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Minor Thesis

**Visual Working Memory Content: Guiding or Misleading  
Attention?**

A behavioral and pupillometry study

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## Abstract

Representations in Visual Working Memory (VWM) are thought to guide visual attention – a phenomenon known as *memory-driven attentional capture*. Whether attention is automatically biased towards (distractor) objects that match the VWM content is yet unclear. Our main objective was to test whether attentional capture is memory-driven, and how this interaction is modulated by 1) the match/nonmatch of distractors with the VWM content and 2) the storage format of visual information – continuous (detailed, sensory representations)/categorical. In addition, we aimed to replicate evidence that pupils are larger while maintaining continuous information in VWM due to being more effortful. In doing so, we collected independent measures of behavior (reaction times) and pupil size in two studies. Results from the behavioral study showed no evidence that attention gets *automatically* captured by memory-matching distractors; rather, the VWM content was used *strategically* to benefit target selection in visual search. In the pupil study, memory-matching probes drove a stronger visual response than non-matching probes, yet the initial stronger constriction made it unclear whether attention got captured later. The storage format did not modulate the memory-driven capture effect, yet it strongly affected the visual response during maintenance: The pupils were smaller (instead of larger as predicted) while maintaining information in continuous representations, likely reflecting a sensory response, than mental effort. Despite focusing on different aspects of VWM – attentional capture and mental effort – our results depict essentially the same thing: Vision is dynamically shaped in a both stimulus-driven and goal-directed manner, via interactions between bottom-up and top-down processes - that are likely mediated by executive functions to serve behavior.

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## 1. INTRODUCTION

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Humans heavily rely on working memory on a daily basis for reasoning and decision-making. Also known as “short-term memory”, this capacity-limited storage system acts like a temporary workspace where information that is relevant for a current task is actively processed for brief periods of time (in the order of seconds). For example, every time we are looking for something, we keep an active representation of that object in visual working memory (VWM) to guide attention and action accordingly. Although it is widely assumed that attention aids working memory by selecting which information to *encode* (Oberauer, 2019; Posner & Boies, 1971; Schmidt, Vogel, Woodman, & Luck, 2002;), other studies suggest the reverse is also true – specifically, information we keep in VWM guides attention by selecting what we *attend* to (Desimone & Duncan, 1995; Olivers, Meijer, & Theeuwes, 2006; Zhou, Lorist, & Mathôt, 2020).

A long-standing dilemma in the field of visual perception is whether attention is automatically captured by any object in the environment that matches the memory content, despite it being relevant or not for our current goal. According to the *biased competition model* of Desimone and Duncan (1995), objects that match a representation in VWM have an automatic advantage in the competition for attention. In visual search, features of a (previously attended) target object get preactivated through the memory representation (Chelazzi et al., 1993), hence making the target *stand out* and easier to find. This feature-based mechanism of visual selection (Olivers, Meijer, & Theeuwes, 2006) implies that attention is drawn to objects in the environment that share similar physical traits with an item from VWM. This is particularly beneficial if you were, for example, to look for a redshirt among dark clothes: The redness of the shirt pops out and immediately captures attention. However, looking for the red shirt in a pile of other red-colored clothes becomes harder since attention gets likely (mis)guided to color-matching distractors (Zhou, Lorist, & Mathôt, 2020), thus hindering the search.

The above-described phenomenon is known as (automatic feature-based) *memory-driven attentional capture* (Olivers, Meijer, & Theeuwes, 2006), and it plays a crucial role in visual search and - as we will discuss later - in vision altogether.

### *Memory-driven attentional capture*

#### **Behavioral approach**

As in early theories on automatic capture (Desimone & Duncan, 1995), recent evidence (Olivers, Meijer, & Theeuwes, 2006; Zhou, Lorient, & Mathôt, 2020) shows that observers are faster to find a target object if it matches the VWM content (i.e., they share the same features, such as color), but slower when distractors also match the item in VWM.

One of the main paradigms to study attentional capture by memory content is a combination of memory-search tasks. Zhou and colleagues (2020) had participants memorize two colors prior to a visual-search task (VST), in which either the target or a distractor could match the colors held in VWM. They found robust evidence of memory-driven attentional capture as shown by differences in response times (RTs) at the VST: Participants were faster to find the target when it matched a memory color, as compared to when a distractor matched a memory color. This shows - at least at the behavioral level - that attention is automatically drawn onto memory-matching objects, thus facilitating search when the target matches the memory content and interfering with search when a distractor matches the memory content.

Following the same dual-task paradigm, Dowd and colleagues (2017) took the behavioral evidence further with computational techniques. They assumed that if VWM and attention are indeed strongly connected, we should be able to predict what someone is holding in VWM based on what they attend to. Using multivariate pattern analyses, they trained classifiers to decode the contents of VWM based on reaction times in a memory-search task: The RTs were faster for memory-matching targets and slower for memory-matching distractors in their experiment. They replicated memory-driven capture effects and successfully predicted the memory content by reaction times. Exceptionally, the classifiers decoded VWM content even across different groups of individuals than that they were trained on, highlighting the generalizability of the phenomenon as independent of individual differences.

The biased competition theory (Desimone & Duncan, 1995) was also supported by evidence from single-cell recordings in macaques. In one of their experiments, Chelazzi and colleagues (1993) presented the animals with a (target) picture to remember. After a delay interval, they were shown multiple pictures and had to choose the target by an eye movement. They found that the (target) picture elicited neural activity that persisted during the delay interval, suggesting that representations are kept in VWM through sustained firing activity of neurons (Curtis & D'Esposito, 2003). When the search display appeared in their experiment, the neurons

that responded to the memory item (target picture) were already in a more active state, showing how features of a previously attended object get preactivated at the neural level via the mental representation of that object (Gayet, et al., Visual Working Memory Enhances the Neural Response to Matching Visual Input, 2017).

Other studies, however, failed to support a memory-driven guidance effect (Downing & Dodds, 2004), despite using similar procedures. Some even found the opposite effect. Woodman and Luck (2007) predicted that (distractor) objects matching the items in VWM automatically capture attention in a visual search task. Specifically, when the memorized item would appear as a distractor, participants will be slower to find the target, as expressed by reaction time. Contrary to their expectations, they found no increase in RTs in the VST when distractors matched the VWM content. Strikingly - they even found a decrease in some conditions, suggesting that participants strategically avoided attending to memory-matching distractors. They concluded that the VWM content does not bias attention towards any matching object but instead can be used to inhibit (matching) distractors that compete for attention.

Counterevidence for automatic attentional capture comes from electrophysiology studies as well. Using event-related potentials (ERPs), Sawaki and Luck (2011) presented participants with task-irrelevant probes that could either match or not a color they kept in VWM. They found that the matching probes elicited an ERP component indicator of inhibition (the Pd), suggesting that (irrelevant) visual information that matches the memory content is automatically detected, yet immediately overridden by top-down suppression to prevent attentional capture.

Despite strong evidence for an *automatic* capture effect (Desimone & Duncan, 1995; Dowd, Pearson, & Egner, 2017; Kiyonaga, Egner, & Soto, 2012; Olivers, Meijer, & Theeuwes, 2006; Zhou, Lorist, & Mathôt, 2020), the findings of Woodman, Sawaki, and Luck (2007, 2011) suggest that representations in VWM work *flexibly* on attention: first, by guiding attention to the target, and second, by suppressing matching distractors. In such a case, representations in VWM would always benefit search through distinct mechanisms that activate based on the situation.

In summary, we are left with contradicting evidence on attentional capture. This points to the fact that visual attention and VWM are intimately related in ways that we do not fully understand; and for which additional measures are necessary to complement the behavioral data.

For example, with cognitive pupillometry (Mathôt & Vilotijević, 2022) we might be able to see how attention is affected by VWM from the moment visual input is detected.

### **Pupillometry approach**

One of the reasons why we visually attend to certain objects at the expense of others has to do with *saliency* i.e., what makes an object stand out in the visual field. Or, more relevant for the current study - what *catches the eye*. Generally, attention is grabbed by objects that contrast with the environment: either in terms of physical traits (saliency) or relevance (a searched-for object). When it comes to interactions between attention and VWM, it has been long assumed that the memory representation of an item makes matching objects stand out and gain attention over competing objects (Desimone & Duncan, 1995; Olivers, Meijer, & Theeuwes, 2006; Zhou, Lorient, & Mathôt, 2020), despite their relevance for a current goal. This has been repeatedly observed in visual search experiments where a target object should be found among distractors, as discussed in the earlier section.

Another promising tool for studying VWM and attention is pupillometry: taking measures of the size of the pupils. One of the great advantages of (cognitive) pupillometry is that it allows us to track changes in pupil size in a timely-sensitive manner (across the full pupil response to a stimulus) - from the earliest phase when visual input is detected, until later when cognitive processes come into play. Pupillometry has various applications in the study of cognition, but here we focus on only two of them. First, Kahneman and Beatty (1966) showed that the pupils increase in size with the number of items being held in WM. Here, pupil diameter was used as a measure of mental effort, a technique that I will describe later in this section. Second, pupillometry was only more recently used to investigate interactions between VWM and attention. Two studies in particular have used pupil constriction as a proxy for memory-driven attentional capture, as described below.

First, Olmos-Solis and colleagues (2018) tested whether the pupil response can be used to differentiate stimuli that match the VWM content from stimuli that do not match the content. In doing so, they followed a similar approach to the combined memory-search paradigm: Observers had to remember a color to be searched for in a subsequent visual search task. During the retention interval, they briefly presented task-irrelevant probes that could be the same, or a different color than the memory item. They found that the memory-matching probes elicited a

more prolonged pupil constriction than the non-matching probes, as expressed by the slower recovery of the pupil to the baseline. Although there was no difference in the initial pupil constriction, the prolonged constriction suggests that attention was *dwelling* on the memory-matching probes, perhaps reflecting capture effects that occur in the later stages of visual processing.

To replicate and extend the results of Olmos-Solis et al. (2018), Wilschut & Mathôt (2022) used the same paradigm, yet with a crucial difference. Instead of match versus non-match, they compared matching with ‘slightly mismatching’, or ‘completely mismatching’ probes. In the slight-mismatch condition, the match and non-match probes were relatively close to each other on a HSV (hue-saturation-value) color circle (e.g., if the memory color was green, the non-match color was yellow); this was comparable to the ‘non-match’ condition in Olmos-Solis et al.’s study (2018). Conversely, in the complete-mismatch condition, the colors were opposite on the color circle (180° apart, e.g., if the memory color was green, the non-match color was purple). They replicated the results of Olmos-Solis et al., but only in the slight-mismatch condition: The pupil constriction was indeed prolonged to memory-matching probes when compared to non-matching probes that were not far away on the color circle. However, when they contrasted matching probes with maximally different probes (‘completely mismatching’), the results changed: The initial pupil constriction was strongest for the non-matching probes, effect that dissipated later in time. They concluded that visual adaptation may have affected saliency in the complete-mismatch condition, in that vision had already adapted to the previously attended item, thus perceiving new stimuli as more salient (and triggering a stronger initial constriction). This early pupil response may have subsequently prevented capture effects from being measurable later in time.

The results of Wilschut & Mathôt (2022) extend the findings of Olmos-Solis et al. (2018) by revealing not only capture effects by memory content, but also how saliency is modulated at different levels of visual processing. First, a sensory level, where saliency is *determined* by low-level features of a stimulus (like novelty), hence the initial pupil constriction to (completely) mismatching probes in their study. On the other hand, a later, higher level, where top-down control from VWM *enhances* saliency through recognition of an object from memory; hence, the prolonged pupil constriction to memory-matching stimuli. Although conceptually sensation and



cognition are distinct processes, the findings of Wilschut & Mathôt show that vision is dynamically shaped by changes in pupil size that are sensitive to both sensory input and higher cognition. Digging into the intricacies of visual perception is far beyond the scope of this paper; however, it is relevant to consider how saliency is affected at the earliest stage of visual processing, which is crucial for perception and attentional selection. To rule out adaptation problems and clearly identify capture effects, we use in our study non-matching probes analogous to the ‘slightly mismatching’ probes in Wilschut & Mathôt’s study (i.e., sampled from adjacent categories to the memory color; 2022).

Another way in which pupillometry has been used to study (a different aspect of) working memory dates back in the 60s. Kahneman and Beatty (1966) demonstrated that the pupils enlarge with the number of items maintained in WM, suggesting that pupils dilate in response to mental effort. One of the latest findings in this direction come from Zhou et al., 2021. They showed that mental effort indeed leads to larger pupils, yet in a slightly different approach than previously done. Instead of merely increasing the memory load, they tested whether the formatting style of information in VWM - in continuous/categorical representations - affects pupil size by means of mental effort; assuming that storing items in continuous, detailed representations (remembering fine-tuned features of an object) is more effortful and leads to larger pupils, than storing them in discrete representations (remembering an object by the category it belongs to).

To do so, they experimentally defined seven color prototypes (to correspond to categorical representations, e.g., the red color), with ambiguous colors standing at the boundary between adjacent colors (to correspond to continuous representations, e.g., red-orange). Then, they had participants remember one-to-four colors randomly drawn from the list of pre-defined hue values, that would be either prototypical or ambiguous; during the retention interval, they measured the pupil size in each condition. The assumption was that it is more effortful to remember ambiguous, than prototypical colors, since it takes more resources to remember objects in high resolution, than in less detail (categories). Indeed, the pupils were larger while maintaining ambiguous, as compared to prototypical colors, likely due to mental effort in the former.

Our study is therefore threefold. First, we build on the findings of Zhou (2020), Wilschut (2022) and colleagues, to study memory-driven attentional capture by means of reaction time and

pupil constriction. We use a two-step approach and combine independent measures of behavior and pupil size, as explained in the *Methods* section. Second, we aim to replicate the results of Zhou et al. (2021) that pupils dilate more when storing information in continuous, than categorical representations in VWM. We use the pre-defined prototypical and ambiguous colors in their study.

Additionally, we want to see whether the storage format of information in VWM also modulates the memory-driven capture effect, via different brain areas involved in VWM maintenance. For example, continuous information is stored in rich, detailed representations, which are thought to recruit sensory areas (Harrison & Tong, 2009; Yörük, Santacrose, & Tamber-Rosenau, 2020). On the other hand, categorical representations rely on more abstract operations, like categorization and learning, which would recruit the prefrontal cortex (Freedman, Riesenhuber, Poggio, & Miller, 2002; Wang, et al., 2018). In consequence, continuous representations would drive a stronger capture effect; since (previously attended) objects are already stored more ‘vividly’ in sensory formats, rather than ‘labelled’ in categories at the abstract level.

## 1.1 Objectives

After decades of research on working memory and attention, the question of whether attention is guided by the contents of VWM remains. Even more intriguing is whether different styles of maintenance in VWM affect how we respond to visual stimuli. Studies so far have focused on categorization as a way to reduce mental effort (Zhou, Lorist, & Mathôt, 2021), or on the neurophysiology of visual category-learning (Minamimoto, Saunders, & Richmond, 2010); yet no prior study investigated the effect of storage format on attention.

As such, our main objective is to test whether attentional capture is memory-driven, and how this interaction is modulated by 1) the match/nonmatch of distractors with the VWM content and 2) the storage format of visual information. We use previously defined color categories from Zhou et al.’s study (2020) to correspond to either categorical (e.g., a prototypical shade of blue), or continuous representations (e.g., an ambiguous shade of blue at the boundary between blue and green). We combine independent measures of behavior and pupil size to study attentional capture in reaction time (Zhou, Lorist, & Mathôt, 2020) and pupil constriction respectively (Wilschut & Mathôt, 2022).

Second, we aim to replicate the findings of Zhou et al. (2021) that pupils dilate more when maintaining ambiguous, as compared to prototypical, colors in VWM.

By this, we hope to strengthen previous evidence for memory-driven attentional capture, and ultimately improve our understanding of how vision is shaped by interactions between cognition and sensation.

## 1.2 Hypotheses

- RTs are slower when a distractor matches the VWM content, with a stronger effect for ambiguous colors.
- Pupils constrict for longer to matching, compared to nonmatching probes, with a stronger effect for ambiguous colors.
- Pupils dilate more when holding ambiguous, compared to prototypical, colors in VWM.

## 2. METHODS

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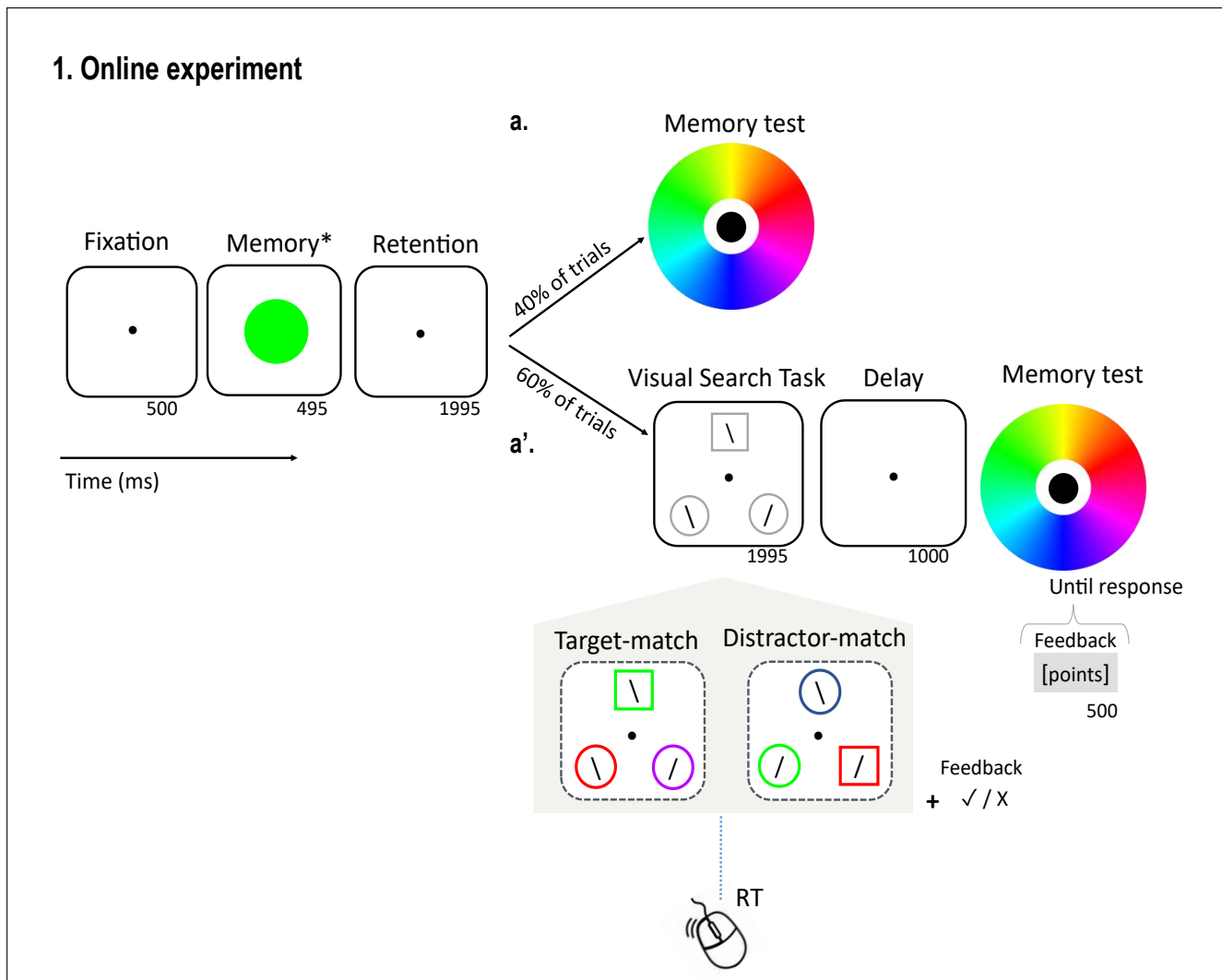
To replicate capture effects in behavior and pupil size we conducted two experiments: first, a behavioral online experiment, and second, a pupillometry experiment in the lab of Heymans Institute, Groningen. The study protocol was approved by the Ethics Committee of the University of Groningen (approval code: PSY-2122-S-0189). First-year students from the University of Groningen volunteered to participate in exchange for course credits, with the condition that all participants have normal or corrected-to-normal vision, normal color perception, and no epilepsy. Both experiments were designed in OpenSesame (version 3.3; Mathôt, Schreij, & Theeuwes, 2012). Methods and results for each experiment are described in turn.

### 2.1 Behavioral study

To test our first hypothesis and identify capture effects in behavior, we conducted an online experiment comprised of a memory-search task (see **Figure A**). Essentially, participants always had to remember a color for later reproduction; sometimes, they would get a visual search task during the retention interval, in which either the target, or a distractor, could match the color being kept in VWM. We measured the RTs in the VST to compare how fast participants respond

when the target versus when a distractor matches the memory color; with the assumption that they are slower when a distractor matches the VWM content, especially for ambiguous colors. **Figure A** illustrates a brief representation of the sequence of trials and conditions in the first experiment.

To foresee the results, we found a strong effect of Target/Distractor-Match on search times, but opposite than expected: Participants were faster to find the target in the VST when a distractor, instead of when the target, matched the memory color, as expressed by decreased RTs in the former. Contrary to our expectation, we found no interaction with Color type, suggesting that the storage format (as represented here) did not affect search time in our first experiment. However, Color Type did affect accuracy in the VST, as well as performance at the memory test, such that participants made overall more errors when responding to ambiguous, than to prototypical colors.



**Figure A.** Sequence of trials in the online experiment. Participants were presented a colored circle for later reproduction. On 40% of the trials, the memory test followed the retention interval (*Memory trials*; 1a). On 60% of the trials, participants got a VST followed by a delay and the memory test (*Search trials*; 1a'). In the VST, participants had to look for the target among distractors (i.e., the unique shape; here, the square among circles) and report the orientation of the line inside it by a mouse click. Feedback was given immediately for the VST (correct/incorrect), and at the end of each block for the memory test (cumulated points within block).

### ***Participants***

Sixty-three first-year students from the University of Groningen participated in exchange for course credits. Written informed consent was given before the start of the experiment. Participants were provided with step-by-step instructions for the task, followed by a short practice block. After excluding 21 participants who scored at chance level on the visual search task, we kept for further analysis 41.

### ***Stimuli, design, and measures***

The experiment comprised one practice block and six experimental blocks with a total of 180 trials, 72 *Memory trials* and 108 *Search trials*; The total duration was roughly 25 minutes.

Each trial started with a 500ms fixation point, followed by a 495ms memory display where a colored circle was presented centrally; the colors were randomly drawn from a 360° HSV color circle, with 7 prototypical colors (red, pink, purple, blue, green, yellow, and orange) and 7 ambiguous colors (at the boundary between color categories; Zhou et al., 2021). Participants were instructed to remember the exact shade of the memory color as they can gain (feedback) points at the end of each block. (This allowed us to encourage VWM maintenance in different formats, while keeping the participants motivated throughout the experiment.) On 40% of the trials, the memory test appeared after a 1995ms retention interval (the *Memory trials*). Here, participants had to indicate the color they saw in the beginning on an HSV color wheel which was randomly rotated trial-by-trial.

On 60% of trials, they got a VST after the retention interval (the *Search trials*), followed by the memory test. In the search display, three colored shapes appeared for 1995ms, each containing a Gabor patch with different orientations (tilted to the left or to the right). Participants had to find the target among distractors (i.e., the unique shape; this was either a circle among

squares, or a square among circles, randomly mixed between trials) and report the orientation of the lines inside it as fast and accurately as possible (left or right mouse click). After response, participants were given immediate feedback displayed for 500ms as a check mark for correct, and a cross for incorrect.

The first manipulation was that either the target, or a distractor, could match the color from VWM; second, the colors would be either ambiguous, or prototypical. Although studies on color perception show that attentional capture can occur even when visual stimuli only resemble, but are not identical, with a color from VWM (e.g., different shades of red), in our experiment the matching colors were always the exact same hue value as the memory color. Moreover, to avoid visual adaptation problems (Wilschut & Mathôt, 2022), the non-matching colors in our study were always 50° away from the memory color in HSV color space: If the memory color was prototypical, the non-match color would always be prototypical, sampled from one of the adjacent categories. (Same for ambiguous colors.)

To summarize, we had a two-by-two factorial design with Match (of Target/Distractor) and Color type (Ambiguous/Prototypical) as factors with two levels, and reaction time as outcome variable.

### ***Data processing and analysis***

All data were processed and analyzed in Python 3.9. First, we excluded the practice block and checked the experimental data individually for each participant. This resulted in removing 22 participants who scored at chance level in the VST, remaining with 41 participants and a total of 7380 observations.

Our first prediction was that participants are slower to find the target in the VST when a distractor matches the memory color, with a stronger effect for ambiguous colors. We performed a two-way repeated measures ANOVA (RM-ANOVA) on *Search trials* to analyze the effect of Match: Target/Distractor, and Color type: Ambiguous/Prototypical, on RTs, as well as interactions between factors. In short, we found a strong effect of Match on RTs, but no interaction between factors.

Then, although not in our main interest, we also looked at performance at the memory test as a function of Color Type, since previous studies reported a strong effect of categories on

memory accuracy (Zhou, Lorist, & Mathôt, 2020). In doing so, we calculated the response error for each color type by taking the distance between the memory hue (that was presented) and the response hue (that was reproduced) on the color wheel. Here, we found a large effect of Color Type on memory performance.

Next, we used the biased-memory toolbox (Zhou et al., 2021) to fit the mixture model to the distribution of response error by two parameters: Precision and Guess Rate. To test the effect of Color Type on precision and guess rates, we ran two RM-ANOVAs using the JASP software, with Color Type as factor and Precision and Guess Rate as dependent variables in turn.

### ***Results and discussion***

Analyses revealed a strong effect of Match on search times ( $F=9.121$ ,  $p<.01$ ; **Fig B. a**), yet opposite than expected: The RTs were slightly faster when one of the distractors matched the memory color, and slower when the target matched the memory color. Unlike predicted, Color Type did not affect RTs, nor interact with the factor; however, it did affect accuracy, such that participants were more accurate at reporting the line-orientation when the target matched the memory color, especially when the color was prototypical (**Fig B. b**). Although not significant here, this is in line with previous findings (Zhou, Lorist, & Mathôt, 2020) that search accuracy is higher when the target, compared to when a distractor, matches the VWM content.

Finally, we found that the overall performance at the memory test was greatly affected by Color Type ( $F=27.735$ ,  $p<.0001$ ; **Fig B. c**), with higher guess rates ( $F=5.333$ ,  $p<.05$ ) and lower precision ( $F=6.195$ ,  $p>.01$ ) for ambiguous, compared to prototypical colors. Although Color type did not affect behavior in the VST, it did predict performance at the memory test, such that participants performed better when they had to reproduce prototypical, than ambiguous colors.

Our results from the VST are surprising, yet potentially insightful. In summary, we found that participants were faster at finding the target when distractors matched the memory color. This is against our hypothesis and previous evidence showing that the presence of memory-matching distractors interferes with search and results in longer search times when a target object has to be found (Olivers, Meijer, & Theeuwes, 2006; Zhou, Lorist, & Mathôt, 2020); in our experiment, however, this was not true. Instead, our results are closer to those of Woodman &

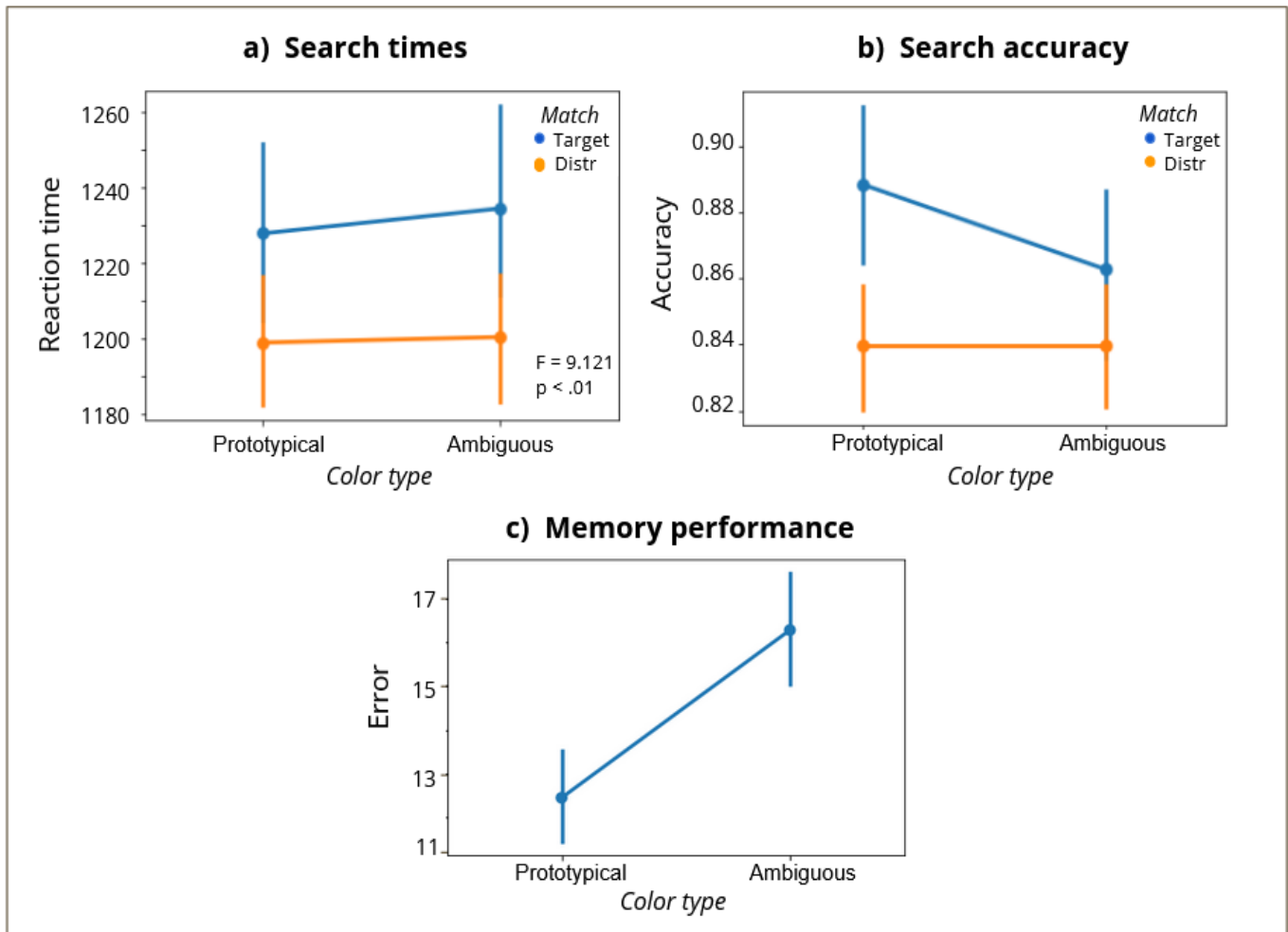
Luck (2007), who found that search was optimized when distractors, compared to when the target, matched the VWM content.

Although unexpected, the behavioral effect in our study is relevant in at least two ways. First, it supports an alternative view on how representations in VWM modulate visual selection - via *flexible* (rather than *automatic*; Desimone & Duncan, 1995; Olivers, Meijer, & Theeuwes, 2006) top-down mechanisms used strategically to either enhance (in the case of matching target), or inhibit (in the case of matching distractors; Sawaki & Luck, 2011; Woodman & Luck, 2007) the saliency of visual information such that attention is deployed to benefit behavior.

Second, it reveals a phenomenon that has been extensively studied in the context of both visual attention and experimental designs: Statistical regularities across trials in visual search can bias attentional selection (Li & Theeuwes, 2020). In our case, such regularities are present in the regularity of matching distractors: The search display always contained one target shape among two distractor shapes, hence a distractor-match would occur on 2/3 of times. Although the shape of target/distractor was randomly mixed between trials to avoid learning of distractor co-occurrence (Thorat, Quek, & Peelen, 2022), the regularity of matching distractors was always constant. As such, participants may have learned and used that information to optimize search. This may explain the reversed effect in our study compared to that of Zhou et al., where the match of target/distractor occurred equally often across trials.

Altogether, our results suggest that 1) representations in VWM are used strategically to control the deployment of attention in a task-specific way, and 2) observers can learn to extract regularities in the search display for a more efficient target selection. In real world, this seems like a viable mechanism for visual selection since such regularities are seen everywhere in natural environments, and cognition has likely evolved accordingly.





**Figure B** Depiction of results from the behavioral study. **Figure a)** illustrates the measured RTs at the VST (*Search trials*) by two factors: Match (of Target/Distractor with the memory color), and Color type (Ambiguous/Prototypical); **Figure b)** shows the Accuracy for the same factorial model. **Figure c)** shows the performance at the memory test (*Memory trials*) for Prototypical/Ambiguous colors, measured in the absolute error: the circular distance between the memory hue (that was presented) and the response hue (that was reported) on a 360° HSV wheel.

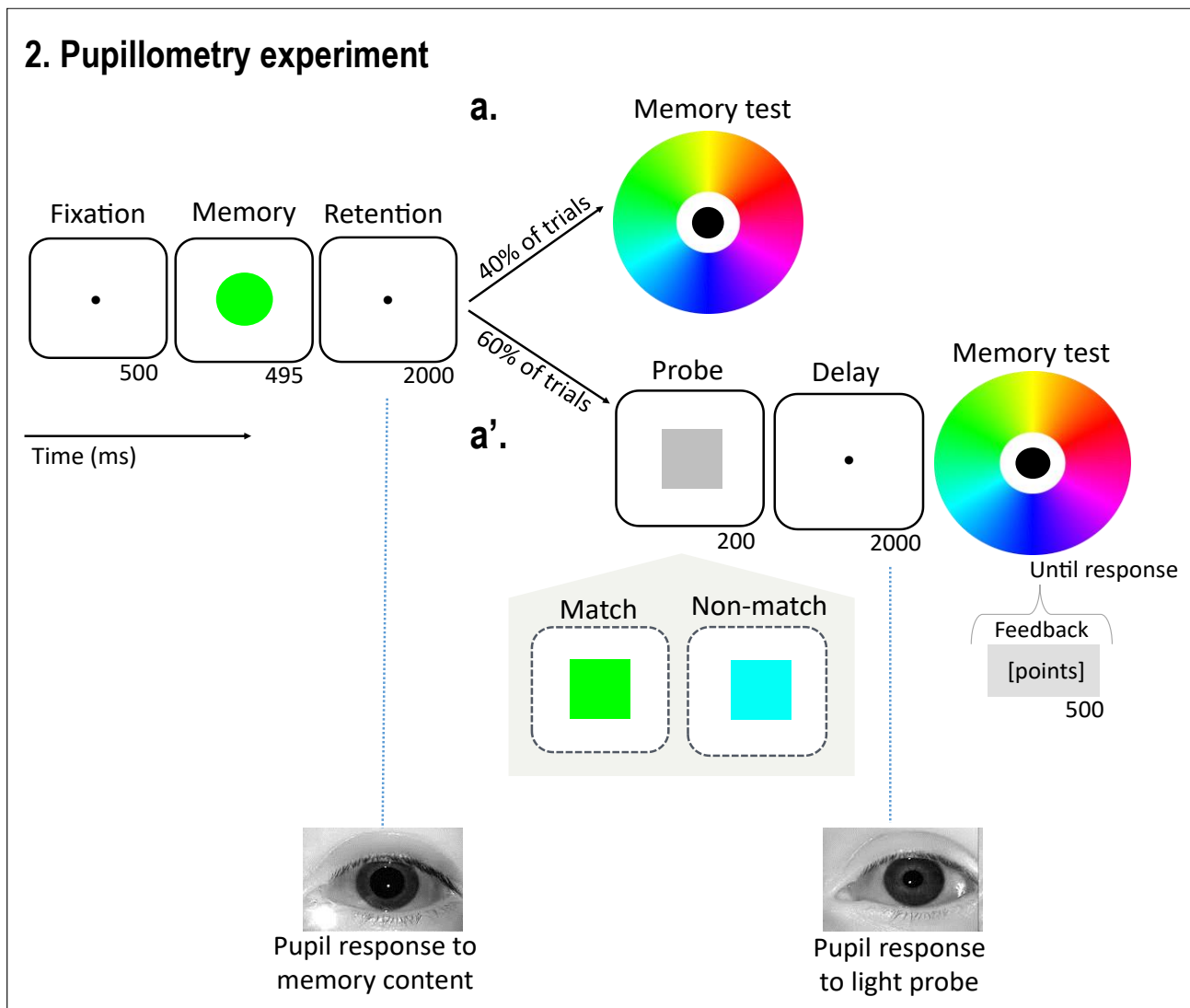
## 2.3 Pupil study

In the second part of our study, we conducted a pupillometry experiment at the Heymans Institute of the University of Groningen. The experiment was structurally the same as in the behavioral study, except that we replaced the *Search trials* with *Probe trials*. As such, participants always had to memorize a color for later reproduction; sometimes they were also presented with task-irrelevant light probes that would be the same or a different color than the

one being held in VWM. **Figure C** illustrates a brief representation of the sequence of trials and conditions in the pupillometry experiment.

First, to replicate the findings of Wilschut and Mathôt (2022) that pupils constrict for longer to matching light-probes, we took measures of pupil size after the probe-onset (*Probe trials*). We found a stronger visual response to memory-matching probes, but – unlike in their study – this was reflected in the initial constriction, and not in the slower recovery of the pupil to the baseline. As such, our result is rather indicator of low-level detection, than of attentional capture.

Next, to replicate the findings of Zhou et al. (2021) that pupils are larger when maintaining visual information in continuous formats, we measured the pupil size during the retention interval (*Memory trials*). Unlike predicted, we found that pupils were smaller for continuous, than for categorical formats, likely reflecting a sensory response, rather than mental effort.



**Figure C.** Sequence of trials in the pupillometry experiment. Participants were presented a colored circle for later reproduction. On 40% of the trials, the memory test followed the retention interval (*Memory trials*; 2a). On 60% of the trials, we briefly presented task-irrelevant light-probes prior to the delay and memory test (*Probe trials*; 2a'). We took measures of pupil size during the retention interval in the *Memory trials*, and after the probe-onset in the *Probe trials*. As in the behavioral study, feedback for the memory test was shown in points at the end of each block.

### ***Participants***

Thirty first-year students from the University of Groningen participated in exchange for course credits. Participants gave written informed consent before the start of the experiment. Instructions for the task were provided step-by-step and followed by a short practice block. At a first check of the data, we removed one participant with missing data and kept for further analysis 29 participants.

### ***Stimuli, design, and measures***

Participants were seated in a dimly lit cubicle-room with their chin placed on a head rest in front of the computer to avoid head movements. Pupil size was measured binocularly with a 60Hz Gaze Point eye tracker (Cuve, et al., 2022; Mannaru, et al., 2017) positioned centrally below the monitor screen. Gaze position was calibrated individually for each participant before the start of the experiment with a nine-point calibration procedure. Stimuli were presented using OpenSesame (version 3.3; Mathôt, Schreij, & Theeuwes, 2012) and Pygaze toolbox (Dalmaijer, Mathôt, & Van der Stigchel, 2014). The experiment comprised one practice block and eight experimental blocks with a total of 240 trials, 96 *Memory trials* and 144 *Probe trials*; the total duration was roughly 25 minutes.

The experiment started after fixation with a colored circle presented centrally for 495ms. We used the same HSV color-set with ambiguous and prototypical colors as in the behavioral study (Zhou, et al., 2021). Participants were instructed to remember the color as accurately as possible to gain points for performance at the memory test. This allowed us to encourage memorization in one of the two formats: continuous for ambiguous colors, and categorical for prototypical colors. As a difference from what Zhou (2021), Wilschut (2022) and colleagues did in their pupillometry experiment, we used a set size of one, meaning that participants were presented with only one memory item to be remembered; as such, stimuli were always presented centrally.

On 40% of trials, the memory test followed a 2000ms retention interval (the *Memory trials*) and stayed on until response. On 60% of trials, task-irrelevant light probes were briefly flashed on the screen (for 200ms) before the memory test (the *Probe trials*). Participants were instructed to ignore the probe and wait for the memory test. Probes were either a perfect match (i.e., identical to the memory color) or a non-match (i.e., a different color sampled from one of the adjacent categories to the memory color). (Probes were square-shaped to be distinguishable from the memory circle across trials.). Importantly, the non-matching probes were always the same color type as the memory color, 50° apart on the HSV circle. The match/non-match and color type of the stimuli were mixed randomly within blocks.

We took measures of pupil size after the probe-onset (in the *Probe trials*) to replicate memory-driven capture effects in pupil constriction (Wilschut & Mathôt, 2022). Here, we had a two-by-two factorial design with Probe type (Match/Non-match) and Color type (Ambiguous/Prototypical) as independent variables with two levels, and the pupil response to the probe as outcome variable.

Additionally, we measured the pupil size during the retention interval (in the *Memory trials*) to test the assumption that continuous representations in VWM are more effortful to maintain and lead to larger pupils (Zhou, Lorist, & Mathôt, 2021). Here, we had a factorial design with Color type as independent variable and pupil size to memory content as outcome variable.

### ***Data processing and analysis***

All data were processed and analyzed in Python 3.9. One participant with incomplete dataset was removed, remaining with 29 participants and a total of 7134 observations. Baseline pupil size was determined by subtracting the average pupil size during the first 50ms after the onset of the memory item from each sample. We kept only the samples with baseline pupil size within two standard deviations away from the mean, which resulted in removing 362 outliers; 6772 trials were included in further analyses.

To smooth out noisy data resulted from poor blink reconstruction, we adjusted the blink-reconstruction parameters to fit the refresh rate of the GazePoint eye-tracker (60Hz). Then, subtractive baseline correction was done for *Probe trials* and *Memory trials*, separately.

Our second aim of the study was to replicate capture effects in the maintained pupil constriction to memory-matching probes. In doing so, we conducted a linear mixed-effects model (LMER) on *Probe trials* using the R package *lme4* (v.1.1-26; Bates et al., 2015), with pupil size as dependent variable and Probe type (match/non-match) as fixed effect with random by-participant intercept and slopes. To test interactions between Probe type and Color type, we ran a separate LMER with Probe type and Color type as fixed effects, with random by-participant intercept and slopes for all fixed effects.

To test our third assumption that pupils are larger when memorizing ambiguous colors, we conducted a LMER on *Memory trials* with pupil size as dependent variable and Color type as fixed effect with random by-participant intercept and slopes.

Finally, to analyze behavior, we first calculated the absolute error at the memory test by taking the distance between the memory hue and the response hue. Next, we fitted the mixture model to the distribution of response error using the biased-memory toolbox (Zhou, Lorist, & Mathôt, 2021), which resulted in two parameters: Precision and Guess Rate. Further, we ran separate RM-ANOVAs using the JASP software, with Color Type as factor and Precision and Guess Rate as dependent variables in turn.

## ***Results and discussion***

### **Memory-driven attentional capture in pupil constriction**

Analyses revealed a strong effect of *Probe type* on pupil response, with a stronger constriction to matching probes. **Figure D a)** depicts the change in pupil diameter after the probe onset; significant effects are observed starting around 200ms after probe onset ( $p < .05$ ), with the highest significance around maximal constriction (700ms after probe onset;  $p < .001$ ).

Unlike predicted, we found that pupils responded stronger, and not for longer (Olmos-Solis, van Loon, & Olivers, 2018; Wilschut & Mathôt, 2022) to matching probes; which suggests that memory-matching visual input appeared more salient (than non-matching input) early before high-level cognition would come into play. This is partly in line with the findings of Wilschut & Mathôt. In their case, the slower recovery of the pupil to matching, compared to mismatching probes (accompanied by no difference in the initial constriction) suggests that saliency was later enhanced for the matching stimuli by top-down control from VWM (resulting in attentional

capture and prolonged constriction to the light-probe). On the other hand, the initial stronger constriction to completely mismatching probes in their study suggests that completely new stimuli are perceived as more salient initially, due to visual adaptation to the already attended objects (the memory item).

Since we controlled for visual adaptation by using slightly mismatching probes (adjacent to the memory color), the initial constriction to matching probes is unlikely explained by visual adaptation here. Instead, it could be explained by the emerging idea that VWM and attention draw upon a shared neural substrate in the visual cortex (Harrison & Tong, 2009; Yörük, Santacrose, & Tamber-Rosenau, 2020) - which would make early detection of memory-matching input possible without executive control.

However, for attention to remain on a stimulus after detection, top-down intervention from VWM might occur in the later stages of visual processing. Nevertheless, because cognitive processes have a slower temporal onset, such top-down effects are hard to identify in the pupil recording since they are likely obscured by faster, sensory responses (as was the case here and in the study of Wilschut & Mathôt).

As such, we conclude that 1) memory-matching visual input is always detected at the sensory level, and 2) saliency is highly sensitive to low-level features of a stimulus, which makes it difficult to tell whether and/or to what extent cognition affects attention (when studied in the pupil response).

### **Mental effort in pupil dilation**

Our final objective was to replicate the findings of Zhou et al. (2021) that pupils are larger while maintaining ambiguous colors in VWM due to resorting to detailed representations and being more effortful. Unexpectedly, we found the opposite effect: Pupils were smaller to ambiguous colors, and larger to prototypical colors. **Figure D b)** shows the change in pupil diameter during the retention interval for ambiguous and prototypical colors. Significant effects are observed from the first 500ms ( $p < .05$ ) throughout the full pupil response, with the highest significance at maximal constriction ( $p < .001$ ).

One crucial difference between our experiment and that of Zhou et al. (2021) may account for our inconsistent results: In their study, the memory display always contained four colors

around fixation, with the memory color/s being indicated by arrows, whereas we used only one memory color presented centrally, which may have caused a stronger visual response. Nevertheless, this unravels a similar phenomenon as earlier: High-level processes (top-down control on attention, or mental effort here) are hardly noticeable in pupil measures when they are preceded by faster, sensory responses.

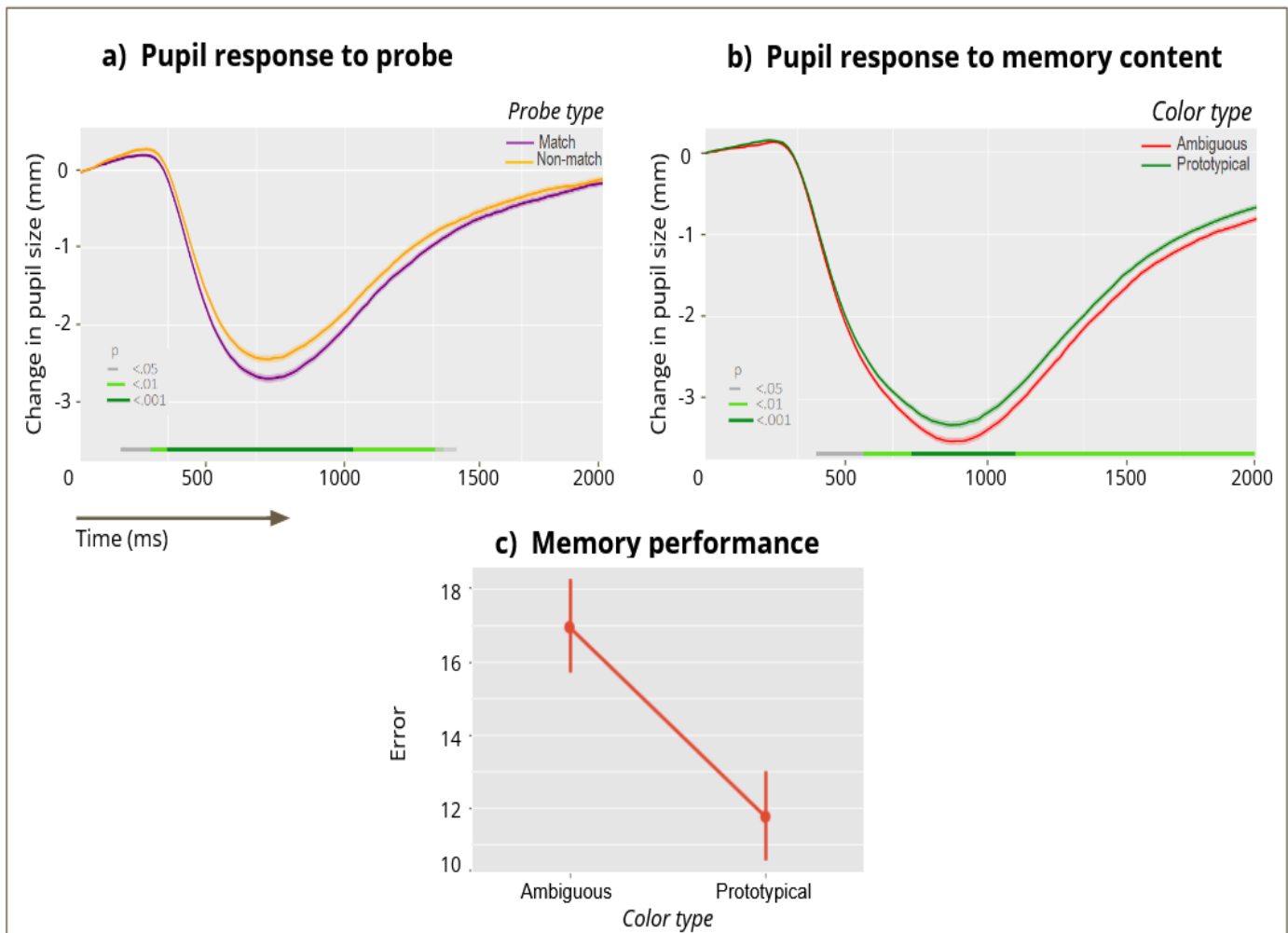
Although the results are inconsistent with our prediction and theories of mental effort on pupil dilation (Kahneman & Beatty, 1966), it does not mean that the ambiguous colors were less effortful to maintain than the prototypical colors. Instead, it reflects a different, more low-level aspect of vision – the more ambiguous a stimulus is, the more ‘unique’ it may appear (and more salient), and the stronger the visual response. Crucially, even more strongly attention gets captured: The initial constriction to ambiguous colors stayed pronounced until (at least) 2000ms after stimulus-onset, suggesting that ambiguous colors appeared more salient initially, but also required more attentional resources to aid maintenance in VWM (compared to prototypical colors, which are easier to categorize and remember).

In addition, the storage format (as represented by Color type here) only influenced pupil size during maintenance (*Memory trials*, experiment 2) and not at all search times (*Search trials*, experiment 1) or the pupil response to memory-matching probes (*Probe trials*, experiment 2). In terms of performance, however, it strongly affected accuracy at the memory test in both experiments, with lower precision for ambiguous colors. Unlike in the study by Zhou et al. (2021) where memory performance for ambiguous colors was lower only for set sizes larger than two (in which case VWM likely relied on categorical representations also for ambiguous colors), we found that even at a set size of one, continuous representations are more fragile than categorical representations.

We conclude from the pupil study that the storage format in VWM does not *necessarily* affect the memory-driven capture effect since previously attended objects are already ‘preactivated’ at the neural level (Chelazzi et al., 1993), hence the VWM representation *per se* could render memory-matching objects ‘equally salient’ in the face of unattended objects (regardless of the format in which they are stored). On the other hand, the storage format becomes relevant when trying to maintain an ambiguous stimulus in VWM, for which vision is enhanced to aid more accurate maintenance of that object in VWM - however, such (continuous)

representations are also less stable in time, which makes reproduction from memory less accurate.

Altogether, despite treating different aspects of VWM – attentional capture and mental effort –, our results from the pupil study depict essentially the same thing: Sensory representations in VWM are associated with stronger visual responses, perhaps via a shared neural substrate that supports VWM maintenance and attention (Harrison & Tong, 2009).



**Figure D** Visual representation of the LMER results in the pupil study. **Figure a)** shows the evoked change in pupil diameter after presentation of Matching/Non-matching probes (*Probe trials*). **Figure b)** shows the pupil size during the retention interval for Ambiguous/Prototypical colors (*Memory trials*). **Figure c)** shows the performance at the Memory test for Ambiguous/Prototypical colors, calculated in the same way as in the behavioral study.



## 4. DISCUSSION & CONCLUSIONS

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The current study aimed to replicate memory-driven capture effects in behavior (Zhou, Lorist, & Mathôt, 2020) and pupil constriction (Wilschut & Mathôt, 2022), and whether these effects are modulated by the formatting style of information in VWM (assuming that different formats resort to different brain areas, hence affecting attention differently). Additionally, we aimed to replicate evidence that continuous representations lead to larger pupils due to being more detailed and, thus, more effortful to maintain (Zhou, Lorist, & Mathôt, 2021).

In short, we found that memory-matching visual stimuli drive a stronger visual response than non-matching stimuli, yet no behavioral evidence that attention gets automatically captured by memory-matching distractors, or that the type of representation in VWM modulates this effect. Although repeatedly demonstrated that visual search is impaired when distractors match the VWM content, in our experiment search was optimized - at least in terms of reaction time (in terms of accuracy, participants made more errors in the distractor-match condition). It could be that visual input that matches a representation in VWM is automatically detected at a sub-perceptual level yet immediately overridden by top-down control of VWM on attention (Sawaki & Luck, 2011). In other words, memory-matching objects may appear more salient initially, but whether or not attention gets captured later depends on the situation.

In order to untangle our results, it is necessary to first consider how VWM and attention are wired at the neural level. Two (more or less) distinct models are briefly presented further, with greater emphasis on the more recent one and the relevance for our paper. First, the classical account of attention selection posits that high-order cortices, like the prefrontal areas, control attention selection through feedback projections of neurons to downstream areas. According to this, control signals modulate visual processing by influencing representations in visual areas in a top-down manner (Gazzaley & D'Esposito, 2007). Second, a *sensory recruitment model* more recently proposed (Harrison & Tong, 2009; Yörük, Santacroce, & Tamber-Rosenau, 2020; Serences et al., 2009) suggests that representations in VWM are stored in the same visual cortices that support early perceptual processes, thus influencing visual selection from the sensory level.

In line with the sensory recruitment account, studies on animal primates suggest that the visual cortex (VC) can even support more complex processes that were traditionally thought to rely on higher-order cortices. Minamimoto and colleagues (2010) demonstrated that monkeys

with or without bilateral removal of the lateral prefrontal cortex (LPFC; a brain area thought to support category-learning of visual stimuli; Ashby & Spiering, 2004; Freedman D. J. et al., 2002) can learn to categorize visual stimuli equally well. This suggests that visual categorization takes place at some early stage of visual processing, even with no input from upstream areas.

Critiques to the sensory model (Lorenc et al., 2018; Xu, 2017) have argued that such overlap in activity in the VC would directly alter perception through interference of memory content with incoming visual information. Indeed, previous perceptions do influence current processing, yet such mechanism is more often adaptive since recent visual cues are useful for predicting future events (Summerfield & de Lange, 2014). Therefore, maintenance in VC may support fast and efficient processing of incoming stimuli, while upstream areas may be responsible for adjusting behavior when such interference becomes detrimental (for which high-level cognition is necessary).

Despite seemingly different in theory, the top-down and sensory models are not mutually exclusive in function. While sensory information may facilitate rapid visual and motor responses to ongoing changes in the environment (without the time-costs of consulting upstream areas), the same stimulus-specific information stored in more abstract formats (e.g., in the LPFC) may act as a support mechanism for adjusting behavior when necessary. For instance, the same VWM representation may be used either as a search template when that information is useful for search (in the case of target-match), or as a template for rejection (Woodman & Luck, 2007) when that information is detrimental for search (in the case of distractor-match). In other words, sensory and abstract representations in VWM are complementary in their roles for visual processing and adaptive behaviors altogether.

This is particularly relevant for the present paper. In our study, the behavioral response (experiment 1.a'; Fig. A) was inconsistent with the visual response (experiment 2.a'; Fig C): The pupils responded stronger to memory-matching stimuli (Fig D.a), yet that was not reflected also in the RTs (Fig. B.a). If visual information that matches the memory content is more salient, why the match of a distractor in our experiment did not impair search (assuming that memory-matching objects automatically capture attention)? From a more integrative view of both models, it may be that representations in VWM are in fact stored in more than one brain area simultaneously, with different functions and differently expressed across visual processing: At

detection, memory-matching objects are perceived as more salient initially (due to maintenance in VC, thus enhancing the visual response; Gayet, et al., 2017; Harrison & Tong, 2009); later, the initial saliency is further enhanced or inhibited (through top-down commands), such that attention is deployed optimally for behavior.

Given the versatility of mechanisms that support visual selection, and the results from the pupil study, it could be that the memory-matching shapes in the VST were always detected at the sensory level, without *necessarily* leading to attentional capture – instead, high-level processing may have modulated the initial response to either ensure or prevent attentional capture based on whether the target or the distractor would match the VWM-content. Even so, this would maximally result in no difference in the RTs between target/distractor-match. We suspect that the faster RTs in the distractor-match condition in our study are likely due to limits in our experiment: The occurrence of matching distractors on 2/3 of trials may have led participants to adopt strategies for finding the target based on the regularity of a distractor-match. Altogether, this points to the fact that attention is dynamically (rather than automatically) modulated by VWM content in a both stimulus-driven (bottom-up) and goal-directed (top-down) manner.

Additionally, because we based our predictions on the idea that VWM maintenance is supported by different brain areas specialized in different types of visual representation, we also expected that the memory-driven capture effect is modulated by the storage format - with stronger effects for continuous (sensory) representations. Unfortunately, we found no evidence that continuous representations in VWM lead to stronger attentional capture to memory-matching stimuli (as predicted by the sensory recruitment model). Interestingly, our results may reveal something else: If visual categorization can occur in the VC, it might be that ambiguous/prototypical stimuli in our study appeared equally salient based on the match with the memory content, regardless of the format in which they were stored. Therefore - at least when it comes to memory-driven visual responses - such distinction between continuous/categorical representation becomes redundant in the case of freshly attended objects, for which the mental representation would be “equally sensory” in either format (assuming they draw upon the same visual area).

However, when it comes to the pupil response during maintenance (experiment 2.a; Fig. C), we found a difference in pupil size for continuous/categorical representations, with smaller

pupils for continuous representations. In this case, visual stimuli that are ambiguous and thus harder to remember may have caused 1) a stronger initial response due to being more salient, and 2) attentional capture to facilitate maintenance in VWM.

Although we could not find evidence of mental effort in pupil dilation (Zhou, Lorist, & Mathôt, 2021), we do not rule out the idea that continuous representations are more effortful to maintain. In fact, this may explain why attention got involved and enhanced the visual response to ambiguous colors. But, considering how salience gets affected by low-level aspects, the difference between the memory display in our study and in that of Zhou may have contributed to the stronger initial constriction.

In other words, whether or not a stimulus is easy to categorize is less relevant when it comes to memory-driven capture effects, but more when trying to maintain it in VWM: The more ambiguous a stimulus is, the harder it is to remember, the more attention gets involved to capture its details. However, the more fragile in time its representation, as seen in the lower memory precision when reproducing ambiguous colors in both experiments. It may be that, while continuous representations are accompanied by stronger visual responses after stimulus-presentation, they are also more sensitive to the time-course of higher-level processes, during which details might get *lost* (or at least *inactive*; Mongillo, Barak, & Tsodyks, 2008).

To conclude, few crucial points derive from our study, that are more or less in line with our predictions, yet with valuable contribution to theory and practice.

First, representations in VWM do not bias attention towards any object that matches the memory content, but instead are used more flexibly on visual selection (perhaps via distributed connectivity in the brain). This would be evolutionary plausible given the amount of information that attempts to our attentional resources on a continuum basis. In order to shape perception into a picture useful for decision-making, cognition may have evolved to select (mostly) the relevant information from the pool of competing stimuli, making use of both cognitive priors and sensory inputs interactively.

Second, the storage format in VWM is less relevant on memory-driven attentional capture, in which case the representation of freshly attended objects is already “more sensory”

*per se*; however, the storage format is crucial for memory performance, with continuous representations being less stable over time.

Third, pupillometry is a viable tool for studying vision, yet with a crucial limitation when it comes to interactions between cognition and sensation – which has to do with how our (1) eyes and (2) neurons (are thought to) work: 1) Sensory responses are faster and stronger and will likely obfuscate measures of subsequent cognitive processes, and 2) The eye-tracker records changes in pupil size on a linear continuum, whereas emerging theories of functional connectivity in the brain propose a more dynamical coding scheme of information processing (Quilichini & Bernard, 2012), with communication between neurons being likely dependent on the physiology of the cells and synapses (Kamiński & Rutishauser, 2020; Mongillo, Barak, & Tsodyks, 2008). In this manner, the processing of information would unfold *across* time, rather than in a *linear* succession of events.

Hopefully, in a recent future, research on VWM and attention could benefit from technology able to track both persistent and activity-silent mechanisms in the brain, and ultimately address questions that are only partially answered by existing theories – most of them based on persistent activity. Meanwhile, combined pupillometry with behavior and, more recently, with EEG, is a powerful approach to studying interactions between VWM and attention across all levels of visual processing; provided that experiments are designed to consider how saliency gets affected at the lowest level. As a future recommendation when studying VWM and attention with pupillometry and colored stimuli, it might be worth exploring how pupils respond to different colors - since retinal cells respond differently to luminance, and would likely contribute to variations in the pupil response.

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