# Electrophysiological measures of flexible attentional control and visual working memory maintenance

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# Abstract

Top-down attentional control can be used to both guide attention toward and away from items according to their goal relevance. When given a feature-based cue, such as the colour of an upcoming target, individuals can allocate attention and memory resources according to the item's priority. This distribution of resources is continuous, such that the amount that an item receives is dependent on its likelihood of being probed. However, top-down goals are often challenged by bottom-up stimulus salience of distractors. One's ability to avoid attentional capture by distractors is limited by attentional control over bottom-up biases. In particular, individuals with anxiety have attentional biases toward both neutral and threatening distractors, leading to unnecessary storage of distractors in visual working memory (VWM). Using electrophysiology, it is possible to study the time course of these attentional processes to gain a better understanding of how attentional selection, suppression, and VWM maintenance relate to attentional control. The present thesis explores the event-related potential (ERP) correlates and time course of flexible attentional control, as well as how individual differences in anxiety limit this ability.

In the first study, I used positive and negative feature-based cues to demonstrate that attentional selection occurs earlier when guided by target information than distractor information. Additionally, it was found that greater anxiety resulted in selection of the salient distractor, demonstrating that anxiety compromises early attentional control. For the second study, I further examined deficits in attentional control in anxiety. Here, it was demonstrated that individuals with high anxiety had early selection of threat-related distractors, whereas individuals with low anxiety could pro-actively suppress them. Interestingly, this effect did not carry over to VWM maintenance, suggesting that deficits in early attentional control do not necessarily result in poor memory filtering. In the final study, I examined the link between continuous attentional allocation and VWM maintenance, finding that individuals use priority information to flexibly select and filter information from VWM. Together, in this thesis I propose that attentional control over selection, suppression, and VWM filtering processes is flexible, time-dependent, and driven both by external cues and internal biases related to individual differences in anxiety.

***Keywords:*** attentional control, target selection, distractor suppression, anxiety, visual working memory

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# List of Abbreviations

| | |
|---|---|
| **ACC** | Anterior cingulate cortex |
| **ANOVA** | Analysis of Variance |
| **BOLD** | Blood-oxygen-level dependent |
| **CDA** | Contralateral delay activity |
| **CI** | Confidence interval |
| **EEG** | Electroencephalography |
| **ERP** | Event-related potential |
| **fMRI** | Functional magnetic resonance imaging |
| **K** | Estimate of visual working memory capacity |
| **lPFC** | Lateral pre-frontal cortex |
| **N2pc** | Posterior-contralateral negativity |
| **$P_D$** | Distractor positivity |
| **RT** | Reaction time |
| **VWM** | Visual working memory |

# Chapter 1

## General Introduction

At any given moment, our brains are faced with an abundance of visual information, which must be searched through so that goal-relevant items are given further processing and goal-irrelevant items remain ignored. Similar to completing a puzzle, although the most brightly coloured piece may capture attention, that piece is not always the one that we need in the moment (Figure 1-1). Using visual working memory (VWM), we can briefly hold goal-relevant features in mind, such as colour or shape, to effectively guide our attention toward specific pieces. We also know the kind of information that we are *not* looking for, such as when we ignore the grey pieces when we are searching for a blue one. Then, once the coveted piece is found, we must again use working memory to remember its shape so that it can be placed in the correct spot.

Yet, there is a fundamental capacity limitation of both attention and VWM, such that only a small subset of available information can be processed at a time (Cowan, 2001; Cowan et al., 2005; Miller, 1956; Wolfe & Horowitz, 2004). This limitation on capacity requires the ability to strategically allocate cognitive resources amongst items, according to their task relevance. Without this ability, our brains would quickly become overwhelmed with information. How the brain manages to flexibly split attention and VWM resources amongst items, and why individuals differ in their abilities to do this efficiently, is the focus of the present dissertation. Here, I propose that individuals are capable of flexibly allocating cognitive resources by both selecting and inhibiting potential memory items depending on their task relevance. However, I also demonstrate using electrophysiological (EEG) data that attentional control over the allocation of cognitive resources is affected by an interaction between item relevance and individual differences in anxiety.

***Figure 1-1.*** To complete a puzzle, one must use both attention and visual working memory to guide attention toward a target piece and away from irrelevant pieces regardless of their salience.

## Attentional selection and the N2pc

When an individual searches for an item in a cluttered visual scene, it is important that they can appropriately select and attend to that one item without getting too distracted by the others. Theories of attention have largely focused on this process of how goal-related items are selected by attention for additional processing (Bundesen, 1990; Wolfe, 1994). The majority of these theories propose that selection is biased by an interaction between two factors (Bundesen, 1990; James, 1890; Treisman, 1988, 1998; Wolfe, 1994): 1) Bottom-up factors, such as item salience (i.e. brightness or color; Theeuwes, 1992, 2004), and 2) Top-down (or goal-driven) selection that is driven by an observer's internal attentional template of the target item (Bacon & Egeth, 1994; Folk et al., 1992). Beyond these two factors, Awh, Belopolsky, and Theeuwes (2012) propose that selection history and reward also bias attention, and that together, all four factors contribute to an overall 'priority map' for selection (Fecteau & Munoz, 2006; Serences &

Yantis, 2006). In this map, the item that receives the highest weighted priority wins the attention competition and receives additional processing.

This idea of attention as an emergent property of competition between items for limited processing resources is outlined in Desimone and Duncan's (1995) *biased competition model* of attention. The authors of this model propose that visual items compete for limited cognitive and neural resources, and that this competition can be biased by the observer's top-down goals. It is these top-down, goal-driven biases that will be the focus of the current thesis. One way that top-down goals can be maintained is through the use of attentional templates, which can be either feature-based or location-based (Battistoni et al., 2017; Carlisle, 2019). Here, I focus on the role of feature-based attention (also referred to as content-based), such as an object's colour or shape.

Search templates that match features of a goal-relevant item are called *positive search templates*, which generally lead to faster reaction times (RTs) compared to uninformative cues when searching for a template-matching target (Vickery et al., 2005). These templates are likely held in VWM, as it has been found that search items that match the contents of VWM receive more attention, even at the expense of performance (Olivers et al., 2006; Soto et al., 2005, 2008). This has been taken as evidence for involuntary attentional capture by the contents of memory (Soto et al., 2008). However, Woodman and Luck (2007) suggested that individuals may instead *voluntarily* allocate their attention toward memory-matching items as a strategic way to boost their overall task performance. Given this finding, it is likely that the contents of VWM alone are not sufficient to guide attention automatically, and that goal relevance plays a more important role in biasing selection (Carlisle, 2019).

Another way in which the impact of attentional templates on selection can be measured is through the use of electroencephalography (EEG). In particular, researchers have identified an event-related potential (ERP) component that relates to attentional selection called the N2 posterior-contralateral (N2pc; Eimer, 1996; Luck & Hillyard, 1994a; Woodman & Luck, 1999, 2003). The N2pc is a greater negativity over contralateral than ipsilateral electrodes to an attended hemi-field that occurs approximately 200 – 300 ms after the onset of a search array, and is largest over parietal and occipital electrode sites. This component is thought to reflect covert attentional selection or enhancement that occurs at the focus of attention (Luck & Hillyard, 1994a, 1994b; Zivony et al., 2018). In visual search tasks, an N2pc is typically observed toward salient and task-relevant items (Luck & Hillyard, 1994a). However, the N2pc is not target-specific, meaning that it reflects attentional selection regardless of an item's goal relevance (e.g. when task irrelevant items capture attention; Gaspar & McDonald, 2018). It has been proposed that the N2pc does not reflect attentional shifting, as it has been found that N2pc amplitude is unaffected by the informativeness of spatial cues; suggesting that this component reflects item processing that occurs after initial attentional shifts, such as item identification and memory encoding (Kiss et al., 2008; Zivony et al., 2018).

Attentional templates affect the amplitude of the N2pc, such that goal-relevant search targets elicit large and early N2pcs (Carlisle & Woodman, 2011). Goal-relevant templates can also include items that are associated with reward, such that high-reward targets elicit a larger N2pc than low-reward targets (Kiss et al., 2009). However, the N2pc is not always affected by the contents of VWM, as it has been found that memory-matching distractors elicit a weak N2pc in comparison to memory-matching targets (Carlisle & Woodman, 2011, 2013). This finding suggests that top-down attentional control (i.e. regulation of attention allocation) is necessary to deploy an attentional template for item selection, consistent with the behavioural findings that the contents of VWM alone do not automatically bias selection (Olivers et al., 2011). Overall, both the behavioural and neural evidence converge on the importance of goal-relevant templates in attentional control and selection.

## Distractor inhibition and the $P_D$

Attentional control is not just the ability to attend to goal-relevant information, but it is equally one's ability to ignore goal-irrelevant information. There is evidence that individuals can use information about distractor features to actively avoid attending to those items (Duncan & Humphreys, 1989; Geng, 2014; Geng et al., 2019; Treisman & Sato, 1990). For example, when participants knew that the item they were searching for would *not* be in a particular colour (e.g. the target would not be red), they could avoid the memory-matching distractor, speeding up target search compared to when a mismatching distractor was present (Woodman & Luck, 2007). This type of attentional template has been deemed a *template for rejection* or *negative template*, and serves to set low priority weights for template-matching items. Ultimately, information from both positive and negative templates can be used to set weights on the attentional priority map (see Figure 1-2). Negative templates, however, have a different effect on visual cortex compared to positive templates, such that there is a down-regulation of visual cortical activity following a negative template compared to a positive template (Reeder et al., 2017, 2018). This suggests that there is a distinct cortical mechanism for distractor inhibition from target selection, which could be facilitated by attentional control activity in the superior parietal lobule (SPL)/precuneus (Reeder et al., 2017).

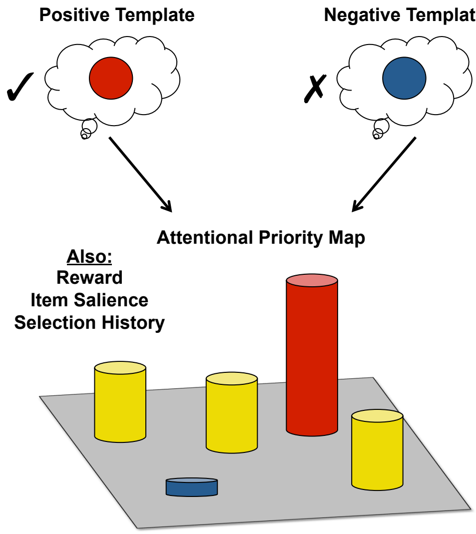

***Figure 1-2.*** Schematic representation of how positive and negative templates can be used to flexibly up- and down-weight item priority as indicated on an overall priority map. Features matching positive templates are enhanced, while features matching negative templates are actively suppressed below baseline. Features matching neither template receive baseline processing. Of note, reward, item salience, and prior selection history also bias attentional priority.

This distinction between positive and negative templates is also present in behavioural studies, which find that although it is possible to use a negative template to benefit search performance (Arita et al., 2012), positive templates result in larger search RT benefits (Zhang et al., 2019). It could be that this smaller benefit for negative templates is driven by a search strategy in which an individual initially searches for the template-matching item, quickly rejects it, and then re-orients attention toward the target item (i.e., *'search and destroy'*; Arita et al., 2012; Moher & Egeth, 2012). This extra disengagement step would therefore cause slower RTs following negative cues compared to positive cues. To examine this possibility, researchers have turned to EEG to track attentional selection using search templates (i.e. the N2pc). Carlisle and Nitka (2019) used a lateralized search array with positive, negative, and neutral colour cues. Participants searched for a target letter C from a large circle of Cs, with each hemi-field sharing the same colour (i.e. left half all red Cs and right half all blue Cs). They found that after a negative cue there was a reliable N2pc only toward the target item (albeit later than following a positive cue). These results suggest that the template-matching distractors did not draw attention, providing evidence against the ‘search and destroy’ mechanism of negative templates.

Although the study by Carlisle and Nitka (2019) provided evidence that negatively cued distractors do not automatically capture attention, the results do not speak to the extent of *active suppression* of negatively cued features. That is, there is a difference between moving attention away from an item, and actively suppressing the representation of that item toward baseline. The *signal-suppression* hypothesis proposes that it is possible to suppress processing of a salient distractor *before* attention is captured by using top-down cognitive control (Gaspelin & Luck, 2018, 2019). Evidence for an active suppression mechanism comes from ERP studies examining posterior parietal activity contralateral to a distractor (Hickey et al., 2009; Kiss et al., 2011). When the distractor is placed on the lateral and the target on the vertical midline, the contralateral waveform is more positive than the ipsilateral waveform, resulting in a positive-going component in the difference waveform. This component is called the distractor positivity ($P_D$), and is observed either before, during, or after the time range of the N2pc, depending on the task design (Sawaki et al., 2012; Sawaki & Luck, 2010, 2011). The early $P_D$ (140 - 190 ms), also referred to as the Ppc, is thought to reflect initial processing of feature discontinuities, which can subsequently guide attentional enhancement and suppression

(Barras & Kerzel, 2016; Fortier-Gauthier et al., 2012; Jannati et al., 2013; but see, Kerzel & Burra, 2020). The later $P_D$ (300 - 400 ms) likely reflects an active suppression process, as it has been found that larger $P_D$ amplitudes predict faster target RTs in the presence of a distractor, suggesting that greater distractor suppression facilitates target selection (Gaspar & McDonald, 2014; Hickey et al., 2009; Sawaki et al., 2012).

## Individual differences in attentional selection and inhibition

Although the evidence presented thus far suggests that individuals are able to flexibly enhance or suppress items depending on their task priority, there is considerable inter-individual variability in these abilities. This is particularly true when it comes to ignoring distracting information. For example, there is evidence that individuals with higher VWM capacities are less captured by distracting stimuli than individuals with lower capacities (Fukuda & Vogel, 2009; Gaspar et al., 2016), and recovery from attentional capture is also faster for those with high capacities (Fukuda & Vogel, 2011). Beyond memory capacity, there is also evidence that older individuals have deficits and delays in inhibiting irrelevant information from being stored in working memory (Gazzaley et al., 2005, 2008; Hasher & Zacks, 1988). This attentional capture by distractors is likely related to variability in top-down attentional control, both between and within individuals (Gaspar & McDonald, 2014; Leber, 2010; Müller et al., 2009).

Deficits in attentional control can also be seen in individuals who have either clinical or subclinical levels of anxiety (Bishop, 2009). In fact, Eysenck and colleagues' (2007) Attentional Control Theory of anxiety (ACT) proposes that anxiety results in both an overall impairment in attentional shifting, and a more specific deficit in distractor inhibition (Derakshan & Eysenck, 2009; Eysenck et al., 2007; Eysenck & Derakshan, 2011). This may be due to increased worry that reduces the amount of attention and VWM resources available for exerting top-down control in the face of salient bottom-up stimuli (Eysenck et al., 2007; Sari et al., 2017). For example, in the antisaccade task, anxious individuals are slower to make a saccade away from an irrelevant distractor (Derakshan et al., 2009). As well, in visual search tasks, individuals with high anxiety are slower to find a target when a salient distractor is present in the search array compared to individuals with low levels of anxiety (Moran & Moser, 2015; Moser et al., 2012).

Interestingly, although the above findings suggest that processing *efficiency* is negatively impacted for individuals with anxiety (i.e. how cognitive resources are used to perform a task), their task *effectiveness* (i.e. overall task performance) is usually unaffected (Eysenck et al., 2007). This suggests that anxious individuals can overcome deficits in attentional control through compensatory strategies, such as exerting more effort into the task to reduce performance-related anxiety (Ansari & Derakshan, 2011; Berggren & Derakshan, 2013). Yet, *how* processing efficiency is impacted by anxiety is less clear from behavioural responses alone, as behaviour reflects a combination of attention, memory, and decision-making processes. Therefore, ERPs have been used to better isolate the role of attentional selection (i.e. N2pc) and suppression (i.e. $P_D$) in anxiety. Gaspar and McDonald (2018) found that individuals with high anxiety had their attention captured by the distractor, as indicated by an early N2pc (but see, Qi et al., 2014), but that they were able to suppress the distractor following initial capture, as indicated by a later $P_D$. This is compared to individuals with low levels of anxiety, who were able to proactively suppress distractor processing, as indicated by an early $P_D$. Similarly, Moran and Moser (2015) found that individuals with higher levels of trait anxiety had larger N2pc amplitudes when a distractor item was presented near a target item, reflecting a need for greater target enhancement in the presence of distraction.

### Anxiety and threat-related attentional control

Although anxiety induces an overall deficit in attentional control, individuals with anxiety have been found to have a specific threat-related bias compared to non-anxious individuals (Bar-Haim et al., 2007; Bishop et al., 2004; Cisler & Koster, 2010; MacLeod et al., 1986). Threat refers to anything that might signal harm, whether physical or social, such as snakes, spiders, angry or fearful faces, and threat-related words (e.g. *injury* or *criticize*; MacLeod et al., 1986). It is thought that the bottom-up attentional orienting system is over-responsive to threat in anxious individuals (Eysenck et al., 2007). This bias in bottom-up processing of threat, combined with deficits in top-down attentional control over distractors, leads to even greater attentional capture by threat-related distractors in anxious individuals (Mogg & Bradley, 2018).

These attentional biases to threat have been examined using the N2pc. It has been found that individuals with anxiety are more likely to have their attention captured by angry faces than neutral or happy faces (Fox et al., 2008). This automatic bias toward threat in anxiety may be driven by an over-reactive amygdala, which signals that threatening distractors should receive additional cognitive resources (Stout et al., 2017). In regards to attentional suppression, it has been found that generally, threatening distractors cause a delayed $P_D$ in comparison to neutral distractors (Burra et al., 2019). However, the effect of *anxiety* on the $P_D$ toward threat-related distractors has not been previously explored.

## Individual differences in visual working memory filtering ability

Following initial attentional selection, suppression, and encoding, information can be temporarily stored in an ‘on-line’ state in VWM to be used in a subsequent task (Baddeley, 1992). One’s ability to prevent distracting information from being stored in VWM, however, at least partially depends on their attentional control over memory resources (Awh et al., 2006; Awh & Vogel, 2008). Because only a small amount of information can be maintained in VWM at a time (Cowan, 2001; Luck & Vogel, 1997), there must be a way to *filter* irrelevant items from memory storage. This filter has been likened to a “bouncer in the brain”; only letting in the most important information while preventing task-irrelevant information from being encoded into memory (Awh & Vogel, 2008). That is to say, the weaker the bouncer, the more memory resources are being used up by task-irrelevant information. If distracting items are maintained erroneously, working memory capacity and performance are negatively impacted (Cowan & Morey, 2006; Fukuda et al., 2015).

One way that filtering ability can be assessed is by examining how much information is stored in VWM. In particular, VWM storage can be tracked by EEG activity during the delay period of lateralized change detection tasks (Ikkai et al., 2010; Klaver et al., 1999; McCollough et al., 2007; Vogel & Machizawa, 2004). When participants are told to remember items on one side of the screen, there is an increased negativity over contralateral electrode sites relative to ipsilateral electrodes (Gratton, 1998). This ERP is called the contralateral delay activity (CDA), which becomes more negative as the number of items held in VWM increases (for a review see, Luria, Balaban, Awh, & Vogel, 2016). Despite its name, this component is not only observed during the delay period of working memory tasks, but is elicited during any task that involves holding information in working memory (e.g. visual search: Emrich, Al-Aidroos, Pratt, & Ferber, 2009). The amplitude of the CDA increases rapidly up to an individual's capacity (Vogel & Machizawa, 2004), supporting this component as an index for the amount of information maintained in VWM.

There is evidence that the better an individual is at preventing distractors from getting into memory (i.e. *filtering efficiency*), the larger their VWM capacity. In a seminal ERP study by Vogel, McCollough, and Machizawa (2005), the researchers investigated how the CDA was affected by distractor filtering. Additionally, they examined how individual differences in filtering efficiency were related to VWM capacity. Participants were told to remember two rectangles in the target color (red), while ignoring the two rectangles in the distractor colour (blue) on one side of the screen. CDA amplitude in this 'filtering' condition was then compared to CDA amplitude when only two or four target items were presented without distractors. If a participant successfully filtered the distractors from VWM, then the CDA amplitude in the filtering condition should be similar to the CDA amplitude when two target items were remembered alone. However, if an individual stored the two distractors in memory, then the CDA amplitude in the filtering condition should be more similar to when four target items were remembered. It was found that individuals with higher VWM capacities had CDA amplitudes in the filtering condition that looked more similar to when two target items were held in memory, whereas lower capacity individuals had CDAs that were closer to the amplitude of four target items (Awh & Vogel, 2008; Vogel et al., 2005). This relationship between capacity and CDA amplitude was continuous, such that the lower one's VWM capacity, the more distractors were being unnecessarily stored in memory.

The CDA has been used as a proxy for filtering efficiency because it measures unnecessary storage in VWM. However, there is evidence from functional magnetic resonance imaging (fMRI) and EEG that filtering-related activity in the pre-frontal cortex and basal ganglia is a better predictor of VWM performance than unnecessary storage alone (Emrich & Busseri, 2015, McNab & Klingberg, 2008, Liesefeld, Liesefeld, & Zimmer, 2014). In a similar filtering task as Vogel, McCollough, and Machizawa (2005), McNab and Klingberg (2008) found that preparatory blood oxygen-level dependent (BOLD) activity in these areas predicted both an individual's filtering efficiency and VWM capacity. These brain areas are distinct from the proposed generator of the CDA (Robitaille et al., 2010): the intra-parietal and intra-occipital sulci (IPS/IOS). This suggests that during filtering tasks there is an interaction between pre-frontal control regions, gating mechanisms in the basal ganglia, and posterior parietal areas involved in VWM storage (Todd & Marois, 2004, 2005). Overall, these findings propose a link between attentional control abilities and VWM filtering efficiency.

## Anxiety, attentional control, and visual working memory filtering

Given that attentional control abilities are affected by anxiety, it is unsurprising that anxiety influences filtering efficiency for both neutral distractors (Qi et al., 2014) and threat-related distractors (Stout et al., 2013). In a VWM filtering task using fearful and neutral faces, Stout, Shackman, and Larson (2013) found that individuals with high anxiety had poor filtering efficiency when a fearful distractor face was presented with a neutral target face. That is, the greater an individual's anxiety level, the smaller the difference in CDA amplitude between the two neutral targets condition and the neutral target plus fearful distractor condition. This suggests that those with anxiety were inappropriately storing the fearful face in memory, resulting in a CDA that was more similar to when two items were held in memory than one.

In a later study using fMRI, Stout and colleagues (2017) expanded upon this finding by demonstrating that the relationship between anxiety and filtering inefficiency was mediated by amygdala activity. That is, individuals with higher anxiety had greater amygdala reactivity in response to a threat-related distractor (but not a neutral distractor, unlike in Qi et al., 2014), which then predicted working memory mis-allocation. Although it was proposed that mis-allocation was a downstream consequence of an over-active amygdala, the point at which this mis-allocation occurred could not be explored due to the low temporal resolution of fMRI. Therefore, it remains an open question whether amygdala reactivity predicts inappropriate attentional enhancement, insufficient suppression, or gating deficits of threat-related distractors.

## A more flexible visual working memory filter

Visual working memory filtering ability has often been conceptualized in an all-or-none way: Either an item is completely task relevant or it is irrelevant and should be ignored. In some situations, however, there are no completely task-irrelevant items; rather, some items are simply more relevant than others. It could be that instead of being left out of VWM all together, less relevant items are given fewer memory resources. When an item receives fewer resources, such as when memory load is high, that item is not remembered with as much detail, and is therefore maintained as a less *precise* memory representation (Bays & Husain, 2008). Probe likelihood also affects representational precision, as there is evidence that when one item is more likely to be probed than the others, its colour or orientation can be reported with greater precision than the un-cued items (Gorgoraptis et al., 2011; Zhang & Luck, 2008; for a review of VWM models, see Ma et al., 2014). The effects of probe likelihood on representational precision suggest that like attentional control, the VWM filter may also be more flexible than once thought.

Recent behavioural studies support the idea that memory resources can be flexibly distributed amongst items based on their relative task priorities (Dube et al., 2017; Emrich et al., 2017; Klyszejko et al., 2014). By varying the probability that an item would be probed, Klyszejko and colleagues (2014) found that items with greater probe likelihoods (i.e. higher attentional priority) were reported more precisely than lower priority items. Similarly, using spatial cues, Emrich, Lockhart, and Al-Aidroos (2017) varied the probability that an item would be probed across a range between 8 and 100%. It was found that memory precision varied continuously with the likelihood that the item would be probed, such that the relationship followed a power law. Dube, Emrich, and Al-Aidroos (2017) replicated and extended this finding using feature-based cues (i.e. shape and colour). They found that individuals had volitional control over the strength of their memory filter, such that item priority predicted memory precision across a wide range of probabilities. Importantly, these studies demonstrate the effect of item priority on memory precision without any explicit distractors in the memory array. Given these findings, Dube, Emrich, and Al-Aidroos (2017) called for an update to the traditional filtering account, proposing that attention can be used to assign memory resources amongst memory items depending on their task priority, instead of simply granting or restricting memory access.

There is also evidence that top-down attentional control of memory precision affects CDA amplitude. At low set sizes, it has been found that individuals can wilfully change the precision with which information is held in VWM, and that this change in precision is reflected by the CDA (i.e. greater amplitude for more precise representations; Machizawa, Goh, & Driver, 2012). The CDA is also affected in a similar manner by the precision with which object location is stored in VWM (McCants et al., 2019). This suggests that beyond the number of items stored in working memory (i.e. the load account), the CDA may also reflect the quality of these memory representations (i.e. the information load account; Alvarez & Cavanagh, 2004; but see, Gao, Yin, Xu, Shui, & Shen, 2011).

## Summary of the present thesis

The overall goal of the present dissertation is to examine the neural correlates of, and individual differences in, the flexible control of attention and working memory resources. By ‘flexibility’, I mean the ability to continuously modulate the amount of resources an item receives by either enhancing (up-weighting) and/or suppressing (down-weighting) attentional allocation of resources to these items. In Chapters 2 and 3 I focus on the role of individual differences in this process by investigating how anxiety impacts attentional control in the face of neutral and threat-related distractors.

Given that both attentional selection and active suppression are likely involved in flexible attentional control over search templates, in Chapter 2 I examine the effect of positive, negative, and neutral feature-based cues on the N2pc and $P_D$. Template type was manipulated on a trial-by-trial basis, as well as whether a target or distractor item was presented laterally in the search display. In this way, both the up- and down-weighting of item priority could be observed in the same task. Ultimately, I present evidence that attentional control is flexible, such that individuals use positive attentional templates to direct attention *toward* targets, and negative templates to *suppress* distractor processing. In this way, the priority map can be updated by top-down control to guide search effectively.

Further, I propose that the ability to effectively use search templates depends on individual differences in anxiety. Previous ERP studies that examined the correlations between anxiety, attentional selection, and distractor suppression have used only positive cues (i.e. the target was consistently defined by one shape). In contrast, here, it is found that individuals with anxiety are able to use positive templates to direct attention toward a target item, but anxiety hinders the ability to pro-actively suppress distractor features given a negative template. In fact, those with higher levels of anxiety inappropriately allocate attention toward items that match negative feature templates. This is in comparison to individuals with lower levels of anxiety, who are able to quickly inhibit negatively cued distractors. Overall, in Chapter 2, I argue that the ability to flexibly up- or down-weight item priority using search templates is related to individual differences in anxiety. Individuals with higher levels of anxiety have a specific deficit when using negative templates, which require the ability to pro-actively suppress distracting information using top-down attentional control.

The above findings support the idea that individuals with anxiety have a general deficit in processing efficiency that arises during early attentional selection. In Chapter 3, I further explore how anxiety affects attentional enhancement and suppression of salient, *threat-related* stimuli. To examine how attentional biases impact memory storage, I use a combination visual search and VWM task. Although there is prior evidence that attentional control over threatening distractors is affected by anxiety, no prior study has investigated the relationship between anxiety, attention (i.e. N2pc/$P_D$), and filtering efficiency (i.e. CDA amplitude) in one task. By examining all three components, it is possible to observe the link between attentional selection/suppression and what is subsequently stored in VWM, instead of looking at attention or memory-related processes in isolation. Here, it was hypothesized that the relationship between anxiety and filtering efficiency that was found in the paper by Stout and colleagues (2013) is mediated by N2pc amplitude toward threat-related distractors.

The results presented in Chapter 3 suggest that although N2pc amplitude toward a fearful distractor is greater for individuals with high levels of anxiety, CDA amplitude for that fearful distractor is not affected by anxiety. Therefore, I propose that when task load is low (i.e. attentional control resources are not taxed), individuals with anxiety are able to overcome filtering deficits despite attentional capture (Holmes et al., 2014). Here, I argue that although anxiety increases attentional biases toward threatening distractors, it does not necessarily result in impairments to VWM filtering abilities. This suggests that individuals with anxiety are capable of using compensatory strategies to prevent threatening, yet task-irrelevant, information from being stored in memory when overall task demands are low.

Together, Chapters 2 and 3 provide evidence that individuals can use positive and negative templates in a flexible manner, and that the effectiveness of attentional selection and suppression can determine what information is subsequently stored in memory. However, recent behavioural evidence suggests that it is possible to use search templates in an even more flexible way than once thought. That is, individuals can *continuously* control the amount of memory resources an item will receive based on its probability of being task relevant, even in the absence of explicit distractors. This has been demonstrated using manipulations of the likelihood that an item will be probed, anywhere from 0 to 100% probability (e.g. squares are 30% likely and circles are 70% likely to be probed). Therefore, if individuals are capable of using positive templates in a continuous manner, at what point in processing is this priority information implicated? It could be that information about item priority is used to modulate attentional enhancement of high priority items, suppression of lower priority items, or how much information is stored in VWM.

To answer this question, in Chapter 4 I use a similar lateralized design as in Chapters 2 and 3 to examine the neural correlates of flexible attentional control. Here, item priority is continuously manipulated using both spatial and feature-based cues. In these tasks, participants were informed about the likelihood (between 16.67% and 100%) that a certain item would be probed using either a concurrent line cue (Chapter 4, Exp.1) or a predictive shape-based cue (Chapter 4, Exp. 2). It is shown that the probability that an item will be probed in a VWM task influences both attentional enhancement (i.e. N2pc) and memory storage (i.e. CDA) in a continuous way. That is, the more likely an item is to be probed, the greater the amplitude of both the N2pc and CDA. Finally, it is demonstrated that even without a priority cue, lateral items that receive more memory resources have greater CDA amplitudes, regardless of lateral memory load (Chapter 4, Exp. 3).

Together, the findings presented in Chapter 4 provide evidence that the N2pc and CDA are not only markers of all-or-none filtering, but these components are also an index for the dynamic distribution of attention and memory resources amongst items, even when all items are task-relevant. These results not only have implications for our understanding of the N2pc and CDA, but also for the broader conceptualization of the how information is organized in VWM based on top-down attentional control over item priority.

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# Chapter 2

## Drawn to distraction: Anxiety impairs proactive distractor suppression of known distractor features in visual search

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## Introduction

Given the abundance of visual information in the world, and the brain's limited processing capacity, it is necessary that we use top-down control to delegate cognitive resources toward goal-relevant items. Without sufficient attentional control, one runs the risk of becoming distracted by salient but task-irrelevant items, which are competing for representation. This competition between goal-driven and stimulus-driven factors for attention can be biased toward relevant items using an attentional set, or template (Corbetta & Shulman, 2002; Desimone & Duncan, 1995). For example, knowing that a target item will be in a certain color or shape (i.e. a featured-based template) allows attention to be guided toward the template-matching item, speeding search times despite the presence of distractors (Bacon & Egeth, 1994; Folk et al., 1992). This type of template is referred to as a *positive template*, and results in the selective attentional enhancement of goal-relevant over irrelevant information for further processing.

Beyond attentional prioritization of template-matching information, there is recent evidence that templates can also be used to down-weight the processing of goal-irrelevant items (Carlisle, 2019; Chang & Egeth, 2019). For example, it has been found that when given information about an upcoming distractor feature (referred to as a *negative template*; Arita et al., 2012), individuals can ignore that item during search, resulting in a search benefit. Negative templates, however, are not always effective in guiding search, as there is behavioral evidence that individuals first attend to the features matching the negative template instead of proactively inhibiting them (Chang et al., 2019; Moher & Egeth, 2012). This process has been termed the 'search and destroy' mechanism of negative templates, suggesting that individuals do not proactively inhibit template-matching distractors. These findings point to a more reactive than proactive attentional mechanism of negative templates, such that suppression only occurs *after* the selection of template-matching distractors.

Evidence for both proactive and reactive suppression given negative templates has largely been supported by behavioral measures, which are a summation of perceptual, attentional, and decision-making processes. However, using time-sensitive electrophysiological (EEG) recordings of brain activity, it is possible to identify the underlying time-course of attentional suppression and selection. For example, Carlisle and Nitka (2019) examined the N2pc – an event-related potential (ERP) related to attentional selection and enhancement – during a visual search task using positive and negative search templates. When attention is directed toward a lateral item, the N2pc is observed as an increased negativity over contralateral compared to ipsilateral electrode sites from 200 – 300 ms post-stimuli onset (Eimer, 1996; Hickey et al., 2009; Luck & Hillyard, 1994). They found an N2pc toward the target hemi-field following both cue types, suggesting that participants were not initially attending to the distractor following the negative cue. Contrary to the search and destroy hypothesis, these findings suggest that template-matching distractors are not always attended (i.e. the ‘search’ part of search and destroy).

Given the inconsistent findings in the literature concerning whether negative templates are beneficial to visual search performance, it remains possible that there are individual differences in how negative templates are used. For positive templates, it has been found that individuals with higher levels of anxiety have greater attentional capture by distractors than less anxious individuals, suggesting that anxiety is related to an overall deficit in top-down inhibitory control (Eysenck et al., 2007). Indeed, Gaspar and McDonald (2018) found that individuals with high levels of anxiety had an early, distractor-elicited N2pc, which was absent for those with lower levels of anxiety (but see, Qi et al., 2014). They also examined an additional ERP component called the distractor positivity ($P_D$). The $P_D$ measures the suppression of salient, task-irrelevant items, and is observed as an increased positivity over contralateral compared to ipsilateral electrode sites when a distractor is presented laterally and a target is on the vertical midline (Hickey et al., 2009; Sawaki et al., 2012). Gaspar and McDonald (2018) demonstrated that although individuals with high anxiety initially showed attentional capture by the target item, both high and low anxiety individuals had a later $P_D$, suggesting that those with high anxiety suppressed the distractor, but only after it had initially diverted attention. Importantly, given that the $P_D$ can occur before, during, or after the time range of the N2pc (Jannati et al., 2013), this component can be used to distinguish between early *proactive* suppression and later *reactive* suppression. Thus, though the findings of Gaspar and McDonald (2018) support a reactive mechanism of distractor inhibition for individuals with anxiety when given a *positive* template, the time course of how *negative* templates affect attention, with or without anxiety, remains unclear.

Consequently, the goal of the present study is twofold: 1) To examine whether negative templates are used to proactively or reactively inhibit processing of template-matching distractors, and 2) to examine whether anxiety affects the timing of attentional selection and suppression given negative search templates. By examining the relative time course of the N2pc and $P_D$, we can observe whether participants are able to proactively suppress the distractor (early $P_D$ with no N2pc), or if they can only suppress the distractor after it has been attended ($P_D$ only after the N2pc). Furthermore, given that individuals with high levels of anxiety have reduced inhibitory control, we predict that negative templates will amplify this deficit. That is, we predict that compared to less anxious individuals, participants with higher levels of anxiety will not be able to proactively suppress template-matching distractors, as reflected by decreased early $P_D$ amplitudes, and will lead to larger subsequent distractor-elicited N2pcs.

## Methods

### Participants

Procedures were approved by and conducted in accordance with the Brock University Bioscience Research Ethics Board. We aimed to collect a sample of 48 healthy participants (normal vision, normal color vision, no history of neurological or psychological disorders, etc.) after data rejection, in line with previous studies that found medium effect sizes for individual differences in anxiety on the N2pc and $P_D$ (Gaspar & McDonald, 2018; Qi et al., 2014). A total of 12 participants were excluded due to experimenter recording error (3), task noncompliance (1), EOG artifacts (3), and low trial counts resulting from inaccurate behavioral responses and/or trial time-outs (5). The final sample consisted of 48 participants between the ages of 17 and 30 ($M_{age}$ = 20.3, 7 male, all right-handed).

### Apparatus

All tasks were completed on a Windows PC with a 41-cm NEC MultiSync LCD 2090UXi monitor (1,600 x 1,200 pixels, 60 Hz refresh rate) in a dimly lit room. Anxiety questionnaires and the change detection task were presented using PsychoPy 1.90.3

(Peirce, 2009), and the visual search task was presented using PsychoPy 3.2.4 (Peirce et al., 2019) on a black background, with a viewing distance of approximately 57 cm.

### Anxiety Questionnaires

At the beginning of the session, participants first completed a change detection task as part of our standard protocol (Luck & Vogel, 1997; not reported here). Next, participants completed both the state and trait anxiety inventories on the computer (STAI; Spielberger et al., 1983). Each questionnaire consists of 20 questions on a 4-point Likert scale and has a minimum score of 20 and maximum of 80. In the present sample both state (*M* = 37.5, *SD* = 9.9, range of 23 – 60) and trait (*M* = 42.3, *SD* = 10.9, range of 24 – 63) anxiety scores were similar to norms for undergraduate samples (Spielberger et al., 1983; Stout et al., 2013).

### Visual Search Task

After EEG cap setup, participants completed the cued visual search task (Figure 2-1). On each trial, following an ITI of 1,000 ms (fixation dot radius of 0.3°), participants were presented with a cue (800 ms) that indicated the likelihood (i.e. *0%* or *100%*, white text, 1° tall, presented above fixation) that the target line would be within a circle of a particular color (diameter = 1.5°, presented at fixation). In the neutral cue condition, a grey circle was presented at fixation without text.

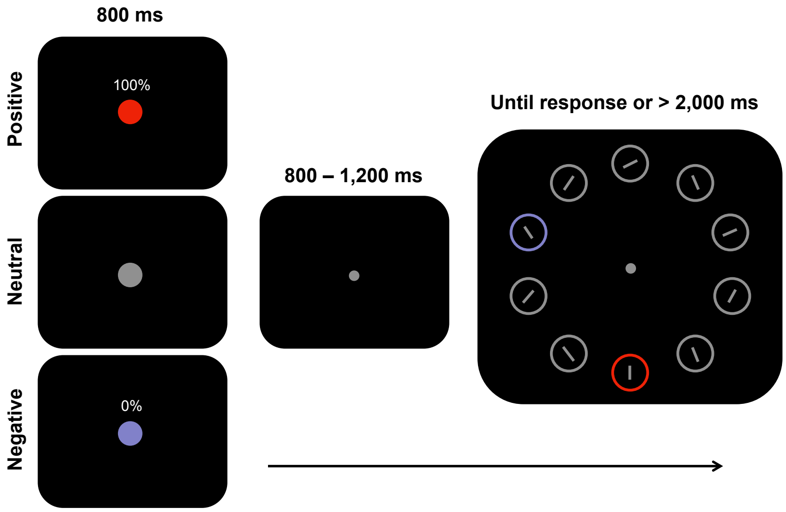

***Figure 2-1***. Task schematic for the lateralized visual search task. A positive, negative, or neutral cue was presented followed by a jittered fixation interval. The search array was present until a key response or 2 seconds elapsed. Example depicted is of a distractor lateral, target midline trial.

Following a delay (800 – 1,200 ms), a search array consisting of 10 rings (width of 0.25°, diameter of 3°) was presented on an imaginary circle around fixation (10° from fixation to center of ring). Eight of the 10 rings were grey, and 2 were colored (red, blue, yellow, or green; all ~7 cd/$m^2$). On the critical 83.33% of trials, one of the colored rings was presented on the lateral and the other on the vertical.

Each ring had a grey line within it (1° long, 0.25° wide) that was either task irrelevant, (angle pseudorandomly chosen every 18° from 0 to 360°) or a target, (angle of 0° or 90°). Participants were instructed to find the vertical or horizontal line within a colored ring, and to report its orientation as quickly as possible while also maintaining accuracy. The search array stayed on the screen for 200 ms before participants were provided with accuracy feedback (i.e. '*Incorrect*'; 800 ms), or the trial terminated after 2 seconds. There was a total of 1,152 trials, 960 of which were used in the final analysis (lateralized positions only).

## EEG Recording and Analysis

EEG was recorded and analyzed according to our standard procedures (see Supplemental Methods). For each participant, contralateral and ipsilateral waveforms were obtained in reference to the lateral target or distractor item at channel pair PO7/PO8 (correct trials only, $M_{incorrect} = 8\% \pm 5\%$). Mean amplitude was measured from these difference waveforms for each participant and condition. This resulted in 6 measurements per ERP component (N2pc and $P_D$): Positive cue/Target lateral, Positive cue/Distractor lateral, Negative cue/Target lateral, Negative cue/Distractor lateral, Neutral cue/Target lateral, and Neutral cue/Distractor lateral. Whether the item on the lateral was a target or distractor is referred to as Lateral Relevance.

Early suppression was measured as the mean amplitude between 100 – 200 ms post-search array onset (Fortier-Gauthier et al., 2012; Sawaki & Luck, 2010). Following the early $P_D$, N2pc mean amplitude was measured from 200 – 300 ms post-search array onset (Salahub et al., 2019; Salahub & Emrich, 2019). Lastly, the later $P_D$ was analyzed as the mean amplitude from 300 – 400 ms post-stimuli onset (Gaspar & McDonald, 2018; Kiss et al., 2011). We also conducted a signed-area permutation analysis on the early and late $P_D$ (see Supplemental Methods).

## Data Analysis

Statistical analyses were completed using JASP Version 0.12 (JASP Team, 2020) and custom scripts in MATLAB R2017a. RTs greater or less than 3 SDs from that participant's mean were removed (*M* = 1.5%, *SD* = 3%). Incorrect and no response trials were also excluded from analysis (*M* = 8%, *SD* = 5%). We excluded any individual participant ERP component amplitudes that were ±3 SDs away from the mean in any condition (and any difference scores created from that condition). However, the pattern of results did not change when outliers were included in the analyses. Any participant whose data had less than 90 trials in any condition (N = 4) or less than 100 trials in more than two conditions (N = 1) was replaced. There was on average 132 trials per condition. Greenhouse-Geisser corrected degrees of freedom and p-values are reported wherever sphericity was violated. Post-hoc tests were one-tailed where a priori hypotheses were present. Bayes factors (BFs) for repeated-measures ANOVAs compared to the null model are reported where applicable (r scale prior width of 0.5, default Cauchy prior centered on 0, 10,000 Monte Carlo samples).

## Results

### Behavioural

To assess the effect of Cue Type on search speed, we first compared search RTs for each cue condition. There was an overall main effect of Cue Type, $F(1.39, 64.12) = 90.75$, $p < .001$, $\eta^2_p = .66$, $BF_M = 1.36^{19}$, such that mean RTs were faster following a positive cue ($M = 731$ ms, $SD = 100$ ms) than a neutral cue ($M = 791$ ms, $SD = 94$ ms), $t(46) = 11.34$, $p_{holm} < .001$, $d = 1.66$, $BF_{10} = 1.03^{12}$, or a negative cue ($M = 795$ ms, $SD = 97$ ms), $t(46) = 11.97$, $p_{holm} < .001$, $d = 1.75$, $BF_{10} = 4.97^9$. However, there was not a significant difference between RTs in the neutral and negative cue conditions, $t(46) = 0.62$, $p_{holm} = .54$, $d = 0.09$, $BF_{10} = 0.24$. Neither state nor trait anxiety correlated with RTs in any cueing condition, $r$s < .22, $p$s > .15.

### Early $P_D$ (100 – 200 ms)

Figures 2-2 and 2-3 display the grand-averaged contralateral/ipsilateral waveforms and their difference scores for each cue condition, respectively. To examine whether there was proactive suppression of the distractor before a shift in attention, we measured mean $P_D$ amplitude from 100 – 200 ms in all conditions. It was found that mean amplitude was not significantly greater than 0 when the positively cued target was presented on the lateral ($M = 0.01$ µV, $SD = 0.66$ µV), $t(47) = 0.11$, $p = .456$, $d = 0.02$, $BF_{10} = 0.17$, and it was greater than 0 in all other conditions, $t$s > 2.3, $p$s < .01, $d$s > 0.32, $BF_{10}$s > 3.26 (see Supplemental Results for permutation analysis).

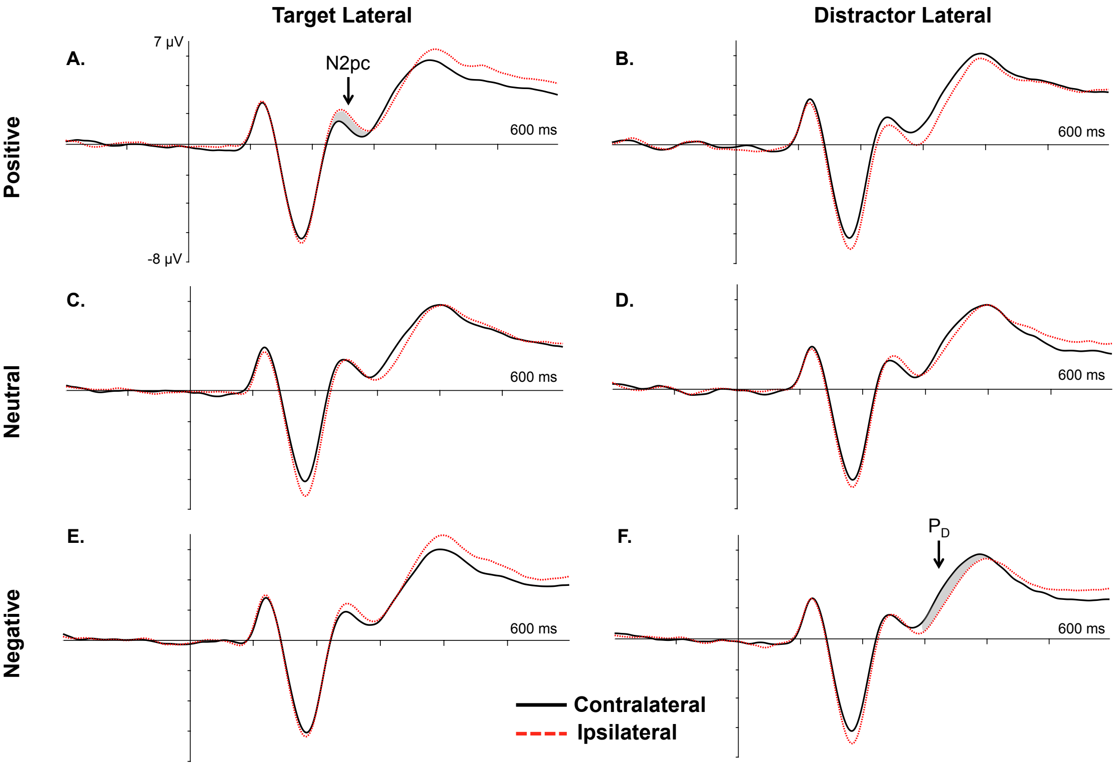

***Figure 2-2.*** Contralateral (black solid lines) and ipsilateral (red dashed lines) waveforms, in reference to the lateral item, at channel pair PO7/PO8 for each condition. A) Positive cue condition, lateral target. B) Positive cue condition, lateral distractor. C) Neutral cue condition, lateral target. D) Neutral cue condition, lateral distractor. E) Negative cue condition, lateral target. F) Negative cue condition, lateral distractor.

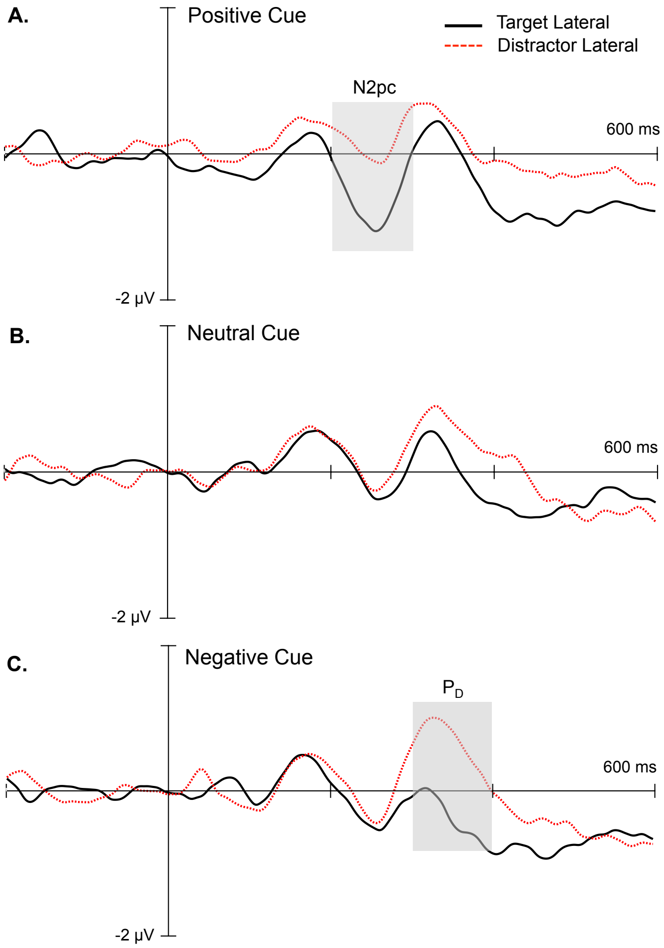

***Figure 2-3.*** Grand-averaged difference waveforms at channel pair PO7/PO8 in A) the positive cue condition, B) neutral cue condition, and C) negative cue condition. Black solid lines reflect activity toward a lateral target, and red dashed lines for a lateral distractor. Waveforms are filtered at 30 Hz for illustrative purposes only.

Cue Type did not affect the early $P_D$ amplitude, $F(2,88) = 2.06$, $p = .134$, $\eta^2_p = .045$, $BF_M = 0.54$. Additionally, lateral targets ($M_M = 0.18$ µV, 95% CI = [0.08, 0.29]) and distractors ($M_M = 0.31$ µV, 95% CI = [0.21, 0.42]) elicited $P_D$s of similar magnitude, $F(1,44) = 3.75$, $p = .059$, $\eta^2_p = .079$, although there is anecdotal evidence for the inclusion of this factor in the model, $BF_M = 1.97$. Cue Type did not interact with Lateral Relevance, $F(2,88) = 0.48$, $p = .621$, $BF_M = 0.04$. Therefore, although it did not reach statistical significance, there is some weak evidence that the early $P_D$ differed in amplitude depending on whether a target or distractor was presented laterally.

**N2pc (200 – 300 ms)**

To investigate whether negatively cued distractors were attended, we compared mean N2pc amplitudes between Cue Type and Lateral Relevance conditions. Compared to 0, there was only an N2pc present when a lateral target was preceded by a positive cue ($M = -0.58$ μV, $SD = 0.78$ μV), $t(46) = -5.12$, $p < .001$, $d = -0.75$, $BF_{10} = 3,154$. Mean amplitudes were not significantly different from 0 in any other condition, $p$s > .11, $BF_{10s} < 0.53$. These results suggest that the lateral distractor did not initially capture attention, in disagreement with the 'search and destroy' mechanism of negative templates.

There was no overall effect of Cue Type on mean N2pc amplitude ($p = .142$). However, across Cue Types, lateral targets elicited a greater negativity ($M_M = -0.25$ μV, 95% CI = [-0.4 -0.1]) than lateral distractors ($M_M = 0.11$ μV, 95% CI = [-0.05, 0.26]), $F(1,45) = 19.51$, $p < .001$, $\eta^2_p = .30$. Importantly, there was an interaction between Cue Type and Lateral Relevance, $F(2,90) = 6.26$, $p = .003$, $\eta^2_p = .12$. The model with the interaction term had the most support ($BF_M = 17.37$) compared to the models with only a Cue Type main effect ($BF_M < 0.001$) or a Lateral Relevance main effect ($BF_M = 0.74$). Mean lateral target amplitude was affected by Cue Type, $F(2,90) = 7.55$, $p < .001$, but there was not an effect of Cue Type on distractor amplitude, $F(2,90) = 1.31$, $p = .276$. Focusing on the lateral target conditions only, mean amplitude was more negative following a positive cue ($M = -0.58$ μV, $SD = 0.78$ μV) than a negative cue ($M = -0.20$ μV, $SD = 0.84$ μV) or a neutral cue ($M = -0.05$ μV, $SD = 0.69$ μV), $t$s > 2.6, $d$s > 0.40, $p_{holms} < .018$, $BF_{10s} > 4.3$. There was no difference in target amplitude between the negative and neutral cue conditions, $t(45) = -0.92$, $d = -0.14$, $p_{holm} = 0.362$, $BF_{10} = 0.31$.

### Late $P_D$ (300 – 400 ms)

To determine whether Cue Type affected later suppression of the distractor, we examined a time window from 300 – 400 ms, following the N2pc. Indeed, it was found that for all three cue types, the $P_D$ was significantly greater than 0 when a distractor was presented laterally, *t*s > 2.5, *p*s < .015, *d*s > 0.36, $BF_{10s}$ > 2.87. Mean amplitude in the negatively cued *target* condition was significantly more *negative* than zero during this later time window (*M* = -0.37 µV, *SD* = 1.03 µV), *t*(47) = -2.50, *p* = .016, *d* = 0.36, $BF_{10}$ = 2.57. Amplitudes in the other conditions were not significantly different from 0, *t*s < 1.51, *p*s > .12, $BF_{10s}$ < 0.46. The signed-area permutation analyses differed in that there was a marginally significant difference from noise in the positive and neutral cue target lateral conditions, $p_{positive}$ = .048, $p_{neutral}$ = .025 (see Supplemental Results).

Next, to examine how Cue Type differentially affected processing of targets and distractors, we conducted a repeated-measures ANOVA. There was not a significant main effect of Cue Type, *F*(2,92) = 1.99, *p* = .142, $\eta^2_p$ = .04. However, there was an overall effect of Lateral Relevance, *F*(1,46) = 23.06, *p* < .001, $\eta^2_p$ = .33, such that there was a greater positivity toward lateral distractors ($M_M$ = 0.51, 95% CI = [0.33, 0.70]) than to lateral targets ($M_M$ = -0.05, 95% CI = [-0.24, 0.13]). Lastly, there was a significant interaction between Cue Type and Lateral Relevance, *F*(2,92) = 3.64, *p* = .03, $\eta^2_p$ = .07. Bayesian analysis provided the most support for the model with only a main effect of Lateral Relevance ($BF_M$ = 7.9) compared to the Cue Type only model ($BF_M = 8.7^{-6}$) and the model with the interaction term ($BF_M$ = 1.07).

Mean amplitude for lateral targets was affected by Cue Type, *F*(2,92) = 4.25, *p* = .017. There was a non-significant effect of Cue Type on lateral distractor amplitudes,

$F(2,92) = 1.57$, $p = .214$. When the target was on the lateral, mean amplitude following a negative cue was more negative than following a neutral cue ($M = 0.16$ µV, $SD = 0.71$ µV), $t(47)= 3.12$, $p_{holm} = .009$, $d = .46$, $BF_{10} = 10.51$. There was no statistical difference in target-related amplitudes between the negative and positive cue conditions, $t(47) = 1.89$, $p_{holm} = .129$, $BF_{10} = 0.91$, or the neutral and positive conditions, $t(47) = 0.74$, $p_{holm} = .462$, $BF_{10} = 0.21$. Overall, these results suggest that lateral distractors elicited equivalent $P_D$s in all cue conditions, and that there was an increased *negativity* toward the negatively cued target during this later time window.

**Anxiety correlates with impaired early suppression of negatively-cued distractors**

Although the whole-group results provide evidence for both early and late suppression of template-matching distractors, it is possible that there are individual differences in inhibitory ability. To this end, we examined correlations between anxiety scores and mean amplitudes of all three ERP time windows. For the early $P_D$, we found that state anxiety correlated with mean amplitude toward the negatively cued distractor, such that the greater an individual's anxiety score, the smaller their early $P_D$, $r = -0.33$, $p = .027$, 95% CI = [-0.04, -0.57], $BF_{10} = 1.96$ (see Figure 2-4). There were no significant correlations between state anxiety and mean amplitude toward the positively cued distractor, $r = .014$, $p = .64$, $BF_{10} = 0.18$, or the neutrally cued distractor, $r = .03$, $p = .841$, $BF_{10} = 0.19$. All of the above correlations were not present with trait anxiety, $r$s < 0.2, $p$s > .2, $BF_{10s} < 0.42$.

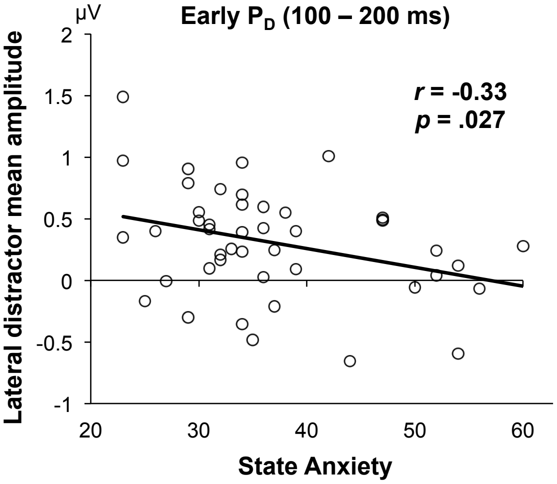

***Figure 2-4.*** Correlation between state anxiety scores and early $P_D$ amplitudes (100 – 200 ms) toward a negatively cued lateral distractor (N = 46).

During the N2pc time window, we found that neither state nor trait anxiety correlated with the target-elicited N2pc amplitude following any of the cue types, *r*s < .1, *p*s > .5. However, state anxiety did correlate with mean amplitude toward the negatively cued distractor, such that greater anxiety scores correlated with larger distractor-elicited N2pcs, $r = -0.38$, $p = .009$, 95% CI = [-0.1, -0.6], $BF_{10} = 4.82$ (Figure 2-5a). This distractor-related correlation was not observed in the positive cue condition ($r = -.02$, $p = .87$) or the neutral cue condition ($r = -.06$, $p = .71$). Further, when looking at the difference in amplitude toward the negatively cued target minus the distractor, we found that greater anxiety correlated with more attention toward the lateral distractor than to the target, $r = .39$, $p = .008$, 95% CI = [0.1, 0.6], $BF_{10} = 5.57$ (Figure 2-5b). All of the above correlations were not present with trait anxiety, *r*s < .2, *ps* > .17. Finally, we examined how later distractor suppression was related to anxiety scores. We found that there was no correlation between anxiety scores and $P_D$ amplitude to lateral distractors following any cue type, *r*s < 0.29, *p*s > .05, $BF_{10s} < 1.15$.

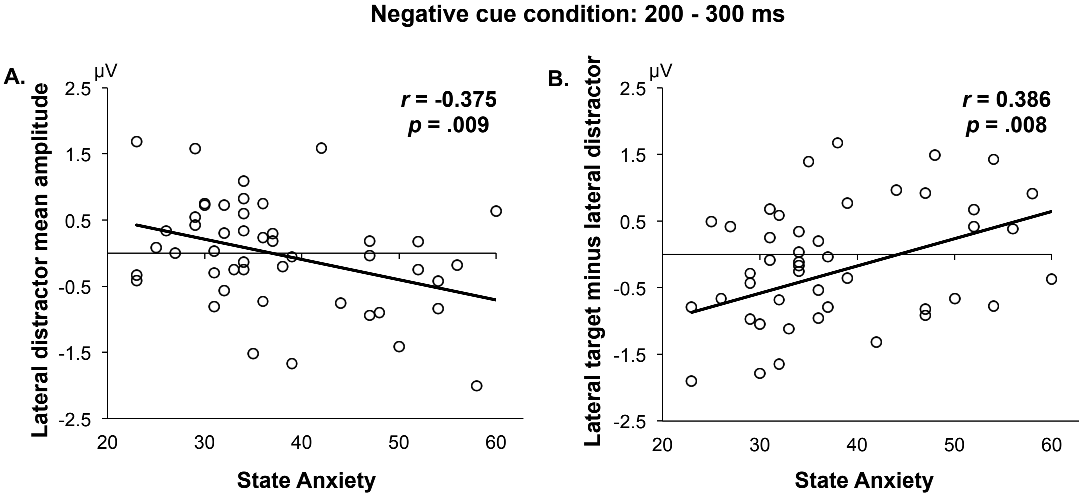

***Figure 2-5.*** Correlations between state anxiety scores and mean amplitudes (200 – 300 ms) in the negative cue condition. A) Mean amplitude toward the lateral distractor (N = 47). B) Mean amplitude toward the lateral target minus the lateral distractor. More negative values reflect greater negativity (N2pc) toward the target than the distractor (N = 46).

## Discussion

The main goal of the present study was to investigate whether individuals use negative templates to proactively suppress distractors, or whether the template-matching distractor is first enhanced instead. Additionally, we predicted that the ability to use negative templates in a proactive manner would be related to anxiety. In brief, we found evidence of both early and late suppression, but that attentional mechanisms differed by individuals' anxiety levels. That is, individuals with greater anxiety scores were more likely to attend to negatively cued distractors, followed by later suppression; whereas individuals with lower anxiety levels could proactively suppress and avoid attentional capture by the template-matching distractor.

Our conceptualization of early and late suppression is based on two competing hypotheses about the attentional mechanisms of negative cues: The early suppression account (Gaspelin & Luck, 2018; Zhang et al., 2019) and the 'search and destroy' account (Moher & Egeth, 2012). If individuals can proactively suppress negatively-cued distractors, then we would predict an early $P_D$ followed by no distractor-elicited N2pc. Conversely, if individuals were initially attending the distractor, then we would predict no early $P_D$, but rather a distractor-elicited N2pc ('search') followed by a later $P_D$ ('destroy'). We found that early distractor suppression was present following all cue types. Thus, the presence of an early positivity in the negative cue condition provides some evidence for the early suppression account; however, this suppression was not stronger for negative than positive or neutral cues.

Following the early positivity, there was a target-elicited N2pc in the positive cue condition only. The absence of a N2pc following a negative cue suggests that negative cues were less effective in guiding attention, consistent with slower RTs following negative cues. Contrary to previous studies, we did not observe a significant N2pc toward the lateral target in the neutral cue condition. However, the present task design differed from Gaspar and McDonald (2018) in that there we no distractor absent trials. Therefore, in the neutral cue trials, participants always had to attend to both locations (lateral and vertical) to determine the orientation of the target line. Perhaps the difficulty of the search was so easy that the participant's response could be made while keeping this diffuse state of attention. That is, if participants did not need to enhance processing of the lateral item to make an accurate response, then we would not expect to observe an N2pc.

Importantly, we did not find an N2pc toward the negatively cued distractor, suggesting that participants did not initially search for the distractor feature. However, there was what appeared to be an attentional shift toward the lateral target *after* the N2pc. This negativity did not appear to be as peaked as a typical N2pc, which may reflect increased between-subject or trial-by-trial variability. This potential delayed target selection is in agreement with Carlisle and Nitka (2019), and may explain why we did not observe an RT benefit in the negative cue condition. However, it is also possible that we did not observe a behavioral benefit following negative cues because the search task was not sufficiently difficult–making it not 'worth it' for participants to use these counterintuitive cues (participants do prefer positive cues; Heuer & Schubö, 2019; Rajsic et al., 2020). For example, it has been found that individuals only use negative cues when the search array consists of larger set sizes (>4 items), or high target/distractor similarity (Arita et al., 2012; Conci et al., 2019). Future research is needed to determine the effect of search difficulty on ERP measures of target selection given negative cues.

Following the N2pc, there was a $P_D$ that was equivalent in amplitude across all cue conditions, suggesting that participants were suppressing the distractor. We also observed a target-related $P_D$ in the positive and neutral conditions during this later window, as determined by the signed area measurements. Although this may seem contradictory, there is evidence that this positivity can also reflect the termination of attention following initial selection (Sawaki et al., 2012). This pattern has been likened to inhibition of return (Posner & Cohen, 1984), such that once the target is selected, it is subsequently suppressed so that search does not return to that location in the future. This positivity was not present for the negatively cued target, consistent with the finding that target selection was delayed following the negative cue.

Although the primary aim of this study was to determine at what time point individuals suppress or enhance negative template-matching distractors, our results provide evidence for both an early suppression and later suppression account. However, the second main objective of the present paper was to examine whether and how individual differences in anxiety modulate distractor suppression given positive and negative search cues. We predicted that individuals with greater levels of anxiety would have deficits in their ability to proactively suppress negatively cued distractors. Indeed, we found that individuals with greater state anxiety scores had both reduced early positivity amplitudes and larger early N2pcs toward the negatively cued distractor than individuals with lower anxiety scores. During the time window of the N2pc, individuals with lower anxiety scores seemed to be more likely to have *positive* amplitudes, supporting an early suppression account (as seen in the scatterplot).

It is possible that this early component does not reflect active suppression, but rather a sensory-related process or a marker of feature discontinuities in the display, used to guide subsequent attention (Ppc; Fortier-Gauthier et al., 2012; Jannati et al., 2013). Here, the search display was identical across conditions, such that there were always two colored rings in a lateral and vertical position. Yet, we did not observe a significant early positivity toward the lateral positively-cued target. This suggests that the early positivity reflects more than an identification of featural discontinuities in the display. Moreover, the presence of a correlation between anxiety and this component, only in the negative cue condition, suggests that this activity reflects cognitive, rather than sensory, processing. However, even if this component does reflect sensory-related processing, this suggests that anxiety impacts early visual activity, before attention is deployed; perhaps reflecting greater arousal or vigilance, such as seen in stress (Shackman et al., 2011). Further research is needed to determine what process this early positivity reflects (i.e., suppression or sensory-related activity).

Contrary to previous studies, we did not find any significant correlations with *trait* anxiety, only *state* anxiety. It has been suggested that state anxiety is more closely linked to attentional alerting and orienting, whereas trait anxiety is related to deficits in executive control (Crocker et al., 2012; Pacheco-Unguetti et al., 2010). Therefore, the anxiety-related correlations observed in the present task likely resulted from increased alerting toward negatively-cued distractors (as indicated by the N2pc). This finding points to a later, reactive suppression strategy for individuals with higher levels of anxiety and an earlier suppression mechanism in individuals with low anxiety, consistent with Gaspar and McDonald (2018). However, unlike the task used by Gaspar and McDonald (2018), we did not find this correlation in the positive cue condition, but only in the *negative* cue condition.

One possible reason that we did not find a correlation between anxiety and distractor processing following a positive cue is that negative cue trials were interspersed with positive and neutral cue trials, preventing participants from building up a strategy over time (Noonan et al., 2016). Therefore, in the context of all three cue conditions, the negative cue may have felt the most difficult to use (participants do prefer positive cues; Heuer & Schubö, 2019; Rajsic et al., 2020). This may be particularly true for individuals with anxiety, who already have inhibitory deficits that are more pronounced when greater demands are placed on cognitive control resources (Berggren et al., 2012, 2013; Eysenck et al., 2007). Additionally, anxiety did not correlate with later suppression, suggesting that regardless of anxiety level, individuals were able to compensate by subsequently suppressing the distractor. Therefore, anxiety mainly affected early control over attentional selection and not later inhibitory processes (Gaspar & McDonald, 2018).

Overall, the present results suggest that negative templates can be used to proactively suppress distractors, but that without sufficient attentional control abilities, distractors may capture attention instead. We propose that there is not a universal mechanism for negative templates, and that individual differences in anxiety affect how search templates are used.

## Open Practices Statement

All EEG and behavioral data, as well as task scripts, will be publicly available on the Open Science Framework at: https://osf.io/5ak2y/?view_only=fdb3e67e60134c44884ce693b47c99fe (peer-review link). This experiment was not formally pre-registered.

# Supplemental Methods

## EEG Pre-processing

EEG was DC recorded at 512 Hz using a 64 Ag/AgCl electrode cap at the standard 10-20 sites (ActiveTwo system; BioSemi, Amsterdam, The Netherlands). The signal was online referenced to the common-mode sense and driven right leg electrodes. Pre-processing was completed in MATLAB with EEGLAB (Delorme & Makeig, 2004; version 14.0.0b) and ERPLAB (Lopez-Calderon & Luck, 2014; version 6.1.2) toolboxes and custom scripts. Data were re-referenced offline to the average of the mastoids and filtered with a 40 Hz low-pass and 0.1 Hz high-pass Butterworth band-pass filter (slope: 12 dB/octave). Baseline correction was performed from -200 to 0 ms relative to the search array onset, and epochs were created between -200 and 600 ms.

Horizontal electro-oculogram (HEOG) was measured from bipolar external electrodes placed laterally beside each eye. Vertical electro-oculogram (VEOG) was recorded as the difference between external electrodes placed below the eyes and activity at FP1 or FP2. Trials with HEOG activity ±32 μV and/or VEOG activity ±80 μV between -200 ms and 400 ms relative to search array onset were excluded. Any trials with voltage ±100 μV over the posterior channels (P1/2, P3/4, P5/6, P7/8, P9/10, PO3/O4, PO7/O8, and O1/2) were also removed. Across the entire epoch, no participant had average residual HEOG voltages more than 3.75 μV. Participants whose data had >35% of total trials rejected due to EOG artifacts were replaced (N = 3). In the final data set, an average of 11.7% (*SD* = 7.2%) of trials were rejected due to EOG artifacts.

**Permutation Analysis**

To reduce the chance of a false positive due to the choice of measurement window from the grand-averaged waveform (Luck & Gaspelin, 2017), we conducted a signed-area permutation analysis on the early and late $P_D$ (positive area only: 100 – 200 and 250 – 400 ms. In this analysis, the positive area measurement will never be less than 0, so a non-parametric permutation approach must be used to determine whether the $P_D$ was greater than chance in each condition (Gaspelin & Luck, 2018b; Sawaki et al., 2012). This method estimates a null distribution from the noise inherent in the difference waveform by randomizing the left/right trial labels within each condition, and then measuring the positive area from the noise-only difference waveform. One thousand permutations were completed and then compared to the observed values from the grand-averaged waveform. The *p* values were then calculated as:

$$p = \frac{\text{Number of permuted positive areas } \geq \text{ Observed positive area}}{1{,}000}$$

# Supplemental Results

## Permutation Analysis

### Early $P_D$.

From 100 – 200 ms, the permutation results confirmed that there was a significant positivity in all conditions (*p*s < .02), except for when the lateral target was positively cued ($p = .243$) and when the lateral distractor was preceded by a neutral cue ($p = .091$).

### Late $P_D$.

The mean positive area from 250 – 400 ms was significantly greater than noise in all of the lateral distractor conditions: $p_{negative} = < .001$, $p_{positive} = .003$, $p_{neutral} = .005$. There was no evidence for a positivity in the negative cue, target lateral condition, $p = .195$. However, departing from the mean amplitude results, there was a marginally significant difference from noise in the positive and neutral cue target lateral conditions, $p_{positive} = .048$, $p_{neutral} = .025$. This is likely due to the larger measurement window and may reflect suppression of the target following initial processing (see Discussion).

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# Chapter 3

## Fear not! Anxiety biases attentional enhancement of threat without impairing working memory filtering

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## Introduction

Humans are wired to attend to and identify threat, such as a potentially dangerous snake in the grass (Öhman et al., 2001; Öhman & Mineka, 2001). Even when these threatening stimuli are task-irrelevant, they manage to capture attention, suggesting that threat detection is a relatively automatic process (Beck & Clark, 1997; Hodsoll et al., 2011; Mogg & Bradley, 1999; but see, Pessoa, 2005). Although it is important to notice these dangers, threat-detection can become disadvantageous if task-irrelevant information cannot be ignored in favor of task-relevant information. This is especially true for individuals with anxiety disorders, who are more likely to attend to threatening stimuli, delay disengagement from those stimuli, and to interpret ambiguous information as threatening (Bishop, 2007; Fox et al., 2001; Mathews & Mackintosh, 1998). Even for individuals with subclinical levels of anxiety, there is a threat-related attentional bias toward irrelevant information (Bar-Haim et al., 2007; Stout et al., 2013), implicating general prefrontal attentional control deficits across a range of anxiety levels, and not just for individuals who are clinically diagnosed (Bishop, 2009; Bishop, Duncan, Brett, et al., 2004).

Although it is widely known that anxiety is related to deficits in attentional control abilities, this deficit does not always impact behavioral performance. Instead, anxiety is thought to affect neural processing efficiency, (i.e. how cognitive resources are used to achieve a goal), whether that be through greater attentional capture or delayed suppression of threatening distractors (Eysenck et al., 2007; Gaspar & McDonald, 2018). It has been proposed that individuals with anxiety can compensate for inefficient processing by investing more cognitive effort into the task, allowing them to maintain performance at the same level as less anxious individuals (Berggren & Derakshan, 2013; Derakshan & Eysenck, 2009; Eysenck et al., 2007; Gaspar & McDonald, 2018).

Because processing efficiency cannot be inferred from behavioral performance alone, event-related potentials (ERPs) have been used to examine attentional selection and suppression of distracting emotional information. One ERP component that has been used to assess attentional enhancement and selection of stimuli is the N2 posterior contralateral (N2pc), which occurs 200 – 300 ms after the onset of a search display (Eimer, 1996; Hickey et al., 2006; Luck & Hillyard, 1994a). The N2pc is affected by stimulus emotionality, with larger and earlier N2pcs toward threat-related than neutral or happy stimuli, regardless of their task relevance (Burra et al., 2016; Eimer & Kiss, 2007; Feldmann-Wüstefeld et al., 2011; Holmes et al., 2009; Kappenman et al., 2015). Attentional enhancement of threatening stimuli is magnified for individuals who have high levels of anxiety (Fox et al., 2008). This bias extends to neutral distractors, as there is evidence that non-emotional distractors also elicit an N2pc in anxious individuals (Gaspar & McDonald, 2018; Moran & Moser, 2015; but see, Qi, Ding, & Li, 2014).

Beyond attentional enhancement of distractors, it has also been found that active attentional suppression of threatening information is impaired in anxious individuals (Ansari & Derakshan, 2011). An ERP component called the distractor positivity, or $P_D$, has been used to measure active inhibition/suppression of salient distractors (Burra & Kerzel, 2014; Gaspelin & Luck, 2018; Hickey et al., 2009; Sawaki et al., 2012). There are two main time windows where the $P_D$ is typically found: early (140 – 190 ms) and later (200 – 400 ms). The early $P_D$ (also referred to as the Ppc), is thought to reflect pre-attentive sensory imbalances in item salience, or suppression of the “attend-to-me” signal

(Fortier-Gauthier et al., 2012; Gaspelin & Luck, 2018; Sawaki & Luck, 2010; Weaver et al., 2017); whereas the later $P_D$ occurs during or after the time range of the N2pc, and indicates an active suppression process, regardless of initial attentional capture (Gaspar & McDonald, 2014; Sawaki & Luck, 2013; for a review, see Jannati et al., 2013).

Active suppression is more difficult when the distractor is threatening, such that $P_D$ amplitudes are larger for angry face distractors than for happy distractors (Burra et al., 2017). Additionally, the timing of distractor suppression is delayed by threatening stimuli such as spiders (Burra et al., 2019). To our knowledge, no study has examined the correlation between anxiety and $P_D$ amplitude toward threat-related distractors. However, there is evidence that individuals with high anxiety are capable of suppressing non-emotional distractors, as individuals with anxiety exhibit a late $P_D$ following initial attentional capture (Gaspar & McDonald, 2018). This finding suggests that attentional enhancement (N2pc) may be more critically affected by anxiety than distractor suppression ($P_D$).

Deficits in attentional control for anxious individuals extend to visual working memory (VWM) storage. In particular, individuals with anxiety fail to filter irrelevant, threat-related faces from VWM (for a review see, Gambarota & Sessa, 2019). Impaired filtering can be measured by an ERP that is associated with the amount of information maintained in VWM: the contralateral delay activity (CDA; Ikkai et al., 2010; McCollough et al., 2007; Vogel et al., 2005). Stout and colleagues (2013) found that dispositional anxiety correlated with CDA amplitude when fearful face distractors were present in the memory array, such that the more anxious the individual, the more likely that a threatening distractor would be erroneously stored in memory (also seen with salient neutral distractors, Qi et al., 2014). Further, using fMRI, Stout and colleagues (2017) found that this anxiety-driven mis-allocation of VWM resources toward threat-related distractors could be observed in the posterior parietal cortex, dorsolateral prefrontal cortex, and fusiform face area. They proposed that this mis-allocation of memory resources was driven by increased amygdala reactivity to threat in highly anxious individuals. In both of these fMRI studies, however, the paradigms were not designed to differentiate between attentional control-related processes and VWM maintenance.

Although the CDA has been used to track unnecessary storage following filtering, it does not directly reflect the activity associated with attentional selection and distractor filtering (although for evidence of distractor suppression in the closely-related CDA$_P$, see Feldmann-Wüstefeld & Vogel, 2019). Indeed, there is evidence that once accounting for filtering-related activity, unnecessary storage no longer predicts VWM performance (Emrich & Busseri, 2015). Additionally, the temporal limitations of fMRI make it difficult to examine quick shifts in attention that may later bias memory. Therefore, although these studies demonstrate that VWM resources are mis-allocated, *how* they are mis-allocated, (whether by attentional enhancement or suppression) remains unclear.

Given the anxiety-related biases in attentional capture and suppression of threatening stimuli, we predicted that deficits in attentional control drive the mis-allocation of VWM resources toward threat-related distractors. In particular, we hypothesized that anxiety would correlate most strongly with attentional enhancement (i.e. N2pc) of a threatening distractor, which is then stored in VWM. However, this model has not been directly tested in a VWM task with threat-related targets and distractors. Here, we aimed to examine the relationship between anxiety, attentional selection and/or suppression, and VWM maintenance using a combination visual search and VWM task with fearful and neutral faces. One face was always defined as the target, and the other as a distractor, by the color of its surrounding border. Participants were required to hold the target face in VWM to determine whether the face identity changed after a brief delay. To disentangle the N2pc from the $P_D$, we used a systematic lateralization procedure for stimuli presentation (see Methods). In brief, this procedure allowed us to isolate brain activity related solely to the face presented on the lateral, unaffected by the vertically presented item. Therefore, we could examine target and distractor-specific processing in a task that requires simultaneous presentation.

If the increase in VWM storage of threatening information in anxiety is due to overall impaired attentional control abilities, then there should be an increased N2pc and decreased $P_D$ toward fearful face distractors for individuals with high anxiety. But, if increased storage is due primarily to attentional capture of the threat-related distractor, then anxiety should only correlate with N2pc amplitude. We also predicted that individuals with higher anxiety would have an increased CDA for threatening distractors compared to neutral distractors. Finally, there should be a correlation between the magnitude of one's attentional control deficit and the unnecessary storage of threatening distractors.

## Methods

Some of the methods and analyses of the present study were pre-registered at https://aspredicted.org/cf7jn.pdf.

## Participants

Sixty undergraduate students participated for either course credit or monetary compensation ($15/hour). All participants provided written, informed consent before the experiment began. Procedures were approved by and conducted in accordance with the Brock University Bioscience Research Ethics Board. We aimed to stop data collection once we reached a sample of 48 participants after data rejection (right handed, normal color vision, no history of mental illness or neurological disorder), although this goal was not reached due to the number of participants rejected and time constraints on data collection. Ten participants' data were excluded due to ocular EEG artifacts on more than 35% of trials, and 4 were excluded due to recording errors during the experimental session. The final sample consisted of 46 participants (10 male, $M_{age} = 20.8$, $SD_{age} = 3.52$).

## Apparatus

All tasks, including the anxiety questionnaires, were completed on a Windows PC with a 41-cm NEC MultiSync LCD 2090UXi monitor (1,600 x 1,200 pixels, 60 Hz refresh rate). Tasks were programmed and presented using Psychopy v1.90.3 (Peirce, 2009) with a viewing distance of approximately 57 cm.

## Anxiety Scores

Participants completed both the state and trait anxiety inventories on the computer (STAI; Spielberger, Gorsuch, Lushene, & Vagg, 1983). These questionnaires have high internal consistency (Cronbach's $\alpha = 0.91$ state, 0.90 trait) and test-retest stability ($r = 0.70$ state, 0.88 trait; Barnes, Harp, & Jung, 2002). Each questionnaire consisted of 20 questions on a 4-point Likert scale measuring how anxious the individual was in the moment (e.g., *I feel nervous*) and in general (e.g., *I worry too much over something that really does not matter*). Both scales have a minimum score of 20 and maximum of 80. In the present sample, both state scores (*M* = 34.39, *SD* = 9.28, range of 20 – 63) and trait scores (*M* = 40.46, *SD* = 9.35, range of 27 – 64) were similar to norms for undergraduate samples (Spielberger et al., 1983; Stout et al., 2013). State and trait anxiety were significantly correlated, $r = .48$, $p < .001$, $BF_{10} = 40.46$.

### Face Stimuli

The face images used in the present study were the same as used in Stout, Shackman, and Larson (2013). There were a total of 52 equal luminance black and white faces (2° wide x 2.5° tall), half fearful and half neutral, with all non-facial features removed. On each trial, there was one face presented on the vertical and another on the lateral midline (3° from fixation). A red (~29.4 cd/$m^2$) or blue (~11.9 cd/$m^2$) border surrounded either of the two faces (7 pixels wide). Opposite the face images, there were scrambled face images surrounded by a grey border (~15.4 cd/$m^2$).

### Procedures

Participants first completed a standard visual working memory change detection task (Luck & Vogel, 1997; see Supplemental Materials and Results). Following EEG cap set up, participants performed a rapid eye-fixation training task on the computer (Guzman-Martinez et al., 2009). This task consisted of a circle containing a flickering pattern of 50% black and 50% white pixels (37.5 Hz, 13.3msec/frame). Participants were instructed to maintain fixation on a cross (24 pixels wide) in the center of the circle and to not move their eyes or blink. When the eyes remain stationary, the flickering pattern subjectively appears grey, but the grey screen becomes disrupted when the eyes are moved such that the pattern is perceived to 'pop out' at the observer. Participants were informed that every time they saw the pattern jump this meant they had moved their eyes, and that they should try to maintain the grey color by minimizing eye movements. Each trial lasted 5 seconds and was initiated by any key press. Participants completed trials until they could consistently maintain the grey color by self-report (approximately 2.5 minutes).

Next, participants completed a systematically lateralized change detection task with fearful and neutral faces (see Figure 3-1). Participants were told to find and remember the target face, defined by the color of the box surrounding the face (red or blue, counterbalanced across participants). Each trial began with a fixation screen (fixation dot of 3° diameter; 500 – 1,500 ms) followed by the search array (100 ms). The search array consisted of two faces that were either fearful or neutral in expression, with one face on the lateral (left or right of fixation) and the other on the vertical midline (top or bottom). Positions opposite the faces contained scrambled face images that served to balance the visual display. In this design, the face presented on the vertical midline elicits equivalent contralateral and ipsilateral activity and is therefore cancelled out in the difference waveform. We used this lateralized search array so that we could observe the target and distractor specific N2pc, $P_D$, and CDA (Feldmann-Wüstefeld & Vogel, 2019; Hickey et al., 2006, 2009; Woodman & Luck, 2003).

There were 6 conditions defined by the Emotion and Relevance (target/distractor) of the lateral face: 1) Lateral target fearful face/Vertical distractor neutral face, 2) Lateral target neutral face/Vertical distractor fearful face, 3) Lateral target neutral face/Vertical distractor neutral face (baseline target condition), and 4-6) the same as conditions 1-3 except with distractors on the lateral. Emotion and Relevance were counterbalanced across all possible position combinations.

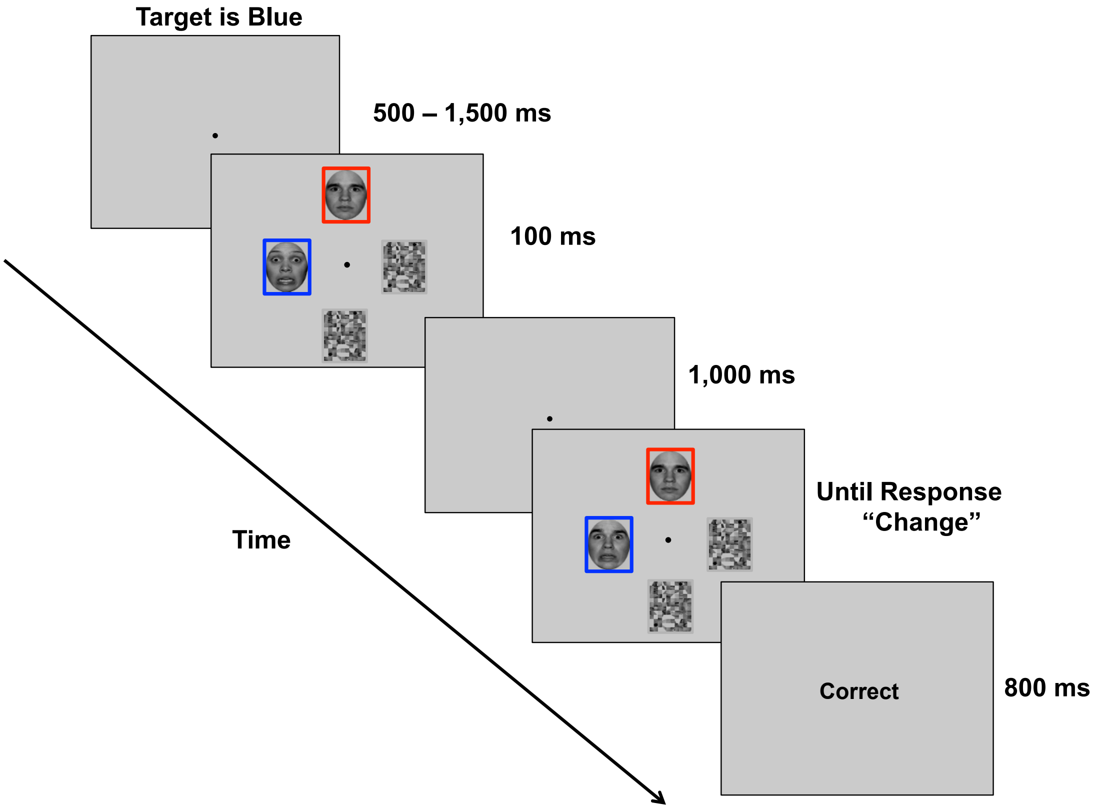

***Figure 3-1***. Task schematic for the lateralized visual working memory face change detection task. Participants were instructed at the beginning of the task which color would be their target color (blue in this example). Participants then must locate the face within a border of the target color and hold the face in memory over a brief delay. A probe screen is then presented where the participant responds whether the target face changed identity (50% of trials) or stayed the same.

After the search display, there was a delay period (1,000 ms) followed by the response screen, which consisted of two faces in the same positions as in the search array. The participants' goal was to determine whether the face surrounded by the target color changed (50% of trials) or stayed the same between initial presentation and the probe array. The distractor face always stayed the same. Participants were instructed to press the 'z' key to indicate a change had occurred or the 'm' key for no change. After a response was made, accuracy feedback was provided (800 ms). There was a total of 624 trials: 208 Fear Lateral/Neutral Vertical (104 fear target, 104 fear distractor), 208 Neutral Lateral/Fear Vertical (104 neutral target, 104 neutral distractor), and 208 Neutral Lateral/Neutral Vertical (neutral baseline condition; 104 lateral target, 104 lateral distractor).

**EEG Recording and Pre-Processing**

EEG was DC recorded at 512Hz using a 64 Ag/AgCl electrode cap at the standard 10-20 sites (ActiveTwo system; BioSemi, Amsterdam, The Netherlands). The signal was online referenced to common-mode sense and driven right leg electrodes. Pre-processing was completed in MATLAB with EEGLAB (Delorme & Makeig, 2004) (version 14.0.0b) and ERPLAB (Lopez-Calderon & Luck, 2014) (version 6.1.2) toolboxes and custom scripts. Data were re-referenced offline to the average of the mastoids and filtered with a 0.01 - 40 Hz Butterworth band-pass filter (slope: 12dB/octave). Baseline correction was performed from -200 to 0 ms relative to the search array onset, and epochs were created between -200 and 1,100 ms, time-locked to the search array.

Horizontal electro-oculogram (HEOG) was measured from bipolar external electrodes placed laterally beside each eye. Vertical electro-oculogram (VEOG) was recorded as the difference between external electrodes placed below the eyes and activity at FP1 or FP2. Trials with HEOG activity ±32 μV and/or VEOG activity ±80 μV between search array onset and the end of the trial were rejected. Additionally, any trials with voltage ±100 μV over the posterior channels (P1/2, P3/4, P5/6, P7/8, P9/10, PO3/O4, PO7/O8, and O1/2) were removed. Average residual HEOG activity from 0 to 400 ms was 1.91 μV (*SD* = 1.48 μV), and from 400 to 1,100 ms was 3.27 μV (*SD* = 2.76 μV). Individuals did not make larger saccades toward the lateral fearful face than to the lateral neutral face during either an early (0 – 400 ms) or later (400 – 1,100 ms) time window (see Supplemental Results).

Participants whose data had > 35% of total trials rejected were replaced (N = 10). In the final data set, an average of 12.16% of trials were rejected (*SD* = 9.05%). Both correct and incorrect trials were included in the grand average waveforms, consistent with previous studies of similar design (Stout et al., 2013). Mean contralateral minus ipsilateral activity was measured at channel pair PO7/PO8 for each participant and condition, resulting in 6 grand averaged waveforms. All ERP measurements were taken from the difference waveforms as mean amplitudes. To quantify the N2pc, we collapsed across condition and measured negative peak latency between 200 – 300 ms at channel pair PO7/PO8 in the lateral target waveform for each participant (Feldmann-Wüstefeld & Vogel, 2019). Then, we averaged across participants and measured N2pc amplitude as ±50 ms from that peak. Therefore, N2pc amplitude was measured as the mean amplitude between 210 – 310 ms.

For the $P_D$, upon examining the lateral distractors grand average waveform (regardless of emotion), we did not observe a clear positivity in the proposed time range of 200 – 375 ms; therefore, we chose to not analyze the $P_D$ (see Discussion). Consistent with previous studies (Feldmann-Wüstefeld & Vogel, 2019; Ikkai et al., 2010; McCollough et al., 2007), the CDA was measured as the mean amplitude during the delay period (400 – 1,100 ms).

### Data Analysis

All statistical analyses were completed using JASP Version 0.12 (JASP Team, 2020), SPSS Version 25.0 (IBM Corp., Armonk, N.Y., USA, 2017), and custom scripts in MATLAB R2017a. Behavioral responses were analyzed for accuracy (proportion correct) and sensitivity (Böckmann-Barthel, 2017) between the 3 main target emotion conditions (fear target/neutral distractor, neutral target/fear distractor, and neutral target/neutral distractor).

For the ERP analyses, we excluded any individual participant component amplitudes that were ±3 SDs away from the mean in any condition (and any difference scores created from that condition). However, results did not change when outliers were included in the analyses. For each ERP component of interest, one-way repeated-measures ANOVAs were run separately for the lateral target and distractor conditions. Each ANOVA had 3 levels defined by the combination of the lateral and midline face emotions (Fear Lateral/Neutral Midline, Neutral Lateral/Fear Midline, and Neutral Lateral/Neutral Midline). A priori planned contrasts were run where appropriate. Greenhouse-Geisser corrected degrees of freedom and p-values are reported wherever sphericity is violated. P-values for all post-hoc tests are Bonferroni-corrected and two-tailed. Bayes factors (BFs) for repeated-measures ANOVAs and contrasts are reported where applicable (r scale prior width of 0.5, default Cauchy prior centered on 0, 10,000 Monte Carlo samples).

## Results

### Behaviour

Accuracy was above chance across all participants and conditions, (*M* = 75%, *SD* = 7.7%, range from 57.7% - 91.2%). There was a significant effect of target Emotion on accuracy, $F(2,90) = 9.23$, $p < .001$, $\eta^2_p = .18$, $BF_{10} = 105.72$, such that changes to a fearful target were detected more accurately (*M* = 76.4%, *SD* = 7.5%) than to the neutral baseline target ($M$ = 74.1%, $SD$ = 8.1%, $t(45) = 2.99$, $p_{bonf} = .01$, d = .42, $BF_{10} = 7.81$). Accuracy for a neutral target in the presence of a fearful distractor ($M$ = 73.2%, $SD$ = 8.8%) was not significantly different from a neutral baseline target, $t(45) = 1.15$, $p_{bonf} = .77$, d = .17, $BF_{10} = 0.30$.

The same pattern of results was observed for measures of sensitivity, such that there was a main effect of target Emotion on d', $F(2,90) = 7.03$, $p = .001$, $\eta^2_p = .32$, $BF_{10} = 19.81$. Overall, participants were more sensitive in detecting changes to fearful target faces ($M$ = 1.95, $SD$ = 0.49) than to a neutral target face in the presence of a neutral distractor ($M$ = 1.82, $SD$ = 0.50, $t(45) = 3$, $p_{bonf} = .013$, d = .44, $BF_{10} = 37.36$). Once again, there was not a significant difference in sensitivity between the neutral target/fearful distractor ($M$ = 1.80, $SD$ = 0.53) and the neutral target/neutral distractor conditions, $t(45) = 0.26$, $p_{bonf} = 1$, d = .04, $BF_{10} = 0.17$). Neither state or trait anxiety was correlated with accuracy or sensitivity in any Emotion condition, $r$s < .22, $p$s > .14. This suggests that individuals with higher anxiety levels were performing the task as accurately as less anxious individuals.

**Electrophysiology**

**N2pc.** Contralateral and ipsilateral waveforms for all conditions can be seen in Figure 3-2 A-F. When the target was presented laterally, there was no effect of face configuration on the amplitude of the N2pc, $F(2,90) = 0.87$, $p = .423$, $\eta^2_p = .02$, $BF_{10} = 0.15$ (Figure 3-3 A1 and A2; see Table 3-1 for descriptive statistics). There was, however, an effect of face configuration when the *distractor* was presented laterally, $F(1.7, 76.4) = 5.54$, $p = .008$, $\eta^2_p = .11$, $BF_{10} = 6.63$ (Figure 3-3 B1 and B2). Planned contrasts revealed that there was a greater N2pc to the lateral fear distractor than to the neutral baseline distractor, $t(90) = 2.99$, $p = .004$, $BF_{10} = 2.94$. Comparing the two conditions where a neutral face was presented laterally, there was no significant difference in N2pc amplitude, $t(90) = 0.23$, $p = .816$, $BF_{10} = 0.17$. These findings suggest that averaged across individuals, threat-related distractors captured attention more than neutral distractors.

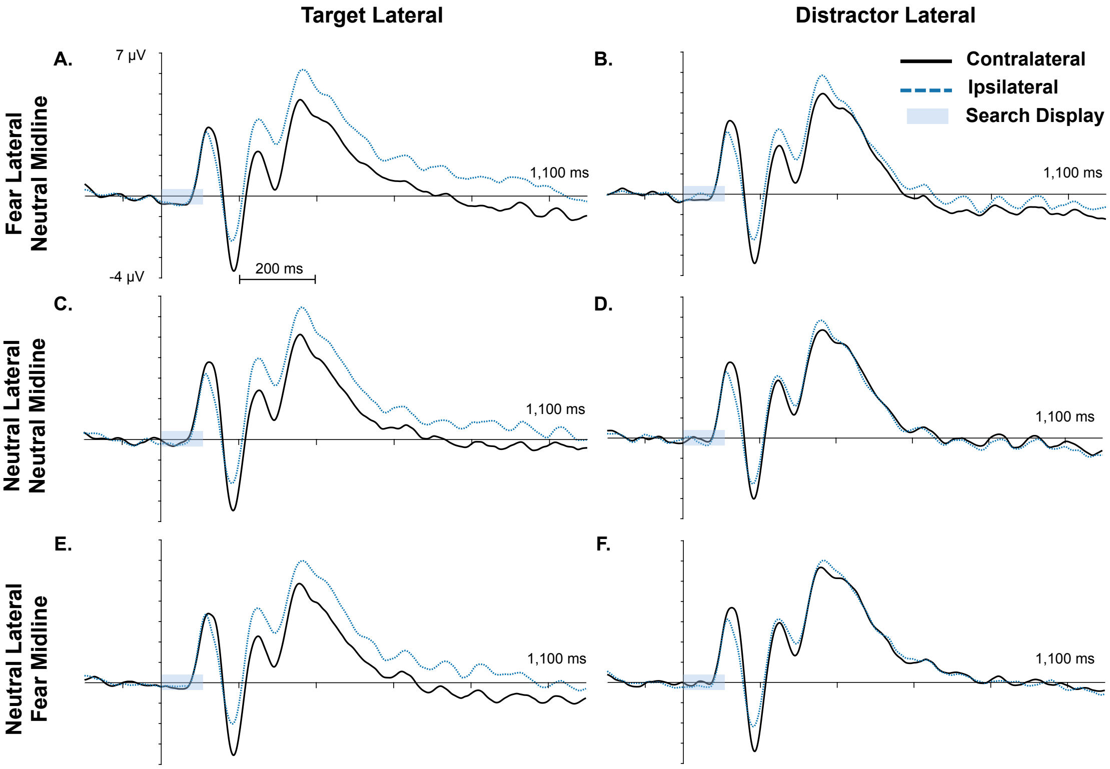

***Figure 3-2.*** Contralateral (black solid lines) and ipsilateral (blue dashed lines) waveforms at channel pair PO7/PO8 for each condition. Filtered at 30 Hz for illustrative purposes only. Y-axis scales are the same for all sub-figures. (A) Fear Lateral/Neutral Midline target and (B) distractor conditions. (C) Neutral Baseline target and (D) distractor conditions. (E) Neutral Lateral/Fear Midline target and (F) distractor conditions.

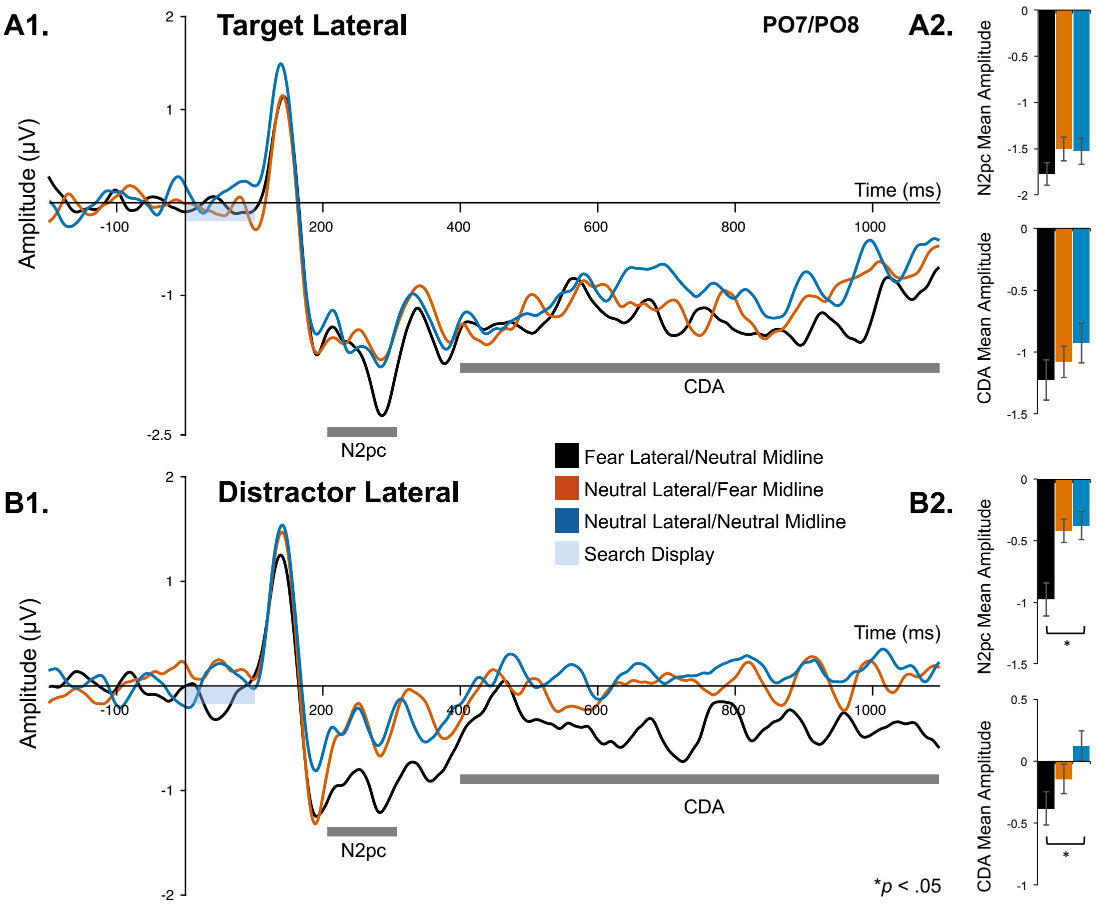

***Figure 3-3.*** Grand average difference waveforms (N = 46) measured at channel pair PO7/PO8, time-locked to stimuli onset. Filtered at 30 Hz for illustrative purposes only. (A1) Waveforms for target lateral conditions. (A2) Bar graphs of mean N2pc and CDA amplitudes by target lateral condition. Within-subject error bars reflect ±1 SEM. (B1) Waveforms for distractor lateral conditions. (B2) Bar graphs of mean N2pc and CDA amplitudes by distractor lateral condition. Within-subject error bars reflect ±1 SEM

***Table 3-1***

*Descriptive Statistics for N2pc and CDA Amplitudes by Condition*

| | N2pc (μV) | | CDA (μV) | |
|---|---|---|---|---|
| Condition | *M(SD)* | 95% CI | *M*(SD) | 95% CI |
| Target Lateral/Distractor Midline | | | | |
| Fear/Neutral | -1.78(1.72) | [-2.25 -1.30] | -1.22(1.52) | [-1.64 -0.81] |
| Neutral/Fear | -1.51(1.63) | [-1.98 -1.03] | -1.08(1.41) | [-1.49 -0.66] |
| Neutral/Neutral | -1.53(1.51) | [-2.00 -1.05] | -0.93(1.34) | [-1.35 -0.51] |
| Distractor Lateral/Target Midline | | | | |
| Fear/Neutral | -0.98(1.38) | [-1.34 -0.61] | -0.38(1.09) | [-0.73 -0.12] |
| Neutral/Fear | -0.42(1.23) | [-0.79 -0.06] | -0.15[a](0.92) | [-0.73 -0.12] |
| Neutral/Neutral | -0.37(1.13) | [-0.74 0.01] | 0.12(1.10) | [-0.22 0.39] |

[a] All *n*s = 46 except for noted condition wherein *n* = 45 due to outlier removal

**CDA.** When the target was presented laterally, face configuration did not have a significant effect on CDA amplitude, *F*(2,90) = 0.64, *p* = .531, $\eta^2_p$ = .01, $BF_{10}$ = 0.12 (see Table 3-1 for descriptive statistics). Similarly, when the distractor was on the lateral, CDA amplitude did not significantly differ between the three face configurations, *F*(2,90) = 2.71, *p* = .072, $\eta^2_p$ = .06, $BF_{10}$ = 0.99. Based on the prediction that CDA amplitude would be greater for lateral fearful faces than for neutral faces, we examined planned contrasts for both targets and distractors. CDA amplitude was not significantly greater for the lateral fear target than the neutral baseline target, *t*(90) = 1.13, *p* = .262, $BF_{10}$ = 0.26. However, CDA amplitude was greater for the fear distractor than the neutral baseline distractor, *t*(88) = 2.32, *p* = .023, $BF_{10}$ = 1.4. This provides weak evidence that participants were holding the fearful distractor in memory more often than the neutral distractor.

**N2pc and CDA correlations.** To test whether changes in attention allocation to fearful versus neutral faces led to greater memory storage of those fearful faces, we created N2pc and CDA difference scores between the Fear Lateral/Neutral Midline and Neutral Lateral/Neutral Midline conditions for both lateral targets and distractors. N2pc amplitude correlated positively with CDA amplitude for fearful versus neutral targets, $r = .725$, $p < .001$, $BF_{10} = 1.25^6$, and fearful versus neutral distractors, $r = .605$, $p < .001$, $BF_{10} = 2,159$. These findings demonstrate that the more an individual paid attention to the fearful target or distractor, the more likely that face was to be held in memory, regardless of their level of anxiety.

### Anxiety predicts attention toward a fearful face distractor

To determine how anxiety affected attention toward a distracting threat-related face, we examined mean N2pc amplitude difference scores between the fearful distractor face and the neutral distractor baseline condition (i.e., Neutral distractor lateral/Neutral target midline). More negative scores indicate a larger N2pc toward the fearful than to the neutral distractor. It was found that more anxious individuals had greater N2pc amplitudes toward a fearful distractor compared to the neutral baseline distractor, $r(44) = -.35$, $p = .018$, 95% CI [-.58, -.06], $BF_{10} = 2.76$ (Figure 3-4A). In contrast, there was no correlation between state anxiety and N2pc amplitude toward a lateral fearful target compared to the neutral baseline target, $r(45) = .15$, $p = .333$, 95% CI [-.15, .42], $BF_{10} = 0.29$ (Figure 3-4B).

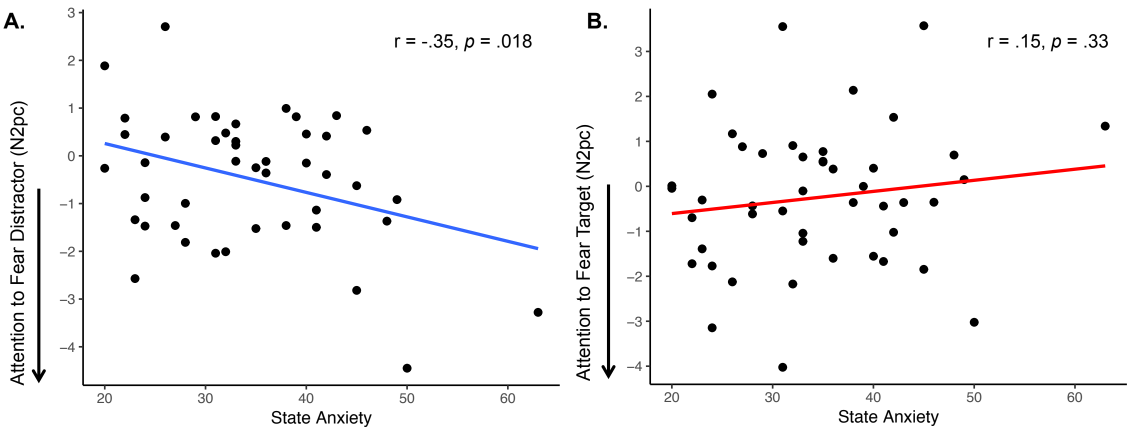

***Figure 3-4.*** Scatterplots between state anxiety scores and mean N2pc amplitudes. (A) Greater state anxiety correlates with greater N2pc amplitudes toward a lateral fearful face distractor compared to a lateral neural distractor (difference score). More negative scores indicate greater attention toward the fearful face distractor than the neutral baseline distractor. (B) Greater state anxiety does not correlate with N2pc amplitude toward a fearful face target compared to the neutral baseline target (difference score).

To examine whether the relationship between anxiety and N2pc amplitude was specific to threat-related distractors, we also analyzed amplitude difference scores between the lateral neutral/vertical fearful condition and the neutral baseline condition (for both targets and distractors). More negative scores indicate greater attention toward the neutral face in the presence of the fearful one, than to the neutral face in the baseline condition. In contrast to when fearful faces were presented laterally, state anxiety scores did not predict greater N2pc amplitudes toward lateral neutral faces in either the target, $r(45) = -.06$, $p = .685$, 95% CI [-.35, .23], $BF_{10} = 0.2$, or distractor conditions, $r(45) = -.273$, $p = .067$, 95% CI [-.52, .02], $BF_{10} = 0.94$. There were no significant correlations between N2pc amplitudes and trait anxiety in the same comparisons, *r*s < .19, *p*s > .21, $BFs_{10} < 0.38$. When including residual HEOG as a covariate, the pattern of results did not change (see Supplemental Results). Therefore, our findings suggest that individuals with greater state anxiety levels are only biased toward fearful faces when they are distractors and not when they are targets, and that this bias does not extend to neutral distractors.

### Anxiety does not predict memory storage of a distracting fearful face

To examine the correlation between VWM storage and anxiety we created mean amplitude CDA difference scores for the same conditions as was done for the N2pc (i.e. lateral fearful minus lateral neutral baseline). In contrast to previous findings (Qi et al., 2014; Stout et al., 2013), we did not observe a correlation between CDA amplitudes and anxiety. State anxiety did not predict greater CDA amplitude for a lateral fearful target, *r*(45) = .203, *p* = .176, 95% CI [-.06, .47], $BF_{10} = 0.45$, or for a fearful distractor, *r*(45) = -.199, *p* = .184, 95% CI [-.46, .1], $BF_{10} = 0.43$. State anxiety also did not correlate with memory storage of a neutral target in the presence of a fearful distractor, *r*(45) = .105, *p* = .489, 95% CI [-.19, .38], $BF_{10} = 0.23$, or a neutral distractor in the presence of a fearful target, *r*(44) = -.215, *p* = .152, 95% CI [-.48, .08], $BF_{10} = 0.50$. There were also no correlations between trait anxiety and CDA amplitudes in these same comparisons, *r*s < .17, *p*s > .26, $BFs_{10} < 0.34$. Overall, these results suggest that in this task, anxiety does not predict greater memory storage of a threat-related compared to a neutral face, whether that face is a target or a distractor.

## Discussion

In the present study, we aimed to examine how anxiety biases attentional enhancement (N2pc), distractor suppression ($P_D$), and VWM storage (CDA) of threat-related distractors. We found that across all individuals, regardless of anxiety level, there were significantly larger N2pc and CDA amplitudes toward fearful distractors than neutral distractors. However, when the fearful face was a target (i.e. task relevant), it was not attended to or remembered more often than a neutral target. These findings are consistent with a large body of literature which suggests that threat-detection of fear-related stimuli is automatic (LeDoux, 2000; Öhman, 2005). This bottom-up capture by threat-related faces is likely driven by the amygdala, which subsequently biases activity in the fusiform face area, prefrontal, and parietal cortices (Öhman, 2005; Stout et al., 2017). Individuals with higher levels of anxiety have amplified amygdala reactivity, resulting in greater attentional biases toward threat-related information than their less anxious counterparts (Shackman et al., 2016; Stout et al., 2017). This is in agreement with our finding that individuals who had higher state anxiety also had larger N2pc amplitudes toward fearful distractors than for neutral distractors. Therefore, the present study supports the idea that individuals with anxiety have an attentional bias toward task-irrelevant, threat-related information; caused by both impaired top-down cognitive control and increased attentional guidance by bottom-up stimuli salience (Eysenck et al., 2007).

Yet, inconsistent with prior studies, we did not find that N2pc and CDA amplitudes were larger for threat-related compared to neutral targets. For example, Feldmann-Wüstefeld and colleagues (2011) found that these two ERP components were larger for angry targets compared to happy targets. Similarly, Stout and colleagues (2013) found larger CDA amplitudes for two fearful face targets than for two neutral targets. These studies differ from the present one in that they presented several faces on the lateral, both neutral and emotional (but see, Sessa et al., 2011). Here, only a single target was presented laterally, such that even if the face were remembered, the CDA amplitude for that one item would be quite small overall. Therefore, the present effect sizes may be too small to distinguish between the target conditions.

Contrary to our hypotheses, anxiety levels did not correlate with CDA amplitude toward fearful distractors, suggesting that anxious individuals had an attentional bias toward threatening distractors, but did not necessarily hold that irrelevant information in memory. This finding is at odds with several studies that have found poor distractor filtering of threat in anxiety, as measured by the CDA (e.g., Sessa et al., 2011; Stout et al., 2013). This discrepancy could be explained by differences in methodological design, as in these previous studies the face stimuli were presented for at least 200 ms, compared to the 100 ms used here. We may have only observed an early attentional bias, and not a memory bias, because memory storage of faces requires a longer encoding time (Curby & Gauthier, 2007).

There are several additional methodological differences between the present study and prior experiments, which may in part explain discrepancies from previous findings. For example, some studies used all fearful or neutral faces in the display without different emotion distractors (Kiss & Eimer, 2008; Sessa et al., 2011). Others did not have a condition where a fearful target was presented with a neutral distractor (Stout et al., 2013), or a neutral target condition (Feldmann-Wüstefeld et al., 2011). Studies also differ by type of face stimuli used, such as schematic faces (Weymar et al., 2011) or angry faces (Burra et al., 2016; Holmes et al., 2009). Participant strategy is also likely affected by the task, whether that be a speeded visual search task (Feldmann-Wüstefeld et al., 2011), or an un-speeded VWM task, such as is used here. Future studies should closely consider the influence of task design and stimuli parameters to better synthesize the literature on anxiety and threat-related filtering.

Deficits in attentional control have been consistently observed in individuals with high trait anxiety (Fox et al., 2008; Gaspar & McDonald, 2018; Qi et al., 2014; Stout et al., 2013). Yet, here we found a correlation with *state* anxiety only. This could be due to an absence of participant pre-screening, however, given that state and trait anxiety were highly correlated, the limited range of the sample cannot fully explain the absence of a correlation between trait anxiety and N2pc amplitudes. There is also evidence that state anxiety is correlated with amygdala reactivity to threat, regardless of whether the threat was attended or unattended; whereas trait anxiety has a greater influence on prefrontal attentional control (Bishop, 2009; Bishop, Duncan, & Lawrence, 2004; Bishop et al., 2007). Therefore, in a task that does not require a lot of cognitive control (such as in the present study), we would expect to observe a greater effect of state anxiety on amygdala reactivity to fearful stimuli than trait anxiety's impact on top-down attentional control.

Beyond biased attentional selection of fearful distractors, we also predicted that attentional control deficits would emerge as impaired active suppression of irrelevant threatening stimuli, as measured by the $P_D$. However, we could not test this hypothesis, as we did not observe a clear $P_D$ component in the distractor waveforms. It could be that because only one distractor was present, the distractor was easy to ignore without needing an active suppression process. Indeed, there is evidence that the $P_D$ amplitude increases with the number of lateralized distractors in a VWM task (Feldmann-Wüstefeld & Vogel, 2019) and with perceptual load (Bretherton et al., 2017). However, even with multiple distractors the $P_D$ is quite small (Feldmann-Wüstefeld & Vogel, 2019).

Another possibility for the absence of a $P_D$ is that the grand average waveform was overall more negative than is usually observed in lateralized visual search tasks.

Therefore, if a more positive-going potential were to have occurred following the N2pc, from around 300 – 400 ms, it would still be measured as negative-going (although this does not appear to be the case from visual inspection of the grand average waveform). This overall increased negativity of the grand average waveform seemed to be driven by a negative-going component occurring directly before the N2pc in the time range of 170 – 200 ms. This negativity could reflect a lateralized N170, a component that reflects the encoding of faces more than non-face stimuli (Bentin et al., 1996; Eimer, 2000). However, there is evidence that the N170 is not affected by selective attention (Cauquil et al., 2000), and therefore its presence should not affect later attention and memory-related components such as the N2pc and CDA.

There was also a lateralized positivity present in the time range of the P1, suggesting that despite our procedures to balance sensory differences, some overall physical imbalances in the display remained. This imbalance was likely due to our use of scrambled faces as a sensory balance (unlike the masks used by Kiss and Eimer, 2008). This positivity could also reflect an early $P_D$ (also referred to as the Ppc; Fortier-Gauthier et al., 2012; Jannati et al., 2013; Luck & Hillyard, 1994b). Because the positivity was equivalent in amplitude across all conditions, $F(4.19, 188.43) = 1.91$, $p = .107$, however, it most likely does not reflect early suppression. Instead, it could indicate pre-attentive activation of the salience map, which is used to guide subsequent attention (Jannati et al., 2013). However, as this component was not the focus of the present study, further research is required to determine whether the early $P_D$ influences attentional selection and suppression of emotional stimuli.

Our final hypothesis was that the relationship between anxiety and VWM storage of fearful distractors would be mediated by attentional enhancement of those distractors. However, because CDA amplitude was not correlated with anxiety, we could not test that model. Yet, we did find that averaged across individuals, greater attention toward a fearful face (regardless of task relevance) correlated with memory storage of that face; that is, greater changes in N2pc amplitudes in response to fearful faces resulted in greater changes in CDA amplitudes. If anxiety does not always correlate with VWM storage, this brings into question whether gating deficits are a defining feature of anxiety-related threat processing. When this ‘gating deficit’ occurs has been inconsistent in the literature, and it is unclear whether gating occurs pre- or post- attentional selection. There is evidence that inefficient filtering arises prior to working memory storage, resulting from attentional control processes in the prefrontal cortex and basal ganglia (Liesefeld et al., 2014; McNab & Klingberg, 2008). Consequently, the N2pc could be a marker of the filtering process itself (Jannati et al., 2013). Regardless of the timing of this gating deficit, we propose that attentional biases, and not memory storage, are the more reliable indicator of an individual’s anxious state.

Accordingly, there is evidence that unnecessary storage does not predict VWM performance as well as the preceding attentional control-related brain activity (Emrich & Busseri, 2015). In addition, several studies have found that a strict all-or-none memory filter (wherein all targets are let into memory and all distractors are denied access) is not sufficient to describe memory performance (Dube et al., 2017; Emrich et al., 2017; Salahub et al., 2019). The ability to flexibly allocate memory resources amongst items may be related to attentional control, a likely candidate for the underlying mechanism driving the relationship between anxiety and the mis-allocation of VWM resources observed in prior studies. Therefore, instead of anxiety causing a threat-related gating deficit, it seems likely that anxiety impairs attentional control abilities, such that threatening irrelevant items receive more enhanced processing than neutral relevant items. To better understand the underlying mechanism of unnecessary VWM storage for threat-related distractors, future studies should examine how item priority interacts with anxiety.

The present findings support a large body of literature that finds an attentional bias toward threat-related distractors for individuals with anxiety. Here, we found that individuals with anxiety do not always unnecessarily store that attended information in VWM. Instead, we show that anxious individuals have an attentional control deficit, resulting in enhanced selection, and not a failure in suppression, of salient threat-related distractors.

**Open Practices Statement:** The methods and analyses in the present study were pre-registered at https://aspredicted.org/cf7jn.pdf. The data from this experiment are not available online due to the absence of participant consent. Task and data analysis scripts are available upon request.

**Author Contributions:** CS and SME contributed equally to the experimental design, data analysis, and manuscript preparation. CS collected the data.

## Supplemental Results

### Residual horizontal eye movements

In the visual search task, participants were instructed not to move their eyes during the search display, however, there is evidence that individuals make more saccades to threat-related than neutral stimuli (Bannerman et al., 2010; Hopkins et al., 2016). Because these eye movements can reduce the amplitude of the ERPs, we conducted an exploratory analysis to compare residual HEOG activity across conditions during both an early (0 – 400 ms) and later (400 – 1,100 ms) time window. These time windows correspond to the time range of the N2pc/$P_D$ and CDA, respectively (see Table S3-1 for descriptive statistics).

**Table S3-1**

*Descriptive Statistics for Residual HEOG (µV) during Early and Late Time Windows*

| | Early (0 – 400 ms) | Late (400 – 1,100 ms) |
|---|---|---|
| Condition | *M(SD)* | *M*(SD) |
| Target Lateral/Distractor Midline | | |
| Fear/Neutral | 2.35(2.03) | 3.86(4.11) |
| Neutral/Fear | 2.47(2.25) | 4.66(4.75) |
| Neutral/Neutral | 2.32(2.00) | 4.43(3.98) |
| Distractor Lateral/Target Midline | | |
| Fear/Neutral | 1.40(0.76) | 2.25(1.14) |
| Neutral/Fear | 1.57(1.08) | 2.25(1.40) |
| Neutral/Neutral | 1.40(0.79) | 2.18(1.18) |

*Note.* N = 46. Averaged across side (left vs. right).

A 2 (Side) x 3 (Face configuration) repeated-measures ANOVA was conducted separately for target and distractor lateral conditions in each time window. During the early time window, there was no effect of face configuration condition on residual HEOG amplitude when either the target or distractor was presented laterally, *F*s < 2.34, *p*s > .1, $\eta^2_p$s < .05. That is to say, individuals were not moving their eyes more to lateral fearful faces than to neutral faces, whether the face was a target or distractor. There was a main effect of which side the face was presented on (left vs. right), such that there were greater eye movements toward lateral targets and distractors than toward the scrambled face on the opposite side of the screen, *F*s > 15, *p*s < .001, $\eta^2_p$s > .25.

Similarly, during the later time window, there was not a significant effect of facial configuration on the residual HEOG for lateral targets or distractors, *F*s < 3, *p*s > .05, $\eta^2_p$s < .07. When the target was presented laterally, individuals were moving their eyes toward the target face more than to the scrambled face on the opposite side of the screen, regardless of the target face's emotion, $F(1,45) = 25.19$, $p < .001$, $\eta^2_p = .36$. There was also an interaction between Side and Face configuration condition, such that when the target was presented on the left, there was an effect of face configuration on residual HEOG amplitudes, $F(2,90) = 3.46$, $p = .036$, $\eta^2_p = .07$. Follow-up post-hoc t-tests revealed that there were greater eye movements to the left in the Neutral Lateral/Fear Vertical condition than in the Fear Lateral/Neutral Vertical condition, $t(45) = 3.58$, $p_{\text{holm}} = .003$. As this was in the opposite direction to what would be predicted if individuals were making saccades toward fearful faces, this result is not further explored. When the distractor was presented laterally, there was no effect of stimulus side, $F(1.76, 79.08) = 2.41$, $p = .103$, $\eta^2_p = .05$, nor an interaction between Side and Face configuration, $F(2,90) = 1.07$, $p = .349$, $\eta^2_p = .02$.

### Individual differences and residual HEOG

Anxious individuals may look at fearful faces more than less anxious individuals (e.g. Mogg et al., 2007), reducing the amplitude of their subsequent ERP components. Therefore, to examine whether residual HEOG affected the correlations between anxiety and N2pc/CDA amplitudes, we included residual HEOG as a covariate. For correlations with the N2pc residual HEOG was measured during an early time window (0 – 400 ms), whereas it was measured during a later time window (400 – 1,100 ms) for correlations with the CDA.

Controlling for residual eye movements, there remained a significant correlation between state anxiety and N2pc amplitude toward a fearful distractor compared to a neutral baseline distractor, partial $r(44) = -.341$, $p = .024$. All other correlations did not reach significance, for both state and trait anxiety, $r$s < .26, $p$s > .09.

### Whole-report change detection task

Participants were first presented with a fixation dot (radius of 0.1°; 500 ms) followed by the memory display (500 ms) of 2, 4, or 6 colored squares (1° x 1°, 8 colors). Square positions were chosen pseudo-randomly from 12 possible positions around an invisible circle, 4° from fixation. Following the memory array, there was a 1,000 ms delay with fixation dot. Next, all squares appeared on the screen again in the same positions, and participants had to indicate whether any one of the squares changed color from the memory array (‘z’ key, half of trials) or whether none of the squares changed color (‘m’ key). Responses were untimed, although both speed and accuracy were stressed. There were a total of 150 trials, 50 of each set size. Participants were first given 18 practice trials to ensure that they were pressing the appropriate keys, and were given a break every 25 trials during the task. Visual working memory (VWM) K-estimates were calculated using the formula for Pashler's K (Pashler, 1988).

### Visual working memory capacity does not predict greater attentional selection and memory storage of fearful distractor faces

As pre-registered at https://aspredicted.org/cf7jn.pdf, we conducted several exploratory correlations between VWM capacity and the ERP components. This investigation was based on previous findings that individuals with lower VWM capacities have decreased attentional control, especially over salient distractors (Fukuda et al., 2015; Gaspar et al., 2016; Ye et al., 2018). It was hypothesized that individuals with lower K-scores would inappropriately attend to and store both neutral and fearful distractors in memory (as seen in Ye et al., 2018).

In the present sample, the mean K-score was 3.62 (*SD* = 0.77). Capacity did not correlate with N2pc amplitude toward the Neutral Lateral distractor/Neutral Midline, $r = -0.051$, $p = .738$; or with the Fear Lateral distractor/Neutral Midline, $r = -0.052$, $p = .733$. Similarly, K-scores did not predict CDA amplitude for the neutral distractor, $r = 0.185$, $p = .218$, or the fearful distractor, $r = -0.064$, $p = .673$. Therefore, contrary to the findings from Ye and colleagues (2018), we did not find evidence that VWM capacity predicted attention toward or memory storage of task-irrelevant distractors. This finding is consistent, however, with Stout, Shackman, and Larson (2013), who found no correlation between VWM capacity scores and filtering efficiency (as measured by the CDA). This suggests that the relationship between memory capacity and unnecessary storage of distractors is tenuous and may be limited to tasks that use angry faces. That is to say, although initial attention toward fearful and angry faces may be equivalent (Mogg et al., 2007), filtering of angry distractors from memory may be more difficult than fearful distractors. Further research is required to directly examine how VWM capacity influences filtering of angry versus fearful distractors.

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# Chapter 4

# Electrophysiological correlates of the flexible allocation of visual working memory resources

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**Note:** Experiment 1 of this paper was designed and collected by Holly A. Lockhart as part of an undergraduate Honours thesis project conducted at Brock University. Christine Salahub analyzed and prepared the data from this study for the following manuscript.

## Introduction

More likely than not, it is much easier for you to recall the names of the characters from the last television show that you watched than what you were wearing while you watched it. This bias in memory is in part due to the fact that what we allocate more attention to is remembered with greater detail (Chun & Turk-Browne, 2007). Indeed, numerous studies of long-term memory have established that attention prioritizes relevant information to be encoded into memory (deBettencourt et al., 2017; Sundby et al., 2018; Turk-Browne et al., 2013). Attention also affects the maintenance and quality of information stored over shorter periods of time, such as in visual working memory (VWM; Adam et al., 2015; Fukuda & Vogel, 2011; Klyszejko et al., 2014). In fact, given that VWM is limited in capacity, several models of VWM have suggested that attention may play a critical role in determining what information gains access to these finite storage resources (Awh et al., 2006; Cowan et al., 2005; Engle, 2002; Fukuda et al., 2015).

One potential mechanism through which attention may drive working memory performance is by filtering out irrelevant distractors (Cowan & Morey, 2006). Filtering efficiency has been quantified using measurements of electrophysiological brain activity related to working memory storage – specifically an event-related potential (ERP) called the contralateral delay activity (CDA; Luck & Vogel, 2013; McCollough et al., 2007; Vogel et al., 2005; Vogel & Machizawa, 2004). CDA amplitude increases with the number of items stored in VWM, saturating as memory load increases beyond a few items (Bays, 2018). Interestingly, when distractors are presented alongside targets in a memory display, lower-capacity individuals exhibit larger CDA amplitudes than those with higher capacities, reflecting the fact that they have encoded and stored more distractors in memory (Vogel et al., 2005). This finding has been taken as evidence that poor filtering efficiency, resulting in unnecessary storage, is a critical determinant of VWM capacity.

Several recent studies have demonstrated that it is also possible to bias attentional resources toward and away from certain items in a flexible manner, independent of the need to filter out irrelevant distractor items. This bias can be induced by associating certain stimuli with monetary incentives, or by simply varying instructions indicating the probability that an item will be probed on any given trial (Klyszejko et al., 2014). In this way, the proportion of attentional resources allocated to any given memory item can continuously vary anywhere between 0 and 100%. In these past studies (Dube et al., 2017; Emrich et al., 2017), it was found that working memory performance (i.e., raw error = 1/precision) was best predicted by the likelihood that an item would be probed on a given trial, independent of the overall memory load. Importantly, this relationship between probe likelihood and memory precision, which followed a power-law, could also account for changes in performance across loads; for example, the change in precision from one to two items was consistent with each item only receiving half as many attentional resources. This framework suggests that attention does more than just restrict or grant access to VWM; rather, it also flexibly distributes resources amongst objects based on their respective priorities. In other words, how attention is allocated between targets is as important to memory performance as whether or not it is allocated to distractors (Emrich & Busseri, 2015; Yoo et al., 2018).

If attention can be flexibly allocated across items in VWM, how might this be reflected by neural measures of attention and VWM maintenance? There is evidence that the CDA is well-described by a saturation model, which predicts a continuous increase in CDA amplitude that saturates as set size becomes larger, instead of increasing discretely and plateauing at memory capacity (Bays, 2018). This finding suggests that the CDA, much like VWM performance, may be more flexibly affected by memory load than previously thought. Yet, it is currently unknown whether the CDA is also flexibly affected by the prioritization of memory items instead of, or in addition to, changes in memory load.

Prioritization could also be tracked by ERP components that precede memory maintenance, such as attentional selection and suppression. That is, one way that flexible prioritization could be accomplished is through the specific up-weighting of goal-relevant over irrelevant information (as opposed to down-weighting of goal-irrelevant information). Attentional selection can be tracked by the N2pc, a lateralized component which specifically reflects the enhancement of an item (Eimer, 1996; Hickey et al., 2006, 2010). Alternatively, it could be that prioritization is accomplished through the active suppression or down-weighting of goal irrelevant information. This can be measured by the distractor positivity ($P_D$): a lateralized component that is observed when distractors are presented laterally in the stimulus display (Burra & Kerzel, 2014; Gaspar & McDonald, 2014; Hickey et al., 2009; Sawaki & Luck, 2013). These two components can thus be used to disentangle the underlying mechanisms of prioritization: whether through selective enhancement of relevant information (N2pc) or suppression of irrelevant information ($P_D$).

Consequently, to determine the effect of resource allocation on the CDA, as well as whether prioritization is driven by selective enhancement of high-priority items or inhibition of low-priority items, we conducted three experiments in which the allocation of memory resources across items was manipulated in a continuous-report delayed-recall task. For these experiments, we use the term *memory load* to refer to the number of items with greater than zero percent likelihood of being probed. We use the terms *resource allocation* or *probability* to refer to the likelihood that one item, or a set of items, will be probed. In Experiment 1, we examined how changes in resource allocation amongst memory items influenced the CDA in comparison to the typical effect of memory load. To do this, participants were asked to remember the colors of four laterally presented items that were either equally likely to be probed, or where a spatial cue indicated that one item was more likely to be probed than the others (i.e. 50% or 100% likely to be probed). Thus, while participants should always be allocating 100% of memory resources to all four items, how the resources were distributed across items varied. If the CDA is unaffected by resource allocation, and is only affected by memory load, then CDA amplitude should only reflect the total number of items to be stored, regardless of attentional priority.

In Experiments 2 and 3, we took advantage of an attribute of the CDA, N2pc, and $P_D$ – that these components are only sensitive to laterally presented stimuli and not stimuli presented on the vertical midline – to separately manipulate the effects of memory load and resource allocation. In Experiment 2, two items were presented laterally and two vertically, and a featural cue indicated whether the lateral or vertical items were more likely to be probed. Thus, this design allowed us to manipulate the proportion of memory resources specifically allocated to lateral items. If these ERP components reflect strategic resource allocation, then they should increase in amplitude with increasing probe likelihood (i.e., greater resource allocation). However, if these components are only affected by overall load, then item prioritization should have no effect.

In Experiment 3, we tested whether the CDA reflects the allocation of memory resources even in the absence of prioritization cues. To do so, we manipulated the total number of to-be-remembered items (four or six), while systematically changing the number of items presented laterally. In this way, we could simultaneously manipulate lateral memory load and proportion of memory resources allocated to the lateral items. We predicted that if the CDA tracks resource distribution across the lateral and vertical items, then CDA amplitude should reflect the proportion of total memory resources allocated to lateral items in addition to lateral memory load.

## Results

### Behavioural: Experiments 1 – 3

Because we manipulated proportion of memory resources per item across all three experiments and were interested in how behavior changed as a function of resource allocation, behavioural results were collapsed across experiments.

To compare how performance changed as a function of resource allocation, all data points were fit to a power-law function. Consistent with past findings (Dube et al., 2017; Emrich et al., 2017), this provided a good fit (Figure 4-1), with the model accounting for around 79% of the variance in the data, adjusted-$R^2 = .79$, *RMSE* = 6.26. These results demonstrate that the proportion of memory resources allocated to an individual item was highly predictive of behavioral precision for that item. Moreover, percent of memory resources allocated to an item better predicted behavioral precision than memory load alone: adjusted-$R^2 = .35$, $RMSE = 10.97$, $\Delta BIC = 9.71$. Thus, regardless of the behavioural manipulation (i.e., spatial cues; feature-based cues; lateralized memory load), precision is strongly predicted by the percentage of resources allocated to the probed item.

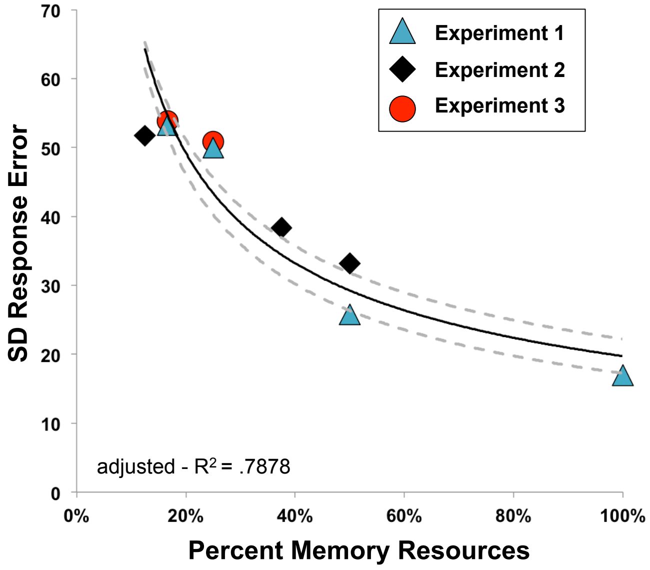

***Figure 4-1.*** Standard deviation of raw response error by percent memory resources in each experiment, fit with a power-law. Dashed grey lines represent fits performed on the 95% confidence interval of the condition means.

## ERPs

### Experiment 1

In this experiment, we sought to examine how the prioritization of one item over the others affected the CDA. Four lateral memory items were always presented, and spatial cues indicated the number of items to be remembered, as well as the likelihood of a given item to be probed (Figure 4-2A). Based on past demonstrations that the CDA primarily reflects VWM load, we expected there to be a larger CDA amplitude in the 4-Cues/100%-Valid condition than the 1-Cue/100%-Valid condition; remembering four items results in a larger CDA than remembering a single item. What remains an open question, however, is how the CDA changes when resources are distributed unequally across the four memory items. Thus, comparing the 4-Cues/100%-Valid and the 1-Cue/100%-Valid conditions to the 1-Cue/50%-Valid condition provides an initial test of how resource allocation affects CDA amplitude.

### CDA.

The spatial prioritization cues influenced CDA amplitude (Figure 4-2B; main effect of Condition, $F(2,38) = 5.83$, $p = .006$, $\eta^2_p = .24$, $BF_{10} = 6.94$). Consistent with a memory load effect, there was a more negative CDA amplitude when all four items were cued ($M = -0.55$ µV, $SD = 0.66$ µV), than when one item was cued at 100% validity ($M = -0.17$, $SD = 0.70$ µV), $t(19) = 3.43$, $p = .003$, d = 0.77, $BF_{10} = 14.94$. CDA amplitude in the 1-Cue/50%-Valid condition ($M = -0.29$ µV, $SD = 0.52$ µV) was not significantly different from the 1-Cue/100%-Valid condition, $t(19) = 0.98$, $p_{bonf} = 1$, d = 0.22, $BF_{10} = 0.36$, or from the 4-Cues/100%-Valid condition, $t(19) = 2.38$, $p_{bonf} = .084$, d = 0.53, $BF_{10} = 2.20$. Thus, though the CDA amplitude in the 1-Cue/50%-Valid condition was numerically smaller than in the 4-Cues/100%-Valid condition, this difference was not born out in the inferential statistics. Instead, the CDA amplitude in the 1-Cue/50%-Valid condition appeared to be in between the amplitudes of the other conditions (see Figure 4-2C).

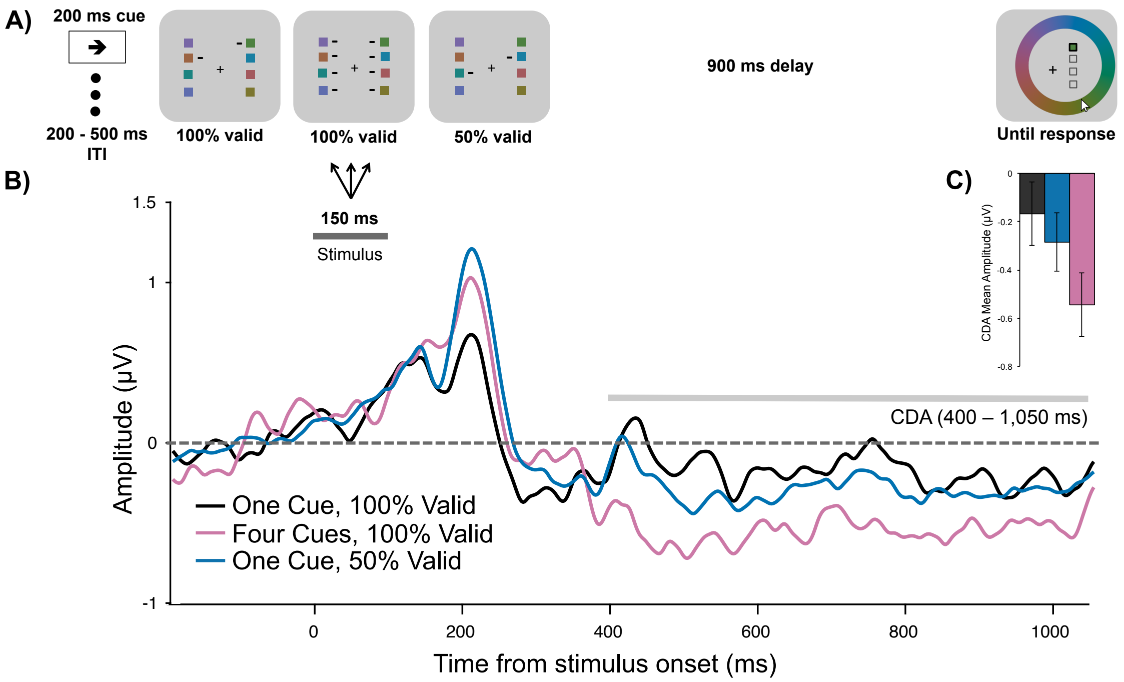

*Figure 4-2*. A) Task schematic of Experiment 1.B) Grand average difference waveform (N = 20) at the average of 5 posterior channel pairs, time-locked to stimulus onset. Positive is plotted up. Filtered at 30 Hz for visualization purposes only. C) Bar chart of mean CDA amplitudes in each condition. Error bars reflect within-subject 95% confidence intervals.

### Experiment 2

In Experiment 1, the typical effect of memory load on CDA amplitude and the behavioural effect of resource allocation on memory precision were replicated. However, the effects of resource allocation on CDA amplitude were less clear, as both high and low probability items were presented together laterally, resulting in a mixed electrophysiological signal. To better isolate the effects of prioritization on CDA amplitude, in Experiment 2 the items in the memory array were separated along the horizontal and vertical midlines and used feature-based priority cues (Figure 4-3A). Specifically, all memory arrays comprised two items presented laterally, and two presented on the vertical midline, with the lateral items either 100%, 75%, 25%, or 0% likely to be probed, depending on the shape of those items. Because lateralized ERP components are only sensitive to laterally presented stimuli, it was possible to systematically manipulate the proportion of lateral memory resources and thus its effect on the N2pc, $P_D$, and CDA. If these components reflect strategic resource allocation, then their amplitudes should increase continuously with item priority. However, if these components reflect memory load alone, then their amplitudes should remain stable regardless of the priority manipulation.

**N2pc.**

Feature-based priority influenced the amplitude of the N2pc (Figure 4-3B; main effect of Condition, $F(2.17, 41.24) = 10.85$, $p < .001$, $\eta^2_p = .36$, $BF_{10} = 1871.28$). Overall N2pc amplitude was more negative when the items were 100% ($M = -0.37$ μV, $SD = 0.74$ μV) likely to be probed than when they were 0% ($M = 0.17$ μV, $SD = 0.58$ μV), $t(19) = 4.82$, $p < .001$, d = 1.08, $BF_{10} = 238.64$, or 25% likely to be probed ($M = 0.06$ μV, $SD = 0.52$ μV) , $t(19) = 3.22$, $p = .005$, d = 0.72, $BF_{10} = 10.02$. The N2pc was also larger when the lateral items were 75% likely ($M = -0.19$ μV, $SD = 0.72$ μV) compared to 0%, $t(19) = 3.32$, $p = .004$, d = 0.74, $BF_{10} = 12.21$, or 25% likely to be probed, $t(19) = 2.57$, $p = .019$, d = 0.57, $BF_{10} = 3.05$. There were no significant differences between N2pc amplitudes in any other condition comparison, *p*s > .069, ds < 0.44, $BFs_{10} < 1.08$. However, the overall N2pc amplitude did become linearly more negative as item priority increased, adjusted-$R^2 = .99$, $RMSE = 5.54$, linear contrast: $t(19) = 5.66$, $p < .001$, suggesting that individuals could flexibly allocate their attention toward an item depending on how important it was to the trial (see Figure 4-3C). Interestingly, fractional peak latency did not differ between conditions, $F(1.81, 29.03) = 1.70$, $p = .202$, $\eta^2_p = .10$, $BF_{01} = 2.29$. Therefore, participants were not selecting high priority items any faster than low priority items.

### $P_D$.

Permutation tests indicated that the positive area of the grand average waveform between 250 – 400 ms was not significantly different from noise in any of the conditions, 100%: $p = .529$, 75%: $p = .30$, 25%: $p = .306$, 0%: $p = .087$. Although the $P_D$ was not significant, it could be that priority still had an influence on its amplitude. There was a small but non-significant effect of priority on the positive area of the $P_D$, $F(1.84, 34.96) = 2.95$, $p = .070$, $\eta^2_p = .13$, $BF_{10} = 1.36$. Therefore, there was little evidence of active attentional suppression in this task.

### CDA.

Similar to the N2pc, priority affected the amplitude of the CDA (main effect of Condition, $F(2.02, 38.42) = 6.43$, $p = .004$, $\eta^2_p = .253$, $BF_{10} = 85.42$). More information was stored in VWM when the items were 100% likely to be probed ($M = -0.69$ µV, $SD = 0.78$ µV) than 0% ($M = -0.02$ µV, $SD = 0.41$ µV), $t(19) = 3.34$, $p = .003$, d = 0.75, $BF_{10} = 12.53$. Similarly, the CDA was more negative in the 100% condition than the 25% condition ($M = -0.14$ µV, $SD = 0.36$ µV), $t(19) = 2.75$, $p = .013$, d = 0.61, $BF_{10} = 4.18$. When the items were 75% likely to be probed, the CDA amplitude ($M = -0.49$ µV, $SD = 0.68$ µV) was more negative than in the 25%, $t(19) = 2.15$, $p = .045$, d = 0.48, $BF_{10} = 1.52$, and 0% conditions, $t(19) = 2.38$, $p = .028$, d = 0.53, $BF_{10} = 2.20$. No other comparisons were significant, *t*s < 0.18, *p*s > .18, ds < 0.31, $BFs_{10} < 0.52$. However, similar to the N2pc, CDA amplitude was linearly related to priority, adjusted-$R^2 = .99$, *RMSE* = .03, linear contrast: $t(19) = 4.33$, $p < .001$ (see Figure 4-3C). Therefore, the more likely the items were to be probed, the greater the amplitude of the CDA.

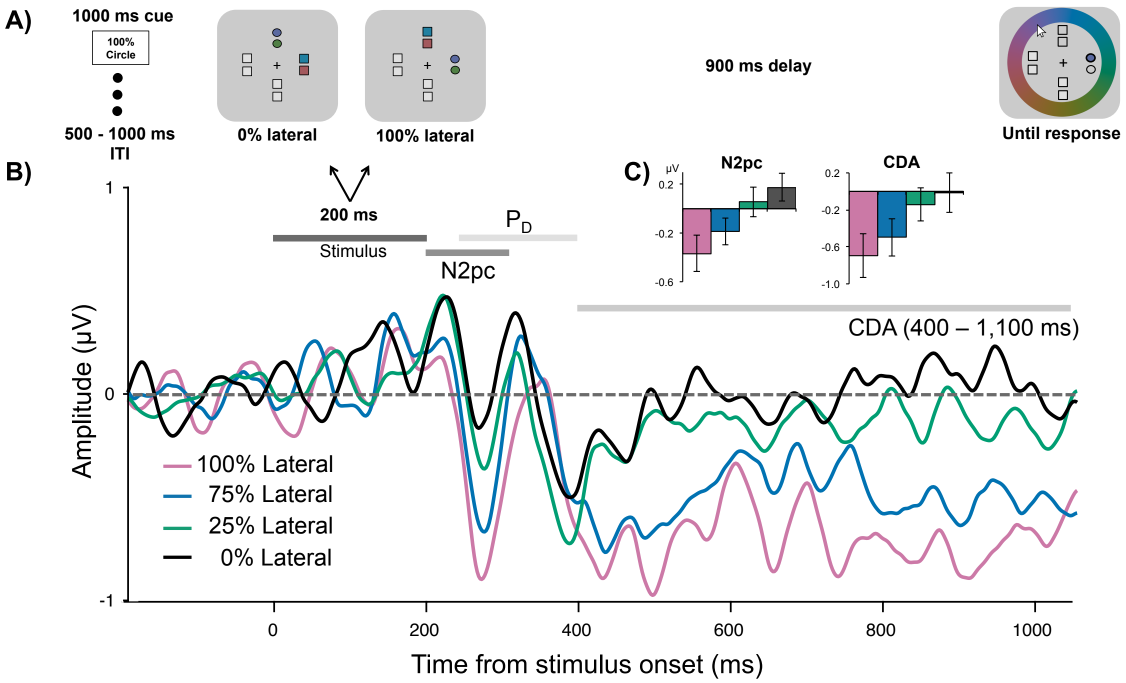

***Figure 4-3.*** A) Task schematic of Experiment 2. In this example, it was 100% likely that the color of a circle would be probed. B) Grand average difference waveform (N = 20) at the average of 5 posterior channel pairs, time-locked to stimuli onset. Filtered at 30 Hz for visualization purposes only. C) Bar chart of mean N2pc and CDA amplitudes in each condition. Error bars reflect within-subject 95% confidence intervals.

### N2pc and CDA amplitudes predict behavioural precision.

To examine whether memory resource-related changes in N2pc and CDA amplitudes predicted changes to VWM response error, a repeated-measures correlation was performed (Bakdash & Marusich, 2017; Emrich, Riggall, LaRocque, & Postle, 2013) between mean amplitude and response error across three lateral resource conditions (25%, 75%, and 100%). It was found that attention toward the lateral shapes, as measured by the N2pc, predicted how precisely the color of the probed shape was reported, $r_{rm}(39) = 0.55$, 95% CI = [.28, .74], $p = < .001$ (Figure 4-4A). There was also a correlation between raw error and mean amplitude of the CDA, $r_{rm}(39) = 0.44$, 95% CI = [0.15, 0.67], $p = .004$ (Figure 4-4B). These findings indicate that more precise reports of the probed color were associated with larger neural responses related to attentional enhancement and memory maintenance.

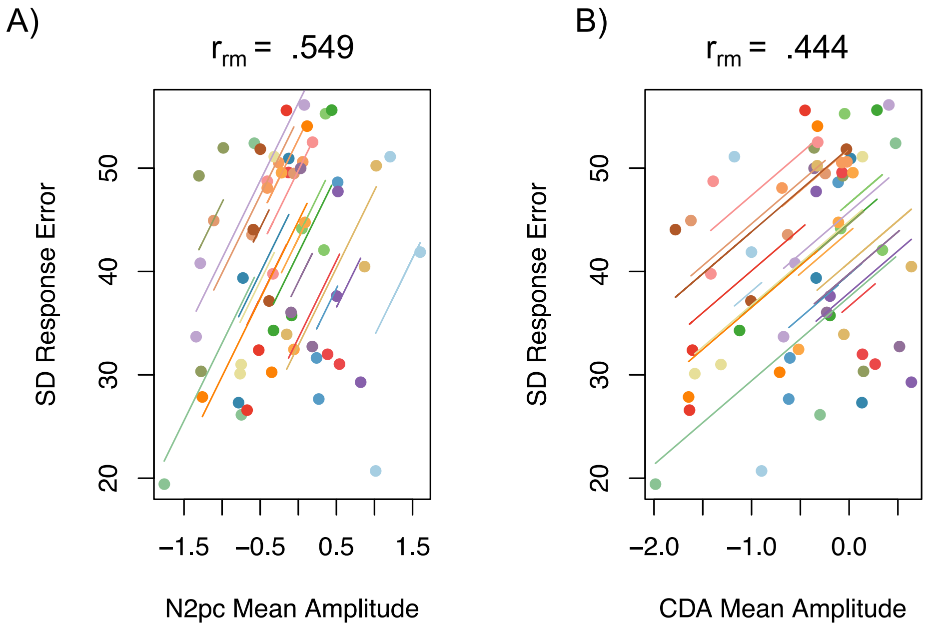

***Figure 4-4.*** Repeated-measures correlations plots. Each colored line is the fit for three data points from each individual participant from the 100%, 75%, and 25% lateral likelihood conditions. A) Correlation between N2pc mean amplitude and standard deviation (SD) of raw response error. Lower SD indicates more precise responding. B) Correlation between CDA mean amplitude and SD of response error.

### Experiment 3

Experiment 2 provided evidence that attentional prioritization not only affects behavioural precision in a delayed-recall task, it is also associated with a proportional increase in the amplitude of ERP components associated with attentional enhancement (N2pc) and memory maintenance (CDA). Interestingly, previous studies have found that the effect of load on behavioural precision is identical to those of prioritization; thus, splitting resources across two items results in similar memory precision as an item with 50% cue validity (Emrich et al., 2017). Consequently, to test whether the CDA similarly reflects resource allocation in the absence of prioritization cues we manipulated how many items were presented laterally, and how many vertically (Figure 4-5A). There were three conditions: one item lateral and three vertical (Load 4, 25% lateral), three items lateral and one vertical (Load 4, 75% lateral), and three items lateral and three items vertical (Load 6, 50% lateral). Thus, these last two conditions had the same lateral memory load but a change in the proportion of memory resources allocated to those items. We predicted that CDA amplitude would become more negative as the proportion of lateral memory resources increased.

### CDA.

CDA amplitude was affected by Condition (Figure 4-5B), $F(2,38) = 7.60$, $p = .002$, $\eta^2_p = .29$, $BF_{10} = 24.31$, such that the amplitude was more negative when 75% of memory resources were allocated to three lateral items ($M = -0.78$ µV, $SD = 0.64$ µV) than when 25% were allocated to one lateral item ($M = -0.25$ µV, $SD = 0.54$ µV), $t(19) = 3.4$, $p = .003$, d = 0.76, $BF_{10} = 14.17$. When 50% of memory resources were allocated to three lateral items ($M = -0.57$ µV, $SD = .60$ µV), the CDA amplitude was more negative than when 25% of resources were allocated to one item, $t(19) = 2.27$, $p =.035$, d = 0.51, $BF_{10} = 1.83$. CDA amplitude in the 50% lateral condition was numerically, but not significantly, smaller than in the 75% lateral condition, $t(19) = -1.92$, $p = .069$, d = 0.43, $BF_{10} = 1.08$. Importantly, CDA amplitude was linearly related to the proportion of lateral resources, adjusted-$R^2 = .91$, $RMSE = .10$, $t(19) = 3.4$, $p = .009$, such that amplitude became more negative as the amount of resources increased (Figure 4-5C). Together, these findings suggest that even in the absence of prioritization cues, the CDA may reflect a combination of memory load *and* the amount of attention/memory resources allocated toward these items.

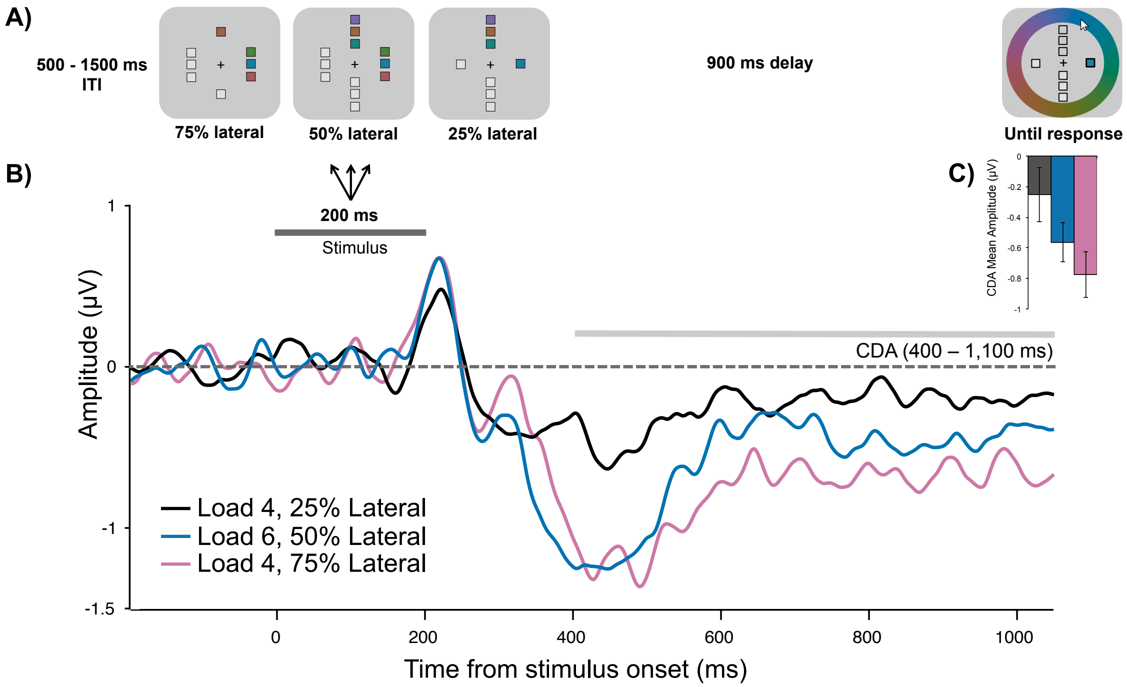

***Figure 4-5.*** A) Task schematic of Experiment 3. B) Grand average difference waveform (N = 20) at the average of 5 posterior channel pairs, time-locked to stimuli onset. Positive is plotted up. Filtered at 30 Hz for visualization purposes only. C) Bar chart of mean CDA amplitudes in each condition. Error bars reflect within-subject 95% confidence intervals.

## CDA amplitude continuously reflects both VWM load and resource allocation

Across three experiments, the manipulation of resource allocation – whether by spatial cues, feature-based cues, or memory load – affected the amplitude of the CDA. Although these effects were sometimes small, they are consistent with previous behavioural findings (also observed here) that the magnitude of the effect on memory performance depends on the magnitude of the change in resource allocation. However, although small changes in resource allocation may only produce small effects, these effects tend to follow a predictable pattern along a continuous power-law in behavioural studies (Emrich et al., 2017). Thus, it is possible that the effect of resource allocation on ERP measures of memory maintenance should similarly follow a continuous pattern, wherein the amplitude of the CDA changes with the proportion of resources allocated to laterally presented items. It is also possible that, although resource allocation is a better predictor of memory performance than load alone, CDA amplitude may reflect a mixture of signals that combine effects of load *and* resource allocation. To examine this prediction, we tested whether the CDA amplitudes observed in Experiments 2 and 3 (which involved similar stimulus displays) were best described by one of three models: one in which CDA amplitude was predicted by load alone, another with resource allocation alone, and a model using a scaled combination of memory load and resource allocation (see Methods).

When CDA amplitudes were compared to memory load alone (Figure 4-6A), the model accounted for 50% of the variance in the data, adjusted-$R^2 = 0.50$, $RMSE = 0.28$, BIC = -17.52. However, when examining the best-fit line, the direction of this function was in the opposite direction to what was predicted, such that CDA amplitude appears not to saturate, but continues to increase with increasing memory load. This suggests that a power function does not well describe the data when fitting CDA amplitude with load, at least within the range of set sizes tested here. CDA amplitudes were even less well fit with proportion of memory resources alone (Figure 4-6B), adjusted-$R^2 = 0.33$, $RMSE = 0.32$, BIC = -15.62. However, when fitting CDA amplitude to the weighted sum of both memory load and proportion memory resources, there was the best fit (Figure 4-6C), adjusted-$R^2 = 0.52$, $RMSE = 0.27$, BIC = -18.35. This demonstrates that the amplitude of the CDA follows a predictable continuous function that is affected both by the number of lateral items to be remembered, and by the proportion of total resources allocated to those items.

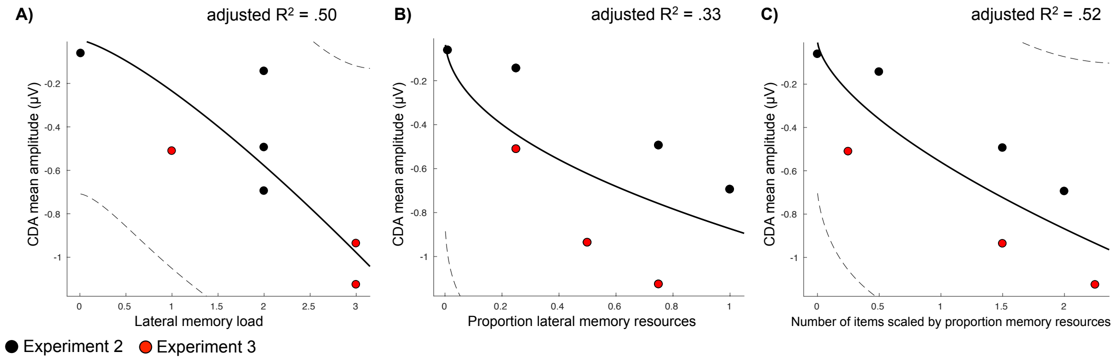

***Figure 4-6.*** Power-law models and fits. Dotted lines represent 95% CIs of the model fit. Black dots represent condition means from Experiment 2 and red dots from Experiment 3. A) Fit between CDA mean amplitude and lateral memory load. B) Fit between CDA amplitude and proportion lateral memory resources. C) Fit between CDA amplitude and number of items scaled for both memory load and memory resources.

## Discussion

In this study, we sought to examine the effect of prioritization on ERP markers of attentional enhancement, distractor suppression, and working memory maintenance, to better understand flexible allocation of memory resources. In Experiment 1, we found that the CDA was somewhat smaller when prioritizing one item over others than when all items were prioritized equally. In Experiment 2, we implemented a stronger manipulation of resource allocation using a systematic lateralization procedure (Hickey et al., 2009; Sawaki et al., 2012), demonstrating that the CDA tracked overall proportion of memory resources allotted laterally. We also found that the N2pc was reflective of priority, providing evidence that the allocation of neural resources toward to-be remembered items occurs via attentional enhancement. Moreover, both N2pc and CDA amplitudes correlated with behavioral precision in this task. Finally, in Experiment 3 we manipulated the proportion of memory resources that should be allocated to lateral items by controlling the number of items presented laterally while manipulating overall load. Consistent with the first two experiments, we found that CDA amplitude tracked the proportion of memory resources allocated toward the lateral items in the memory array.

When comparing across Experiments 2 and 3, we also found that CDA amplitudes were best predicted by a weighted sum of memory load and resources. This finding points to the CDA as a proxy of more than memory load alone, suggesting that this component may also reflect the total amount of memory resources allocated to lateral items.

One potential argument against the resource allocation interpretation is that instead of flexibly distributing resources across all items in the display, individuals alternated strategies *probabilistically* across trials: encoding higher probability items on most trials and lower probability items less often. If items were being encoded probabilistically, then one might expect that, on the majority of trials, participants would pay attention to and encode the higher probability items first. This would result in an earlier N2pc, consistent with previous findings in visual search tasks (Woodman & Luck, 1999, 2003). In contrast to this hypothesis, there was no difference in the timing of the N2pc across conditions in Experiment 2, suggesting that all items were being attended to at the same time, regardless of priority.

One interpretation of the probabilistic account is that participants alternate across trials between encoding high or low probability items; however, this interpretation can be ruled out based on the behavioral estimates of guess rates obtained from the two-component mixture model (Zhang & Luck, 2008) (see Supplemental Results). In Experiment 2, for example, if differences in CDA amplitudes were due to participants probabilistically encoding items, then the number of encoded items in the 75/25% condition should reflect this. That is to say, if participants encoded the two higher priority items on 75% of trials, and the two lower priority items on 25% of trials, this would lead to the same difference in CDA amplitude between conditions as was observed here, but with a total estimated number of encoded items of 2. However, the total number of encoded items in these conditions was 2.9, significantly greater than what would be predicted by the probabilistic encoding account.

Even if participants weren't probabilistically encoding items, they may have been selectively encoding the higher priority items on the majority of trials, which could affect the CDA amplitude. However, this strategy cannot be ruled out based on estimates of the total number of items encoded, as increased guessing can also result from low resource allocation (Emrich et al., 2017; van den Berg & Ma, 2018). Indeed fluctuations in CDA amplitude across trials is likely a feature of all CDA measurements (Adam et al., 2018), as changes in the number of items and amount of information encoded have been observed due to spontaneous fluctuations in attention (Adam et al., 2015; deBettencourt et al., 2019; van den Berg et al., 2012; Yoo et al., 2018), and top-down strategies (Cusack et al., 2009; Linke et al., 2011). Thus, although the experiments presented here may include some measure of strategic differences in resource allocation across trials, resulting in some change in the number of stored items, *spontaneous* changes in resource allocation across trials may be an additional source of variance within past CDA studies that has been previously unidentified.

There are several implications that arise from these findings, such as the role of attentional enhancement in prioritization. In Experiment 2 we found that the N2pc, but not the $P_D$, tracked the priority of the lateralized items, while also predicting the precision of memory report. This suggests that when using feature-based cues, participants relied on up-weighting relevant information depending on their respective priorities, in comparison to down-weighting irrelevant information using active suppression. This is consistent with previous findings, which found that when given a pre-cue to up- or down-regulate memory encoding processes, participants could only up-regulate processing to benefit performance (Sundby et al., 2018). Additionally, it has been found that when using reward to prioritize items, only target selection is impacted and not distractor suppression (Hickey et al., 2011). This speaks to the importance of attentionally selecting and enhancing target information to VWM, instead of only inhibiting and filtering distractors. That is, although previous work has focused on the link between unnecessary memory storage of distractors and VWM capacity (Liesefeld et al., 2014; McNab & Klingberg, 2008), a full account of working memory performance should require a mechanism wherein resources are allocated amongst items when they are all relevant to the task (Fukuda et al., 2015). The present results begin to point to potential mechanisms.

Finally, our results provide some information about the neuronal underpinnings of the CDA. The finding that the CDA follows a power-law when fit with a combination of resources and memory load is consistent with the saturation model of delay period activity proposed by Bays (2018). In this model, as input increases, neuronal activity also increases. However, as the input becomes increasingly large, it produces a consequent smaller increment in neuronal activity, saturating at some maximum level (Bays, 2018). Although the power-law examined here tests a similar pattern, the present experiments did not test a large enough range of set sizes to delineate between capacity-limited models and limitless models. Moreover, it could be that prioritization is only possible within a limited range of stored items.

Our results do suggest that it is possible that different types of information can independently affect the CDA. Consistent with this interpretation, there are a few studies that have found memory precision can modulate the CDA independent from memory load (Machizawa et al., 2012; McCants et al., 2019) (but see, Gao et al., 2011)). These previous findings support an account of VWM that encompasses both discrete item units, as well as continuous modulations in representational quality (Brady et al., 2011; Xu & Chun, 2006). Consistent with this finding, a previous study observed independent effects of the number of items and complexity on the CDA at different channel pairs (Wilson et al., 2012). Thus, while the results of the experiments presented here cannot fully adjudicate between different models of VWM architecture (i.e., whether or not memory resources are tied to discrete units), they are consistent with the idea that how resources are allocated should be considered in addition to overall load in neural and behavioral models of VWM.

## Methods

### Participants

Informed, written consent was obtained from all participants. Procedures were approved by and conducted in accordance with the Brock University Bioscience ethics review board. We aimed for a sample size of 20 participants in each Experiment (Fukuda, Kang, & Woodman, 2016; Vogel & Machizawa, 2004; Vogel et al., 2005) (right handed, normal-color vision, no history of mental illness). To reach these targets, a total of 30 participants were run in Experiment 1, 33 in Experiment 2, and 28 in Experiment 3. Distinct samples (N = 20) were used for each experiment (Exp 1: $M_{\text{age}} = 22.0$, $SD_{\text{age}} = 3.0$, 10 male; Exp 2: $M_{\text{age}} = 22.6$, $SD_{\text{age}} = 4.2$, 9 male; Exp 3: $M_{\text{age}} = 21.6$, $SD_{\text{age}} = 3.9$, 3 male).

### Stimuli and Procedures

All tasks were completed on a Windows PC with a 41-cm NEC MultiSync LCD 2090UXi computer monitor (1600 x 1200 pixels, 60 Hz refresh rate). Stimuli were rendered using Psychopy v1.90.3 (Peirce, 2007) and presented on a grey background (RGB = 128 128 128) with a central fixation dot (radius of 0.3°). Viewing distance was approximately 57 cm. In all experiments, participants first completed a standard change detection task (Luck & Vogel, 1997). These data are not included.

The colors for the squares in the continuous report VWM tasks were chosen pseudo-randomly from a 360-degree isoluminant color wheel (CIE L*a*b* color space, [L = 70, a = -6, b = 14, radius = 49]), which was calibrated to the testing monitor. Memory stimuli colors were separated by at least 30 degrees on the color wheel.

#### Experiment 1.

At the beginning of each block, participants were instructed on cue-validity, both with on-screen and verbal instructions: In the 1-Cue/100%-Valid condition, the one cued item was always probed; In the 4-Cues/100%-Valid condition, the probed item was randomly selected from all four items; In the 1-Cue/50%-Valid condition, the cued item was probed on 50% of trials, un-cued items were probed on the remaining trials. Each trial began with an arrow indicating which side of the screen was task relevant (3° tall, 200 ms), followed by a jittered fixation interval (200 – 500 ms). The memory array (150 ms) consisted of four squares on both sides of the screen (1° x 1°, 4° from fixation) along with horizontal spatial line cues (2° long x 3 pixels wide, 2° from fixation). After a delay (900 ms), participants reported the color of the bolded square (line width of 3 pixels vs. 1 pixel) from the color wheel (diameter of 7°) with the mouse. There were 240 trials in both the 1-Cue/100%-Valid and 4-Cues/100%-Valid Conditions, and 480 in the 1-Cue/50%-Valid condition, split equally between both sides of the screen (total 960). One participant's data consisted of only 840 trials due to a recording error.

**Experiment 2.**

In both Experiments 2 and 3 participants first completed a subjective luminance-matching task, which was used to create the placeholder colors (see Supplemental Methods).

Each trial began with a feature-based cue (i.e. *100% Circle*; 1,000 ms, 1.5° tall) followed by a jittered interval (500 – 1,000 ms). Next, eight shapes were presented in clusters of two at each cardinal position 3° from fixation (to center of shape cluster) and 1.2° apart (vertical center to center; 200 ms). There were always two colored squares (1° x 1°) and two colored circles (diameter of 1°). The remaining four items were filled with the subjectively luminance-matched grey and were always the un-cued shape. Shapes were presented in all possible position configurations equally (16 unique positions). After a delay (900 ms), participants made a response to the probed shape on the color wheel with the mouse (pseudo-randomly chosen from top or bottom shape in cluster). There were a total of four conditions defined by the probability that the lateral shapes would be probed: 100%, 75%, 25%, and 0%. Participants completed a total of 816 trials (100% lateral: 200, 0% lateral: 200, 75% lateral: 208, 25% lateral: 208). One participant completed 806 trials due to a programming error, and another completed 807 trials due to an interruption to the recording session.

### Experiment 3.

Participants were instructed that all items were equally likely to be probed. Each trial began with a jittered ITI (500 – 1,500 ms) followed by the memory array (200 ms). Then, after a delay (900 ms), participants made a response to the probed shape on the color wheel with the mouse. There were three conditions: 1) Load 4 with three colored squares presented in a vertical cluster to the left or right of fixation (1° x 1°, 1.2° apart center-to-center, 3° from fixation) and one colored square presented vertically. 2) Load 4 with one square presented laterally and three squares on the vertical. 3) Load 6 with three squares presented laterally and 3 vertically. Participants were given feedback after their response (800 ms), where 'Correct' was considered within 40° of the target color. Participants completed a total of 900 trials, 300 of each condition.

## EEG Recording and Pre-Processing

All EEG pre-processing was done in MATLAB with the EEGLAB (Delorme & Makeig, 2004) (Version 14.0.0b), and ERPLAB (Lopez-Calderon & Luck, 2014) (Version 6.1.2) toolboxes. EEG was DC recorded at a 512 Hz sampling rate from a 64 Ag/AgCl electrode cap placed at the standard 10-20 sites (*BioSemi ActiveTwo System Amsterdam, The Netherlands*). The signal was online referenced to the common mode sense (CMS) and the driven right leg (DRL) electrodes. Data were re-referenced off-line to the average of the mastoids, baseline corrected to -200 ms before memory array onset, and filtered with a 40-Hz low-pass and 0.1-Hz high-pass Butterworth filter (slope: 12dB/octave). Data were epoched between -200 and 1,050 ms (Experiment 1) or -200 and 1,100 ms (Experiment 2 and 3), time-locked to the memory array.

### Artifact rejection.

Horizontal electro-oculogram (HEOG) was recorded from bipolar external electrodes placed laterally beside the eyes. Vertical electro-oculogram (VEOG) was recorded as the difference between external electrodes placed below the eyes and FP1 or FP2. Trials with VEOG activity > ±80 μV or HEOG activity > ±32 μV between stimuli onset and the end of the trial were removed, as were trials in which the voltage over posterior channels (P1/2, P3/4, P5/6, P7/8, P9/10, PO3/O4, PO8/O7, and O1/2) was > ± 100 μV. Participants with more than 35% of trials rejected were replaced. An average of 21.4% of trials were rejected in Experiment 1, (*SD* = 10.4%), 11.6% in Experiment 2 (*SD* = 7.8%), and 13.3% in Experiment 3 (*SD* = 10.1%). Across studies, each participant had more than 100 trials in each condition bin.

In Experiments 2 and 3 participants whose average residual HEOG activity was greater than ± 4 μV between memory array onset and the end of the epoch were also replaced. Resulting in absolute residual HEOG values of 1.61 μV (*SD* = 1.02 μV) in Experiment 2 and 1.61 μV (*SD* = 1.00 μV) in Experiment 3. The total number of replaced participants was 10 in Experiment 1, 12 in Experiment 2, and 8 in Experiment 3.

## Data Analysis

### Behavioural data.

Performance was assessed using the trial-by-trial raw response error (i.e., the difference in degrees between the color of the probed item and the participant's response). Lower values reflect more precise responding. Data from all experiments were fit to a power-law function:

$$y \propto ax^{-k}$$

Bayesian information criterion (BIC) values were computed to compare model fits. Raw error values were calculated using custom scripts in MATLAB. Goodness of fit was computed using nonlinear least squares regression in MATLAB's Curve-Fitting Toolbox using a bisquare robust fitting procedure with the group data averaged across conditions.

**ERP data.**

Difference waves were calculated at electrode pairs: P3/4, P7/8, PO7/O8, PO3/O4, and O1/2 (Hakim, Adam, Gunseli, Awh, & Vogel, 2019). Across all experiments, there was no significant Condition x Channel interaction for any of the ERP components (*F*s < 2.24, *p*s > .055, $\eta^2_p$s < .11). Therefore, activity was averaged across these electrode sites for all ERP measurements.

Repeated-measures ANOVAs were used along with follow-up linear contrasts and fits where reported. Where violations of sphericity exist, Greenhouse-Geisser corrected degrees of freedom and *p* values are reported. Two-tailed t-tests were Bonferroni-corrected only where a priori hypotheses were not present. Bayesian repeated-measures ANOVAs and post-hoc tests are reported where applicable (r scale prior width of 0.5, default Cauchy prior centered on 0, 10,000 Monte Carlo samples). Statistical analyses were completed using JASP Version 0.8.4(JASP Team, 2018) and MATLAB R2017a.

In all experiments, the CDA was measured as the mean amplitude during the delay period from 400 ms post-stimuli offset to the end of the trial (Adam et al., 2018; Ikkai, McCollough, & Vogel, 2010). An N2pc was only visually observed in Experiment 2 and was measured as the mean amplitude from 200 – 300 ms post-stimuli onset (Kiss, Velzen, & Eimer, 2008; Luck & Hillyard, 1994; Mazza, Turatto, & Caramazza, 2009; Woodman & Luck, 1999). The negative 50% fractional peak latency of the N2pc was measured between 200 – 300 ms (Luck, 2014). In Experiment 2, the $P_D$ was measured as the positively signed area from 250 – 400 ms (Feldmann-Wüstefeld & Vogel, 2018; Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016). A nonparametric permutation approach was used to determine the presence of the $P_D$.

The $p$ values for the permutation tests were estimated using the following formula with 1,000 permutations (Gaspelin & Luck, 2018):

$$p = \frac{\text{Number of permuted areas } \geq \text{ observed area}}{\text{Total number of simulated permutations}}$$

**Modelling CDA data.**

In Experiments 2 and 3, the CDA amplitudes were fitted to a power-law model. The weighted-product values were calculated by the following formula:

$$\% \text{ of lateral resources} \times \text{number of lateral items}$$

Model fits were completed using the Curve Fitting Toolbox in MATLAB and custom MATLAB scripts to calculate BIC values to compare model fits.

**Data Availability:** The datasets generated or analysed during the present study are unavailable due to the absence of consent.

**Code Availability:** Psychopy task scripts, R code, and MATLAB code used to pre-process EEG data as well as to fit models are available online at: https://osf.io/r73c5/

**Author Contributions:** C.S., H.A.L., N.A., and S.M.E conceived of the designs. C.S., H.A.L., and S.M.E. analyzed the data; C.S., H.A.L., and B.D. collected the data. C.S. and S.M.E. took the lead in preparing the manuscript. All authors discussed the interpretation of results and contributed to the final manuscript.

## Supplemental Materials

### Methods

**Luminance-matching task.** This task was used in Experiments 2 and 3 to obtain an individual grey color that was subjectively matched in brightness to the color wheel colors. This grey was used in the main experiment as the fill color for the placeholder shapes to visually balance the display. In this task, participants were presented with a screen that was vertically divided in half with a fixation point (0.3° x 0.3°) in the middle. The left half of the screen was filled with a color from the color wheel and the right half was filled with grey. Twelve colors were selected from the color wheel (in 30° steps). Each color was presented four times: twice each with a grey that was ~5 cd/m$^2$ greater or less than the average brightness of the 12 colors (~25.1 cd/m$^2$). Participants were instructed to match the brightness of the grey half of the screen to that of the color using the left and right arrow keys. Each press of the right arrow key increased the lightness of the grey by 0.01 units closer to white, and the left arrow key decreased the lightness by 0.01 units closer to black (-1 to 1 RGB color space where [0, 0, 0] is grey). To make their final response, participants pressed the enter key. For each individual participant, their averaged grey luminance ratings were used across all 48 ratings as the fill color for the placeholders in Experiment 2 ($M$ = [-.02 -.02 -.02] or ~35.6 cd/m$^2$, $SD$ = .087) and Experiment 3 ($M$ = [-.047 -.047 -.047] or ~29.3 cd/m$^2$, $SD$ = .041).

## Results

### Standard mixture model estimates of visual working memory capacity.

Behavioural data from all three experiments were analyzed using the two-component standard mixture model (Zhang & Luck, 2008). This model provides two parameter estimates per experimental condition: $P_m$, the probability that the probed item was encoded and stored in memory; and standard deviation (SD), which reflects the precision of the memory representation. Here, the analysis was focused on the effect of experimental condition on $P_m$ as a way to examine whether participants were probabilistically encoding items into memory in each experiment. To calculate the number of items held in memory, the following calculation was used:

$$P_m \times Load$$

Where Load refers to the total number of items that should be held in memory if performing the task correctly. $P_m$ can also be calculated as (1 – Guess Rate).

**Experiment 1.** In this experiment, Load was defined as 1 when one item was cued with 100% validity and 4 when 1 item was cued at 50% validity or when all 4 items were cued. A repeated measured ANOVA was conducted on the estimates of memory load for each condition. It was found that there was a main effect of overall Condition, $F(1.39, 26.40) = 87.51, p < .001, \eta^2_p = 0.82, BF_{10} = 1.42 \times 10^{14}$. More items were held in memory when all 4 items were cued with 100% validity ($M = 1.98, SD = 0.58$), than when only 1 item was cued with 100% validity ($M = 0.97, SD = 0.02$), $t(19) = -7.78, p_{bonf} < .001$, d = 1.74, $BF_{10} = 6.29 \times 10^4$. However, participants held more items in memory when 1 item was cued with 50% validity ($M = 2.23, SD = 0.35$) than when all 4 items were cued, $t(19) = 2.86, p_{bonf} = .03$, d = 0.64, $BF_{10} = 5.14$, and more than when 1 item was cued with 100% validity, $t(19) = 16.32$, $p_{bonf} < .001$, $d = 3.65$, $BF_{10} = 5.65 \times 10^9$ (see Table S4-1 for a summary of the guess rates and memory load estimates). Contradictory to the pattern of CDA amplitudes, these findings suggest that more items were being held in memory when 1 item was cued at 50% validity than when all 4 items were cued with 100% validity. This suggests that in this condition, participants were not strategically holding only the highest probability item in memory on the majority of trials.

**Experiment 2.** Here, the analysis was focused on $P_m$ in the 75/25% condition to determine whether participants were probabilistically encoding the memory items. If participants were encoding the two higher priority items on 75% of trials, and the two lower priority items on the remaining 25% of trials, this would result in a pattern of CDA amplitudes similar to what was observed in the current study. However, this probabilistic pattern of responding should be reflected in behavioural estimates of memory load (i.e. $P_m$ * Set Size). That is to say, if participants were encoding the two 75% likely items on 75% of trials, an average of $75 * 2 = 1.5$ items should be encoded into memory. Adding this to the number of items encoded on the remaining 25% of trials results in a total average of $1.5 + 0.5 = 2$ items. Therefore, if participants were probabilistically encoding items into memory, the number of items in memory in the 75/25% condition should not be significantly different from 2. Similarly, if participants were only holding the higher priority items in memory, it would also be expected that 2 items would be held in memory on average. However, if participants were instead using flexible resource allocation amongst all items in the memory display, then the number of items in memory should be greater than 2.

Although the analysis was focused on 75/25% condition, all estimates per Condition are presented in Table S4-2 (excluding the 0% priority condition). Collapsed across probed item priority, an average number of 2.92 items were held in memory in the 75/25% condition (*SD* = 0.59). This is significantly different from 2, $t(19) = 7.05$, $p < .001$, d = 1.58, $BF_{10} = 1.74 \times 10^4$. When the same analysis was applied to each probed condition separately, it resulted in a number of poor model fits. Nevertheless, the total number of items encoded in memory (*M* = 2.33, *SD* = 0.64) was significantly greater than the 2 predicted by the probabilistic account, $t(19) = 2.33$, $p = .031$, $BF_{10} = 2.04$. These findings suggest that participants were not probabilistically encoding the items in the 75/25% condition, and were instead using flexible resource allocation to encode all items in the display.

**Experiment 3.** Guess rates and estimates of the number of items held in memory for Experiment 3 are presented in Table S4-3. A paired samples t-test comparing the number of items held in memory in the Load 4 condition (collapsed across which item was probed) and the Load 6 condition, showed that more items were stored in memory at Load 4 (*M* = 1.90, *SD* = 0.47) than in the Load 6 condition (*M* = 1.63, *SD* = 0.71), $t(19) = 2.99$, $p = .007$, d = .67, $BF_{10} = 6.58$. Using the same logic as presented in Experiment 2, in the Load 4 condition if participants were holding 3 items in memory on 75% of the trials, then they would on average store 2.25 items in memory. This is then added to the 25% of trials where 1 item was remembered, resulting in an average of 2.25 + 0.25 = 2.5 items for the Load 4 condition. Similarly, for the Load 6 condition, the probabilistic account would predict that 50% of the time only three items are being remembered, resulting in an average of 3 items. Thus, although the total number of encoded items was less than what would be predicted, there were a greater number of items encoded in the Load 4 condition, contrary to the probabilistic account.

**Table S4-1**

*Guess Rate and Memory Load Estimates by Condition in Experiment 1*

| Condition | $M(SD)_{Guess}$ | $M(SD)_{Load}$ |
|---|---|---|
| 1 Cue, 100% Valid | 0.03 (0.02) | 0.97 (0.02) |
| 1 Cue, 50% Valid | 0.44 (0.09) | 2.22 (0.35) |
| Cued Item Probed | 0.09 (0.08) | 0.91 (0.08) |
| Non-Cued Item Probed | 0.68 (0.27) | 0.96 (0.81) |
| 4 Cues, 100% Valid | 0.51 (0.15) | 1.98 (0.58) |

*Note.* N = 20.

**Table S4-2**

*Guess Rates and Memory Load Estimates by Condition in Experiment 2*

| Condition | $M(SD)_{Guess}$ | $M(SD)_{Load}$ |
|---|---|---|
| 100/0% | 0.18 (0.10) | 1.64 (0.20) |
| 75/25% | 0.27 (0.15) | 2.92 (0.59) |
| 75% Probed | 0.24 (0.11) | 1.52 (0.23) |
| 25% Probed | 0.59 (0.34) | 0.81 (0.69) |

*Note.* N = 20.

**Table S4-3**

*Guess Rates and Memory Load Estimates by Condition in Experiment 3*

| Condition | $M(SD)_{Guess}$ | $M(SD)_{Load}$ |
|---|---|---|
| Load 4 | 0.52 (0.12) | 1.90 (0.47) |
| 25% Probed | 0.24 (0.14) | 0.76 (0.14) |
| 75% Probed | 0.61 (0.15) | 1.16 (0.44) |
| Load 6 | 0.73 (0.12) | 1.63 (0.71) |

*Note.* N = 20.

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# Chapter 5

# General Discussion

The overall goal of the present dissertation was to examine the neural mechanisms of, and individual differences in, the flexibility of attentional control. Given recent behavioural findings that attention can be used to continuously up- and down-weight the priority of search and memory items (Arita et al., 2012; Dube et al., 2017; Emrich et al., 2017), I sought to examine the electrophysiological correlates of this process, as well as the consequences of poor attentional control for VWM maintenance. The goal was to test the hypothesis that attentional control is much more flexible than has been previously thought, such that attention can be dynamically moved toward relevant items and suppress irrelevant items in a continuous manner. Additionally, consistent with the Attentional Control Theory (ACT) of anxiety, it was proposed that individual differences in anxiety would affect one's ability to use priority cues to split attention appropriately across items, based on the idea that individuals with higher anxiety have general deficits in attentional control in the face of distraction (Eysenck et al., 2007). Across five experiments, I examined ERPs related to attentional selection (N2pc), suppression ($P_D$), and memory maintenance (CDA) using systematically lateralized search and memory displays (Hickey et al., 2009). Using this technique, it was possible to separately analyze the precise timing of attentional enhancement and suppression for high versus low priority items.

In Chapter 2, I examined how individuals use information about upcoming target versus distractor features to guide attention during visual search, and how this ability varies across individuals. I found a significant early $P_D$, a component that reflects active distractor suppression or detection of feature discontinuities in the display. This component negatively correlated with state anxiety scores, such that higher anxiety scores related to greater amplitudes. When given information about an upcoming target feature (positive cue), it was found that observers could quickly attend to and select the target item, as indicated by large and early N2pc amplitudes. Following attentional selection of the target, the positive cue led to active suppression of the distractor, as indicated by the $P_D$. However, when given information about an upcoming distractor feature (negative cue), participants were slower to locate the target, as reflected by both increased RTs and a delayed contralateral negativity. During this later time window, negatively cued distractors were also suppressed. Important to the main goal of this thesis, I demonstrated that individuals were capable of both up-weighting high priority items using attentional selection, and down-weighting low priority items with active suppression. The ability to suppress the negatively cued distractor was related to individual differences in anxiety levels, such that the more anxious an individual was, the greater their early visual processing and attentional selection of the distractor. This finding suggests that flexible control over attentional selection is limited by an interaction between individual differences and cue type, such that salient, task-irrelevant items are more difficult to ignore for anxious individuals.

In Chapter 3, I used a similar lateralized search array to further explore the limits of attentional control when the distractor is threat-related. It was found that individuals with anxiety had a specific deficit when it came to inappropriately attending to a fearful distractor face (i.e. greater N2pcs), as compared to a neutral distractor. This finding supported my prediction that limits in attentional flexibility are related to individual differences in anxiety. This is particularly true for threat-related stimuli, as anxious individuals have greater attentional biases toward perceived threat. Following capture, I also assessed whether deficits in attentional control predicted the storage of distractors in VWM. However, contrary to previous findings in the literature (Stout et al., 2013), I did not observe that anxious individuals stored the threat-related distractor in VWM (as indicated by the CDA) more so than their less anxious counterparts. This suggests that despite attentional control deficits, anxious individuals are not always more likely to have impaired VWM filtering abilities. That is to say, there is a distinction between what one pays attention to and whether that item is subsequently stored in memory. This study provides further support for the idea that the ability to appropriately up- and down-weight stimuli priority depends on attentional control.

Finally, in Chapter 4 I used ERPs to probe the extent to which information about item features could be used *continuously* to bias selection and memory maintenance. That is, in addition to conditions telling participants that some items were task relevant and the others task irrelevant, I also included continuous manipulations of attentional priority, such that the items had a moderate chance (i.e. 25% or 75%) of being probed. Across three experiments, I found evidence for continuous up-weighting of higher priority than lower priority items. Both attentional selection (N2pc) and memory maintenance (CDA) tracked the relevance of the lateral items. Additionally, N2pc and CDA amplitudes predicted behavioural precision of responses. Together, these findings support the proposal that individuals can continuously allocate attention and memory resources toward items based on their priorities, even when all items are task relevant.

## Flexibility in the attentional priority map

The concept of a priority map to guide attentional selection is integral to many major theories of attention (Desimone & Duncan, 1995; Itti & Koch, 2001; Treisman, 1988; Treisman & Gelade, 1980; Wolfe, 1994). For example, in Wolfe's Guided Search Model of attention (1994), there is a proposed interaction between top-down goals and bottom-up capture, which are then combined to create an 'attention map'. Similarly, in Desimone and Duncan's (1995) Biased Competition model, items compete for representation on the basis of potential task-relevance from top-down goals. These goals determine an individual's *attentional control setting*, that is, what the individual aims to do in the moment (Folk et al., 1992). The priority map likely uses a combination of spatial and feature-based information; however, the present thesis focuses mainly on the role of top-down attentional guidance by feature-based search templates.

The majority of attentional theories have focused on how attention is used to boost target processing in the face of distractors. More recently, researchers have begun to consider the role of active distractor suppression, both in visual search and VWM tasks (Carlisle & Woodman, 2011; Feldmann-Wüstefeld & Vogel, 2018; Gaspelin & Luck, 2018a; Sawaki & Luck, 2010). Although on the surface these processes may seem to be two sides of the same coin, there is a distinction to be made between reduced activation of a distractor compared to the target, and *active inhibition* of that distractor. Behavioural and electrophysiological findings support the idea of flexible attentional templates, which can be used to guide attention toward targets or away from distractors depending on the task demands (Arita et al., 2012; Carlisle, 2019; Chang & Egeth, 2019).

The attentional priority map has often been conceptualized as a guide for target selection, and not for distractor inhibition (Fecteau & Munoz, 2006). However, given the findings that attentional control can work like a 'dial' to turn up target processing and to turn down distractor processing, this suggests that the priority map is also likely more flexible than once thought (Carlisle, 2019). However, it's difficult to distinguish between moving attention away from a location and actively suppressing processing in that location from behavioural findings alone (but see, Chang & Egeth, 2019). Although the studies presented here attempted to provide electrophysiological evidence for the flexible attentional control hypothesis, the findings mostly point toward an enhancement-focused model. That is, in the majority of the present studies, I found that item priority had a greater impact on attentional selection (i.e., N2pc) than active distractor suppression (i.e., $P_D$). Additionally, a continuous pattern of activity based on probe likelihood was only observed for target enhancement, and not inhibition (Chapter 4), highlighting the dynamic nature of attentional focusing.

Nonetheless, distractor suppression was observed when participants were explicitly told about an upcoming distractor feature using a negative cue (Chapter 2). Therefore, suppression may only occur when the task demands highlight the need for inhibition. This idea is in accordance with conclusions made by Arita, Carlisle, and Woodman (2012) that negative cues are only used when it is strategically beneficial to use them, such as when the search task is difficult. The results presented here suggest that individuals may use distractor suppression under certain circumstances, but that control is most often employed as a strategic enhancement of target features. Here, I propose that target-related activation has a stronger guiding effect on the feature-based priority map than distractor-related suppression.

### Attentional control and learned versus top-down distractor suppression

Many theories of attention specify that there is an interaction between top-down and bottom-up factors on attentional guidance (Folk et al., 1992; James, 1890; Kastner & Ungerleider, 2000; Posner, 1980). In these theories, top-down control is defined as attention being driven by internal factors, such as an individual's goals, which are unrelated to bottom-up stimulus salience (Awh et al., 2012). In the present dissertation, two of the studies focused on top-down attentional control as manipulated by trial-by-trial priority instructions (i.e., Chapter 2 and Chapter 4, Exp. 2); and in Chapter 3, a consistent feature-based cue was provided at the beginning of the task. These instructions were explicitly stated, informing participants which items were task relevant as well as the items' priority level. These explicit priority manipulations differ from a large area of attention research that focuses on statistical learning through *implicit* probability manipulations of target and distractor locations (Druker & Anderson, 2010; Ferrante et al., 2018; Geng & Behrmann, 2002; Wang & Theeuwes, 2018a). In these past studies, targets were detected faster when presented in high probability locations (Chun & Jiang, 1999), and distractors captured less attention when they consistently appeared in one location (Wang & Theeuwes, 2018a).

The effect of statistical learning on attention is thought to arise from a bias in *selection history*: the prioritization of previously attended to items (Awh et al., 2012). Interestingly, selection history is unrelated to both top-down goals and bottom-up stimuli salience. Therefore, it can be argued that statistical learning is a distinct type of attentional bias. Wang and Theeuwes (2018b) examined the difference between statistical learning (i.e. selection history) and trial-by-trial distractor location cueing (i.e. top-down control). It was found that in contrast to implicit learning, following an explicit location cue, participants did not actively suppress the distractor location. Therefore, statistical learning is capable of changing weights on the priority map, such that the distractor location is suppressed (Wang & Theeuwes, 2018b); whereas this change in weights cannot be accomplished using active, top-down suppression. These findings highlight the importance of considering the separate effects of learned and top-down suppression on the priority map.

Yet, in the attentional capture literature, learned and top-down suppression are sometimes treated as one in the same. For example, when testing the *signal suppression hypothesis* using ERPs, the presence of an early $P_D$ toward the location of the learned distractor is often taken as an indication that suppression can be used to proactively prevent attentional capture (Gaspelin & Luck, 2018a; Sawaki & Luck, 2010). However, it is important to note that this effect is only observed in tasks that involve learned suppression; that is, when individuals are not volitionally using spatial or feature-based pre-cues. Therefore, a distinction must be made between the mechanisms of involuntary and volitional top-down control on distractor suppression (see Gaspelin & Luck, 2018b for a discussion about the definition of 'top-down').

What this early $P_D$ reflects has been contested in the literature. This component (also referred to as the Ppc) may indicate pre-attentive sensory imbalances in the display, or an initial processing of feature discontinuities which marks the locations of potential targets and distractors, used to later guide attention (Fortier-Gauthier et al., 2012; Leblanc et al., 2007; Sawaki & Luck, 2010). Whether this component reflects suppression or sensory-related activity, my findings in Chapter 2 suggest that anxiety has an impact on early visual processing. For example, Shackman and colleagues (2011) found that stress induced by threat of shock increased N1 amplitudes, which are reflective of early visual processing in extrastriate cortex. By increasing vigilance, anxiety likely has a similar effect on these earliest cascades of information processing (Bishop, 2007). Future research is needed to pinpoint the exact underlying process that this early positivity reflects.

In Chapter 2, I found that feature-based pre-cues elicited a late $P_D$; and in Chapters 3 and 4 (Exp. 2) I found no evidence for a $P_D$ at all (only an N2pc). My findings support the idea that (voluntary) top-down attentional control cannot be used for early suppression of a distractor but can be used to stop later attentional processing of the distractor. It must be noted that there are likely differences between spatial and feature-based attention, as there is evidence that these two processes occur at different times and through separate neural mechanisms (Carlisle, 2019; Hillyard & Münte, 1984; Luck & Hillyard, 1994).

Why might there be such a difference between learned and top-down biases on distractor suppression? One possibility is that top-down suppression is difficult, especially when the distractor feature changes on a trial-by-trial basis. Indeed, there is evidence that participants prefer to use positive over negative cues when given the choice (Rajsic et al., 2020), consistent with anecdotal evidence that negative cues are ‘counterintuitive’ (Heuer & Schubö, 2019). Similarly, Wang and Theeuwes (2018b) proposed that participants may have actively tried to use the distractor cue on each trial but were not able to suppress the location. The reason behind this failure in suppression needs to be further examined, as it remains unclear why inhibition may fail and when individuals, consciously or subconsciously, give up on an active suppression strategy. Overall, my findings agree with the idea that top-down suppression given negative cues is difficult, as despite the presence of a late $P_D$ in Chapter 2, there was no behavioural benefit following a negative cue. Additionally, in Chapter 4 (Exp. 2) when items were cued as 0% likely to be probed (i.e., a negative cue), the absence of a $P_D$ could indicate that participants did not adopt an active suppression strategy at all. Finally, the existence of individual differences in inhibitory abilities suggests variability in the perceived usefulness of top-down suppression.

## Individual differences in attentional control abilities

Since the introduction of Eysenck and colleague's (2007) Attentional Control Theory (ACT) of anxiety, there has been a surge of research on inhibitory control in individuals with anxiety. The ACT proposes that anxious individuals have deficits in processing *efficiency*, which encompasses both the ability to use top-down control to guide attention, and the extent to which bottom-up salience drives attentional capture (an extension of processing efficiency theory: Eysenck & Calvo, 1992). Yet, it has been found that individuals with anxiety do not perform any less *effectively* than their less anxious counterparts; maintaining behavioural accuracy on a wide variety of tasks (Berggren & Derakshan, 2013). This suggests that anxious individuals have developed compensatory strategies to overcome inefficient attentional processing (Ansari & Derakshan, 2011; Eysenck & Derakshan, 2011). The findings from the present thesis are in agreement with this tenet of the ACT, as I found no correlation between anxiety scores and behavioural outcomes (i.e., RT and accuracy). This pattern held true for both neutral (Chapter 2) and threat-related stimuli (Chapter 3), suggesting that the compensatory strategy is relatively robust regardless of the task demands or stimulus emotion. However, these findings do not elucidate the underlying mechanism(s) of this strategy. Perhaps this mechanism is linked to activity in the mid-cingulate cortex, as there is evidence that mid-frontal theta oscillations are related to cognitive control processes, especially in individuals with anxiety (Cavanagh & Frank, 2014; Cavanagh & Shackman, 2015). Therefore, future work using self-report or electrophysiological measures (such as oscillatory power) is needed to better understand the different strategies used by individuals with anxiety to maintain performance at the same level as less anxious individuals.

Here, despite having no discernible impact on behavioural performance, anxiety scores did correlate with ERP measures of attentional control. That is, greater anxiety predicted more attentional capture by distractors, as indicated by the N2pc. The present findings support the idea that anxiety causes impairments in proactive distractor suppression. This interpretation would lead to the conclusion that individuals with anxiety have an overall deficit in top-down control, as indicated by activity in the anterior cingulate cortex (ACC) and lateral pre-frontal cortex (lPFC; Basten et al., 2011; Bishop, 2009; Bishop et al., 2004), or by decreased functional connectivity in fronto-parietal networks (Sylvester et al., 2012). However, it is also possible that the present findings reflect an over-active attentional orienting system in anxiety, driven by biases in bottom-up salience (Eysenck et al., 2007). This is usually observed with attentional biases toward threat, as indicated by increased reactivity in the amygdala (Stout et al., 2017). Yet, it could be said that a stimulus-driven attentional bias still reflects a failure in attentional control, as there was a failure to proactively prevent capture. Therefore, the present findings support the idea of general attentional control deficits in individuals with anxiety, which is specific to inhibition of distractors.

Although it has been widely established that individuals with anxiety have decreased attentional control, less research has been conducted to understand why this deficit exists. One possibility is that worry about potential threat and task failure pre-occupies working memory resources, which are essential for processing task demands (Eysenck et al., 2007; Sari et al., 2017, but see, Moser et al., 2012). This hypothesis could account for the observed attentional deficits in the presence of both threat-related *and* neutral distractors, as although neutral distractors are not objectively threatening, they could be perceived as a threat to task performance. Indeed, there is evidence that for individuals with high anxiety, working memory training decreases neutral distractor interference (Sari et al., 2016).

In the ACT of anxiety (Eysenck et al., 2007), worry is proposed to have a large effect on the central executive, as defined by Baddeley's model of working memory (1992, 2002), which can be described as the command center of attentional control. The present findings, however, cannot speak directly to the impact of worry on deficits in flexible attentional control, and further research is needed to support this mechanism of failures in control. Self-report measures of worry could be compared to electrophysiological measures of working memory storage (i.e. CDA) and search preparedness (e.g. pre-trial theta or alpha) to determine the impact of worry on attention (for an example of EEG measures of fluctuations in attentional control, see Adam et al., 2015, 2018).

## Flexibility in visual working memory filtering

There is a close link between attention (whether selective or sustained) and memory (Chun & Turk-Browne, 2007; deBettencourt et al., 2017; Hasher & Zacks, 1988). Specifically, it has been shown that top-down attentional control predicts what is subsequently remembered or forgotten (Turk-Browne et al., 2013). In the VWM literature, the ability to prevent distractors from being stored in memory is referred to as *filtering efficiency* (Awh & Vogel, 2008; Cowan & Morey, 2006). VWM filtering has traditionally been conceptualized as an all-or-none process, contrary to recent behavioural findings that attentional control can be used to flexibly allocate memory resources (Dube et al., 2017; Emrich et al., 2017). Activity related to filtering has been observed in the basal ganglia and pre-frontal cortex (Liesefeld et al., 2014; McNab & Klingberg, 2008), similar to the proposed origins of top-down attentional control (Miller & Cohen, 2001; van Schouwenburg et al., 2015).

Given the similarities between VWM filtering and attentional control activity, neural markers of flexible attentional control may predict measures of VWM storage (Emrich & Busseri, 2015). Here, it was found that attentional control could be used to continuously modulate attentional enhancement of task-relevant items (Chapter 4). This effect carried over to VWM maintenance, as reflected by the relationship between probe likelihood and CDA amplitudes. These results support a model of continuous flexibility in attentional control, which extends to the allocation of VWM resources (Dube et al., 2017; Emrich et al., 2017). However, once again this effect was only observed for target selection, with no evidence for continuous modulations of suppression. In fact, contrary to predictions, there was no $P_D$ present in Chapters 3 and 4, despite the presence of task-irrelevant items. This finding is in direct opposition to findings from Feldmann-Wüstefeld and Vogel (2019), who found that $P_D$ amplitude scaled with the number of distractors in a filtering task and correlated with VWM capacity. This discrepancy could be due to differences in task design, as in Feldmann-Wüstefeld and Vogel (2019), targets and distractors were consistently defined by one shape throughout the task. In contrast, here I used trial-by-trial pre-cues. This difference in task design echoes the previous discussion of statistical learning versus top-down control, demonstrating that individuals do not generally use proactive suppression to distribute VWM resources on a trial-by-trial basis. Yet, it remains an open question whether *implicit* statistical learning affects suppression and VWM filtering in a continuous manner.

Similarly, the findings from Chapter 3 provide support for a model of top-down control in the presence of threat-related stimuli. Overall, there were larger N2pc and CDA amplitudes toward targets than distractors, suggesting that participants were appropriately using the feature-based instructions to orient their attention. However, there were overall greater N2pc and CDA amplitudes for threat-related compared to neutral distractors. In terms of the attentional priority map, this finding indicates that perceived threat is up-weighted, regardless of its task relevance. Additionally, although greater anxiety scores correlated with larger distractor-elicited N2pc amplitudes, anxiety did not correlate with memory storage of distractors. This result provides an example wherein despite deficits in attentional control, memory filtering remained intact. Taken together, the VWM findings from the present thesis suggest that filtering is not a strictly all-or-none process. Instead, it is proposed that although filtering can be flexible and continuous in nature, there are individual differences in this ability, which depend on the task demands and emotional nature of the stimuli.

## A time-dependent model of external and internal influences on attentional control

Attentional mechanisms require time to effectively guide behaviour (Weaver et al., 2017). When not enough time is provided to select and/or suppress an item, attention becomes driven by the stimulus itself, such has been proposed in the *temporal dependency* theory about the link between covert attention and saccades (van Zoest et al., 2004, 2017). In the present thesis, overt eye movements were controlled for, but the importance of time on the development of covert selection and suppression mechanisms is still interesting to consider. One must balance the impact of top-down goals against bottom-up stimuli salience, and the ability to do so may be dependent on the amount of time available to deploy these mechanisms (similar to, Hickey et al., 2010). The balance between top-down and bottom-up control over attention can also be swayed by internal biases, such as anxious individuals' selection of threat-related and salient distracting stimuli. Whether external or internal factors have a greater pull on attention likely depends on the available stimulus processing time. Here, I propose a model of the temporal nature of selection and suppression when both external cues and internal biases are considered in the competition for cognitive resources.

Processing speed is often intuited from behavioural response times. For example, Hickey and colleagues (2010) found that when participants responded slowly, they had a fast distractor-elicited N2pc, followed by the target N2pc. The authors concluded that quick attentional selection is driven by bottom-up stimulus salience, whereas goal-related selection develops over time. Although the present thesis did not focus on an analysis of RTs, I did observe a temporal separation of selection and suppression across studies. This time course of attentional processes is affected by external factors, such as the pre-cues used in the present thesis. When observers were provided with an external trial-by-trial pre-cue, such as in Chapters 2 and 4, attentional selection and enhancement of the target item(s) was early. This was especially true when the cue was positive in nature (Chapter 2), providing information about an upcoming target feature. However, when the external cue contained information about an upcoming distractor, there was no evidence of early target enhancement, accompanied by a lack of behavioural cueing benefit. Similarly, in Chapter 4 selection was early following a continuous positive pre-cue. Together, these findings suggest that target selection is quick and effective following target pre-cues, supporting fast attentional enhancement driven by external cues.

In contrast to target selection, distractor suppression is a slower process following external cues. Supporting this, in Chapter 2, although there was evidence of a $P_D$, it was later overall than the N2pc. Yet, in Chapters 3 and 4, there was no evidence of active distractor suppression at all. One main difference between these studies is stimulus presentation time; such that the search screen was presented for a longer period of time in Chapter 2 (up to 2,000 ms) than in the studies presented in Chapters 3 and 4 (100 – 200 ms). If stimulus presentation time is underlying this difference between studies, then it suggests that active distractor suppression following external cues takes time. For example, inhibition of return to a cued target takes approximately 225 ms to develop (Klein, 2000). Additionally, Zhang, Gaspelin, and Carlisle (2020) found that negative cue RT benefits increase with the amount of processing time provided, with maximal effect at

400 ms. Therefore, it may be that when sufficient time is not provided, proactive suppression is not used. However, this hypothesis was not directly tested in the present thesis, and therefore future studies could manipulate stimuli presentation time to determine the amount of time needed to use attentional suppression mechanisms.

The speed of selection and suppression are also affected by factors internal to the observer, such as the individual differences in anxiety described in the present thesis. This is particularly true when it comes to distracting items, such that salient distractors are selected earlier for individuals with higher levels of anxiety. In contrast, it was found that individuals with lower levels of anxiety were able to avoid capture and proactively suppress distractors; regardless of the amount of time they were provided to process the stimuli. Yet, when provided with extra time (such as in Chapter 2), anxious individuals were capable of suppressing the distractor, as indicated by a late $P_D$ following the N2pc. Therefore, whether attentional selection or suppression of distractors is quick depends in part on internal biases, suggesting the importance of considering individual differences on the timing of attentional control-related processes. Future research could more precisely measure the time course of individual differences in selection and suppression by probing attention throughout the trial, such as in the rapid serial probe presentation paradigm (Grubert & Eimer, 2020). In this paradigm, task-irrelevant probes are presented every 200 ms for a period of 1,400 ms before search array onset. N2pc amplitudes toward the probe indicate that a search template is active, providing information about the time course of attentional preparation for search.

A time-dependent model of flexible attentional selection and suppression must take into account both external cues and internal factors, such as individual differences in attentional biases. Selection of task-relevant information is quick when provided with external cues, whereas suppression of distractors takes more time. Individual differences in attentional control abilities also affect the timing of suppression, such that less anxious individuals can quickly and proactively suppress distractors, whereas more anxious individuals can only inhibit distractors following attentional capture.

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