search preparation (Grubert & Eimer, 2018). In our rapid serial probe presentation (RSPP) paradigm, participants search for colour-defined target objects among multiple distractors, and irrelevant probe displays are presented rapidly (every 200ms) during the interval between successive search displays. Each of these probe displays includes a colour singleton that either matches the colour of the target or a distractor colour. Any attentional capture by target-matching probes indicates that a corresponding colour template is active at the moment when the probe is presented. To measure such probe-induced attentional capture, we recorded EEG during task performance, and computed N2pc components for each individual probe position between two search displays. The N2pc is a negative event-related potential (ERP) component, triggered at posterior scalp electrodes contralateral to objects with task-relevant features around 180-200ms after stimulus onset, that reflects the rapid allocation of attention to candidate target objects (e.g., Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999). The rationale for such probe-related attentional capture builds on the task-set contingent capture literature, in which N2pc components were measured in response to template matching, but task- irrelevant, cues that preceded search onset (e.g., Barras & Kerzel, 2016; Eimer & Kiss, 2008; Goller et al., 2020; Grubert & Eimer, 2016a; Livingstone et al., 2017; Sawaki & Luck, 2013; Schönhammer et al., 2020).

During search for a constant colour-defined target (Grubert & Eimer, 2018), singleton probes that matched the current target colour triggered N2pc components from about 1000ms prior to the onset of the next search display, indicating that a colour-selective target template was activated in a transient fashion during the preparation for search. In contrast, no such N2pcs were elicited by singleton probes in a distractor colour, demonstrating that N2pcs to target-colour probes did not merely reflect salience-driven attentional capture. To investigate whether multiple preparatory target templates can be activated concurrently, a follow-up study employed the same RSPP procedures, except that two possible colour-defined search targets now alternated between trials in a fully predictable fashion between successive search displays (ABAB; Grubert & Eimer, 2020). Reliable N2pcs were now observed both for singleton probes that matched the upcoming (relevant) target colour, and for probes that matched the preceding (now irrelevant) target colour. This observation provides clear electrophysiological evidence for the simultaneous activation of two colour-specific target templates. Notably, the relevance of a colour for the next search episode only affected N2pcs to probes that appeared immediately prior to the arrival of the search display. These probes triggered larger N2pcs when they matched the upcoming target colour (rather than the preceding target colour). In another recent study from our lab, observers also searched for one of two possible colour-defined targets, but these targets now appeared in a random order, so that their identity was no longer predictable (Grubert & Eimer, 2023). In one condition, these colours were equiprobable (50%). In another condition, they differed in their probability (80% versus 20%). Probes that matched either of the two target colours triggered N2pc components from about 600-800ms prior to search display onset, providing further evidence for multiple-template activation. Notably, these probe N2pcs did not differ from N2pcs triggered by probes in a one-colour task where participants always searched for the same colour target. Expectations linked to the a priori probability of a particular target also did not affect the size or time course of these probe N2pcs.

The results of these two studies suggest that during the preparation for two-colour search, both colour-selective templates are activated simultaneously. Because maintaining two target templates at the same time is unlikely to exceed working memory capacity, it may be less demanding to always activate both templates concurrently rather than switching templates, even when only one of them is relevant for the next search episode (ABAB task; Grubert & Eimer, 2020). However, when the number of possible target colours is further increased, limits to the capacity of preparatory target template activation processes may emerge. In the present study, we investigated this possibility by including search tasks in which observers searched for one of three possible colour-defined target objects. Maintaining three colour-specific target templates concurrently might reach (or possibly even exceed) working memory capacity for many observers, and this may result in qualitative differences in the way that these templates are activated during search preparation relative to one-colour or two-colour search.

We employed the same RSPP technique as in our previous work (Grubert & Eimer, 2018, 2020, 2023; see also Dodwell et al., 2024). In Experiment 1, there were three possible colour-defined target objects, but the identity of each target was fully predictable in each trial, because the target colours rotated in a constant order between trials (ABCABC). Thus, Experiment 1 was equivalent to our previous ABAB task (Grubert & Eimer, 2020), except that a third target colour was added. Colour singleton probes were presented rapidly and continuously between search displays, and probes matching each of the three target colours appeared with equal probability and in a random order. The question was whether we would again observe evidence for multiple-template activation under these circumstances. If all three colour templates are activated on any given trial, even though the identity of the target is fully predictable, reliable N2pc components to all colour singleton probes should emerge during search preparation. Alternatively, template activation may be fully colour-selective during predictable three-colour search, so that only the template that matches the upcoming target colour is activated at any time. In this case, only these target-matching probes should trigger N2pc components, whereas no N2pcs should be observed for the two other colour singleton probes.

3.2 Experiment 1

3.2.1 Methods

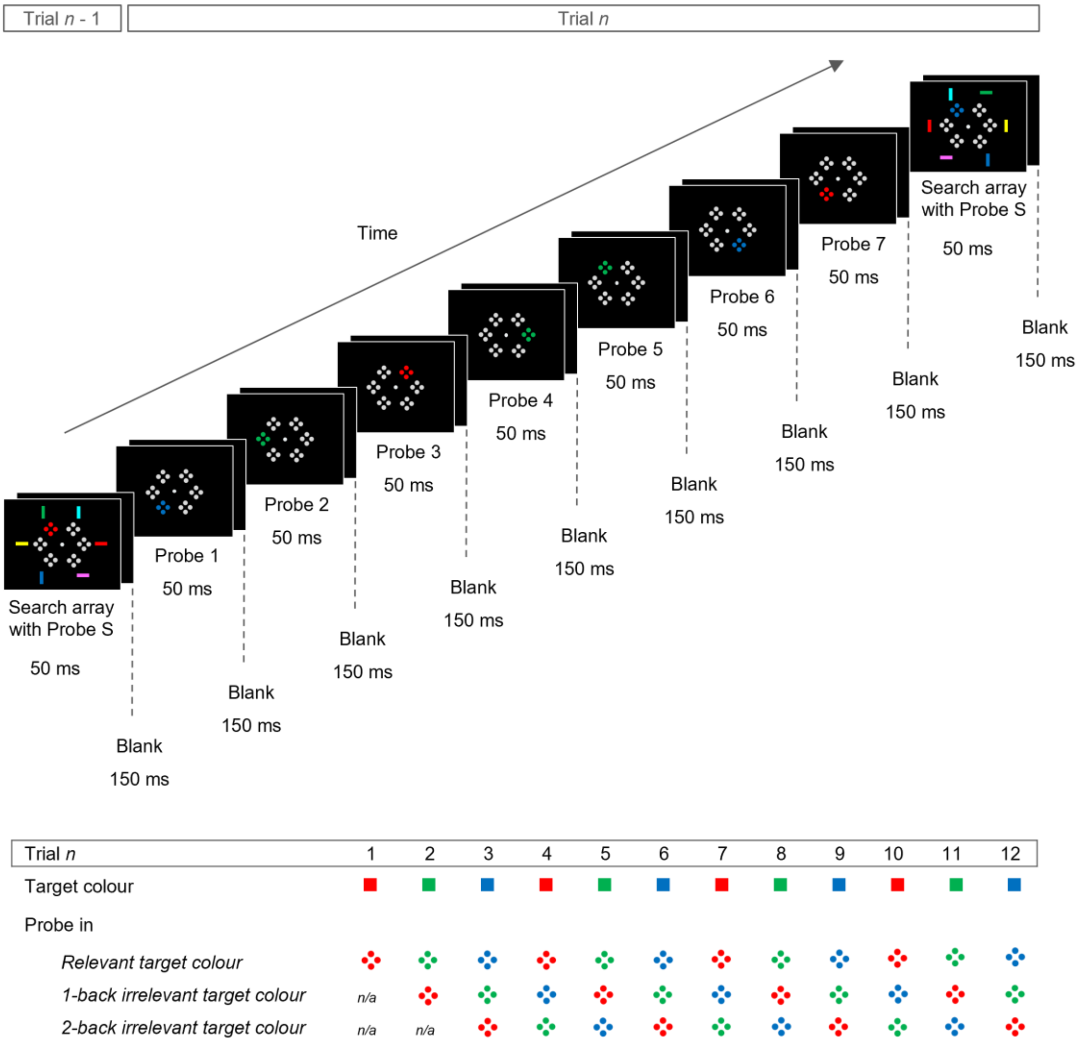
3.2.1.1 Participants

Twenty-two participants were paid at an hourly rate of £10 to participate in Experiment 1. The experiment was approved by the Ethics Committee of the Psychology Department at Durham University and was conducted in accordance with the Declaration of Helsinki. Participants gave informed written consent prior to testing. Four participants were excluded from analysis due to excessive eye movement artefacts (>40% of trials were lost during artefact rejection). The remaining 18 participants were between 19 and 47 years old (mean=30.0, SD=8.7). Thirteen participants were female and five were male. All participants were right-handed. They all had normal or corrected-to-normal vision and normal colour vision (as tested with the Ishihara colour vision test; Ishihara, 1972). The sample size of 18 was calculated by means of an a priori power analysis using MorePower 6.0.1 (Campbell & Thompson, 2012) to detect an interaction in a 2×7×3 factorial repeated-measures ANOVA (within-subject factors laterality, probe number, and probe colour, see Results) with an assumed alpha of .05, power of .95, and a large effect size of 0.4 (Cohen's f) to replicate partial eta squared values (η_p^2) of .14, which we measured in a previous RSPP experiment in which participants searched for two alternating target colours (3-way interaction between laterality* probe number* probe colour in Experiment 1 of Grubert & Eimer, 2020; p.1531).

3.2.1.2 Stimuli and procedures

The experiment was tested in a sound attenuated Faraday cage with dim illumination. The viewing distance from the monitor was approximately 90cm. Stimuli were presented on a 22-inch MSI Optix G272 LCD monitor with a 100Hz refresh rate and a resolution of

1920×1080 pixels. Stimulus presentation, timing, and response collection were controlled using PsychoPy (psychophysics software in Python; Peirce et al., 2019) on an LG Pentium PC with Windows 10. All stimuli were presented on a black background. A central grey fixation point was presented throughout the experimental blocks (CIE x/y colour coordinates: .327/.348; 0.2°×0.2° of visual angle). Each block contained 12 trials with eight stimulus displays that were presented in a continuous serial presentation stream, as illustrated in Figure 13 (top panel). Stimulus displays were presented for 50ms and were separated by a 150ms blank interval (200ms stimulus onset asynchrony). The first seven displays in each trial contained a probe array (probes 1 to 7), the eighth displays contained both the response-relevant search array and a probe array. The probes in the eighth display were only presented for the sake of a consistent visual pattern throughout the blocks. They never triggered any N2pcs in our previous work (e.g., Grubert & Eimer, 2018) and will not be analysed in this study.



Trial *n*	1	2	3	4	5	6	7	8	9	10	11	12
Target colour	🟥	🟩	🟦	🟥	🟩	🟦	🟥	🟩	🟦	🟥	🟩	🟦
Probe in												
Relevant target colour	🔴	🟢	🔵	🔴	🟢	🔵	🔴	🟢	🔵	🔴	🟢	🔵
1-back irrelevant target colour	*n/a*	🔴	🟢	🔵	🔴	🟢	🔵	🔴	🟢	🔵	🔴	🟢
2-back irrelevant target colour	*n/a*	*n/a*	🔴	🟢	🔵	🔴	🟢	🔵	🔴	🟢	🔵	🔴

Figure 13 Schematic illustration of the stimuli and presentation times in Experiment 1 (top panel). Search displays contained three target colour bars (e.g., red, green, blue), and three nontarget colour bars (e.g., yellow, cyan, pink). However, the response-relevant target colour alternated predictably across the 12 trials of each block (e.g., red, green, blue, red, green, blue, etc.; bottom panel). Probe displays were presented every 200ms in the interval between two search displays (probes 1-7) and simultaneously with a search display. They contained a colour singleton that randomly matched the relevant (upcoming) target colour, the previous target colour (1-back irrelevant target-colour probes) or the colour of the target before the previous trial (2-back irrelevant target-colour probes).

Search arrays were presented at an eccentricity of 1.4° from central fixation and contained six vertically (0.2°×0.6°) or horizontally (0.6°×0.2°) oriented bars at the 1, 3, 5, 7, 9, and 11 o'clock positions of an imaginary clock face. The orientations of the six bars were selected independently and randomly for each search array. Each bar had a different colour. They were red (.610/.321), green (.273/.624), blue (.172/.181), yellow (.435/.490), pink (.483/.246), and cyan (.222/.313). All colours were equiluminant (~11.9cd/m^2), and they were allocated randomly to the six bars in each search display. Each participant was assigned three target colours from the set of red, green, blue, and yellow (pink and cyan were dedicated non-target colours only). The four possible sets of target colours were counterbalanced across participants so that five participants searched for red, green, and blue targets, five other participants searched for red, green, and yellow targets, and always four other participants searched for red, blue, and yellow or green, blue, and yellow targets. However, in each trial, only one of the three colours was response relevant: Target colours alternated sequentially across consecutive trials (e.g., red in trial 1, green in trial 2, blue in trial 3, red in trial 4, etc.). The target colour sequence was determined randomly for each participant but remained the same for each participant throughout the experiment. Participants' task was to report the orientation (vertical/horizontal) of the response-relevant target colour bar in each trial by pressing the up/down arrow keys on a standard keyboard. Since search displays always contained all three target colours, participants had to keep track of the target colour sequence for themselves. There were no cues indicating the upcoming target colour during a block, but participants received a reminder about their target colours and the respective target colour sequence in each block break (none of the participants reported forgetting the sequence during a block). The locations of the three target colour bars in each search array were determined randomly and independently of each other. The response-to-key mapping (vertical/horizontal response on arrow up/down key) and the hand-to-key mapping (left/right hand on arrow up/down key) was counterbalanced across participants but was kept constant for each participant for the duration of the whole experiment.

Probe arrays contained six items composed of four closely aligned dots, two on the vertical, and two on the horizontal axis (0.1°×0.1° for each dot, 0.25°×0.25° for each four-dot probe item). The probe items were presented at the same 1, 3, 5, 7, 9, and 11 o'clock positions of an imaginary clock face than the search bars, but closer to fixation (at an eccentricity of 0.5°). Five of the six probe items were uniformly grey, the sixth item was a target colour singleton that randomly matched any of the three respective target colours (as assigned to each participant). Probes that matched the colour of the upcoming search target were *relevant target-colour probes*, probes that matched the target colour of the previous trial were *1-back irrelevant target-colour probes*, and probes that matched the target colour of the target before the previous trial were *2-back irrelevant target-colour probes* (Figure 13, bottom panel). The singleton locations were selected randomly and independently in each probe array with the following two restrictions. Successive probes were equally likely to appear on same or opposite display sides to avoid any hemispheric imbalance in the baseline activity preceding each probe, and immediate location repetitions between probe displays were not allowed to avoid colour masking effects (note that the location variability was therefore reduced in same side as compared to opposite side probes). Participants were informed that probe displays were never response-relevant and could be ignored.

Experiment 1 contained 55 blocks of twelve trials. Blocks were kept as short as possible and participants were instructed not to blink during the blocks, if possible. The twelfth search display in each block was followed by seven additional probe displays to keep stimulus conditions during the post-target response interval identical across all trials in a block. Each block thus contained twelve search displays and 91 probe displays (13 for each probe number 1 to 7). Before the experiment proper, participants practised the task until they felt comfortable with it (usually after two to four blocks). These practise data were not recorded.

3.2.1.3 EEG recording and data analyses

EEG was DC-recorded from 25 scalp sites (at standard positions of the extended 10/20 system; EasyCap, Brain Products), sampled at 500Hz (BrainAmp DC amplifier, Brain Products), and digitally low-pass filtered at 40Hz (no other filters were applied after data acquisition). Impedances were kept below 5kΩ. The left earlobe served as the online reference during data acquisition. Offline, all channels were re-references to linked earlobes. EEG data processing was conducted with the BrainVision Analyzer software (Brain Products GmbH, Gilching, Germany). EEG epochs were locked to the onsets of the probes (probes 1 to 7) and the search displays and included a 100ms pre-stimulus baseline and a 400ms post-stimulus ERP time window. Data from the first and last seven probe displays in each block were excluded from analysis. Probes that were presented prior to search displays with anticipatory (<200ms), very slow (>1500ms), incorrect, or missing responses were also excluded from analysis. Epochs that were contaminated with artefacts were also excluded from analysis. Artefacts were eye movements (±30µV in the bipolar HEOG channel), blinks (±60µV at Fpz), and other muscular activity (±80µV in all channels). Artefact rejection resulted in an exclusion of 8.7% of all epochs (SD=7.2%; ranging between 0.8% and 25.3% across participants). The remaining epochs were averaged separately for each probe number (probes 1-7) for relevant, 1-back irrelevant, and 2-back irrelevant target-colour singletons in the left versus right hemifield (mean number of epochs for each average = 87; SD=10; ranging between 56-97 epochs across participants). Separate averages were also computed for search displays with a target in the left or right hemifield (M=285 per average; SD=19; ranging between 250-319 epochs across participants).

N2pc components to probes were quantified based on ERP mean amplitudes obtained at lateral posterior electrodes PO7 and PO8, contralateral and ipsilateral to the side of a probe, within an 80ms time window starting at 190ms after the respective probe display onset. As in our previous work using analogous rapid serial probe presentation procedures (Grubert & Eimer, 2018), the start of this time window was determined by measuring the point in time (rounded to the nearest 10) when the ascending flank of the averaged probe N2pc (pooled across all relevant target-colour probes in Experiment 1) reached 50% of the peak amplitude (at -0.13μV). Target N2pcs in the search displays were computed within the same 190-270ms post-stimulus time window for consistency. Target N2pc onset latencies were substantiated by means of jackknife-based procedures (Miller et al., 1998). Eighteen grand-average difference waves (contralateral minus ipsilateral ERPs at PO7/8) were computed, each excluding one different participant from the original sample. N2pc onset latencies were defined as the point in time when each subsample difference wave reached an absolute onset criterion of -0.7μV (50% of the peak amplitude of the target N2pc in Experiment 1). All *t*-tests on jackknifed N2pc onset latencies were power-corrected as suggested by Miller et al., (1998) and are denoted with t_c. All *t*-tests reported are two-tailed. Effect sizes are reported in terms of Cohen's *d* (Cohen, 1988), with a confidence interval of 95%, for *t*-tests, and partial eta squared ($\eta_p{}^2$) for *F*-tests and power corrected t_c-tests ($\eta_{pc}{}^2$).

3.2.2 Results

3.2.2.1 Behavioural results

Trials with anticipatory (<200ms) or exceedingly slow (>1500ms) reaction times (RTs) were excluded from analysis (0.5% of all trials). The mean RT in correct trials was 679ms and the mean error rate was 8.3%.

3.2.2.2 N2pc components triggered in the probe displays

To determine the time course of template activation in preparation for search, N2pc components triggered in each of the seven successive probes (probes 1-7) were measured by computing ERPs at posterior sites PO7/8, contralateral and ipsilateral to the side of a probe, separately for probes that matched the upcoming target-colour (relevant target-colour probes), the previous target colour (1-back irrelevant target-colour probes), and the target colour that was relevant before the previous target colour (2-back irrelevant target-colour probes). The ERPs for relevant target-colour probes 1 to 7 are illustrated in Figure 14 (the corresponding ERPs to 1-back and 2-back irrelevant target-colour probes are included in the Supplementary

Materials). Probe N2pc difference waves, obtained by subtracting ipsi- from contralateral ERPs at PO7/8 for each individual probe, are shown in Figure 15. To make the time course of the successive probe N2pcs easier to see, Figure 15 was designed to show the N2pc difference waves for probes 1 to 7 in a temporally continuous fashion, separately for relevant (top panel), 1-back irrelevant (middle panel), 2-back irrelevant (bottom panel) target-colour probes. Note that N2pc components were extracted individually for each probe (probes 1-7) and that Figure 15 simply illustrates these probe N2pcs in a successive fashion. Figure 15 starts with the activity triggered in response to probe 1 (100ms prior to 350ms after onset of probe 1) which was the first probe presented directly after a previous search display. For the subsequent probes (probes 2-7), 200ms intervals (150ms to 350ms after onset of each respective probe) are shown sequentially with interpolated data points between adjacent intervals. The onset of each probe is marked with a vertical line, and the N2pc time window for each probe (190-270ms post-stimulus) is shaded in grey. As probes appeared every 200ms, each individual probe was therefore presented within the N2pc time interval of its immediately preceding probe. As can be seen from Figure 15, relevant target-colour probes triggered N2pc components in the second half of the preparation period before search onset with the N2pc for probe 7, immediately preceding the next search display, being the largest. Relevant target-colour probes that were presented earlier in the trial did not trigger any N2pcs. This N2pc distribution mirrors our previous RSPP findings (e.g., Grubert & Eimer, 2018) and demonstrates that attentional templates are activated in a transient fashion during preparation for search. In contrast to the N2pc pattern triggered by relevant target-colour probes, none of the probes that matched any of the previous target colours (1-back and 2-back irrelevant target-colour probes) seemed to trigger any substantial N2pc components.

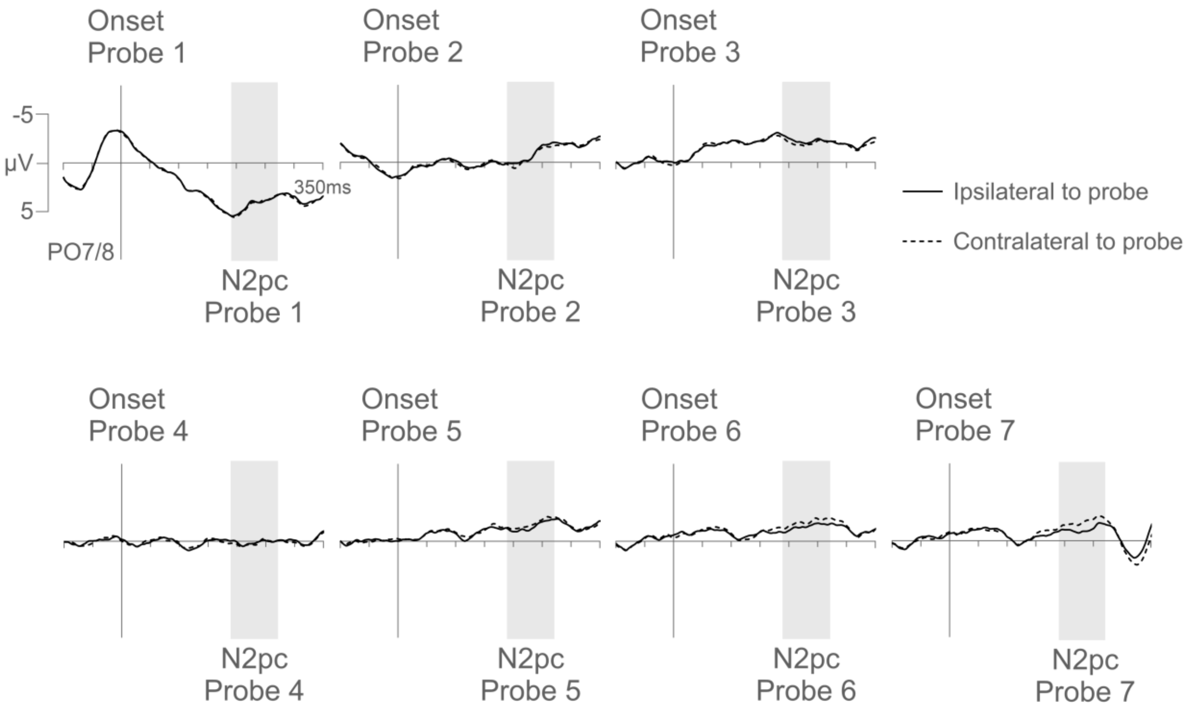


Figure 14 Grand-averaged ERPs triggered at electrode sites PO7/8 contralateral and ipsilateral to relevant target-colour singleton in the seven probe displays presented between consecutive search displays of Experiment 1. Probe 1 is the first probe to follow the previous search display and probe 7 is the probe to immediately precede the next search display. Shaded areas mark N2pc time windows (190-270ms after onset of each individual probe).

Figure 15 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for relevant target-colour probes (top panel), 1-back irrelevant target-colour probes (middle panel), and 2-back irrelevant target-colour probes (bottom panel) in Experiment 1. Here, difference waves for the seven probes (probes 1-7) are illustrated in a temporally continuous fashion, but the seven individual probe N2pcs were extracted independently of each other from the raw signal. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe). Statistically reliable probe N2pcs are marked by asterisks.

Statistical analyses confirmed these informal observations. ERP mean amplitudes measured at PO7/8 in the 190-270ms post probe time windows were fed into a repeated-measures omnibus ANOVA with the factors Probe Colour (relevant, 1-back irrelevant, and 2-back irrelevant target-colour probe), Probe Number (Probe 1, 2, 3, 4, 5, 6, and 7), and Laterality (electrode contralateral and ipsilateral to the hemifield of a probe). There was no main effect of Laterality, $F(1,17)=1.9$, $p=.186$, $\eta_p^2=.10$, but a significant interaction between

Laterality and Probe Number, *F*(6,102)=3.6, *p*=.003, η_p^2=.17, confirming that some of the probes triggered N2pc components, while others did not. There was also an interaction between Laterality and Probe Colour, *F*(2,34)=3.3, *p*=.050, η_p^2=.16, and a significant three-way interaction, *F*(12,204)=1.8, *p*=.046, η_p^2=.10. This suggests that the temporal pattern of probe N2pcs not only differed across consecutive probes but was also different for relevant and irrelevant target-colour probes.

The differences between N2pcs triggered in response to relevant, 1-back irrelevant, and 2-back irrelevant target-colour probes were followed up with three repeated-measures ANOVAs with the factors Probe Number (Probe 1-7) and Laterality (contralateral versus ipsilateral activity). For relevant target-colour probes, the ANOVA produced a main effect of Laterality, *F*(1,17)=6.0, *p*=.025, η_p^2=.26, and a significant interaction between Laterality and Probe Number, *F*(6,102)=5.3, *p*<.001, η_p^2=.24, confirming that probe N2pc amplitudes differed across the preparation period. Follow-up t-tests, comparing ipsi-and contralateral activity for each of the seven consecutive probes separately, revealed that probe 5 (-0.2μV), *t*(17)=2.3, *p*=.044, *d*=.11, probe 6 (-0.3μV), *t*(17)=4.8, *p*<.001, *d*=.17, and probe 7 (-0.6μV), *t*(17)=3.9, *p*<.001, *d*=.39, triggered reliable N2pc components. In contrast, no N2pcs were triggered in response to probes 1 to 4, all *t*(17)<1, *p*>.661, *d*<.01. The same ANOVAs for 1-back and 2-back irrelevant target-colour probes did not produce any main effects of laterality, both *F*(1,17)<1, *p*>.768, η_p^2<.05, and also no significant Probe Number * Laterality interactions, both *F*(1,17)<1.1, *p*>.412, η_p^2<.06, demonstrating that irrelevant target-colour probes never triggered any N2pc components.

3.2.2.3 N2pc components triggered in the search displays

Target N2pcs were substantiated at PO7/8 ipsilateral and contralateral to the side of the target in the 190-270ms time window after search display onset. These ERPs, together with the respective N2pc difference waves are shown in Figure 16 (top panel). A *t*-test comparing ipsi- and contralateral activity confirmed that target N2pc mean amplitudes were reliable (-0.8μV), *t*(17)=5.3, *p*<.001, *d*>.22. The onset latency of the target N2pc was 224ms.

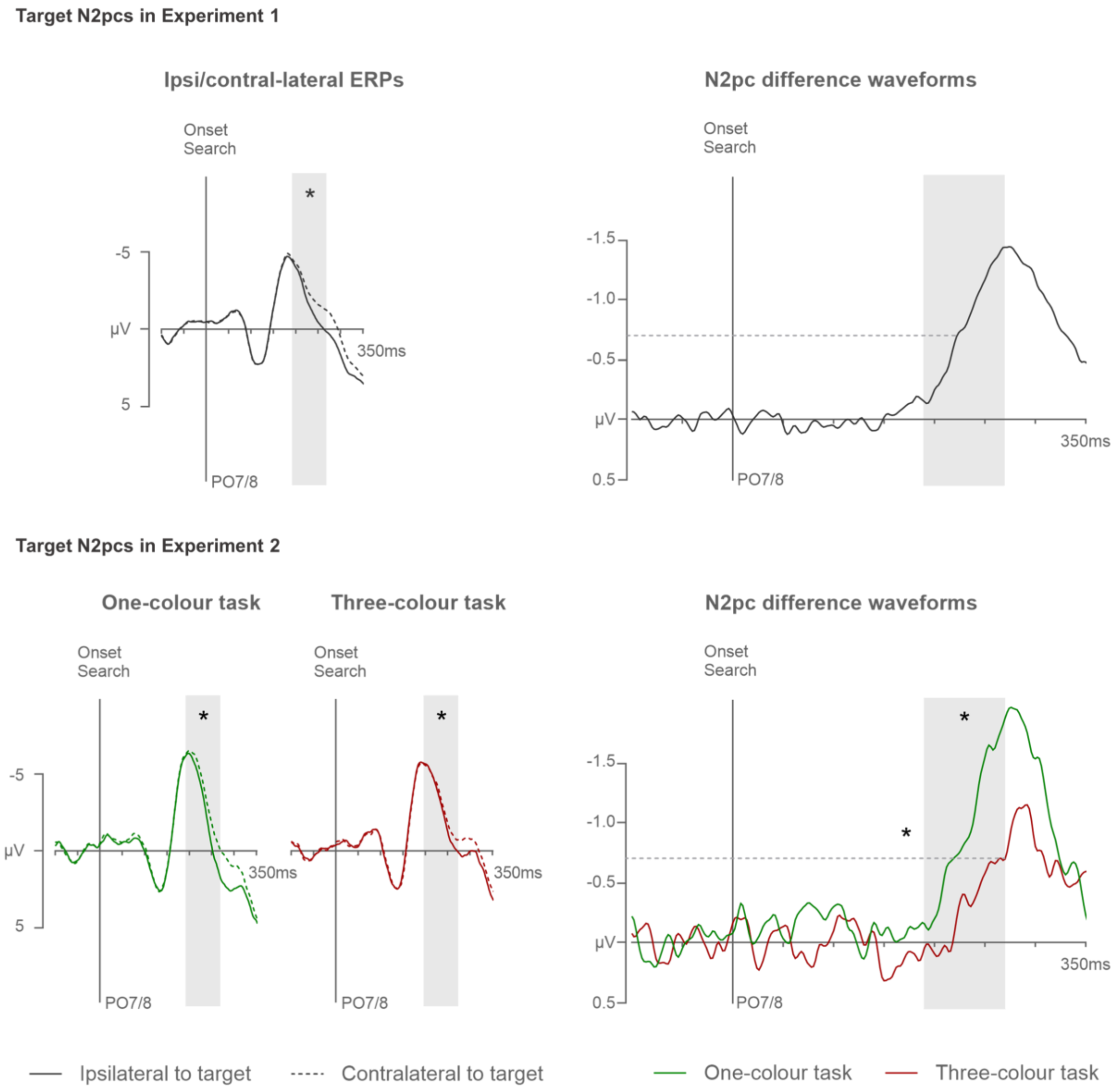


Figure 16 Grand-averaged ERPs triggered at electrode sites PO7/8 contralateral and ipsilateral to the target side in the three-colour search displays of Experiment 1 (top left panel) and the one- and three-colour search displays of Experiment 2 (bottom left panels). The corresponding contralateral-ipsilateral N2pc difference waveforms are shown in the top and bottom right panels, respectively. Shaded areas indicate N2pc time windows (190-270ms after search display onset). Asterisks in the ERP panels (left) indicate significant N2pcs. Asterisks in the difference wave panels (right) represent significant task differences in mean amplitudes and onset latencies (measured at -0.7μV, as indicated by the dashed horizontal lines).

3.2.3 Discussion of Experiment 1

The pattern of probe N2pc results obtained in Experiment 1 was clear-cut. Reliable N2pcs were only triggered by colour singleton probes that matched the known colour of the upcoming target, but not by probes that matched the colours of the other two possible targets. Probes in the currently relevant colour triggered reliable N2pcs when they were presented during the 600ms prior to the next search display (probes 5-7), but not when they appeared earlier in the preparation period (probes 1-4). In line with previous observations (e.g., Grubert & Eimer, 2018), this demonstrates that target-colour templates were only active in temporal proximity to an upcoming search episode, rather than throughout the entire preparation period. In contrast, colour singleton probes that matched the colours of either of the two previous targets failed to trigger any N2pcs at all, suggesting that the corresponding colour templates remained inactive.

These results are qualitatively different from the results of a previous study (Grubert & Eimer, 2020) that used identical procedures except, that participants searched for one of two rather than three predictably alternating targets (ABAB versus ABCABC). Whereas probe N2pcs revealed the concurrent activation of both target colour templates in this earlier study, the addition of a third colour target in Experiment 1 resulted in colour-selective preparation that was limited to the upcoming target colour. This change in search preparation might have been a strategic choice of the participants to reduce working memory load and focus on the one known (as opposed to three possible) target colour(s). Alternatively, it might also reflect capacity limitations, with the number of target templates that can be maintained simultaneously being limited to two. If this was the case, the fact that target colours were fully predictable in Experiment 1 would make the adoption of a single-template strategy the most adaptive choice. Experiment 2 was conducted to test this hypothesis directly and to substantiate potential differences in template activation patterns during three colour search in which all colour templates were equally relevant for the upcoming search.

3.3 Experiment 2

If maximally two preparatory target templates can be activated in parallel, this should have adverse effects on attentional guidance in three-colour search tasks where the identity of each colour target is no longer fully predictable (as in Experiment 1) but instead varies randomly across trials. Template activation under such different task demands was tested in Experiment 2, which included two search tasks. There was a three-colour task that was identical to the ABC task of Experiment 1, with two exceptions. First, and most importantly, the three possible target colours now appeared in random order across search displays, so that each target colour was equally likely to be presented in any given search display. Second, the colour singleton probes now either matched any of the three possible target colours or a distractor colour that also appeared in the search displays. Distractor-colour probes were included in Experiment 2 to rule out the possibility that N2pcs to target-colour probes might at least in part reflect salience-driven attentional capture by singleton probes that are unrelated to any target template activation. In previous studies (Grubert & Eimer, 2018; 2023), such distractor-colour probes failed to trigger any N2pcs. They were still included in Experiment 2 because of the possibility that salience-driven attentional capture might emerge in search tasks where the number of possible target representations exceeds the capacity limits for multiple template activation.

If no more than two colour templates can be activated simultaneously during search preparation, participants will not be able to fully prepare for all potential target colours when three different colour targets vary unpredictably across trials. In such a situation, they may abandon any preparatory template activation altogether, which should be reflected in the absence of any N2pc components in response to target-colour singleton probes. Alternatively, they may randomly activate two target-colour templates on each trial. This should result in an overall reduction of probe N2pc amplitudes, as one third of all target-colour probes will not match either of the active templates, and thus not attract attention and trigger an N2pc. To assess whether target-colour probes are indeed attenuated in the three-colour task, Experiment 2 also included a one-colour task where participants always searched for the same colour-defined target object. Again, colour singleton probes either matched the colour of this target or appeared in a task-irrelevant distractor colour. In this one-colour task, the corresponding attentional template should always be activated during search preparation, resulting in full-size N2pc components in response to target-colour cues. In contrast, if search preparation is limited to two (or one) target colours in the three-colour task, this should result in reliably reduced probe N2pc components in this task relative to the one-colour task. Finally, it might also be possible that three target-colour templates are activated in parallel, but that the colour representations are less precise for three as opposed to two concurrently activated colours (in line with resource models of working memory, e.g., Bays & Husain, 2008). This might also lead to attenuated target-colour probe N2pcs in the three- as compared to the one-colour task. But in this scenario, we would also expect target-similar distractor probes (e.g., pink probes during search for red) to capture attention (e.g., Kerzel, 2019). Distractor-colour probes should therefore trigger N2pc components in the three-colour but not the one-colour task in which target representations should be completely precise and distractor-colour probes should be fully ignored.

In addition to comparing probe N2pcs between the one-colour and three-colour tasks, we also compared the N2pc components triggered by target objects in search displays between these two tasks. Previous studies (e.g., Berggren & Eimer, 2019; Grubert & Eimer, 2016, 2023; Ort et al., 2019) have consistently found that target N2pcs are attenuated and delayed during two-colour as compared to one-colour search, suggesting that the guidance of attentional selectivity is less efficient when two colour templates are active (see also Ort & Olivers, 2020). If only two target templates can be activated concurrently, this difference might be even more pronounced when contrasting one-colour and three-colour search.

3.3.1 Methods

3.3.1.1 Participants

Twenty-three new participants were paid at an hourly rate of £10 to participate in Experiment 2. Participant procedures were identical to Experiment 1. Four participants were excluded due to excessive eye movement activity (>40% trials lost during artefact rejection) and one additional participant was excluded because they did not finish the task. The remaining 18 participants were aged between 20 and 25 years (mean=29.5, SD=10.3). Eleven participants were female and seven were male, all of them were right-handed, and had normal or corrected-to-normal vision and normal colour vision (as tested with Ishihara, 1972).

3.3.1.2 Stimuli and procedures

All experimental procedures were identical to Experiment 1 with some exceptions that are explained below. In Experiment 2, the three target colours assigned to each participant were now presented randomly. Because the response-relevant target colour now changed unpredictably between trials, participants had to activate three colour templates in parallel to enable target detection. Nine of the participants searched for red, green, and blue targets, while pink, yellow, and cyan were the designated distractor colours, and vice versa for the other nine participants. This colour assignment ensured that target colours were separable in colour space so that participants could not adopt a relative colour template for guidance (S. Becker, 2010). Each search display always contained one target colour bar (e.g., red), three distractor colour bars (e.g., pink, yellow, cyan), and two dedicated nontarget colour bars (grey and brown). The six different colours were allocated randomly to the six bars in each search display. Experiment 2 was run on MATLAB using the Cogent 2000

Toolbox and was tested on a different monitor than Experiment 1 (17-inch Samsung wide Syncmaster 753S CRT; 1280×1024-pixel resolution; 100-Hz refresh rate). The colour values therefore slightly differed from Experiment 1: red (.609/.327), green (.296/.581), blue (.174/.149), pink (.216/.110), yellow (.389/.512), cyan (.227/.376), grey (.287/.312), and brown (.540/.400). All colours were equiluminant (~10.9cd/m^2). Half of all probes in Experiment 2 were *target-colour probes* and contained one of the three target colours (e.g., red, green, blue). The remaining probes were *distractor-colour probes* shown in one of the three distractor colours (e.g., pink, yellow, cyan). The exact colour of the probe singleton, from either the target or distractor colour set, was chosen randomly and independently in each probe display. In addition to the *three-colour search*, we also tested a one-colour version of this task in Experiment 2. In the *one-colour task*, each participant searched for one of the three target colours they were assigned to in the three-colour task (e.g., red). The other two colours of the respective target colour set never appeared in the search or probe displays (e.g., green, blue), so that target colours would never become distractors. Half of the colour singletons in the probe displays were shown in the designated target colour (e.g., red) and the other half in any of the three colours from the respective distractor colour set (e.g., pink, yellow, cyan). The one-colour and three-colour search tasks were tested in 30 separate blocks each, with twelve trials per block.

3.3.1.3 EEG recording and data analyses

All EEG procedures were identical to Experiment 1. During artefact rejection, 10.1% of all segments in the one-colour task (SD=8.5%; ranging between 0.3% and 25.0% across participants) and 9.2% in the three-colour task (SD=8.4%; ranging between 0.5% and 29.4% across participants) were excluded from analysis in Experiment 2. Averaged ERP waveforms were computed for probes 1-7 in the left or right hemifield, separately for target and distractor colour probes in the one-colour (mean number of epochs for each average = 77;

SD=6; ranging between 59-83 epochs across participants) and three-colour task (M=72 per average; SD=8; ranging between 58-82 epochs across participants). Separate averages were computed for left- and right-side targets in the search displays in the one-colour (M=152 per average; SD=23; ranging between 104-173 epochs across participants) and three-colour task (M=147 per average; SD=22; ranging between 98-174 epochs across participants).

All data analysis procedures were identical to Experiment 1.

3.3.2 Results

3.3.2.1 Behavioural results

Trials with anticipatory or slow responses were excluded from analysis (0.2% of all trials). RTs in correct trials were faster and error rates were lower in the one-colour (610ms; 4.4%) as compared to the three-colour task (731ms; 13.0%), both $t(17)>4.7$, $p<.001$, $d=.57$.

3.3.2.2 N2pc components triggered in the probe displays

The temporally continuous N2pc difference waves (obtained by subtracting ipsi- from contralateral ERPs at PO7/8) can be seen in Figures 17 and 18. The difference waves are shown separately for target-colour (Figure 17) and distractor-colour probes (Figure 18) in the one-colour (top panels) and three-colour search tasks (bottom panels), respectively. The corresponding ipsi/contra-lateral ERPs can be found in the Supplementary Materials. The temporal pattern of target-colour probe N2pcs mirrored the N2pc pattern observed for relevant target colour probes in Experiment 1, with pronounced N2pcs emerging in the later phase during search preparation. However, distractor-colour probes did not seem to trigger any N2pc components in either the one-colour or the three-colour search task.

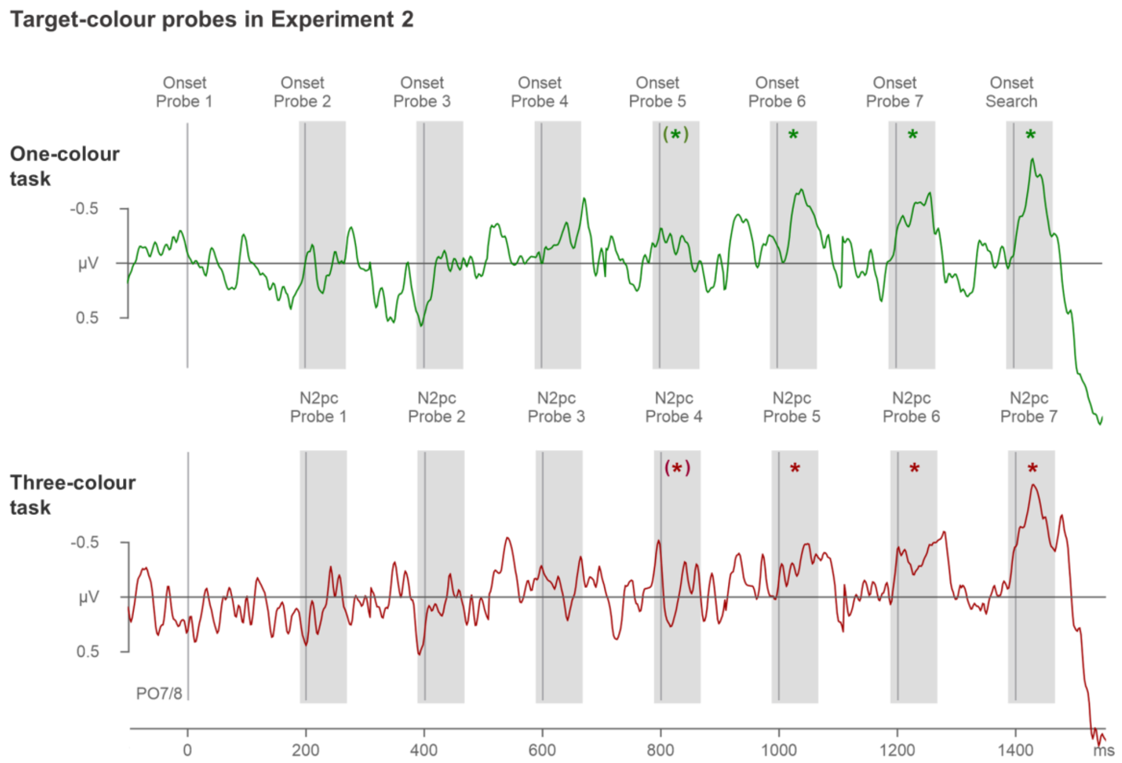


Figure 17 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs triggered by the target-colour probes in the one-colour (top panel) and three-colour tasks (bottom panel) of Experiment 2. Difference waves triggered by individual probes are shown in the same continuous fashion as in Figure 15. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe). Statistically reliable probe N2pcs are marked by asterisks. Note that probe 4 N2pcs were reliable when power was combined across the two tasks (repeated-measures ANOVA), but that individual t-tests for probe 4 N2pcs failed to reach significance in both tasks.

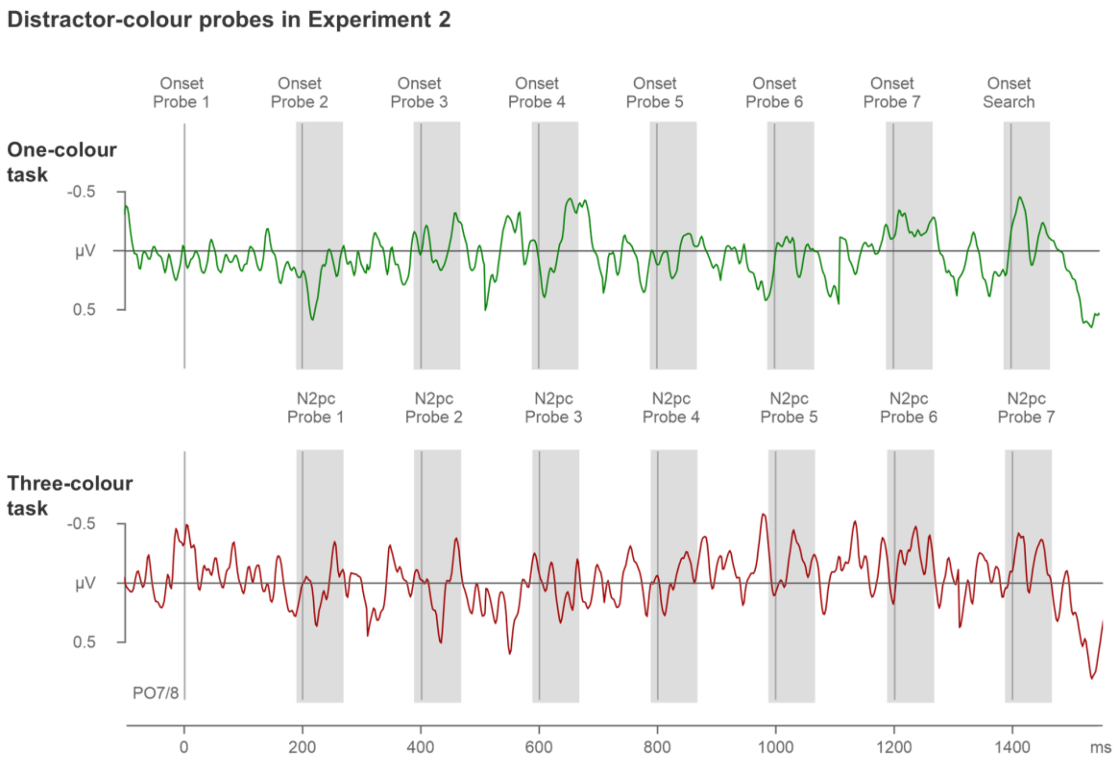


Figure 18 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs triggered by the distractor-colour probes in the one-colour (top panel) and three-colour tasks (bottom panel) of Experiment 2. Difference waves triggered by individual probes are shown in the same continuous fashion as in Figure 15 and 17. Probe onsets are indicated by vertical lines, and probe N2pc time windows by shaded areas (190-270ms after onset of each individual probe). Statistically reliable probe N2pcs would have been marked by asterisks.

ERP mean amplitudes measured at PO7/8 in the 190-270ms post probe time windows were subjected to a repeated-measures omnibus ANOVA with the factors Task (one-colour, and three-colour search), Probe Colour (target-colour, and distractor-colour probe), Probe Number (Probe 1, 2, 3, 4, 5, 6, and 7), and Laterality (electrode contralateral and ipsilateral to the hemifield of a probe). The ANOVA revealed a main effect of Laterality, $F(1,17)=22.2$, $p<.001$, $\eta_p^2=.57$, and two significant interactions between Laterality and Probe Number, $F(6,102)=6.3$, $p<.001$, $\eta_p^2=.27$, and Laterality and Probe Colour, $F(1,17)=24.1$, $p<.001$, $\eta_p^2=.59$. Interestingly, none of the interactions involving the factor Task reached significance, all $F<1$, $p>.688$, $\eta_p^2<.04$.

The effects of Probe Colour were followed up by means of two repeated-measures ANOVAs with the factors Task (one-colour, three-colour), Probe Number (Probe 1-7), and

Laterality (contralateral, ipsilateral activity), separately for target- and distractor-colour probes. The ANOVA on target-colour probe N2pcs uncovered a main effect of Laterality, $F(1,17)=43.8$, $p<.001$, $\eta_p^2=.72$, and a significant interaction between Laterality and Probe Number, $F(6,102)=7.2$, $p<.001$, $\eta_p^2=.30$, indicating that probe N2pc amplitudes differed across the preparation period. The absence of any interaction involving the factor Task, all $F<1$, $p>.992$, $\eta_p^2<.02$, suggests that the pattern of probe N2pcs across the preparation period was identical in the one-colour and three-colour tasks. Follow-up ANOVAs with the factors Task (one-colour, three-colour) and Laterality (contralateral, ipsilateral) revealed main effects of Laterality for probe 4 (-0.2μV), $F(1,17)=4.8$, $p=.042$, $\eta_p^2=.22$[7], probe 5 (-0.3μV), $F(1,17)=15.5$, $p=.001$, $\eta_p^2=.48$, probe 6 (-0.4μV), $F(1,17)=31.6$, $p<.001$, $\eta_p^2=.65$, and probe 7 (-0.6μV), $F(1,17)=34.1$, $p<.001$, $\eta_p^2=.67$. Probes 1, 2, and 3, did not produce any significant N2pcs, all $F(1,17)<3.3$, $p>.089$, $\eta_p^2<.16$. None of these ANOVAs for individual probes produced a reliable interaction with Task, all $F(1,17)<1$, $p>.482$, $\eta_p^2<.03$, indicating that not only the pattern of probe N2pcs, but also the size of the N2pcs triggered by the probes at different temporal positions prior to search were identical in the one-colour and three-colour task.

The ANOVA on distractor-colour probe N2pcs did not produce any main effects of Laterality, $F(1,17)=2.4$, $p=.140$, $\eta_p^2=.12$, or any significant interactions involving the factor Laterality, all $F<1$, $p>.618$, $\eta_p^2<.04$. In other words, none of the distractor-colour probes produced any N2pcs, either in the one-colour or the three-colour task.

3.3.2.3 N2pc components triggered in the search displays

Target ERPs and N2pc difference waves, measured at PO7/8 ipsilateral and contralateral to the side of a target in the 190-270ms time window after search display onset

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[7] *Note that without the combined power of the two task conditions, N2pc components to probe 4 in both the one-colour and three-colour task failed to reach significance, both t(17)<1.3, p>.209, d=.06. All other t-tests for probes 5-7 were significant, all t(17)>2.7, p<.015, d>.23.*

in the one-colour and three-colour tasks, are shown in Figure 16 (bottom panel). A repeated-measures ANOVA with the factors Task (one-colour, three-colour) and Laterality (contralateral, ipsilateral), showed a main effect of Laterality, $F(1,17)=56.2$, $p<.001$, $\eta_p^2=.77$, and a significant Task*Laterality interaction, $F(1,17)=5.9$, $p=.027$, $\eta_p^2=.26$, indicating that targets in both search tasks triggered solid N2pc components, which were significantly larger in the one-colour (-1.0µV) as compared to the three-colour task (-0.7µV)[8]. Target N2pcs in the one-colour task (227ms) were also significantly faster than in the three-colour task (271ms), $t_c(17)=5.0$, $p<.001$, $\eta_{pc}^2=.62$.

3.3.3 Discussion of Experiment 2

In Experiment 1 with alternating target colours, we observed strategic colour-selective preparation that was limited to one rather than three target colours. In the three-colour task of Experiment 2, one of three possible colour-defined targets appeared randomly and unpredictably on each trial. In such a context, optimal search preparation will involve the concurrent activation of all three target colour templates. It is conceivable that the colour-selective preparation observed in Experiment 1 was not strategic, but an effect of capacity limitations on the number of search templates that can be maintained simultaneously. In this case, it should not have been possible to concurrently activate three colour templates in Experiment 2. However, the probe N2pc results obtained in the three-colour task of Experiment 2 do not provide any evidence for the existence of such a rigid capacity limitation. Target-colour probes triggered reliable N2pc components from about 600ms prior to search display onset, demonstrating that colour templates were indeed activated during

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[8] *These amplitude results were the same when the target N2pcs were re-analysed in a time window of 240-320ms that matched the time course of target N2pcs more closely (starting at 50% of the peak amplitude of the pooled one- and three-colour target N2pc). Target N2pcs were reliable, $F(1,17)=70.2$, $p<.001$, $\eta_p^2=.81$, and were significantly increased in the one-colour (-1.6µV) as compared to the three-colour task (-0.8µV), $F(1,17)=22.3$, $p<.001$, $\eta_p^2=.57$. For completeness, the target N2pc in Experiment 1 (-1.2µV) was also reliable in this time window, $t(17)=7.5$, $p<.001$, $d>.32$.*

search preparation. The fact that distractor-colour singleton probes did not trigger any N2pcs showed that the presence of target-colour probe N2pcs was not in any way related to salience-driven attentional capture.

Most notably, there was no difference in the time points when probe N2pcs emerged during the preparation period, or in the size of these N2pcs, between the three-colour and one-colour tasks. This is an important observation because it shows that preparatory template activation processes were equivalent regardless of whether the search task required the activation of one constant or three different colour templates. In order words, it strongly suggests that there is no rigid capacity limitation for the activation of multiple attentional templates, and that at least three templates can be activated in parallel without apparent costs. Further evidence for the absence of any capacity limitations during preparation for three-colour search comes from the observation that distractor-colour probes were fully ignored and did not trigger any N2pcs, neither in the one- or the three-colour task. This suggests that the precision of the target colour representations held in working memory did not suffer in the three- as compared to the one-colour task.

In contrast to the apparent absence of any capacity limits of template activation during the preparation period, clear differences between the one-colour and three-colour tasks emerged once a search display had been presented. There were pronounced behavioural costs associated with multiple-colour search, as RTs were delayed by more than 100ms and error rates were three times higher in the three-colour as compared to the one-colour task. This was mirrored by N2pc components triggered in response to search targets, which were attenuated and delayed during the three-colour search[9]. These behavioural and electrophysiological search costs are in line with previous studies contrasting one- and two-colour search tasks

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[9] *Note that power was sufficient to detect large behavioural and N2pc effects. Because the probe N2pcs contained fewer epochs than the RT averages and target N2pcs it is theoretically possible that small effects of task at the level of the probe N2pcs may have been missed. However, there was no statistical evidence for the existence of such effects (i.e., F-values were <1 for all interactions between task and laterality).*

(e.g., Grubert & Eimer, 2016; Irons et al., 2012), and demonstrate again that attentional guidance and/or subsequent processes involved in search target selection and identification operate less efficiently when the identity of this target is uncertain. The factors that may be responsible for the remarkable contrast between the absence of any multiple-target costs during search preparation and the presence of large costs during the search episode itself will be considered in the General Discussion.

3.4 General Discussion

The goal of this study was to employ ERP markers of target template activation processes during search preparation to investigate capacity limitations associated with activating multiple templates simultaneously, and the costs that arise because of such limitations. Previous work has shown that at least two colour-specific target templates can be activated at the same time (e.g., Grubert & Eimer, 2016, 2023; Irons et al., 2012). To study whether this number represents an upper capacity limit, we employed search tasks where participants searched for one of three possible colour-defined targets, and measured N2pc components elicited by target-matching and target-nonmatching colour singleton probes that appeared in rapid succession during the interval between two search displays.

In Experiment 1, where the three different targets appeared in a fixed order (ABCABC), so that target identity was fully predictable, reliable N2pc components were elicited only by singleton probes that matched the colour of the upcoming target, but not by probes that matched either of the other two target colours. This demonstrates that search preparation was colour-selective and restricted to a single attentional template in this experiment. In contrast, when task demands changed so that the three colour-defined targets were randomly intermixed and target identity was thus no longer predictable (Experiment 2), all three target-matching singleton probes triggered N2pc components. This indicates that three colour templates were activated in parallel during unpredictable three-colour search.

The fact that these N2pc components were equivalent in size to the N2pcs triggered by target-matching probes in a one-colour task where only a single attentional template was task-relevant suggests that multiple target-colour templates can be activated without apparent costs relative to single-template search (but see below for some caveats). Overall, these results imply that template activation during three-colour search can be limited to a single template when target identity is predictable. However, this is not the result of rigid capacity limitations, as it is possible to maintain at least three different preparatory colour templates simultaneously when this is required because three different colour targets are equally likely to appear in any given search display (see also Kerzel & Grubert, 2022, for behavioural support for this conclusion).

The observation that only the colour template that was relevant for the next search episode was activated in Experiment 1 during fully predictable three-colour search (ABCABC) raises the question why two colour templates were activated in our previous study (Grubert & Eimer, 2020) which was identical to this experiment, with the only difference that two (ABAB), as opposed to three, target colours were employed in the earlier study. There are several possible reasons for this difference. First, given that the cognitive load associated with maintaining multiple attentional templates in working memory increases with each template that is added, participants should have a stronger incentive to adopt a single-template strategy during predictable three-colour search than during two-colour search. Second, during three-colour search, displays with a particular colour target were always followed by two search displays with different colour targets. During two colour-search, the same colour target appeared in every second display. The longer interval between search displays with the same relevant target colour in the three-colour task may have further encouraged the preparation of a single colour template in the current Experiment 1 (see Grubert et al., 2024, and Lien et al., 2010, for electrophysiological and behavioural evidence, respectively, of single template activation in AABB designs when the temporal interval between relevant templates is increased as compared to ABAB designs). Both factors (increased cognitive load and longer gaps between target repetitions) may have combined to produce the difference in template activation strategies between predictable two-colour and three-colour search.

The electrophysiological and behavioural results of Experiment 2 present an interesting conundrum. While the pattern of probe-induced N2pc components suggests equally strong target template activation during one-colour and three-colour search, behavioural performance and N2pc components and electrophysiological effects in response to search displays suggest clear capacity limitation for three-colour search. This dissociation is consistent with previous behavioural (Kerzel & Grubert, 2022) and ERP studies (Grubert, et al., 2016; Grubert & Eimer, 2023; Ort et al., 2019), which also found costs for multiple-colour versus single-colour search primarily for target selection but not during search preparation (see also Ort & Olivers, 2020, for further discussion).

One obvious factor that contributes to costs associated with multiple-colour as compared to single-colour search is the fact that target colours are uncertain in the former case but fully predictable in the latter case. Multiple-colour costs may also be the result of the existence of inhibitory links between multiple simultaneously active target templates (e.g., Grubert et al., 2016; Kerzel & Grubert, 2022; Ort et al., 2019). Between-template suppression during two-colour or three-colour search will result in lower overall template activation levels as compared to one-colour search, and this should result in less efficient template-guided target selection, as reflected by behavioural and electrophysiological costs for multiple-colour search observed here and in prior studies (see Kerzel & Grubert, 2022, for specific model predictions). But if there is mutual inhibition between concurrently active templates, why is this not also reflected by a corresponding attenuation of N2pcs to template-matching probes presented during the preparation for multiple-colour as compared to single-colour search? To answer this question, it is important to stress that probe N2pc components do not reflect search template activation levels directly, but instead the allocation of attention to a colour singleton probe that is guided by a matching template. Such interactions between a search template and a template-matching visual object may trigger an additional transient increase in the activation of this particular template (see also Moore & Weissman, 2010, 2014, for similar suggestions), resulting in similar probe N2pc amplitudes during one-colour and three-colour search.

Although this explanation may seem speculative, it can be directly tested based on the data obtained in Experiment 2. If the activation level of a particular colour template in the three-colour task is temporarily enhanced by its match with a colour singleton probe, this should have direct consequences for the attentional processing of search displays. More specifically, if selection of probe 7 that immediately precedes a search display selectively boosts a specific template, this should benefit attentional guidance and target selection on trials where the subsequent search target matches this template. Such a benefit was indeed observed behaviourally for these trials by Kerzel and Grubert (2022) during three-colour search. To obtain more direct electrophysiological evidence for such probe-target colour match benefits, we conducted additional analyses of target N2pc components measured in the one-colour and three-colour tasks of Experiment 2. These N2pcs were computed separately for targets that either matched or did not match the colour of the immediately preceding probe 7. Figure 19 (left panel) shows N2pc difference waveforms for targets in the three-colour task that were preceded either by a colour matching or nonmatching target-colour probe, or by an irrelevant distractor-colour probe. When the target was preceded by a matching target-colour probe, N2pcs were significantly larger (-0.9µV), $t(17)=2.9$, $p=.040$, $d=.59$, and emerged earlier (231ms), $t_c(17)=6.1$, $p<.001$, $\eta_{pc}^2=.71$, than when it was preceded by a non-matching target-colour probe (-0.5µV; 276ms). In contrast, there were no N2pc amplitude or onset latency differences between trials in which targets were either preceded by a non-matching target-colour or a distractor-colour probe (-0.4µV, 270ms), both *t*(17)<1. This demonstrates that a colour match between probe 7 and the subsequent target does indeed facilitate template-guided target selection. Figure 19 (right panel) shows the corresponding target N2pc results for the one-colour task, separately for trials where the target was preceded by a target-colour probe (-1.0µV, 225ms) or by a distractor-colour probe (-1.0µV, 215ms). In this task, there were no N2pc amplitude or onset latency differences associated with the probe-target colour relationship, both *t*(17)<1.1, demonstrating that target selection remained efficient regardless of whether probe 7 matched the colour of the target or a distractor. Moreover, a comparison of trials where targets were preceded by a matching probe between the one-colour and three-colour tasks revealed no N2pc amplitude and latency differences, both *t*(17)<1.

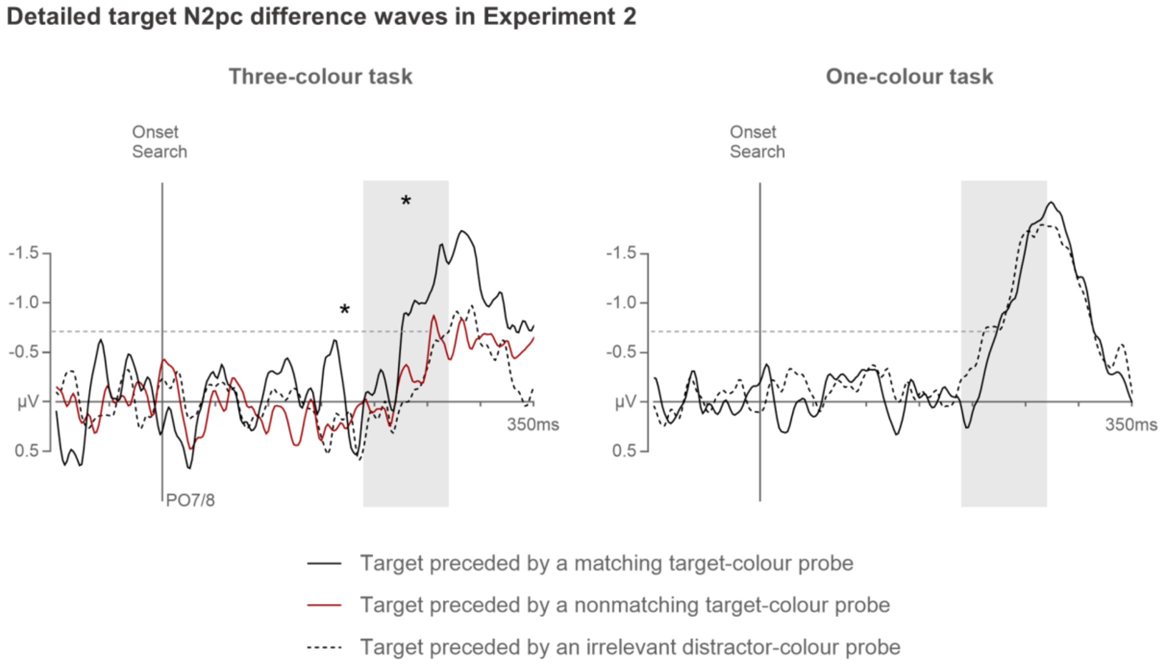

Figure 19 N2pc difference waveforms computed separately for targets that were preceded by colour-matching or nonmatching target-colour probes, or by irrelevant distractor-colour probes in the three-colour (left panel) and one-colour tasks (right panel) of Experiment 2. Shaded areas indicate N2pc time windows (190-270ms after

search display onset). Asterisks represent significant differences in mean amplitudes and onset latencies (measured at -0.7µV, as indicated by the dashed horizontal lines).

These N2pc results were mirrored by the behavioural data. RTs in the three-colour task were significantly faster when the target was preceded by a matching (724ms) versus nonmatching target-colour probe (744ms), *t*(17)=3.0, *p*=.032, *d*=.20. There was no RT difference between trials in which the target was preceded by a nonmatching target-colour or a distractor-colour probe (732ms), *t*(17)<1. In the one-colour task, RTs were virtually identical on trials in which the target was preceded by a target-colour (615ms) or a distractor-colour probe (616ms), *t*(17)<1. However, even though search was faster in the three-colour task when targets were preceded by colour-matching probes, RTs on these trials were still substantially slower than in the one-colour task, *t*(17)=6.4, *p*<.001, *d*=1.3[10]. In other words, while the search costs associated with multiple- as compared to single-colour search on attentional guidance (as measured with the N2pc) can be fully accounted for by probe-target colour relationships, there are additional costs at the behavioural level which are likely to be generated at post-guidance stages of attentional selectivity (see Ort et al., 2019).

Overall, these additional analyses support the hypothesis that between-template competition during three-colour search affects the efficiency of attentional guidance towards search targets and produces search performance costs relative to single-colour search. In this context, it is interesting to note that there were no target N2pc differences between trials where the preceding probe matched a different target colour (resulting in increased activation of a target non-matching template) and trials where this probe matched a distractor colour (producing no additional activation of any target-colour template). This suggests that while

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[10] *Error rates were also still significantly increased in the three-colour (10%) as compared to the one-colour task (4%), t(17)=3.7, p=.008, d=1.2, even when the targets were preceded by target colour matching probes. None of the other comparisons revealed significant differences on error rates, all t(17)<1.*

the prior activation of a matching template facilitates target selection in multiple-colour search, the activation of a different non-matching template produced no additional costs.

In summary, the current study has obtained new insights into the nature of capacity limitations that arise when observers search for one of several possible target objects, and multiple preparatory target templates have to be activated concurrently. First, and most importantly, the presence of reliable N2pc components to target-colour probes during three-colour search when target identity was unpredictable, and the absence of any N2pcs to distractor-colour singleton cues, shows that at least three search templates can be activated in parallel. However, the template-guided allocation of attention towards search targets, as well as search performance, are less efficient during three-colour as compared to one-colour search, and these costs are associated with inhibitory interactions between simultaneously active search templates.

3.5 Supplementary Materials

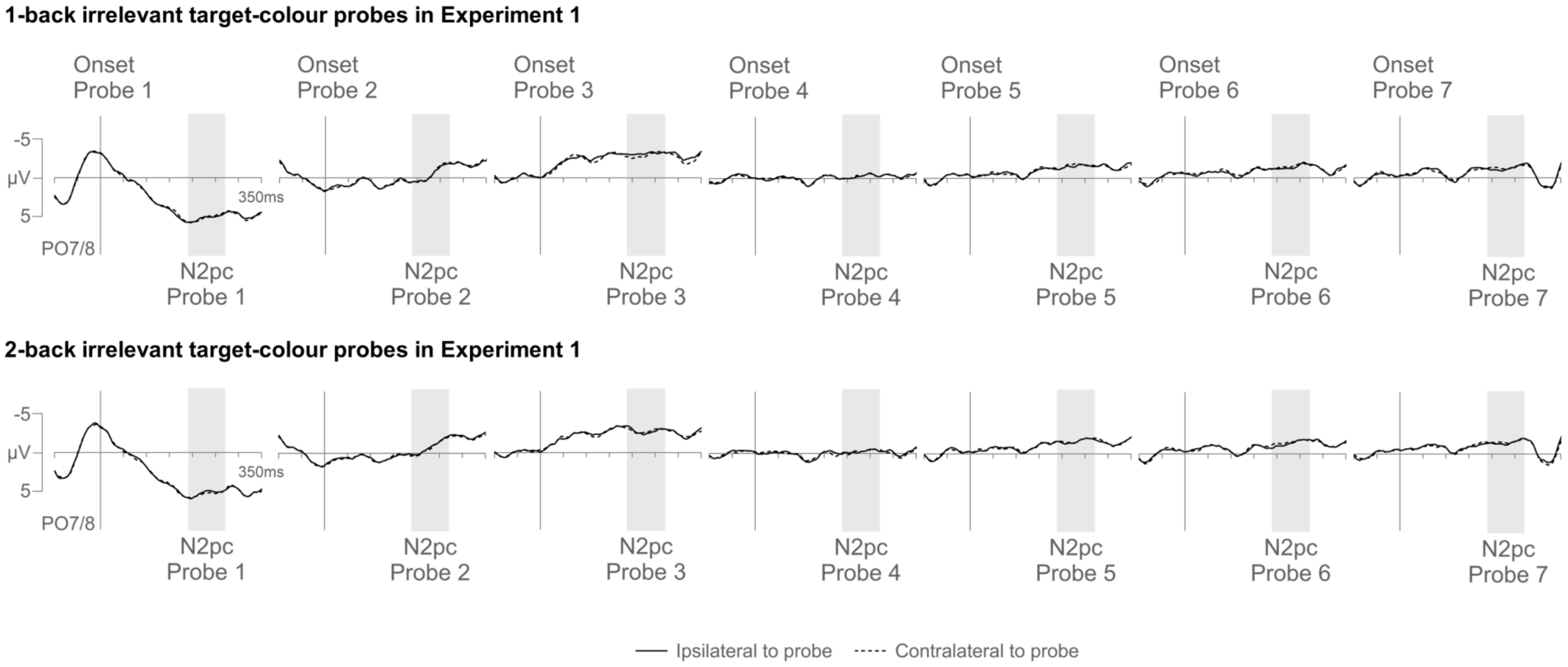

Figure 20 Grand-averaged ERPs elicited at electrode sites PO7/8 contralateral and ipsilateral to 1-back (top panel) and 2-back (bottom panel) irrelevant target-colour probes 1 to 7 in Experiment 1. N2pc time windows are indicated by shaded areas (190-270ms after onset of each individual probe).

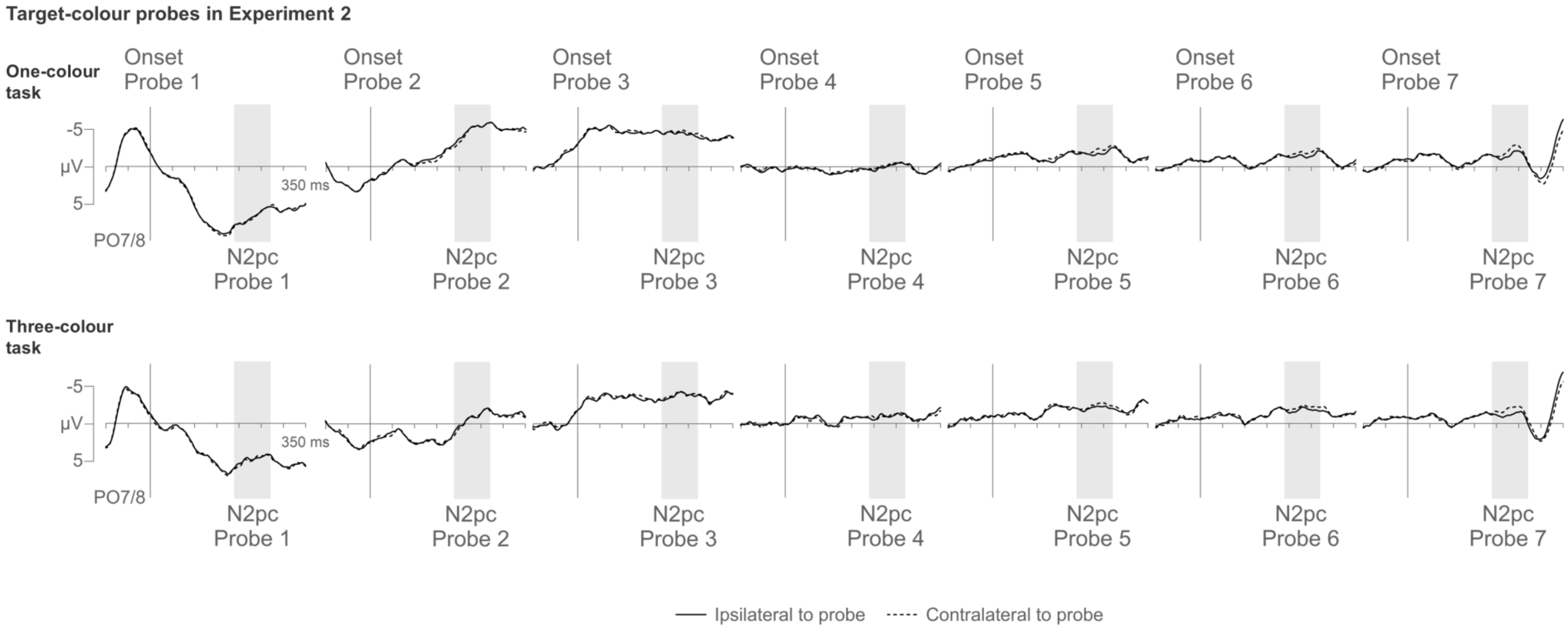

Figure 21 Grand-averaged ERPs elicited at electrode sites PO7/8 contralateral and ipsilateral to target-colour probes in the one-colour (top panel) and three-colour tasks (bottom panel) of Experiment 2. N2pc time windows are indicated by shaded areas (190-270ms after onset of each individual probe).

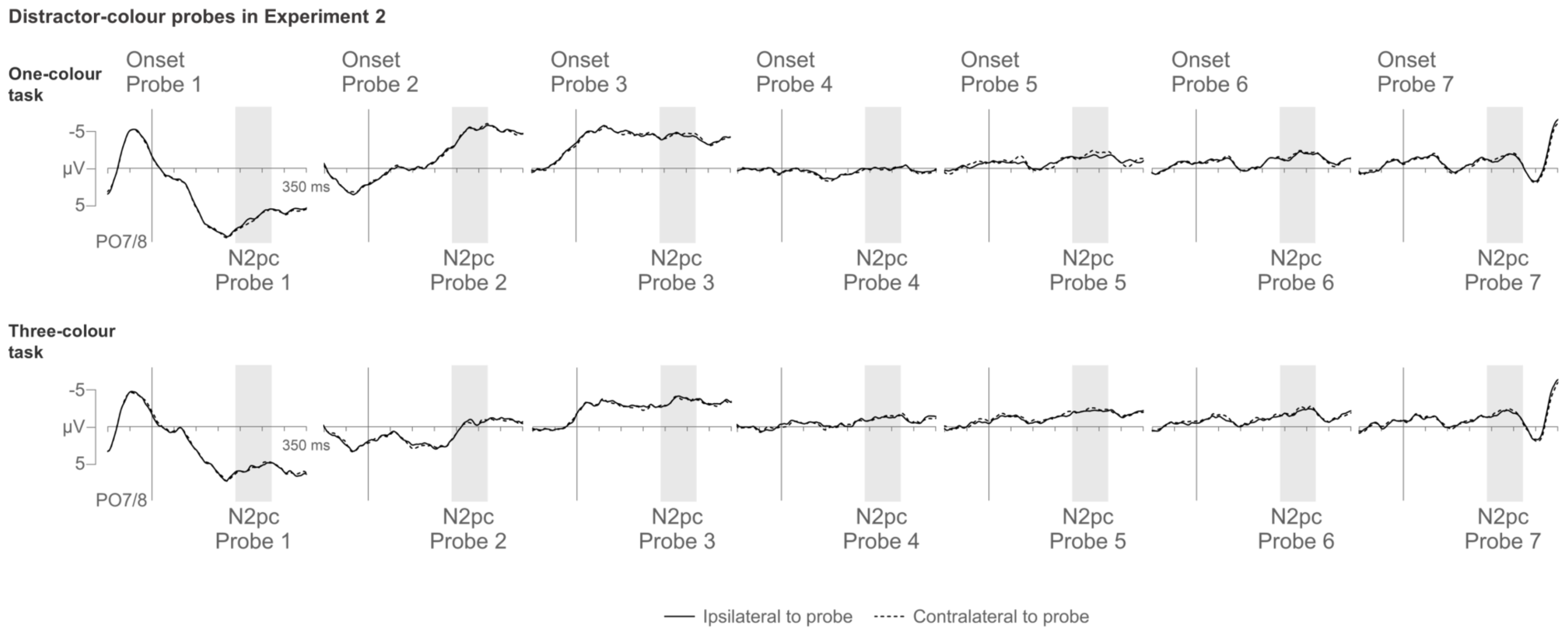

Figure 22 Grand-averaged ERPs elicited at electrode sites PO7/8 contralateral and ipsilateral to distractor-colour probes in the one-colour (top panel) and three-colour tasks (bottom panel) of Experiment 2. N2pc time windows are indicated by shaded areas (190-270ms after onset of each individual probe).

Chapter 4 Activation of multiple attentional templates in colour and shape, but not in conjunction search

4.1 Introduction

Attentional guidance towards task-relevant objects is controlled by attentional templates, i.e., target representations held in working memory (e.g., Duncan & Humphreys, 1992; Olivers et al., 2011; Soto et al., 2008). Attentional templates contain target descriptions, such as a particular colour or shape, which are activated in a preparatory (e.g., Chelazzi et al., 1998) and transient fashion (e.g., Grubert & Eimer, 2018) before the arrival of the search display. Once activated, any object in the visual field that matches the content of the current target template will automatically attract attention (e.g., Desimone & Duncan, 1995; Folk et al., 1992; Grubert & Eimer, 2016a; Martinez-Trujillo & Treue, 2004; Wolfe, 2021) in a spatially global manner (e.g., Berggren et al., 2017; Eimer, 2014; McAdams & Maunsell, 2000; Saenz et al., 2002). However, the content of attentional templates remains a topic of debate. One controversial issue is concerned with the question as to whether attentional templates contain single features per default (e.g., blue), or whether they can contain feature conjunctions (e.g., blue and large) that form a wholistic object representation, e.g., during search for a large blue textbook between other blue but small or large but green books on the bookshelf.

Contemporary theories of visual search propose that the initial analysis of the visual field is feature-based (Bundesen, 1990; Huang & Pashler, 2007; Itti & Koch, 2001; Müller & Krummenacher, 2006; Wolfe, 2021). According to Guided Search 6.0 (Wolfe, 2021), attentional deployment is controlled by a feature-based “priority map” which signals the most likely target location, and which is continuously updated during visual search as stimulus-, user-, and context-dependent parameters change. Only when a potential target location is selected, object features are bound together, and holistic object representations are matched with stored target representations held in long-term memory for target identification (see also Cunningham & Wolfe, 2014). Behavioural (e.g., Becker et al., 2020; Dent, 2023), eye tracking (e.g., Williams & Reingold, 2001), computational modelling (e.g., Rutishauser & Koch, 2007), and electrophysiological studies (e.g., Berggren & Eimer, 2018; Eimer & Grubert, 2014) have delivered empirical evidence for the hypothesis that early visual selection is feature-based even during conjunction search, when multiple task relevant features are presented in the same object. In a study from our own lab (Eimer & Grubert, 2014), participants searched for conjunctive colour and shape targets (e.g., blue square). In some trials, the target was absent, but a colour-matching (e.g., blue circle) or a shape-matching (e.g., yellow square) distractor was presented. We recorded EEG and measured the N2pc component of the event-related potential as an electrophysiological marker of attentional selection in response to these targets and partially matching distractors. The N2pcs is an increased negativity, elicited at around 200ms after stimulus onset at posterior electrode sites over extrastriate visual cortex (e.g., Hopf et al., 2000), contralateral to the side of an attended object (Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999). All objects that contained any of the two target features, i.e., targets, colour-matching and shape-matching distractors, produced solid N2pcs, indicating that attentional selection was guided by individual target features as opposed to holistic object representation (in which case partially matching distractors should have been ignored). Interestingly, the target N2pc was initially identical to the summed N2pc of the partially matching distractors, but after approximately 250ms, the target N2pc became larger than the summed distractor N2pc. This finding suggests that selection was initially guided by signals from the colour and shape dimension independently and in an additive fashion. From about 250ms, however, attentional processing became superadditive and sensitive to the joint presence of both relevant target-defining features within the same object.

In contrast to the feature-specific templates proposed in visual search, empirical evidence from the working memory literature shows that “chunking” single features into holistic object representations is an efficient method to reduce working memory load during information retention (e.g., Cowan, 2001; Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Quinlan & Cohen, 2011). For example, Luck and Vogel (1997; see also Vogel et al., 2001) used a change detection task in which they presented participants with memory arrays of two, four, or six coloured bars of different orientations. After a short retention period, a test display appeared, and participants had to decide whether the bars were identical to the memory array or whether a change had occurred. In the single feature conditions, participants were instructed to only memorise the colour or orientation of the bars, as a change could only occur in either the colour or orientation dimension, respectively. However, in the conjunction condition, participants had to memorise both the colour and orientation of the bars because a change could occur in either feature dimension. If participants can only memorise individual features, this would mean that the memory load would be doubled in the conjunction as compared to the single feature conditions. Already with a set size of two conjunctive objects, this would result in a memory load of four individual features, which would fill up working memory to its capacity (3-4 items; e.g., Cowan, 2001). Memory accuracy should therefore be substantially lower in the conjunction as compared to the single feature conditions. However, results revealed identical accuracy rates in both the single feature and the conjunction condition across all set sizes. This shows that participants successfully integrated the colour and orientation features into a coherent object representation and kept working memory load identical in the conjunction and single feature tasks.

These observations from the working memory literature raise the question as to why attentional templates, which are assumed to be part of working memory (e.g., Duncan & Humphreys, 1992; Olivers et al., 2011; Soto et al., 2008) cannot also hold integrated target representations. Or perhaps they can, and it is just the subsequent guidance mechanism in search that is limited to single features? It might also be that previous search studies have failed to measure activation of conjunctively defined target templates because the memory set size in visual search is typically a single target and therefore rarely exhausts working memory limits. In contrast, change detection tasks often employ memory set sizes that make use of the full capacity of working memory. It might be possible that with an increased working memory load, observers have a stronger incentive to integrate single features into object-based templates for visual search. Berggren and Eimer (2018), for example, found evidence for object-based attentional templates during search for two feature conjunctions, but only under conditions when purely feature-based templates were entirely insufficient to discriminate target from distractor objects. Vice versa, Balaban and Luria (2016), showed that feature integration for conjunction stimuli is not mandatory in change detection and critically depends on stimulus parameters and task demands.

We tested the above hypotheses by presenting participants with single feature tasks in which targets were defined by colours or shapes, and a conjunction task in which targets were defined by combinations of colour and shape. Each task had two working memory load conditions. In low-load trials, targets had a single colour/shape/colour&shape conjunction, while they were shown in one of two possible colours/shapes/conjunctions in high-load trials. The relevant target colours/shapes/conjunctions for each trial were cued prior to search display onset. Load effects (costs associated with the activation of two as compared to one attentional template) were substantiated at consecutive stages of the search process, i.e., during template activation prior to search (CDA, see below), during attentional guidance (N2pc), and at response execution (RTs and error rates).

Several studies, using a variety of search paradigms and measures, have shown that multiple attentional templates can be activated in parallel when multiple target features, e.g., two colours, are task relevant (e.g., Barrett & Zobay, 2014; Beck et al., 2012; Berggren & Eimer, 2020; Christie et al., 2015; Grubert & Eimer, 2016a, 2023; Irons et al., 2012;

Kristjánsson & Kristjánsson, 2018; Moore & Weissman, 2010; Ort et al., 2019). In a previous study from our lab (Grubert et al., 2016), participants searched for one, two, or three possible target colours that were specified by one, two, or three colour cues at the beginning of each trial, respectively. Search displays contained four differently coloured digits and letters, one of which was always shown in (one of) the pre-cued colour(s). Participants' task was to identify the target-colour object as a letter or digit, respectively. Results revealed substantial load costs at the behavioural level with RTs being delayed by more than 100ms for each additional colour that was task relevant. But N2pc components, measured in response to the search targets, were only delayed by about 30ms and 20ms between the one- and two-colour and the two- and three-colour tasks, respectively. While the much more pronounced RT costs are likely generated at post-guidance stages of attentional selectivity (e.g., Ort et al., 2019; and Ort & Olivers, 2020), the significant but small N2pc delays measured at the level of attentional guidance can be explained by mutual inhibition between simultaneously activated attentional templates (e.g., Kerzel & Grubert, 2022; Ort et al., 2019). This assumption was also confirmed by analyses of the contralateral delay activity (CDA) which was measured in response to the colour cues at the beginning of each trial. The CDA component is a sustained negative deflection triggered at posterior electrode sites which is elicited during the active maintenance of target representations in working memory (e.g., Carlisle et al., 2011) and was found to increase in size with increasing memory load (e.g., Vogel & Machizawa, 2004). In our experiment, CDA components systematically increased from one- to two- and then again from two- to three-colour search, demonstrating that participants did activate an increasing number of templates in parallel prior to search. From these observations we can predict that if attentional templates can hold integrated target representations, load effects as measured at the behavioural and electrophysiological level should be identical in single feature and conjunction search. Alternatively, if attentional templates can only hold single features, load effects should be substantially increased in the conjunction task in which the feature load is twice the size than in the feature search tasks.

However, before we were able to test the conjunction search (Experiment 2), we ran Experiment 1 to establish whether colour and shape templates are equally efficient in their attention guiding quality. On the one hand, there is behavioural (e.g., Moutoussis & Zeki, 1997; Wolfe & Horowitz, 2004) and electrophysiological (e.g., Lee et al., 2018) evidence that colour processing is superior to shape processing. And these experiments have support from historical anatomical studies (e.g., Barlow, 1972) as well as more contemporary fMRI studies which found clear segregation between colour and shape processing in the brain (e.g., Lafer-Sousa et al., 2016). On the other hand, there has been growing evidence showing that, since colour and shape are both processed in V4 (see Roe et al., 2012, for a review), colour and shape processing may be more intertwined than historically assumed (see Rentzeperis et al., 2014, for a review).

4.2 Experiment 1

4.2.1 Methods

4.2.1.1 Participants

Eighteen participants were tested in Experiment 1 and received £10 per hour for their work. The experiment was approved by the Ethics Committee of the Psychology Department at Durham University and was conducted in accordance with the Declaration of Helsinki. Participants gave informed written consent prior to testing. Three participants were excluded from data analysis, two of them because of excessive eye movements resulting in a loss of more than 50% of all trials during artefact rejection, and the other one because of accuracy rates below 80%. Of the remaining 15 participants, aged between 19 and 45 years (Mean=26.5, SD=5.9), ten were female and five were male. Three of the 15 participants were left-handed and 12 were right-handed. All participants had normal or corrected-to-normal vision and full colour vision, as verified with the Ishihara colour vision test (Ishihara, 1972). The sample size of 15 was calculated by means of an a priori power analysis using MorePower 6.0.1 (Campbell & Thompson, 2012) to detect a 2×2 interaction (memory load*laterality) in a repeated-measures ANOVA (within-subjects) with an assumed alpha of .05, power of .95, and a large effect size >1.[11]

4.2.1.2 Stimuli and procedures

Participants were seated in a sound attenuated and dimly illuminated Faraday cage. Visual stimuli were presented on a PC monitor at a viewing distance of approximately 90cm. A 17-inch Samsung wide Syncmaster 753S monitor (1280×1024 pixels resolution, 100Hz refresh rate) was employed. Stimulus presentation, timing, and response collection were controlled by an LG Pentium PC running under Windows XP, using the Cogent 2000 toolbox for MATLAB (RRID: SCR_001622; www.mathworks.com/products/matlab/).

Stimuli were presented on a black background. A grey fixation point was presented at the centre of the screen throughout each experiment block (0.2°×0.2° of visual angle; x/y CIE colour coordinates: .317/.359). Each trial started with the presentation of an indicator display for 200ms, which was followed by a 200ms cue display. After an 800ms blank retention period, the search display appeared for 200ms (Figure 23A). The inter-trial interval between the offset of a search array and the onset of the indicator display of the next trial was 2000ms.

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[11] *A large effect size was expected to replicate partial eta squared values (η_p^2) of .55, which we measured in a previous N2pc experiment in which participants searched for one versus two target colours (Colour load*Laterality interaction in Experiment 1 of Grubert, Carlisle, & Eimer, 2016; p.1953). Note that the sample size of that reference study was also 15.*

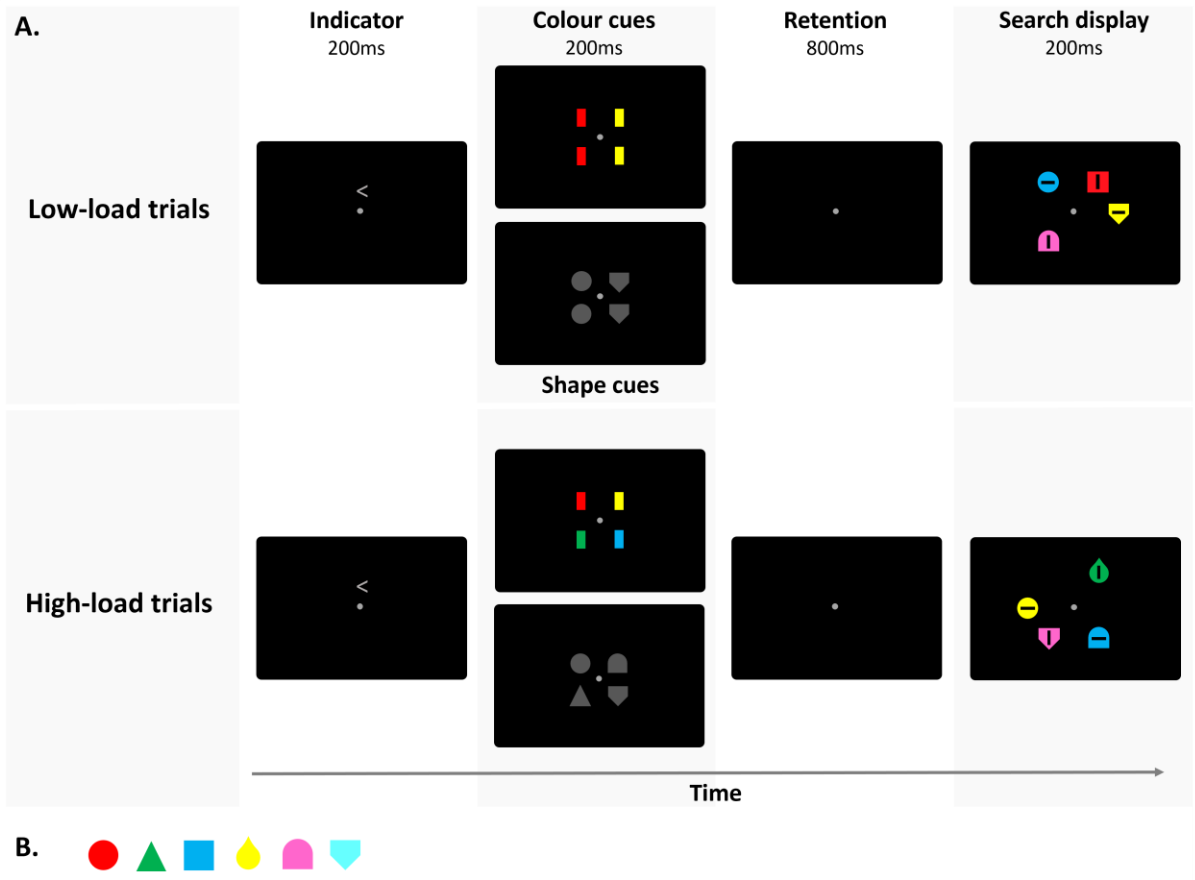

Figure 23 Schematic illustration of the stimuli and temporal trial sequence in Experiment 1. Each trial began with the presentation of an arrowhead pointing to the left or right to indicate the task relevant side for the upcoming cue display. Cues informed participants about the upcoming one (low-load trials) or two (high-load trials) target colours (colour task) or shapes (shape tasks), respectively. Cue displays were followed by a retention period and the search displays which contained four differently coloured shapes randomly presented at four of six possible equidistant positions on an imaginary circle (two in each hemifield). Participants' task was to report the line orientation (horizontal, vertical) shown within the target object that matched the cued target colour or shape, respectively.

Two blocked task conditions were tested in Experiment 1. In the *colour task*, participants searched for a pre-defined target-colour object amongst differently coloured nontargets. In the *shape task*, they searched for a pre-defined target shape amongst different nontarget shapes. Importantly, search displays were physically identical in the two task conditions as they each contained four differently coloured individual shapes (0.5°×0.5°) with a black horizontal (0.4°×0.1°) or vertical (0.1°×0.4°) line inside. Each search array contained two objects at each display side. These were presented randomly at two out of three possible locations in the right (1, 3, or 5 o'clock position of an imaginary clock face) or left hemifield

(7, 9, or 11 o’clock position). All stimulus locations had an eccentricity of 1° from central fixation. There were six possible stimulus colours (Figure 23B): red (.621/.335), green (.285/.616), blue (.180/.176), yellow (.462/.465), pink (.340/.174), and cyan (.217/.355). All colours, including the grey of the fixation point, were equiluminant (~9.5cd/m^2). There were also six possible stimulus shapes (Figure 23B): circle, triangle, square, drop, gate, and inverted house. The drop, gate, and inverted house shapes were created by combining the canonical shapes, mimicking the mixing of the three primary colours to achieve yellow, pink, and cyan. All shapes were matched with respect to size in pixels (36×36).

One of the four objects in each search display contained a cued target colour or shape, respectively, and participants' task was to find this search target and report the orientation (horizontal, vertical) of the black line inside it. Each colour/shape combination was used equiprobably as the target within each block, even though the object shape was task irrelevant in the colour task, and vice versa, the object colour was irrelevant in the shape task. The target location was pseudo-randomised so that, in each block, the target appeared equiprobably in the left and right hemifield. The line orientations within the four search objects were independently and fully randomly selected in each trial.

The target identity was cued prior to search onset and changed in every trial. Cue displays contained two sets of two vertically aligned objects presented bilaterally to the left and right of fixation at a horizontal distance of 0.3° (measured relative to the centre of each cue item). In each hemifield, the two cues were presented at a vertical distance of 0.3° above and below the horizontal midline. In the colour task, the cues were rectangles (0.2°×0.4°) shown in the colours described above. In the shape task, the cue displays contained the shapes described above in grey colour (0.4°×0.4°). Only one side of the cue display was task relevant in each given trial and contained the target colours/shapes for the upcoming search. The relevant cue side was randomised but equiprobable in each block and was determined at the beginning of each trial by means of an indicator display. Indicator displays contained a central grey arrowhead presented above fixation, that pointed towards the side with the target colour/shape cues. In half of the trials, the target colour/shape cues and the subsequent target appeared on the same side, in the other half of the trials, they were presented in opposite hemifields. Each task condition (colour, shape task) contained two equiprobable and intermixed memory load conditions. In *low-load trials*, the two target cues were identical and had the same target colour or shape, respectively. In *high-load trials*, the two target cues showed two different colours or shapes, respectively, either of which could appear in the search display. Note that there was only ever one target in each search display. The other cued target colour/shape never appeared in the search display. The location of the cue (top/bottom) that contained the actual target colour in each trial was fully randomised between trials. The nontarget cues randomly contained one (low-load trials) or two (high-load trials) different colours or shapes, respectively, which always appeared as nontargets in the search display, too.

Responses were given bi-manually on a standard keyboard using the up and down arrow keys, respectively. Response-to-key (top or bottom key for horizontal or vertical line) and hand-to-key assignments (left or right hand on top or bottom arrow key) were counterbalanced across participants but remained the same for each participant throughout the experiment. Each block contained six trials for each combination of memory load (low-, high-load), cue side (left, right hemifield) and target side (left, right hemifield). Both the colour and shape task each contained 12 blocks of 48 trials, resulting in a total of 1152 experimental trials for Experiment 1. Seven of the participants completed the colour task first and then the shape task, and vice versa for the other eight participants. Before the first block of each task, participants completed a practise block to familiarise themselves with the task. These practise data were not recorded.

4.2.1.3 EEG recording and data analyses

The continuous EEG was DC-recorded from 23 scalp electrodes at Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz, plus two HEOG electrodes next to the outer cantus of each eye. EEG data were recorded using the Brain Vision Recorder (RRID: SCR_016331; www.brainproducts.com) at a sampling rate of 500Hz with a 40Hz low-pass filter. No other offline filter was applied after data acquisition. Impedances were kept below 5kΩ. All channels were referenced online to the left-earlobe and re-referenced offline to an average of both earlobes. Data from trials with incorrect or missing responses, or with anticipatory (<200ms) or slow responses (>1500ms), were not included in the analysis. Trials contaminated with eye movements (exceeding ±30µV in the bipolar HEOG channel), eye blinks (exceeding ±60µV at Fpz), and muscular movement artefacts (exceeding ±80µV in all other channels) were removed as artefacts. Artefact rejection resulted in an exclusion of 13.8% of all trials in the colour task (SD=15.2%; ranging between 0.6% and 33.9% across participants) and 12.5% of all trials in the shape task (SD=11.8%; ranging between 0.9% and 35.3% across participants). The remaining EEG was segmented into 500ms epochs ranging from 100ms before to 400ms after search display onset. The first 100ms served as a pre-stimulus baseline. EEG was averaged separately for each combination of memory load (low-, high-load) and target side (left, right hemifield). All EEG data processing was performed using the Brain Vision Analyzer Software (RRID: SCR_002356; www.brainproducts.com). N2pc mean amplitudes were quantified at lateral posterior electrodes PO7 and PO8, contralateral and ipsilateral to the target side, in the 190-290ms interval after search display onset. N2pc onset latencies were calculated based on difference waveforms, computed by subtracting ipsilateral from contralateral activity. Jackknife-based procedures were applied (Miller et al., 1998) in which 15 grand-average difference waves were computed, always leaving out one different participant from the sample. N2pc onset latencies were defined as the point in time when the ascending flank of each subsample difference wave reached -0.8µV (50% of the peak amplitude of the averaged target N2pc, pooled across all targets in all conditions of Experiment 1; see e.g., Grubert & Eimer, 2023, for similar procedures). Jack-knifed F-values (labelled F_c) were power-corrected according to Ulrich and Miller (2001). Effect sizes are reported as Cohen's d (Cohen, 1988) with a CI of 95% for t-tests, and as partial eta squared (η_p^2) for F-tests (η_{pc}^2 for power-corrected F-testes, respectively; see Grubert & Eimer, 2016c, for detailed procedures). When necessary, F-tests were Greenhouse-Geisser corrected and t-tests were Bonferroni corrected. All t-tests were two-tailed. Bayesian statistics (Rouder et al., 2012) were used to provide additional statistical evidence. Bayesian Model Averaging (Hoeting et al., 1999; Wagenmakers et al., 2018) was computed across matched models (reported as BF_{incl}). Bayesian t-tests are report as BF_{10}. Substantial evidence for the alternative hypothesis is marked by Bayes factors $BF>3$ (Jeffreys, 1961), indicating that the empirical data are more than three times more likely under the alternative hypothesis than the null hypothesis. All statistical analyses, including Bayesian statistics were conducted with JASP statistical software (version 0.18.1.0, www.jasp-stats.org).

4.2.2 Results

4.2.2.1 Behavioural results

Trials with anticipatory (<200ms) and slow (> 1500ms) responses were excluded from analysis (2.7% of all trials). Behavioural data are presented as Balanced Integration scores (BI scores; Figure 24A), which account for potential speed-accuracy trade-offs by subtracting the standardised mean RT from the standardised mean accuracy rates (Liesefeld et al., 2015; Liesefeld & Janczyk, 2019). BI scores must be understood to reflect relative performance differences, i.e., whether one condition is more or less difficult than the other. BI scores>0 indicate performance above average, while BI scores<0 reflect below average performance. Therefore, a relatively higher BI score means that participants performed "better" in that condition than another, taking both, RTs and error rates into account at the same time.[12] Mean BI scores were subjected to a repeated-measures ANOVA with the factors task (colour, shape) and memory load (low-, high-load). A main effect of task revealed larger BI scores in the colour (0.92) than shape task (-0.93), $F(1,14)=14.6$, $p=.002$, $\eta^2_p=.51$, indicating that selection was more efficient in the colour task. BI scores were also larger in low-load (0.57) than high-load trials (-0.58), $F(1,14)=49.2$, $p<.001$, $\eta^2_p=.78$, reflecting higher performance levels when participants searched for one as opposed to two possible target colours or shapes, respectively. There was no significant interaction between these two factors, $F(1,14)=1.2$, $p=.284$, $\eta^2_p=.08$, which shows that load effects (difference between low- and high-load BI scores) were identical in the colour (1.84) and shape tasks (1.85). Bayesian Model Averaging also provided clear evidence for the main effects of task ($BF_{incl}=14.1$), and load ($BF_{incl}>100$), and the absence of a Task × Load interaction ($BF_{incl}=0.5$).

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[12] *Separate mean RTs and error rates of Experiment 1 are presented in the supplementary materials (Table 1).*

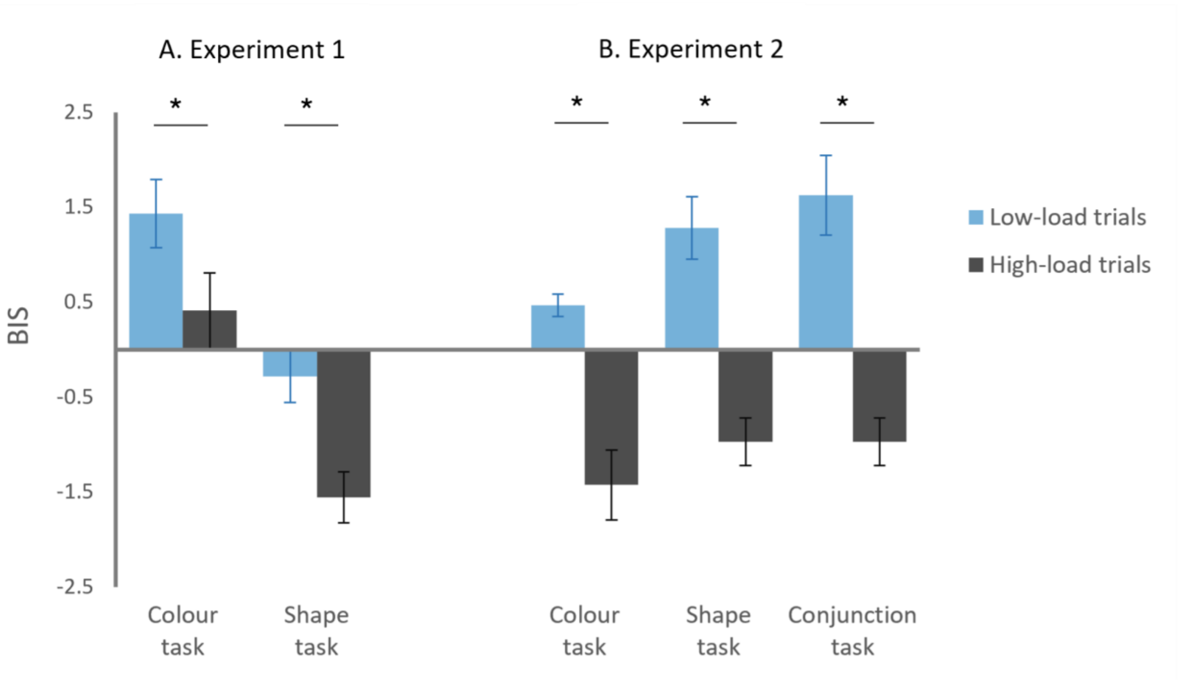

Figure 24 Balanced Integration Scores (BI scores) measured in low- and high-load trials in the colour and shape tasks of Experiment 1 (A) and the colour, shape, and conjunction tasks of Experiment 2 (B). BI scores reflect relative performance differences, taking both RTs and error rates into account at the same time. Higher BI scores indicate more efficient task performance than lower BI scores. Error bars indicate standard error of the mean. Statistically reliable load effects (differences between high- and low-load trials) are marked by asterisks.

4.2.2.2 N2pc results

Figure 25A displays grand-averaged event-related potentials (ERPs) recorded at electrode sites PO7/8 contralateral and ipsilateral to targets in low- and high-load trials of the colour and shape tasks. Clear N2pc components were triggered in the 190-290ms time interval after search display onset in all four conditions. From the corresponding N2pc difference waves (Figure 25B), it can be seen that N2pcs in the shape, as compared to the colour task, were delayed and attenuated. However, memory load effects, i.e., attenuated and delayed N2pcs in high- as compared to low-load trials, appeared to be comparable between the two task conditions.

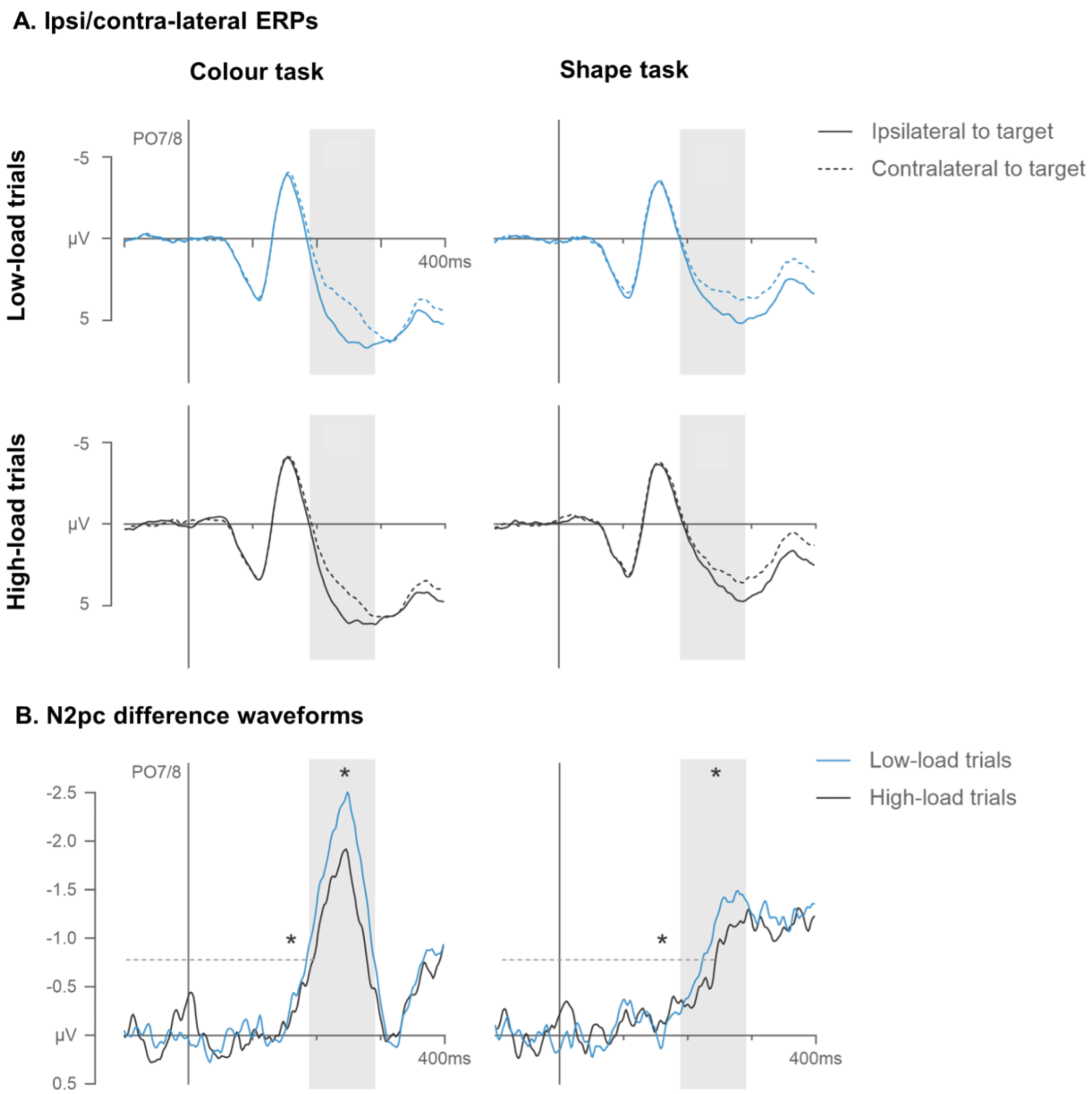

Figure 25 Grand-averaged ERPs measured at electrodes PO7/8 contralateral and ipsilateral to the targets in low- and high-load trials of the colour and shape tasks in Experient 1 (A). The respective difference waves (contra- minus ipsilateral ERPs) are shown below (B). Shaded areas mark the N2pc time windows (190-290ms after search display onset). Asterisks mark statistically reliable load effects measured in N2pc mean amplitudes (low- minus high-load amplitudes) and onset latencies (high- minus low-load latencies).

These observations were confirmed by repeated-measure ANOVAs on N2pc mean amplitudes with the factors task (colour, shape), memory load (low-, high-load), and laterality (electrode contralateral, ipsilateral to the target). The ANOVA revealed a main effect of laterality, $F(1,14)=59.7$, $p<.001$, $\eta^2_p=.81$, which interacted with task, $F(1,14)=28.0$, $p<.001$, $\eta^2_p=.67$, and load, $F(1,14)=11.1$, $p=.005$, $\eta^2_p=.44$, confirming that N2pc components were larger in the colour (-1.6μV) than the shape task (-0.9μV), and in low-load (-1.4μV) as compared to high-load trials (-1.0μV). Most importantly, there was no three-way interaction $F(1,14)=1.5$, $p=.238$, $\eta^2_p=.10$, meaning that the amplitude load effects (low- minus high-load amplitudes) were comparable between the colour (-0.5μV) and shape tasks (-0.3μV). These conclusions were supported by a complementary Bayesian ANOVA, which provided evidence for a main effect of laterality ($BF_{incl}>100$), a Laterality × Task interaction ($BF_{incl}=97.3$), and a Laterality × Load interaction ($BF_{incl}=4.0$), but no substantial evidence for the three-way interaction ($BF_{incl}=.4$).

N2pc onset latencies were subjected to a repeated-measure ANOVA with the factors task (colour, shape) and memory Load (low-, high-load), which produced main effects of task, $F_c(1,14)=66.3$, $p<.001$, $\eta^2_{pc}=.83$, and load, $F_c(1,14)=7.0$, $p=.007$, $\eta^2_{pc}=.33$, but no reliable interaction, $F_c(1,14)<1$, $p=.499$, $\eta^2_{pc}=.03$. In other words, N2pc onset latencies were delayed in the shape (234ms) than colour search *(*192ms), and in high-load (221ms) as compared to low-load trials (206ms). But in line with the behavioural and mean amplitude results, the load effects (high- minus low-load latencies) were comparable between the colour (11ms) and shape tasks (19ms).[13]

4.2.3 Discussion of Experiment 1

Experiment 1 revealed clear memory load costs, with lower BI scores and attenuated and delayed N2pc components in high-load as compared to low-load conditions. The load costs observed in the colour task mirrored findings of previous studies (e.g., Grubert et al., 2016; Grubert & Eimer, 2013; Ort et al., 2019). N2pc amplitudes and latencies were attenuated and delayed, respectively, in high-load as compared to low-load trials when participants had to activate two as compared to one colour template for search. However, the

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[13] *To the best of our knowledge, the issue of how to perform non-parametric statistical tests on jack-knifed data (i.e., to decrease artificially inflated Bayes factors due to reduced error variance in jack-knifed data), has not yet been discussed in the literature. No Bayesian statistics were therefore performed for N2pc latency analyses.*

small N2pc delays (11ms) suggest that two colour templates were activated simultaneously, as a serial switch between two sequentially activated templates was found to be much more time consuming (e.g., 250-300ms; Dombrowe et al., 2011). Load costs of similar magnitude were previously interpreted to be caused by competitive interactions and between-template inhibition of two simultaneously activated attentional templates (e.g., Grubert, et al., under review; Kerzel & Grubert, 2022; Ort et al., 2019).

Experiment 1 confirmed that this parallel template activation pattern is also true for templates that define target shapes rather than colours. In fact, the costs associated with the increased memory load were statistically identical in the colour and shape tasks (-0.5µV vs -0.3µV; 11ms vs 19ms), even though there was an absolute processing advantage for colour over shape, i.e., BI scores were higher and N2pcs were larger and faster in colour as compared to shape search. This seems to suggest that irrespective of the guiding quality of a feature dimension, the processing costs associated with multiple template activation and between-template inhibition are constant across feature dimensions.

4.3 Experiment 2

The preferential processing of colour observed in Experiment 1 might, however, still be a problem during conjunction search. If colour is processed faster, a good search strategy would be to first use the colour template to select all colour-matching objects in the visual field and then use the shape template to simply verify their target status. This seems to have happened in a colour and shape conjunction search conducted by Lee et al. (2018). They measured solid N2pcs to target colour-matching distractors in their visual search, but shape-matching distractors were completely ignored and did not trigger any N2pcs whatsoever. In contrast, we observed both target colour-matching and shape-matching distractor N2pcs during target and shape conjunction search (Eimer & Grubert, 2014; see also Jenkins et al., 2017). In our tasks, the target colours were perceptually more similar than in Lee at al.

(2018), and we only used outline shapes rather than filled objects which also reduced the amount of colour information available. These stimulus differences may have eliminated a strong colour advantage in our previous studies. To equate the perceptual task difficulty in Experiment 2, we therefore used more similar colours than in Experiment 1 and only presented outline shapes (to make the colour task harder). In addition, we also only used canonical shapes and one shape mix (to make the shape task easier).

In addition to the two single feature conditions (colour and shape), we also tested a new conjunction task in Experiment 2 in which targets were defined by combinations of colour and shape. Each target was accompanied by a target colour- or shape-matching distractor. If conjunction search is guided by combined feature templates, these partially matching distractors should be completely ignored because only the target contains a combination of both task relevant features. Alternatively, if conjunction search is guided by individual feature templates, both partially matching distractors should be attended. They should trigger N2pc components that would either merge with the target N2pc when the target and distractor are in the same hemifield or attenuate the target N2pc when the target and distractor are in opposite hemifields.

Each task had two load conditions as in Experiment 1. In low-load trials, participants searched for a single target colour/shape/colour&shape conjunction, while they searched for two target colours/shapes/conjunctions in high-load trials. If templates contain integrated object representations, the memory load should be identical in the feature and conjunction search tasks and load effects as measured on the behavioural level and the level of the N2pc should also be identical. Alternatively, if attentional templates hold single features instead, the feature-based memory load in both the low- and high-load condition would be twice as high in the conjunction than the single feature tasks and memory load effects should be substantially increased in the conjunction as compared to the single feature conditions.

Finally, in Experiment 2 we measured CDA components triggered in response to the target cues at the beginning of each trial. CDAs should be increased in high-load as compared to low-load trials, reflecting the parallel activation of two as compared one attentional template, respectively (e.g., Carlisle, et al., 2011; Grubert et al., 2016). As for the N2pcs, these memory load effects should be identical in the single feature and conjunction conditions if attentional templates hold combined feature representations in conjunction search but should be significantly increased if attentional templates hold single features during conjunction search.

4.3.1 Methods

4.3.1.1 Participants

Fifteen new participants aged 20-40 years (Mean=25.1, SD=5.0) were paid (£10/hour) to participate in Experiment 2. Thirteen were female and two were male. All participants were right-handed and had normal or corrected-to-normal vision without colour deficiency (tested with the Ishihara colour vision test; Ishihara, 1972).

4.3.1.2 Stimuli and procedures

The stimuli and procedural aspects were identical to Experiment 1 with the few exceptions listed below. In addition to the *colour* and *shape tasks* tested in Experiment 1, Experiment 2 contained a third blocked task condition, a *conjunction task*, in which participants searched for targets with a specific colour and shape combination (Figure 26A). To equate the neuronal responses to colour and shape targets, we reduced task difficulty in the shape task by using four, rather than six possible target shapes (circle, triangle, square, and gate; 0.5°×0.5°; Figure 26B). We also used four rather than six colours but made them perceptually more similar to increase task difficulty in the colour task (green: .621/.335, turquoise: .285/.616, cyan: .180/.176, and blue: .462/.465; equiluminant at ~9.5cd/m^2). In addition, all stimuli in the cue and search displays were now outline rather than filled shapes to reduce the amount of colour information available during both template preparation and attentional guidance.

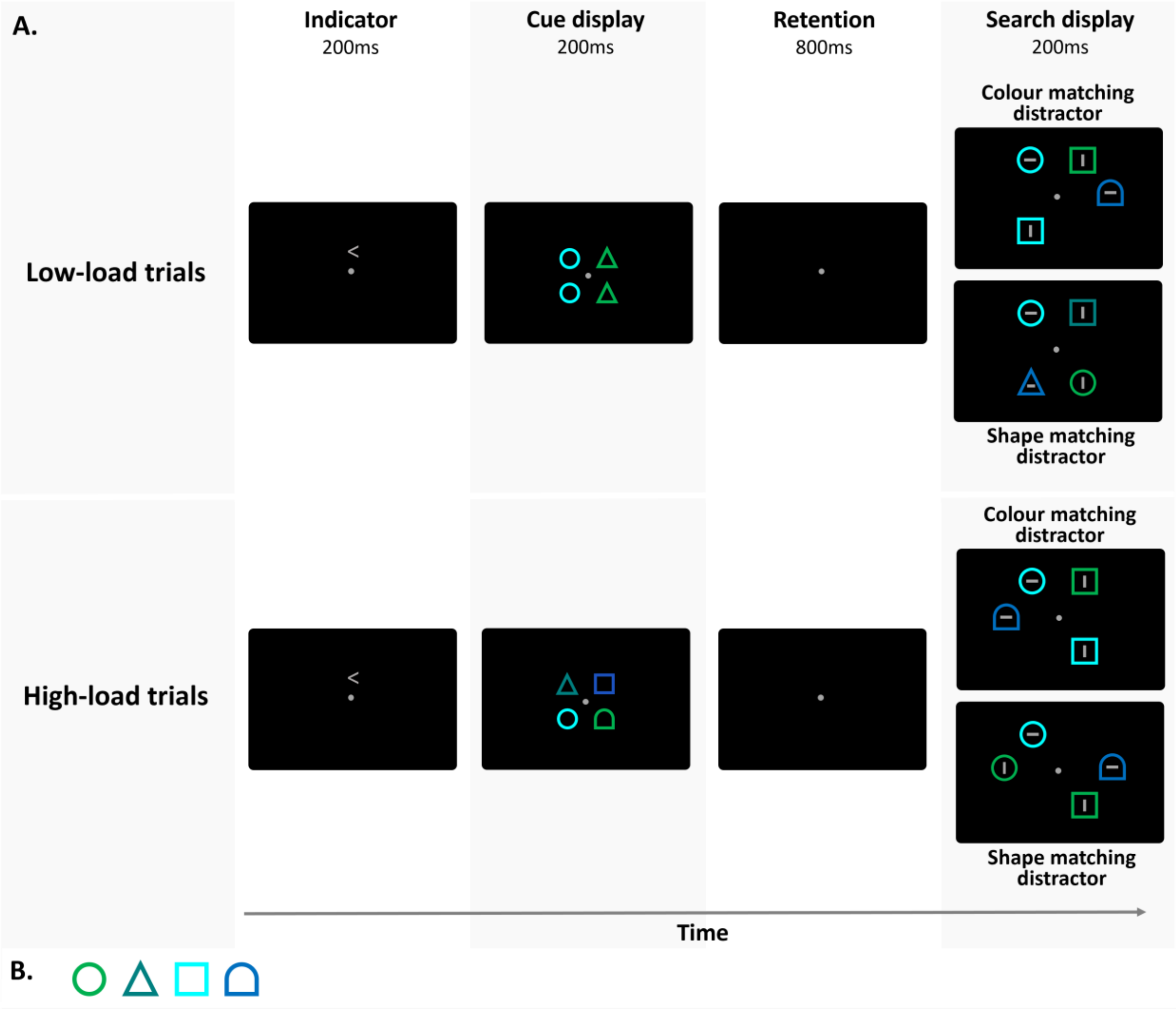

Figure 26 Schematic illustration of the stimuli and temporal trial sequence in Experiment 2. The trial sequence and timing were identical to Experiment 1, but cue displays as well as search displays were now physically identical in all task conditions, i.e., colour, shape, and conjunction task. Participants were instructed to search for the cued colour(s), shape(s), or colour and shape combination(s), respectively.

As in Experiment 1, search displays contained one target and three nontargets, presented at four (two in each hemifield) out of six possible lateralised stimulus locations (equidistant at an eccentricity of 1° from fixation). In each block of the colour, shape, and conjunction task, each of the four colours, four shapes, and 16 colour-shape combinations, respectively, appeared equally often as the target. To ensure that conjunction targets could not solely be found based on the colour or shape information alone, one of the nontargets in the conjunction task either matched the target colour (50% of the trials) or the target shape (50%). In half of all trials, this partially matching distractor was presented on the same side as the target, in the other half, it was presented in the opposite hemifield. To keep the search displays physically identical between task conditions, the same logic was applied in the colour and shape tasks. In the colour task, one of the nontargets matched the shape of the colour target, even though shape was completely task irrelevant, and vice versa, one of the nontargets matched the target colour in the shape task, even though colour was completely task irrelevant. The other non-matching feature of the partially matching distractors, and the colours and shapes for the remaining two nontargets in each search display, were randomly chosen (without replacement) from the set of colours and shapes that were not used for the target. The response-relevant lines within the search objects were grey in Experiment 2 (.317/.359 ~9.5cd/m^2).

In contrast to Experiment 1, the cue displays were now physically identical in all three task conditions and contained smaller versions of the search items (0.4°×0.4°) that were also presented closer to fixation (±0.3° from both the horizontal and vertical axes) to prevent location overlap. *Low-load* and *high-load* memory conditions were equiprobably and were presented in an intermixed fashion in each block. In low-load trial, the two target cues on the relevant side were shown in one target colour/shape/colour&shape combination, while they were shown in two different target colours/shapes/colour&shape combinations in high-load trials. The two target cues in high-load trials always differed with respect to both the target colour and shape. As in Experiment 1, there was only ever one target in each search display and the colours and shapes of the irrelevant target cue never appeared in the search display. The colour(s) and shapes(s) of the two cues on the irrelevant side of the cue display were randomly chosen (without replacement) from the set of colours and shapes that were not used for the target cues on the relevant cue side.

Experiment 2 was tested in two separate sessions because of the large number of trials required. The two sessions were completed by the same participants on two non-consecutive days. Each session consisted of five consecutive blocks for each of the three tasks. Task order was counterbalanced between participants so that each of the three tasks was presented equally often first, second, and last across all participants. The task order of the first session was mirror-reversed for each participant in the second session. All blocks contained eight trials for each combination of memory load (low-, high-load), cue side (left, right hemifield) and target side (left, right hemifield), for 64 trials per block and 1920 trials in total in Experiment 2.

4.3.1.3 EEG recording and data analyses

EEG procedures were identical to Experiment 1. Trials with EEG artefacts, anticipatory, slow, missing, and error response were excluded from analyses. For the N2pc analysis, locked to the onset of the search displays, artefact rejection resulted in an exclusion of 16.7% of all trials in the colour task (SD= 14.1%; ranging between 1.4% and 36.4% across participants), 13.9% of all trials in the shape task (SD=11.9%; ranging between 0.2% and 33.1% across participants), and 16.3% in the conjunction task (SD=13.0%; ranging between 0.7% and 36.7% across participants). EEG on the remaining trials was segmented into 500ms epochs, from −100ms to 400ms relative to the onset of the search display. As in Experiment 1, N2pc mean amplitudes to targets in the search display were measured in the 190–290ms time window after onset of the search displays. The threshold criterion for N2pc onset latencies was -0.7μV in Experiment 2 (50% of the peak amplitude of the averaged target N2pc, pooled across all targets in all conditions of Experiment 2). In addition to the N2pc, in Experiment 2, we measured the contralateral delay activity (CDA) over PO7/8 in the 400-

900ms time widow after cue onset. The same artefact rejection criteria applied as for the N2pc analysis. For the CDA analysis, locked to the onset of the cue displays, artefact rejection resulted in an exclusion of 19.9% of all trials in the colour task (SD= 15.6%; ranging between 1.3% and 49.3% across participants), 18.0% of all trials in the shape task (SD=14.3%; ranging between 1.6% and 48.3% across participants), and 20.1% in the conjunction task (SD=13.8%; ranging between 1.5% and 51.9% across participants).

4.3.2 Results

4.3.2.1 Behavioural results

Trials with anticipatory (<200ms) and exceedingly slow (>1500ms) responses were excluded from analysis (1.6% of all trials). BI scores[14] in Experiment 2 (Figure 24B) were subjected to a repeated-measures ANOVA with factors task (colour, shape, conjunction) and memory load (low-, high-load), which revealed a main effect of load, $F(1,14)=321.2$, $p<.001$, $\eta^2_p=.96$, $BF_{incl}>100$, as participants were generally more efficient during low- (1.12) as compared to high-load search (-1.12). There was no main effect of task, $F(2,28)=3.9$, $p=.064$ $\eta^2_p=.22$, $BF_{incl}=2.52$, but task interacted with load, $F(2,28)=7.6$, $p=.009$, $\eta^2_p=.35$, $BF_{incl}=14.44$, because load effects (difference between low- and high-load BI scores) were significantly increased in the conjunction task (2.60), both in comparison with the colour task (1.89), $t(14)=4.5$, $p<.001$, $d=.42$, $BF_{10}=44.4$, and the shape task (2.25), $t(14)=2.3$, $p=.036$, $d=.60$, $BF_{10}=4.4$. However, load effects on BI scores were comparable in the colour and shape tasks, $t(14)=1.5$, $p=.175$, $d=.42$, $BF_{10}=.67$. Because there were no reliable task and load effect differences between the colour and shape tasks, the two single feature tasks were pooled for the following ERP analyses.

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[14] Separate mean RTs and error rates for Experiment 2 are presented in the supplementary materials (Table 2).

4.3.2.2 N2pc results

Figure 27A shows grand-averaged event-related potentials (ERPs) in response to the targets in the low- and high-load trials of the single feature (pooled for colour and shape[15]) and feature conjunction tasks, together with the corresponding N2pc difference waves (Figure 27B). While the single feature N2pcs mirrored the N2pcs measured in Experiment 1, with slightly attenuated and delayed N2pcs in high- as compared to low-load trials, this load effect seemed to be substantially increased in the conjunction task. To verify these observations, N2pc mean amplitudes were fed into a repeated-measure ANOVA with the factors task (single-feature, conjunction), memory load (low-, high-load), and laterality (electrode contralateral, ipsilateral to the target). The ANOVA uncovered a main effect of laterality, $F(1,14)=64.9$, $p<.001$, $\eta^2_p=.82$, $BF_{incl}>100$, which interacted with task, $F(1,14)=33.7$, $p<.001$, $\eta^2_p=.71$, $BF_{incl}>100$, and load, $F(1,14)=74.4$, $p<.001$, $\eta^2_p=.84$, $BF_{incl}>100$. In other words, N2pcs were generally larger when they were triggered in response to conjunction (-1.3µV) rather than single-feature targets (-0.9µV), and in low-load (-1.5µV) as compared to high-load trials (-0.8µV). Critically, the ANOVA also revealed a significant three-way interaction, $F(1,14)=5.3$, $p=.022$, $\eta^2_p=.32$, $BF_{incl}=62.4$, because the load effects (low- minus high-load amplitudes) were substantially increased in the conjunction (-1.0µV) as compared to the single-feature tasks (-0.4µV).

N2pc onset latencies were fed into an ANOVA with the factors task (single-feature, conjunction) and memory load (low-, high-load). There was no main effect of task, $F_c(1,14)=1.1$, $p=.213$, $\eta^2_{pc}=.07$, but a significant main effect of load, $F_c(1,14)=42.5$, $p<.001$, $\eta^2_{pc}=.75$, and a reliable interaction, $F_c(1,14)=4.1$, $p=.028$, $\eta^2_{pc}=.23$. N2pc onset latencies were generally delayed in high-load (229ms) as compared to low-load trials (203ms), but this load

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[15] *Separate colour and shape N2pc difference waves are shown in Figure 30 in the supplementary materials. Statistics are given in the figure legend to prove that the stimulus changes in Experiment 2 helped to equate neuronal responses to colour and shape targets and that colour and shape N2pcs were statistically identical in Experiment 2.*

effect (high- minus low-load latencies), was substantially increased in the conjunction (35ms) as compared to the single feature tasks (18ms).

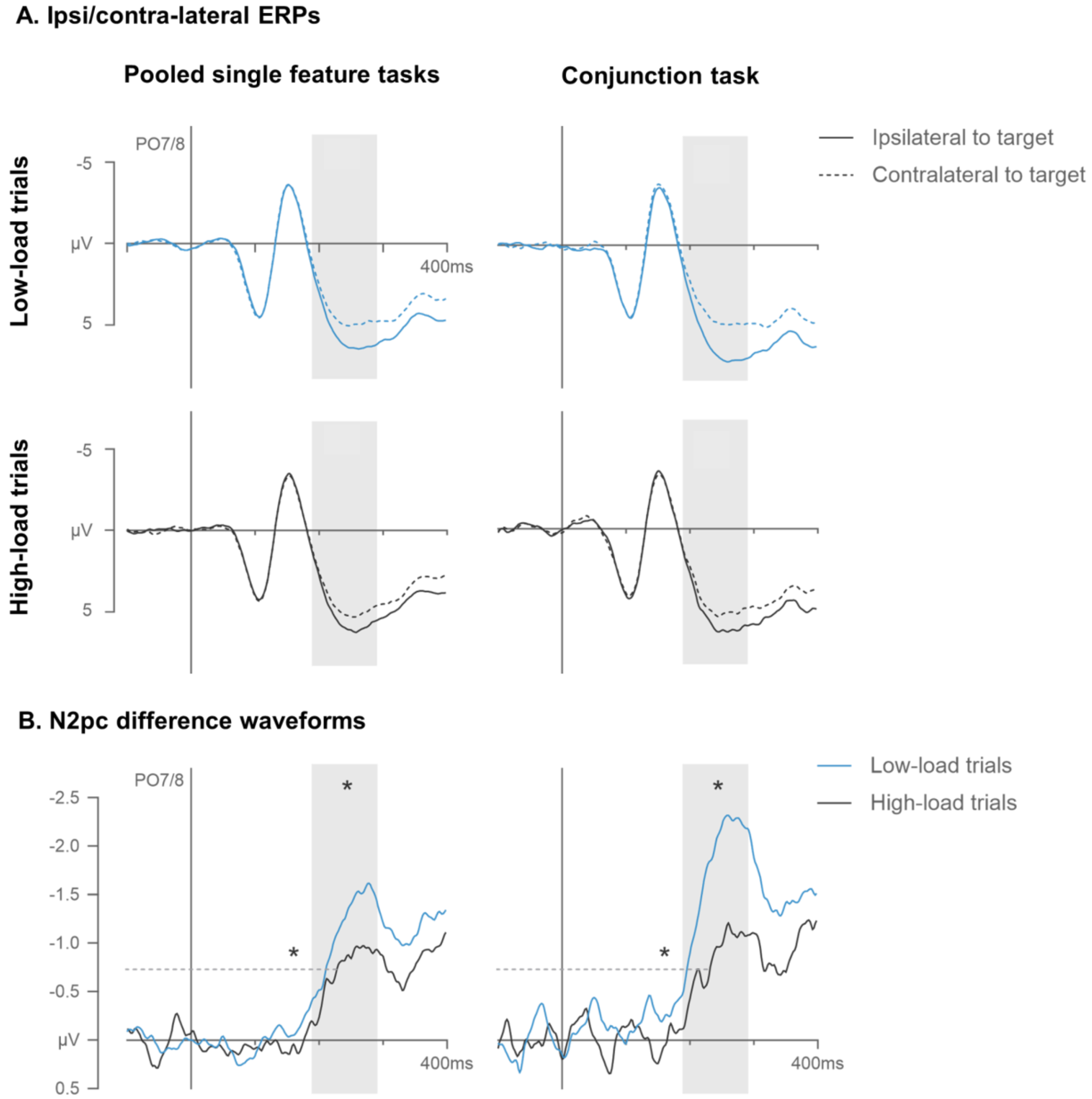


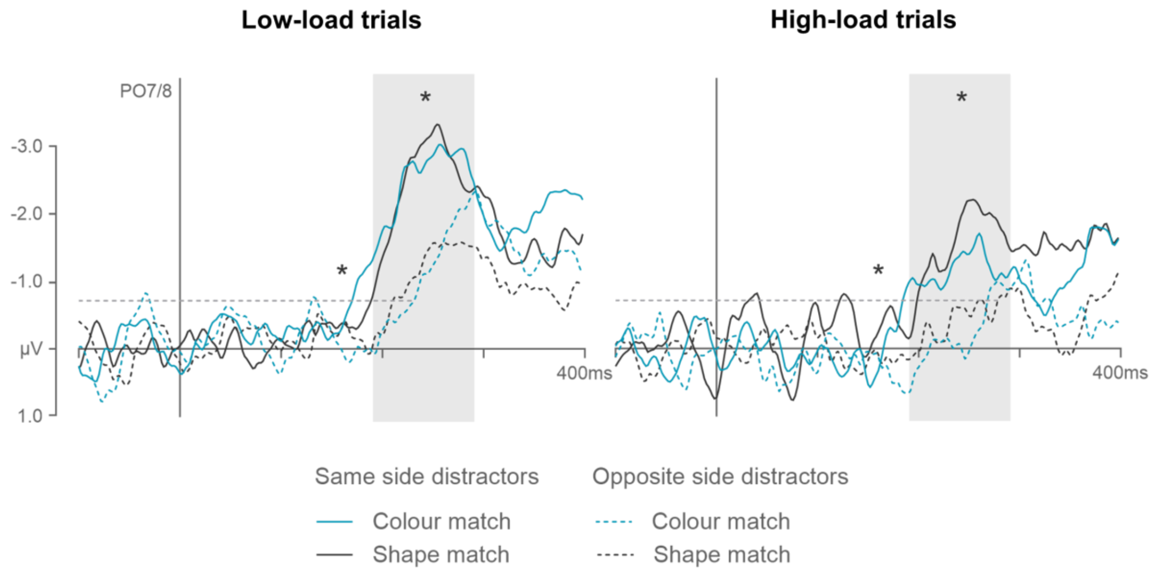
Figure 27 Grand-averaged ERPs measured at electrodes PO7/8 contralateral and ipsilateral to the targets in low- and high-load trials of the single feature tasks (pooled for colour and shape) and the conjunction tasks in Experient 2 (A). The respective difference waves (contra- minus ipsilateral ERPs) are shown below (B). Shaded areas mark the N2pc time windows (190-290ms after search display onset). Asterisks mark statistically reliable load effects measured in N2pc mean amplitudes (low- minus high-load amplitudes) and onset latencies (high-minus low-load latencies).

Effects of partially matching distractors on target N2pcs

We also measured the effects of colour- and shape-matching distractors on single-feature versus feature conjunction targets. Figure 28A shows N2pc difference waves in low- and high-load trials of the conjunction task with a partially matching distractor in the same and opposite hemifield to the target. N2pc mean amplitudes in these trials were subjected to a repeated-measure ANOVA with the factors laterality, memory load, distractor type (colour, shape matching), and distractor side (same, opposite side to target). Apart from the effects already described in the main analysis above, i.e., main effect of laterality and interaction between laterality and memory load, there was also an interaction between laterality and distractor side, $F(1,14)=64.5$, $p<.001$, $\eta^2_p=.82$, $BF_{incl}>100$. This demonstrates that N2pc mean amplitudes were attenuated when a partially matching distractor was presented in the opposite (-0.7µV) as compared to the same side of the target (-1.9µV). This distractor side related amplitude reduction (same minus opposite side amplitudes) was virtually identical for colour and shape matching distractors (-1.2µV), $F(1,14)<1$, $p=.946$, $\eta^2_p<.01$, $BF_{incl}=0.4$, and was also comparable in low-load (-1.4µV) and high-load trials (-1.1µV), since none of the other interactions involving the factors distractor side or distractor type reached significance, all $F(1,14)<2.4$, $p>.145$, $\eta^2_p<.146$, $BF_{incl}<0.9$.

The same pattern was found for N2pc onset latencies. A repeated-measure ANOVA with the factors memory load, distractor type, and distractor side produced a main effect of memory load as described in the main analysis above, and an additional main effect of distractor side, $F_c(1,14)=10.6$, $p=.002$, $\eta^2_{pc} = .43$, indicating that partially matching distractors delayed target N2pcs when the distractor was in the opposite (244ms) as compared to the same hemifield than the target (185ms). This distractor side related delay was comparable for colour matching (72ms) and shape matching (46ms) distractors, $F_c(1,14)=0.5$, $p=.408$, $\eta^2_{pc} = .04$, and in low-load (43ms) and high-load trials (75ms), $F_c(1,14)=1.0$, $p=.229$, $\eta^2_{pc} = .07$.

A. Target N2pc difference waveforms in conjunction task with a partially matching distractor in the same and opposite hemifield



B. Target N2pc difference waveforms in pooled single feature tasks with the task irrelevant feature in the same and opposite hemifield

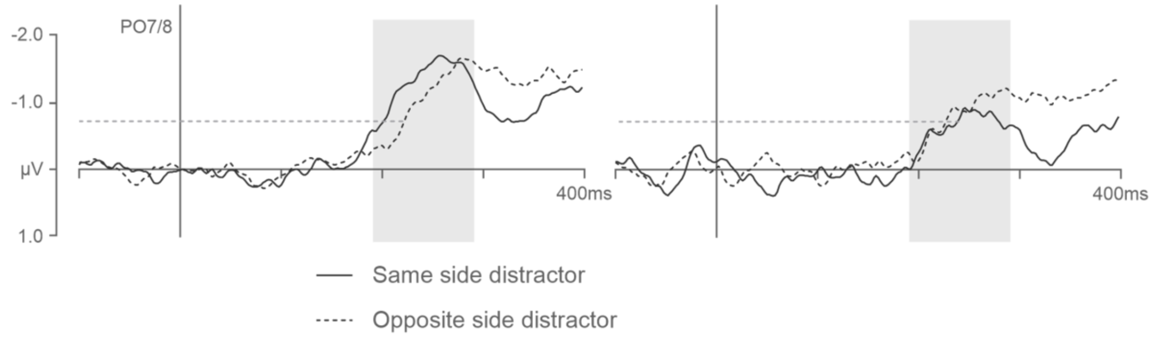


Figure 28 N2pc difference waves in low- and high-load trials of the conjunction (A) and pooled single feature tasks (B), separately for trials in which partially matching distractors were presented in the same or opposite hemifield of the target. In the conjunction task N2pcs are shown separately for distractors that matched the target colour or shape, respectively. In the single feature tasks, partially matching distractors are pooled. Shaded areas mark the N2pc time windows (190-290ms after search display onset). Asterisks mark statistically reliable N2pc amplitude and latency differences between N2pcs triggered in response to targets with same or opposite side distractors.

The very same amplitude and latency analyses conducted on target N2pcs in the single feature tasks in which we presented a distractor that matched the task irrelevant target shape in the colour task and the task irrelevant target colour in the shape task, revealed no such distractor effects at all (Figure 28B). Note that colour and shape matching distractors were pooled for this analysis. None of the ANOVAs produced any significant effects involving the factor distractor side, not for mean amplitudes, $F(1,14)<3.8$, $p>.071$, $\eta^2_p<.21$, $BF_{incl}<1.1$, or onset latencies, $F_c(1,14)<1$, $p=.884$, $\eta^2_{pc}=.01$. N2pc components in the single feature tasks were statistically identical in trials in which the partially matching distractor was presented on same or opposite sides to the target both in low- and high-load trials.

4.3.2.3 CDA results

Figure 29A shows grand-averaged ERPs at electrode sites PO7/8 contralateral and ipsilateral to the target cues in low- and high-load trials of the single feature and feature conjunction tasks. CDA components were elicited in the 400-900ms time interval after cue display onset in all four conditions. The corresponding CDA difference waves are shown in Figure 29B. CDAs were generally increased in high- as compared to low-load trials, but this load effect seemed to be exaggerated in the conjunction as compared to the single feature tasks. This was substantiated by means of a repeated-measure ANOVA with the factors task (single-feature, conjunction), memory load (low-, high-load), and laterality (electrode contralateral, ipsilateral to the target cues). A main effect of laterality, $F(1,14)=11.7$, $p=.004$, $\eta^2_p= .46$, was accompanied by a significant Laterality × Load interaction, $F(1,14)=11.5$, $p=.004$, $\eta^2_p=.45$, and a significant three-way interaction, $F(1,14)=5.0$, $p=.042$, $\eta^2_p=.26$. CDA mean amplitudes were generally larger in high-load (-0.9μV) than low-load trials (-0.6μV), but these load effects (high- minus low-load amplitudes) were substantially increased in the conjunction (-0.6μV) as compared to the single-feature tasks (-0.3μV). These findings were reinforced by a complementary Bayesian ANOVA, which provided support for the main effect of laterality ($BF_{incl}=39.4$), the Laterality × Load interaction ($BF_{incl}=23.8$), and the three-way interaction ($BF_{incl}=7.5$).

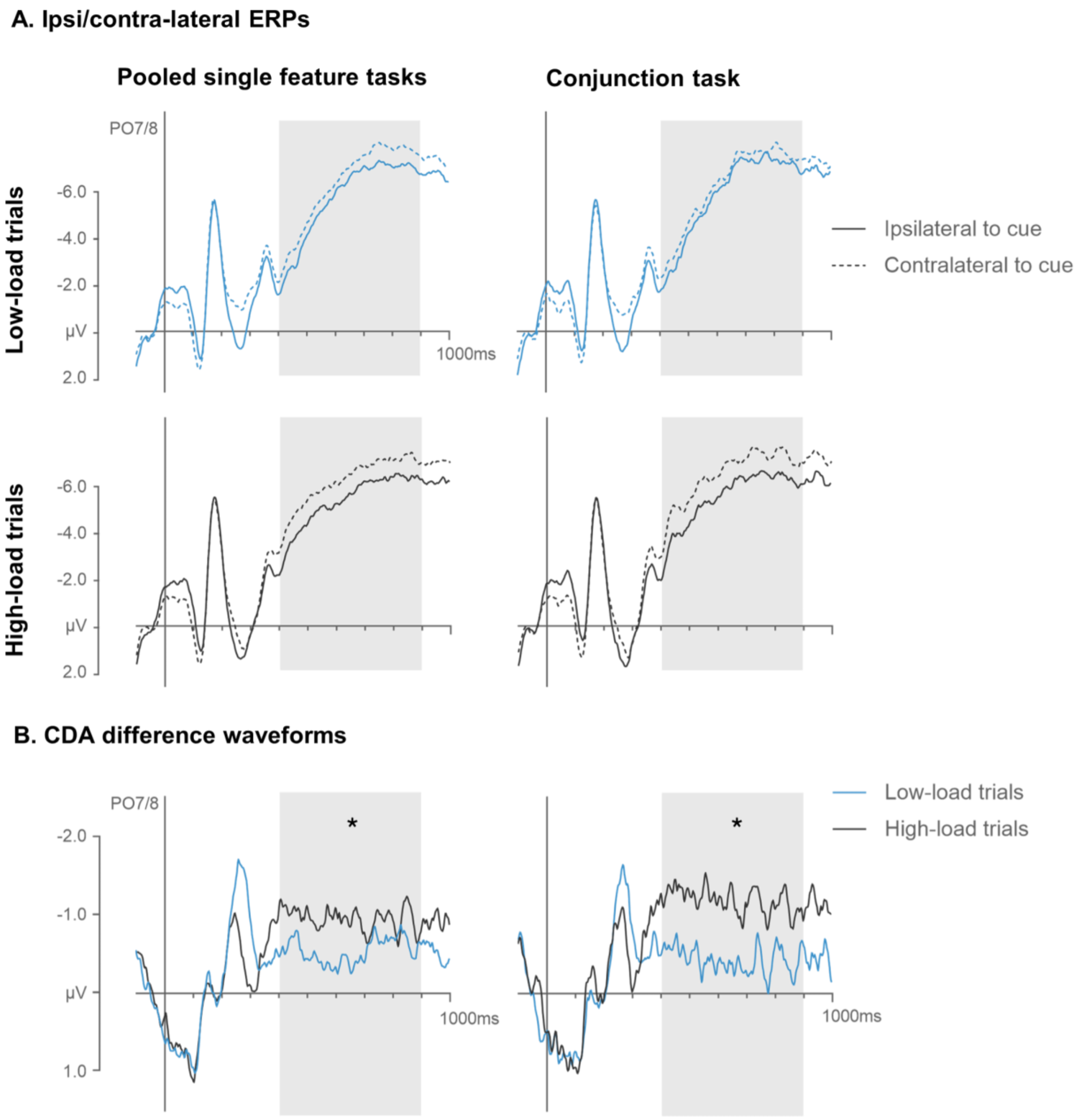


Figure 29 Grand-averaged ERPs measured at electrodes PO7/8 contralateral and ipsilateral to the target cues in low- and high-load trials of the single feature tasks (pooled for colour and shape) and the conjunction tasks in Experient 2 (A). The respective difference waves (contra- minus ipsilateral ERPs) are shown below (B). Shaded areas mark the CDA time windows (400-900ms after cue display onset). Asterisks mark statistically reliable load effects measured in CDA mean amplitudes (low- minus high-load amplitudes).

4.3.3 Discussion of Experiment 2

As in Experiment 1, BI scores were lower in high-load as compared to low-load trials, and these load effects were comparable between the colour and shape tasks. But importantly, load effects were substantially increased in the conjunction tasks in comparison to the single feature tasks, indicating that search efficiency was lower in the conjunction than the two single feature tasks. With the new stimuli, i.e., outline shapes with more similar target colours, we eliminated the main effect of task and the general advantage for colour observed in Experiment 1. BI scores were now comparable between the colour and shape tasks and this was explicitly tested in a follow-up t-test, $t(14)=1.6$, $p=.283$, $d=.40$, $BF_{10}<1$. However, looking at Figure 24B it is plain to see that BI scores in the colour task (-0.48) were numerically lower than in the shape task (0.15) and that colour discrimination was now more difficult than shape discrimination. In fact, BI scores were statistically similar in the shape and conjunction task (0.33), $t(14)<1$, $p=.485$, $d=.19$, $BF_{10}<1$, while they were lower in the colour than the conjunction task, $t(14)=3.6$, $p=.009$, $d=.93$, $BF_{10}=15.25$, raising the question as to whether conjunction search was mainly controlled by shape rather than colour signals in Experiment 2. We do not think that this was the case, because this search asymmetry seems to have been triggered at post-selective processing stages rather than during attentional guidance at search. There were no amplitude or latency differences between colour and shape N2pcs (see Figure 30), and both colour- and shape-matching distractors affected conjunction N2pcs virtually identically (see below).

Also, in line with Experiment 1, N2pc amplitudes and latencies were attenuated and delayed, respectively, in high-load as compared to low-load trials when two as compared to one target colour or shape were task relevant. In fact, amplitude load effects measured in the (pooled) single feature conditions of Experiment 1 and 2 were the same (-0.4μV), and the latency effects were almost identical (15ms vs 18ms in Experiments 1 and 2, respectively). This pattern of N2pc load effects found in the single feature tasks is comparable to previous experiments and indicates that two attentional templates with competitive interactions were activated to guide attention in the high-load trials (e.g., Grubert 2023; Grubert et al., 2016; Ort et al., 2019). In contrast, memory load effects were substantially increased in the conjunction task (-1.0µV; 35ms) as compared to the single feature tasks (0.4µV; 18ms), indicating that template load must have been significantly larger in the conjunction as compared to the single feature conditions.

A straightforward explanation for this is that conjunction search was guided by individual feature templates. While there were one versus two templates active during low- and high-load single feature search, in the conjunction task participants had to activate two versus four templates in parallel, which would have doubled between-template inhibition and consequently decreased the activation level and guidance power of each individual template. Alternatively, it could be argued that the maintenance of objects is more demanding, i.e., because there is additional binding information to be held with objects. Both accounts can also explain the increased target N2pcs in the conjunction as compared to the single feature tasks. The increased N2pcs could either reflect two separate feature-based guidance mechanisms that act additively when the target colour and shape signal are at the same location (e.g., Berggren & Eimer, 2018; Eimer & Grubert, 2014). Alternatively, they could be due to more effortful selection processing when attention is guided to objects as compared to features.

To decide between the two alternative accounts, we re-analysed the target N2pcs by taking the location of the partially matching distractors into account. Target N2pcs were substantially delayed when the target and the partially matching distractor were in opposite as compared to the same hemifield. This means that distractors that either matched the target colour or shape captured attention, which is consistent with the idea of independent parallel selection guided by separate feature templates for colour and shape (e.g., Berggren & Eimer, 2018; Eimer & Grubert, 2014; Lee et al., 2018). It is important to note that the distractor effects were virtually identical for colour- and shape-matching distractors, providing additional evidence that attentional guidance by colour and shape templates was equally efficient in Experiment 2. Also, the same target colour- or shape-matching distractors in the shape and colour task, respectively, had no effect on the target N2pc. This demonstrates that features that are presented at one location, i.e., as cues, are not automatically bound together, if only one of them is task relevant and that search was truly feature-based in the two single feature tasks.

The evidence so far suggests that attentional guidance in the conjunction task was feature-based. However, it is still possible that target templates contained integrated feature representations to lower the memory load in conjunction search and that only the guidance process was feature-based. But looking at the CDA analysis this was clearly not the case. Load effects in the single feature tasks mirrored previous findings of increased CDA components set up in preparation for high-load as compared to low-load search (e.g., Carlisle et al., 2011; Grubert et al., 2016). But these load effects were significantly increased in the conjunction than the single feature tasks (-0.6µV vs -0.3µV), demonstrating that additional features (potentially twice as many) were maintained during the retention period in the conjunction task. These increased load effects very likely reflect the activation of additional features as opposed to binding costs because previous working memory studies which measured integrated object representations held in working memory found that feature- and object-based CDAs were comparable in size, i.e., there was no overhead for binding involved (e.g., Luck & Vogel, 1997; Vogel et al., 2001).

4.4 General discussion

The goal of this study was to measure whether attentional templates can be set up to hold integrated object representations and whether such integrated target representations can guide attention under conditions when chunking was beneficial to decrease working memory load. None of our results support these hypotheses. In chronological order, we observed initial evidence that multiple templates were activated prior to search. CDA amplitudes, measured in response to the cue displays, were generally larger in high- as compared to low-load trials. The important finding is that these memory load effects were substantially increased in the conjunction task. In fact, they were exactly twice as large in the conjunction as compared to the single feature conditions suggesting that twice the amount of information was activated in preparation for conjunction as compared to single feature search (e.g., Vogel & Machizawa, 2004), i.e., one additional template in the feature tasks (one in low-load trails, two in high-load trials), but two additional templates in the conjunction task (two in low-load search, four in high-load search). This is a first piece of evidence that target templates in the conjunction were set up to contain individual target features, as opposed to integrated object representations. This was further confirmed at the level of attentional guidance. Target N2pcs measured in response to the search displays, both in Experiment 1 and 2, were generally attenuated and delayed during high- as compared to low-load search. While these load effects were identical in colour and shape search, they were more than twice as large in the conjunction as compared to the single feature tasks. The reason for this is that the parallel activation of multiple attentional templates leads to between-template inhibition (e.g., Grubert et al., 2016; Kerzel & Grubert, 2022; Ort et al., 2019). Because twice the number of templates was activated in the conjunction task the increased inhibitory links between these additional templates resulted in lower overall template activation levels and more pronounced difference between low- and high-load search efficiency in the conjunction than feature search (see Kerzel & Grubert, 2022, for a model of template inhibition in multiple colour search). In addition to the load effects, we also found that partially matching distractors in the conjunction task (both colour- and shape-matching) attracted attention and triggered N2pc components that either boosted or attenuated target N2pcs when distractors were on the same versus opposite side of the targets. If attentional guidance was based on integrated object representations, these distractors that only ever matched one of the two task relevant target features, would have been ignored. Finally, the reduced level of search efficiency in high- as compared to low-load trials propagated to the level of response execution, i.e., BI scores in both Experiments 1 and 2 were significantly lower in high- as compared to the low-load trials. Both Experiments 1 and 2 confirmed that these load effects were comparable in colour and shape search but Experiment 2 demonstrated that these load effects were significantly increased in the conjunction search as compared to the two single feature conditions.

All in all, our results provide strong evidence that working memory load was increased in the conjunction as compared to the single feature tasks, indicating that single features rather than integrated object representations were activated prior to search and held active during attentional guidance. Our results are therefore in line with visual search theories that assume that initial attentional guidance is feature-based (e.g., Bundesen, 1990; Huang & Pashler, 2007; Itti & Koch, 2001; Müller & Krummenacher, 2006; Wolfe, 2021), and integrate with a vast body of empirical evidence that have supported this assumption (e.g., Becker et al., 2020; Berggren & Eimer, 2018; Dent, 2023; Eimer & Grubert, 2014; Jenkins et al., 2017; Lee et al., 2018; Rutishauser & Koch, 2007; Williams & Reingold, 2001). However, there is an equally large body of evidence that demonstrates that working memory representations can be object-based (e.g., Balaban & Luria, 2016; Cowan, 2001; Delvenne & Bruyer, 2004; Luck & Vogel, 1997; Olson & Jiang, 2002; Quinlan & Cohen, 2011; Vogel et al., 2001). Since attentional templates are part of working memory, it is still unclear why attentional templates cannot also contain object-based representations. How can these diverging findings from the visual search and working memory literature be reconciled? Our study seems to suggest that task difficulty and the need for chunking to reduce working memory load is no reason. Future studies will have to advance this inquiry. For example, in change detection tasks, memory items must simply be retained in working memory until they can be matched with a set of test items. In contrast, in visual search, target locations are typically unknown and attentional templates are designed to guide attention to relevant target locations in a spatially global fashion (e.g., Berggren et al., 2017; Eimer, 2014; McAdams & Maunsell, 2000; Saenz et al., 2002). Also, depending on task requirements, attentional templates must be highly precise to discriminate a target from its surrounding distractors (e.g., Kerzel & Cong, 2021; Yu et al., 2023), for example in conjunction search, when the distractors share features with the target. There already is evidence from working memory studies, demonstrating that integrated object representations are less precise than feature-based representations (e.g., Fougnie et al., 2010). Also, conjunction benefits disappeared when object locations were rendered irrelevant, i.e., when the test objects were presented at different locations than the memory objects (e.g., Wang et al., 2016), which would always be the case in visual search where target locations are unknown. Further research will have to explore the roles of feature precision and location dependence for object-based memory representations used for attentional guidance versus short-term storage.

4.5 Supplementary Materials

Table 1 Mean reaction times (RTs; in milliseconds) and error rates (ER; % of trials) measured in low- and high-load trials of the colour and shape tasks in Experiment 1. Brackets contain standard deviations.

	Low-load trials		**High-load trials**	
	RTs in ms	ER in %	RTs in ms	ER in %
Colour task	700 (79)	4.3 (5.4)	753 (75)	7.5 (7.3)
Shape task	863 (87)	6.0 (3.3)	922 (71)	10.4 (4.7)

Table 2 Mean reaction times (RTs; in milliseconds) and error rates (ER; % of trials) measured in low- and high-load trials of the colour, shape, and conjunction tasks in Experiment 2. Brackets contain standard deviations.

	Low-load trials		**High-load trials**	
	RTs in ms	ER in %	RTs in ms	ER in %
Colour task	757 (82)	10.2 (7.3)	806 (90)	21.5 (6.4)
Shape task	769 (79)	2.4 (2.1)	882 (80)	11.2 (6.8)
Conjunction task	720 (70)	3.8 (2.5)	841 (81)	14.7 (4.5)

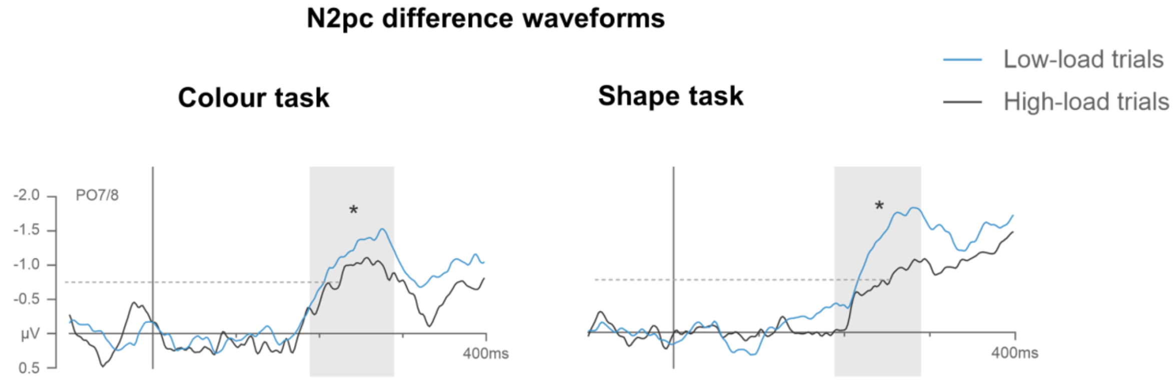


Figure 30 N2pc difference waves in low- and high-load trials in the colour and shape tasks of Experiment 2. Shaded areas mark the N2pc time windows (190-290ms after search display onset). Asterisks mark statistically reliable load effects measured in N2pc mean amplitudes (low- minus high-load amplitudes) and onset latencies (high- minus low-load latencies). Mean amplitudes were subjected to a repeated-measures ANOVA with the factors task (colour, shape), memory load (low-, high-load), and laterality (electrode contralateral, ipsilateral to the target). A main effect of laterality, $F(1,14)=57.1$, $p<.001$, $\eta^2_p=.80$, $BF_{incl}>100$, interacted with load, $F(1,14)=33.0$, $p<.001$, $\eta^2_p=.70$, $BF_{incl}>100$, revealing that significant N2pcs were triggered across task conditions but that these were larger in low-load (-1.2µV) compared to high-load trials (-0.7µV). However, there were no significant interactions involving the factor task, $F(1,14)<2.1$, $p>.167$, $\eta^2_p<.13$, $BF_{incl}<1$, demonstrating that N2pc mean amplitudes (-1.0µV versus -0.9µV, respectively) and load effects (low- minus high-load amplitudes; -0.3µV versus -0.5µV, respectively) did not differ between the colour and shape tasks. The equivalent ANOVA for onset latencies did not produce any significant effects at all, all $F_c(1,14)<2.1$, $p>.094$, $\eta^2_{pc}<.13$. N2pc onset latencies (213ms versus 232ms, respectively) and load effects (high- minus low-load latencies; (20ms versus 34ms, respectively) were identical in the colour and shape tasks of Experiment 2.

Chapter 5 General Discussion

This thesis investigates the temporal dynamics of attentional template activation during visual search, focusing on the capacity limits and strategic control of multiple templates, as well as the organisational properties of features in conjunction search. Comprising six EEG studies across three chapters, it addresses three critical research questions:

1: To what extent is template co-activation under strategic control: Do participants by default activate multiple templates simultaneously, or do they strategically activate a single template based on specific task demands? (Chapter 2)

2: Is there template co-activation possible near the VWM capacity limit: Do template activation patterns change when three templates need to be prepared for search? (Chapter 3)

3: How does template co-activation work during conjunction search when targets are defined by multiple features from different dimensions: Do templates contain features lists or integrated target representations? (Chapter 4)

In the preceding chapters, I have explored different aspects of attentional template formation and activation. In this final chapter, I will integrate the most significant findings and further discuss capacity limitations and the flexibility of template co-activation in feature and conjunction search.

Experiments in Chapter 2 found significant template switch costs when target templates had to be switched as compared to repeated between trials. RTs in switch trials were delayed, error rates were increased, and target N2pcs were delayed and attenuated. These switch cost arose from delayed activation of the relevant upcoming target colour template in each trial as opposed to interference from the irrelevant template that specified the previous target colour. This was uncovered by the N2pcs triggered in response to a series of target colour probes presented prior to search. When these probes matched the relevant target colour, they triggered solid N2pcs from about 800ms before search, indicating that the relevant target template was activated well ahead of search display onset. However, this was only the case in colour repetition trial. In colour switch trial, template activation was delayed and only started about 200ms prior to search. Importantly, irrelevant target colour never triggered any N2cpcs, indicating that they were completely ignored at all times.

The study in Chapter 3 discovered that three target templates can be activated in parallel during preparation for search, if necessary. When the upcoming target colour was unknown, all target-colour probes triggered solid N2pcs from about 800ms prior to search. However, capacity limitations became evident during the actual search for one of these three possible target colours. Especially, target N2pcs were attenuated and delayed in the three-colour as compared to a one-colour control condition in which participants searched for a single colour only. These findings show that while it is possible to activate three attentional templates in parallel, the costs caused by the inhibitory interactions between these co-activated templates still renders search more inefficient than during single colour search. Furthermore, if participant have the opportunity to prioritise one of the three templates, i.e., because the target sequence is fully predictable, they will make use of this opportunity and only activate the relevant templates specifying the upcoming target colour.

Chapter 4 employed a conjunction task involving colour and shape and extends the investigations of this thesis to targets that are defined by multiple features of different dimensions. Results revealed that attention is guided in a feature-based fashion by attentional templates that hold separate target features rather than integrated object representations. Memory load effects (costs of multiple template activation) were measured during search preparation (CDA), during attentional guidance at search (N2pc), and at post-selective stages during response execution (BI scores) both during feature- and conjunction search. However, these load effects were substantially increased, i.e., doubled, in the conjunction task as compared to the single-feature task. Specifically, at the level of the CDA this means that participants activated twice the number of attentional templates in the conjunction than the single feature task. These additional templates increased the level of inhibitory between-template interactions and reduced search efficiency in the conjunction task so that N2pc load effects were also twice the size in the conjunction than the single feature tasks. Furthermore, partially matching distractors that were presented with the target captured attention and reduced the target N2pc when they were located in the opposite hemifield to the target. This is further evidence for the feature-based nature of attentional templates in conjunction search.

5.1 Capacity in template activation without strategic control

VWM is known to have a limited capacity, typically around 3-4 items for visual information (Cowan, 2001; Luck & Vogel, 1997). This capacity limitation has important implications for visual search, as attentional templates guiding search are thought to be maintained in VWM (Eimer, 2014). The series of studies in this thesis investigated the capacity limits of template activation and how these limits affect visual search preparation and performance. Experiments in Chapter 3 directly tested the capacity limit of template activation during preparation and selection of visual search by employing an RSPP paradigm with probes matching target or distractor colours presented before search onset. The results demonstrated that, in an unpredictable three-colour scenario, three potential target colour templates were activated simultaneously, showing optimal search preparation, i.e., if participants do not know the target identity, they simply activate all possible target templates. Critically, distractor-colour probes did not trigger any N2pc, suggesting that the presence of target-colour probe N2pcs was not related to salience-driven attentional capture. These observations confirm and extend previous findings that more than one colour-specific search templates can be activated in parallel (e.g., Beck et al., 2012; Irons et al., 2012; K. S. Moore & Weissman, 2010), even when the target colours are presented randomly with unequal probabilities (Grubert & Eimer, 2023).

Importantly, we observed significant performance costs in both the behaviour and the target N2pcs, consistent with observations of previous studies contrasting one- and two-colour search (e.g., Grubert et al., 2016; Irons et al., 2012). This suggests that attentional guidance and subsequent processes involved in target selection and identification operate less efficiently when the target's identity is uncertain. While critical search performance costs were observed, there were no apparent costs in the probe-related N2pc amplitudes for maintaining and activating multiple templates during search preparation. This is consistent with the findings of Ort et al. (2019) and Ort and Olivers (2020), who concluded that costs primarily exist in the target selection stage rather than in search preparation.

From the results in Chapter 3, we now know that three single-feature templates can be activated simultaneously, but that there are substantial costs for attentional guidance during search for three possible target colours. Following from this, in Chapter 4, it was hypothesised that the co-activation of two conjunction templates, each containing a colour and a shape, should show a similar degree of search performance cost than single feature search. However, the results showed the opposite. The search cost observed with the activation of conjunction templates was nearly twice as high as the cost observed in single feature tasks, suggesting that the two conjunction templates were not activated in the same fashion than the two single feature templates. The possible reason for this might be due to the way target information is stored in the target templates. If the target's colour and shape are integrated into a holistic object, two conjunction templates should behave similarly to two single feature templates, as they are represented as two items in VWM. However, if the conjunction templates are feature-based, for two conjunction templates there are actually four features stored in VWM, reaching VMW capacity. Our results clearly support the feature-based hypothesis. In addition to the N2pc load costs, the difference in CDA amplitudes between two and one conjunction templates was twice as high as that of single-feature templates, indicating that each conjunction template involved two features. Additionally, the partially matching distractors were found to capture attention, further indicating that conjunction templates were feature-based. In the two conjunction search, four individual features must have been activated to guide attention, but with the inhibitory interactions between these templates search was rendered significantly less efficient as compared to the search for two single features. Such an assumed between-template suppression potentially observed in the conjunction task agrees with recent models of template inhibition in multiple-feature search (e.g., Kerzel & Grubert, 2022).

However, even though as much as three templates can be activated simultaneously to guide attention, the predictable three-colour task in Chapter 3 showed that only one target template, the one that matched the immediately upcoming target colour was active at a time. This means that participants make use of strategic template activation to reduce VWM load if it is needed (i.e., during three-colour search) and if they can (i.e., when target colours are predictable). Altogether, the findings from the studies of this thesis suggest a more flexible nature of template capacity, where multiple templates can be maintained simultaneously, albeit with performance costs due to competitive interactions. This understanding challenges the notion of a strict single-template capacity limit (Olivers et al., 2011) and highlights the adaptability of the visual system in managing attentional resources. As we move forward, it becomes crucial to explore how strategic control mechanisms are employed to optimise template activation and manage these competitive interactions effectively.

5.2 The strategic control in template activation

Task switching is a fundamental aspect of cognitive control, requiring flexible reconfiguration of mental sets to meet changing task demands (Monsell, 2003). In the context of visual search, task switching often involves updating attentional templates to guide attention towards new targets (features). It was found that in tasks when participants search for one of several possible targets, performance was impaired on target-change trials relative to target-repeat trials even when the identity of the next target was fully predictable (Rogers & Monsell, 1995). The strategic control of template activation is crucial for efficient performance, particularly when managing multiple potential targets or adapting to changing task requirements, given our limited VWM capacity.

In Chapter 2, we examined the mechanisms involved in switching target templates, where participants were tasked with identifying targets defined by one of two colours, which alternated predictably every two trials in Experiment 1 and every four trials in Experiment 2. A significant finding was the delay in the emergence of probe N2pc components before the target-colour switch trials in both experiments, highlighting a temporal dissociation between the switch and repeat trials. On the target-repeat trials, the template was active from about 800ms prior to search display onset, while on switch trials, a reliable N2pc was only present for the target-colour probe immediately preceding the search display (200ms). This delay seems to reflect the time needed for reconfiguring a target template, akin to task-set reconfiguration processes in the task switching literature (see Monsell, 2003, for a review; Monsell et al., 2000; Rogers & Monsell, 1995; Rubinstein et al., 2001).

Both experiments demonstrated clear behavioural switch costs, despite the predictability of the next target and sufficient time between search displays, in line with previous studies (e.g., Wylie & Allport, 2000). Target N2pcs were also weaker and emerged significantly later on colour-switch relative to colour-repeat trials, indicating that search guidance was more effective on repeat trials. The delay in probe N2pc components on switch trials (approximately 600ms) was significantly larger than the switch costs in RTs (approximately 50ms) and those in target N2pc onset latencies (25-30ms). This suggests a more substantial impact of task switching on preparatory template activation than on subsequent attentional guidance and target selection. This finding also aligns with the previous literature, which suggested that a significant portion of the switch cost arises from the need to reconfigure the cognitive system during preparation (Meiran, 1996; Rogers & Monsell, 1995). Furthermore, maintaining task sets (target sequence in our study) in VWM is a preparatory process. Hence, the capacity limitations could show a disproportionately strong effect during preparation. Another possible factor leading to the preparation delay is task inertia, (i.e., the previous task set persists and interferes with the new one). This inertia primarily affects the initial configuration (preparation) rather than later processing stages (Allport & Wylie, 1999). However, no evidence of template inertia was found, as irrelevant colour probes did not elicit N2pcs on switch trials. This means that a colour-selective template is activated without residual activation of any previous templates, and that there is no competition between the current and any previous target-colour templates.

The absence of any N2pcs to irrelevant colour probes expanded the finding of a previous study that showed parallel activation of two colour templates (Grubert & Eimer, 2020). This difference may be attributed to various search preparation strategies based on task design. The single-template strategy used in the current study, despite leading to switch costs, might be less demanding than activating two templates. The strategic choice of single-template activation was also evidenced in Chapter 3. In predictable three-colour search scenarios, participants strategically activated only the relevant colour template for the upcoming search despite knowing all three potential target colours. As such, participants can flexibly adopt single- or multiple-template strategies based on task demands (Ort & Olivers, 2020). This flexibility suggests that template activation is not a passive process, but instead actively controlled to optimise performance. Overall, the strategic adoption of a single-template strategy in predictable two-colour (Chapter 2) and three-color search (Chapter 3) may be driven by increased cognitive load and longer intervals between target repetitions

(Lien et al., 2010), which encourages a more economical activation strategy even when it is accompanied by performance costs.

5.3 Contents of attentional templates in conjunction search

Chapter 4 investigated how attentional templates manage target representations in visual search tasks. Specifically, the experiments directly contrasted conjunction tasks with single-feature (colour and shape) tasks under low and high VWM load conditions. As hypothesised above, the findings suggest that conjunction tasks are guided by individual feature templates rather than integrated object representations. This conclusion aligns with several prominent visual search theories (e.g., Bundesen, 1990; Wolfe, 2021), which emphasise the role of feature-based attentional guidance. The empirical evidence from our study supports the notion that attentional guidance is fundamentally feature-based, even in complex conjunction tasks, therefore challenges the assumption that integrated representations are employed when task difficulty increases (Qian et al., 2019).

A key observation in Chapter 4 was the capture of attention by partially matching distractors in conjunction tasks. This finding supports the idea of feature-based guidance, as integrated object representations should have been blind for these distractors that only ever matched one of the two target defining features. The ability of distractors that match either the target colour or shape to capture attention suggests that attentional guidance operates independently for each feature. This is consistent with studies by Lee et al. (2018) and Dent (2023), who have demonstrated similar feature-based attentional capture effects. This feature-based attentional capture underscores the efficiency of separate feature templates in guiding attention, even when multiple features are involved in the same target. The CDA findings (reflecting the maintenance of information in VWM) provide further support for the feature-based interpretation. The size of the CDA amplitude differences between low (one template in VWM) to high (two templates in VWM) load conditions was significantly larger in the conjunction than in the single feature task. To be more specific, the load effects in the conjunction task were twice as large than in the single feature task. This finding provides strong evidence that a conjunction template contains separate feature representations instead of an integrated representation.

However, this feature-based interpretation stands against a substantial body of literature from working memory experiments suggesting the prevalence of object-based representations (e.g., Cowan, 2001; Luck & Vogel, 1997; Olson & Jiang, 2002) and an elevated level of colour-shape integration (Huang, 2020). Given that attentional templates are components of VWM, this discrepancy is particularly striking. The current result seems to suggest that task difficulty and the chunking strategy for reducing VWM load may not suffice for integrating features into a holistic object representation. To reconcile these contradictions, we need to contemplate the specific demands of visual search tasks. These tasks often involve spatial uncertainty and require highly precise templates to effectively differentiate targets from distractors. Some VWM studies (e.g., Fougnie et al., 2010) suggested that integrated object representations may lack the precision of feature-based representations. Furthermore, the benefits of forming conjunction representations appear to diminish when object locations are rendered irrelevant (Wang et al., 2016). Weber et al. (2020) examined how VWM stores two features of a single object under increased load within the same or different feature dimensions and failed to find significant coupling in precision across trials for these features. Interestingly, within a single object, increased load in one feature dimension (e.g., colour) affected precision in both the same and other feature dimensions (e.g., size), implying partial integration during maintenance. Consequently, the author proposed a hierarchical model suggesting that VWM capacity is determined not solely by the number of objects stored, but also by the complexity of the information within those objects. Overall, it is suggested that VWM is capable of handling both independent features and integrated objects, depending on the demands of the task at hand. In summary, the current findings strongly support feature-based attentional guidance in visual search, even under conditions that integrated representations may be beneficial.

5.4 Limitations and future directions

Firstly, the behavioural and N2pc differences we observed between the colour and shape search in Experiment 1 of Chapter 4 demonstrate that the effects measured during search for a specific feature dimension cannot blindly be generalised to other feature dimensions. Feature dimensions differ with respect to their guiding quality (e.g., Wolfe & Horowitz, 2004). Both Chapters 2 and 3 focused on colour-defined targets, and the results may therefore not directly translate to other feature dimensions or more complex target definitions.

Furthermore, Chapter 3 demonstrated that at least three colour templates can be activated simultaneously during visual search tasks. However, the maximum number of templates that can be activated concurrently remains unknown. It is important to distinguish between single-feature and conjunction tasks. In single-feature tasks, features can be stored independently to guide attention, whereas conjunction tasks require the integration or binding information of features to select the correct target, imposing additional constraints. That is, in the two conjunction templates search, the items maintain in VWM may not be four features, but four features plus two relationship information, resulting six items. This distinction implies that findings from multiple conjunction searches might not directly apply to the overall limits of template capacity in single-feature tasks. Future research should focus on the role of feature binding in VWM and its impact on the activation of multiple conjunction templates. Specifically, studies could investigate whether the limitations in activating multiple conjunction templates are due to incorrect feature binding or the loss of features during VWM maintenance. For instance, to test if binding information interplays with template activation, future studies could employ a task with a mis-binding condition, where features are allowed to not bind to other feature(s) within the same object. The results may show a reduced the number of items that need to be maintained in VWM and a better overall template activation. Another potential experiment could compare a conjunction template containing four or more features to two conjunction templates, each containing two features. If the template with four features can guide attention as efficiently as single-feature templates, or if there are significant costs associated with the activation of the two conjunction templates, it implies an inference about the binding information related to template activation.

Another emerging question from the current work involves understanding the interactions between attention templates. Findings from Chapters 3 and 4 suggest that inhibitory interactions occur when multiple templates are simultaneously active. However, the specific mechanisms behind these interactions remain unclear. Inhibition becomes particularly crucial when multiple target templates are activated and the target identity is unpredictable. In such scenarios, distractors with high target similarity may also capture attention, leading to a higher cognitive load to suppress such distractors. Future research should further clarify the dynamics and nature of these inhibitory processes. For example, using a similar RSPP paradigm with designated similar versus dissimilar distractor conditions to untangle effects of target template activation from distractor suppression.

5.5 Conclusion

The current thesis investigated the temporal dynamics of attentional template activation during visual search, focusing on how strategic control and capacity limitations influence the activation of multiple templates. The first four EEG experiments convergingly demonstrated that multiple single-feature templates can be activated simultaneously, and that template activation can be strategically controlled depending on task demands and capacity constraints. The last two EEG experiments further showed that conjunction templates for two feature dimensions are likely to be activated as separate features in parallel, instead of integrated object representations. Taken together, these experiments show that three, and possibly even four feature-based templates can be activated in parallel during search preparation, but that mutual inhibitions of these co-activated templates have detrimental effects on visual search. With an increasing number of active templates there is a reduction of the overall activation level of each individual template leading to poorer search performance.

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