

1 Attending and inhibiting stimuli that match the contents of visual working memory: Evidence
2 from eye movements and pupillometry

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Abstract

When you keep a red apple in working memory, your attention is usually—but not always— attracted by other red objects. The conditions under which the contents of visual working memory guide visual attention are still unclear. Here we tested whether attention is indeed biased toward memory-match stimuli, and, if so, whether this bias is transient or sustained. We used a new pupillometric technique, which exploits that the pupil is larger when you covertly attend to dark, compared to bright, stimuli. This allowed us to test whether and when attention was biased toward memory-match stimuli, by placing them either on a dark or a bright background, while measuring pupil size over time. We found that the eyes were captured by memory-match probes early on in the trial. However, the pupillary data suggested that there was no sustained attention bias toward memory-match probes later in time; rather, attention appeared to be biased away from them. Together, our results suggest that: (1) memory-match stimuli automatically capture attention; but (2) they do so only briefly; and (3) they may even become inhibited later in time.

Keywords: visual working memory, visual attention, pupillometry, eye movements

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3 When you selectively attend to a visual stimulus, you enhance its representation in your
4 mind's eye. Compared to non-attended stimuli, attended stimuli appear higher in contrast
5 (Carrasco, Penpeci-Talgar, & Eckstein, 2000), are detected faster and more accurately (Posner &
6 Cohen, 1984), and trigger a stronger pupillary light response (Binda & Murray, 2015; Mathôt, van
7 der Linden, Grainger, & Vitu, 2013). Attention is also the gate to visual working memory
8 (Bundesen, 1990): You need to attend to a stimulus to remember it.

9 Many theories of vision state that the link between attention and working memory goes both
10 ways: Not only are locations that are held in working memory biased toward attended locations
11 (Van der Stigchel, Merten, Meeter, & Theeuwes, 2007), attention is also captured by stimuli that
12 match the contents of working memory (e.g., Duncan & Humphreys, 1989; Folk, Remington, &
13 Johnston, 1992; Wolfe, 1994). For example, if you keep a red apple in working memory, other red
14 objects, such as firetrucks (in countries where these are red), automatically attract attention. The
15 influential biased-competition model explains this in terms of neural activity (Chelazzi, Miller,
16 Duncan, & Desimone, 1993; Desimone & Duncan, 1995). According to biased competition,
17 similar patterns of neural activity are set up when you keep a stimulus in memory, and when you
18 actually see that same stimulus (see also Postle, 2006). Therefore, when you keep a red stimulus
19 in memory, and subsequently see a red and a green stimulus, the red stimulus elicits stronger
20 neural activity (perceptual activity on top of working-memory activity) than the green stimulus
21 (perceptual activity only). In other words, working memory is a 'search template' that guides
22 attention by increasing baseline activity for memorized stimuli in visual cortices.

23 Behavioral studies have provided compelling evidence that working memory can guide
24 attention in the way predicted by biased competition and related theories (e.g., Awh, Jonides, &
25 Reuter-Lorenz, 1998; Downing, 2000; Hollingworth, Matsukura, & Luck, 2013; Mannan,
26 Kennard, Potter, Pan, & Soto, 2010; Olivers, Meijer, & Theeuwes, 2006; Pan & Soto, 2010; Silvis
27 & Van der Stigchel, 2014; Wong & Peterson, 2011). For example, in a study by Olivers and

1 colleagues (2006), participants kept a color (e.g. red) in working memory. Next, they searched for
2 a target among multiple distractors, one of which had a unique color that either matched (a red
3 circle), or did not match (a green circle), the memorized color. The crucial finding was that
4 response times on the visual-search task increased when the distractor color matched the
5 memorized color. This suggests that the memory-match distractor captured attention more
6 strongly than other distractors did; that is, attention was biased toward stimuli that matched the
7 contents of working memory.

8 However, other studies, using similar dual-task designs, found that memorized stimuli do
9 not, or not always, guide attention (e.g., Downing & Dodds, 2004; van Moorselaar, Theeuwes, &
10 Olivers, 2014; Woodman & Luck, 2007). For example, Woodman and Luck (2007) found that the
11 presence of a memory-match distractor did not always affect response times on a visual-search
12 task; and when it did, the effect was sometimes in the opposite direction from that reported by
13 Olivers and colleagues (2006), suggesting that attention could be biased away from, rather than
14 toward, stimuli that matched the contents of working memory.

15 Most evidence for the relationship (or lack thereof) between attention and working memory
16 comes from behavioral studies that have used dual-task designs like those described above (but
17 not all; we will return to other approaches in the discussion). Such experiments are limited in two
18 main ways. First, participants, who are typically less-than-naive university students, undoubtedly
19 guess that there is a link between the visual-search and memory tasks, which may affect their
20 behavior in unpredictable ways—a point also raised by Woodman and Luck (2007). Second, using
21 behavioral responses, it is difficult to test how attention evolves during a trial: Is there a sustained
22 bias of attention toward memory-match items, or do they grab attention only briefly? If attention
23 is grabbed only briefly by memory-match items, this might explain why these items have little or
24 no effect in a slow-paced visual-search task, such as used by Woodman and Luck (2007), whereas
25 they do have an effect in a fast-paced attentional-capture task, such as used by Olivers and
26 colleagues (2006).

27 To bypass these limitations, we used a new pupillometric technique to continuously track the

1 focus of attention in a working-memory task, without requiring an intervening visual-search task.
2 This technique exploits that the pupillary light response is driven mostly by attended stimuli; that
3 is, if eye movements and visual input are controlled, your pupil is smaller when you attend to a
4 bright, compared to a dark, stimulus (e.g., Binda, Pereverzeva, & Murray, 2013; Mathôt et al.,
5 2013; Naber, Alvarez, & Nakayama, 2013; reviewed in Mathôt & Van der Stigchel, 2015). We
6 conducted two experiments with the same overall design. Participants maintained a single color in
7 working memory. During a five-second retention interval, two task-irrelevant probes were
8 presented. One probe was presented on a dark background; the other was presented on a bright
9 background. Because the pupillary light response is modulated by covert attention, this allowed
10 us to track whether and when attention was biased toward (or away from) the memory-match
11 probe. Based on previous studies (e.g., Olivers et al., 2006), we predicted that there would be a
12 sustained bias of attention toward the memory-match probe; therefore, we predicted that,
13 throughout the retention interval, the pupil would be larger when the memory-match probe was
14 presented on a dark, compared to a bright, background.

15 Experiment 1

16 *Methods*

17 *Materials and availability*

18 Participant data, color measurements, experimental scripts, and analysis scripts are available
19 from https://github.com/smathot/materials_for_P0014/.

20 *Participants*

21 Fifteen participants were recruited from Utrecht University (7 women; age range 17 - 36;
22 normal or normal-to-corrected vision). All participants signed informed consent before
23 participating and received monetary compensation. The experiment was approved by the ethics
24 committee of Utrecht University.

25 *Software and equipment*

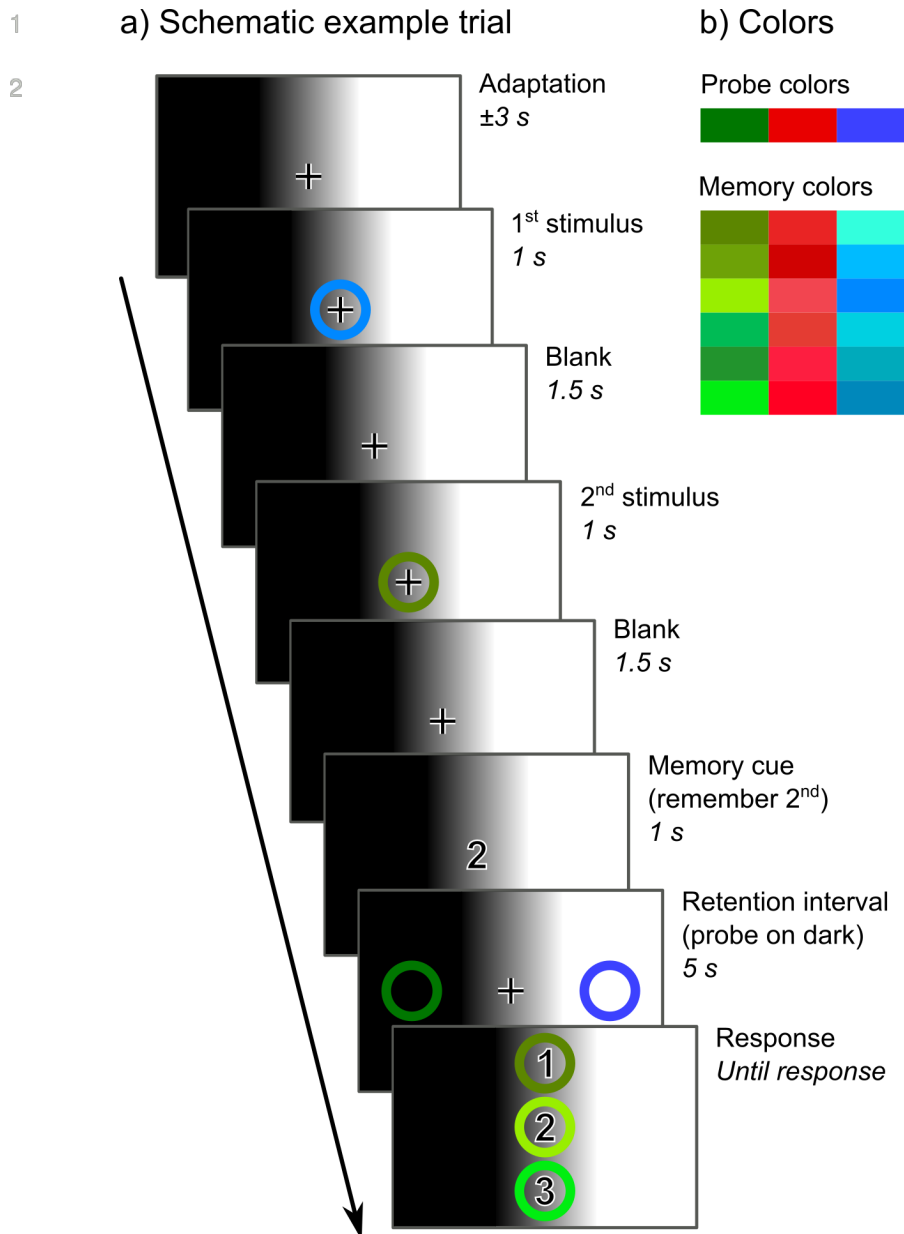
1 Eye position and pupil size were recorded with an Eyelink 1000 (SR Research, Mississauga,
2 Canada, ON), a video-based eye tracker sampling at 1000 Hz. Stimuli were presented on a 19"
3 Nokia Multigraph 446Xpro monitor (1024 x 768 px, 120 Hz). Stimulus presentation was
4 controlled with OpenSesame (Mathôt, Schreij, & Theeuwes, 2012) and PsychoPy (Peirce, 2007).

5 *Procedure*

6 Before the experiment, a nine-point eye-tracker calibration was performed. During the entire
7 trial, the display was divided into a bright (94.7 cd/m²) and a dark (1.19 cd/m²) half, separated by
8 a 9.7° horizontal luminance gradient (Figure 1a). Participants kept their eyes on the display center
9 from the start of the trial until the response interval (i.e. they were allowed to look at the response
10 options). To control for small eye movements, from the onset of the first color stimulus, the
11 central gradient was locked to gaze position; for example, when the eyes drifted slightly to the
12 left, the gradient moved slightly to the left by an equal amount (cf. Exp. 2 from Mathôt et al.,
13 2013). This made sure that the eyes were always exactly in between the bright and dark sides of
14 the screen. The maximum displacement of the gradient was 4.9°.

15 Each trial started with a period of ±3 s during which the pupil adapted to the display, and
16 during which an automatic one-point recalibration (drift correction) was performed (the exact
17 duration depended on the time needed for drift correction). Next, the first color stimulus (an
18 unfilled colored circle; 3.6° diameter) appeared for 1 s, followed by a 1.5 s blank display. The
19 color was randomly selected from six variations of red, green, and blue (Figure 1b; color
20 specifications are included with online materials). Next, the second color stimulus appeared for 1
21 s, again followed by a 1.5 s blank display. The second color was always of a different category
22 than the first; that is, if the first color was green, the second color was either red or blue. Next, a
23 memory cue appeared (a centrally presented “1” or “2”) for 1 s, indicating whether the first or
24 second color should be remembered. We presented two colors, of which only one was to be
25 remembered, to control for priming effects due to visual presentation of the to-be-remembered
26 color. Next, there was a retention interval of 5 s during which two task-irrelevant probes were

1 presented 7.3° to the left and right of the display center. The two probes were different variations
2 of the same color categories as the two color stimuli; that is, if the color stimuli were red and
3 green, the probes were different variations of red and green (labeled 'Probe colors' in Figure 1b).
4 Finally, three colored circles, all of the same color category as the memorized color, were
5 presented. The participant indicated which of the three colors exactly matched the memorized
6 color by pressing the 1, 2, or 3 key on the keyboard.



3 **Figure 1.** The experimental paradigm. a) A schematic example trial.
 4 This example shows a Probe-on-Dark trial, because the memory-
 5 match probe (the green circle shown on the left during the retention
 6 interval) is on a dark background. b) The colors used for the
 7 experiment. (Color specifications are included with online
 8 materials.)

9 The crucial manipulation was the placement of the probe that matched the memorized color
 10 (from now on: *memory-match probe*; in Figure 1a this is the green circle on the left during the

1 retention interval). On Probe-on-Dark trials, the memory-match probe was placed on the dark
2 background (as in Figure 1a); on Probe-on-Bright trials, the memory-match probe was placed on
3 the bright background.

4 The experiment consisted of 24 practice trials, followed by 144 experimental trials, and took
5 ± 1.5 h. Probe Brightness (Probe-on-Dark, Probe-on-Bright) and Probe Side (Left, Right) were
6 randomized within blocks.

7 *Results*

8 *Trial-exclusion criteria*

9 Trials were discarded when horizontal gaze deviation from the display center during the
10 retention interval exceeded the maximum displacement of the central gradient (15.8%; see
11 Methods: Procedure). Due to a technical problem (a buffer overflow in the connection between
12 the EyeLink and experimental PC), manual responses were not logged for some trials; these were
13 excluded (1.3%). No participants were excluded. In total, 1,794 trials remained for further
14 analysis.

15 *Behavioral results*

16 Accuracy was 74.3% ($SE = 1.8$). Mean correct response time (RT) was 2.2 s ($SE = 0.1$).

17 *Eye-movement results*

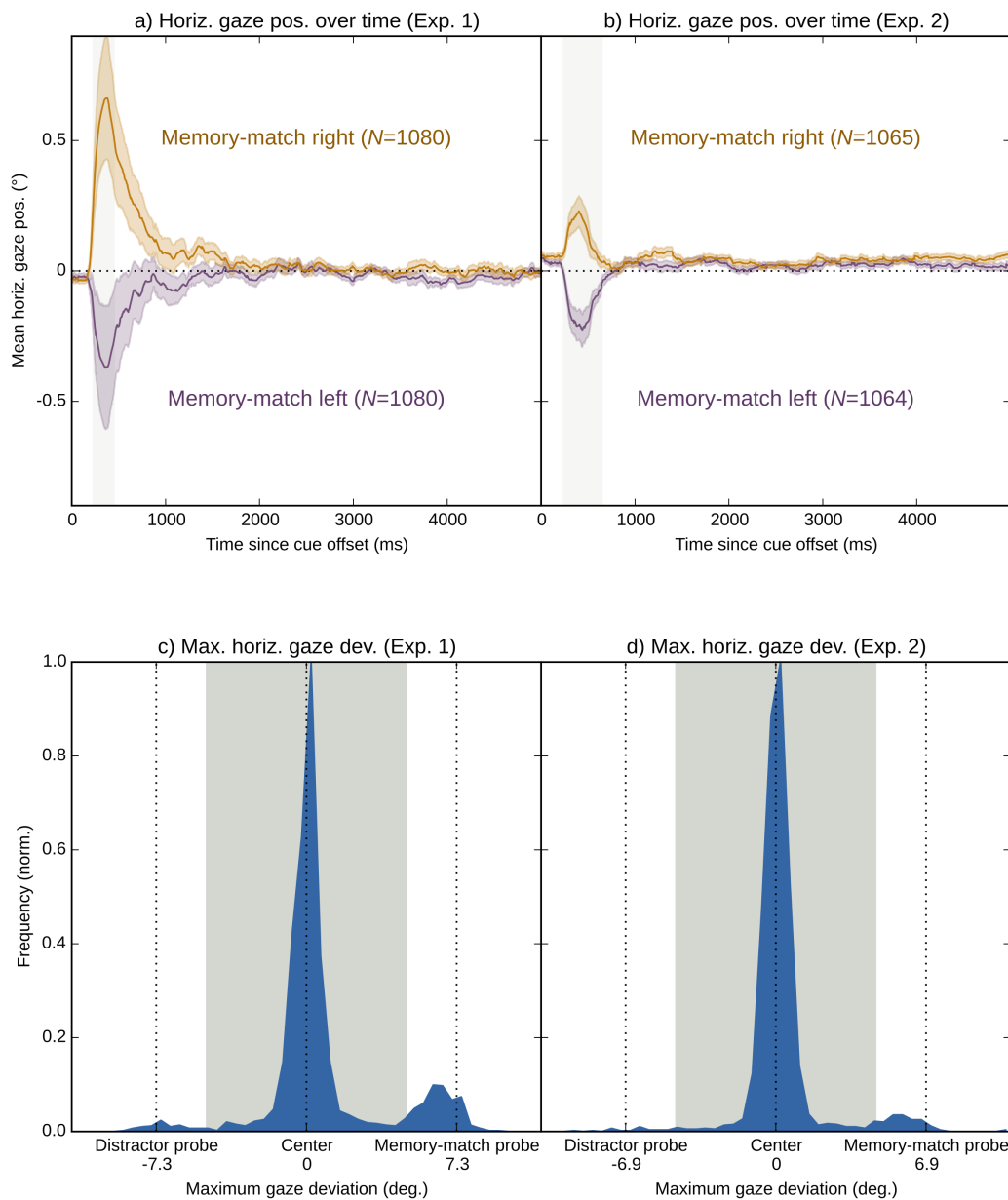


Figure 2. a, b) Mean horizontal gaze position over time for Experiments 1 (a) and 2 (b). Gray shadings indicate a reliable effect of Memory-Match Side. Error bands indicate standard errors. c, d) Histogram of the per-trial maximum gaze deviation toward the memory-match probe for Experiments 1 (c) and 2 (d). The shaded area indicates the maximum displacement of the gaze-locked central gradient; trials that fell outside of this area were removed for the main analyses.

On about 15% of trials, despite that we had instructed participants to maintain central fixation, gaze deviated considerably from the display center; trials with such gaze errors were

1 discarded for the main (pupil-size and behavioral) analyses. However, we used the full,
2 untrimmed data to test whether and when the eyes were captured by the memory-match probe.
3 For each 10 ms period, we conducted an LME with horizontal gaze position as dependent
4 measure, Memory-Match-Probe Position (Left, Right) as fixed effect, and by-participant random
5 intercept and slopes. As shown in Figure 2a, the eyes were sometimes captured by the memory-
6 match probe at the start of the retention interval, but there was hardly any capture later in time
7 (230 - 449 ms; criterion: $t > 2$ for at least 200 ms, cf. Mathôt, Dalmaijer, Grainger, & Van der
8 Stigchel (2014)). The systematic gaze deviation is driven by a small and distinct proportion of
9 trials on which the eyes were captured by the memory-match probe (Figure 2c). Most gaze errors
10 were directed toward the memory-match probe (13.2%); the eyes rarely went to the non-matching
11 probe (2.6%).

12 *Pupil-size results*

13 We analyzed pupil size during the retention interval. Mean pupil size during the last 100 ms
14 of cue presentation was taken as a baseline, and all pupil size measures are reported in area (i.e.,
15 not diameter) relative to this baseline. Pupil size during blinks was reconstructed using cubic-
16 spline interpolation (Mathôt, 2013). Pupil size was smoothed with a 31 ms Hanning window.

17 For each 10 ms period, we conducted an LME with normalized pupil size as dependent
18 measure, Probe Brightness (Probe-on-Dark, Probe-on-Bright) as fixed effect, and by-participant
19 random intercept and slopes (cf. Mathôt, Melmi, & Castet, 2015). Only correct-response trials
20 were included in this analysis.

21 Figure 3a shows pupil size over time as a function of Probe Brightness. There is an overall
22 constriction from about 250 ms after the start of the retention interval; this is a visual response to
23 the onset of the retention-interval display. This constriction is followed by a slow dilation, which
24 is partly a recovery from the initial constriction, and partly an effect of memory load (e.g.,
25 Kahneman & Beatty, 1966). Crucially, and in contrast to our prediction, the pupil was slightly
26 (but not reliably; criterion: $t > 2$ for at least 200 ms) larger, rather than smaller, when the
27 memory-match probe was on a bright (orange line), compared to a dark (blue line), background.

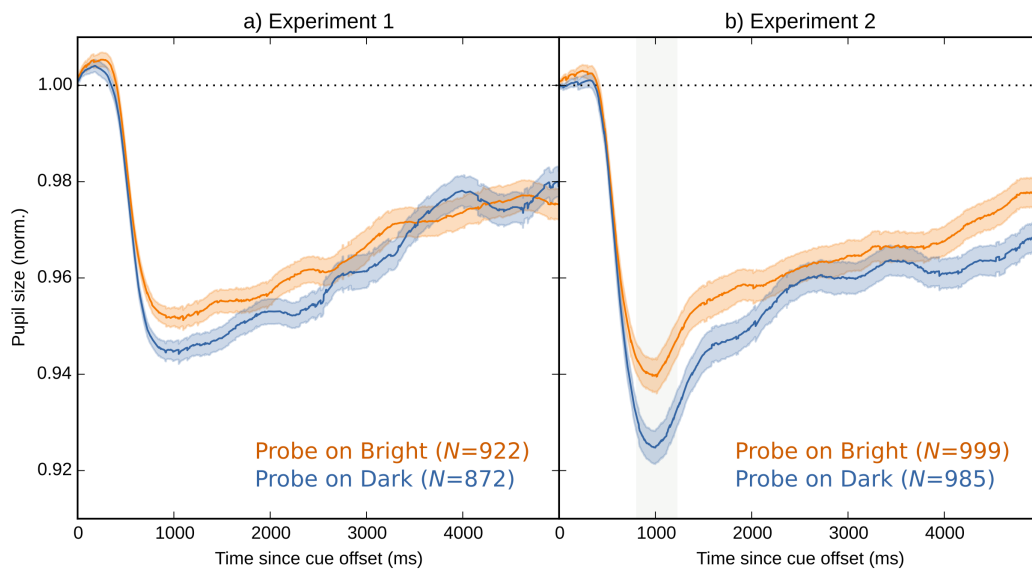


Figure 3. Pupil size over time as a function of Probe Brightness (Probe-on-Bright, Probe-on-Dark). a) Results from Experiment 1. b) Results from Experiment 2. Gray shadings indicate a reliable effect of Probe Brightness. Error bands indicate standard errors.

Discussion

In Exp. 1, we found that, at the start of the retention interval, the eyes were captured by the probe that matched the contents of visual working memory (memory-match probe). However, the pupillary data suggest that this initial gaze bias did not result in a sustained shift of attention toward the memory-match probe throughout the retention interval; that is, when the memory-match probe appeared on a bright background, the pupil was not smaller than when it appeared on a dark background; rather, there was a tendency in the opposite direction.

Experiment 2

In Exp. 1, the memory-match probe was task-irrelevant and presented in peripheral vision; therefore, the memory-match probe could be ignored by narrowing the focus of attention to the fixation point. This ‘attentional tunnel vision’ may have prevented a sustained shift of attention toward the memory-match probe (Pan & Soto, 2010; Theeuwes, 1991). To control for this, we

1 repeated the experiment, but added catch trials in which the probes were task-relevant; therefore,
2 participants could no longer use attentional tunnel vision to ignore the probes throughout the
3 retention interval.

4 *Methods*

5 The methods were similar to those of Exp. 1 with the following differences. Fifteen
6 participants were recruited (7 women; age range 18-26; normal or normal-to corrected vision).
7 Stimuli were presented on a 24" LG 24MB65PM monitor (1280 x 800 px, 60 Hz). Because of the
8 monitor change, stimuli were scaled by 95% (i.e. slightly smaller) compared with Exp. 1. One of
9 every nine trials was a catch trial, in which the probes abruptly changed to patches of white noise
10 at an unpredictable moment during the retention interval. One probe changed 83 ms before the
11 other probe, and the participant indicated which probe changed first by pressing the right (right
12 first) or left (left first) key. The experiment was conducted in two sessions on separate days. Each
13 session consisted of 27 practice trials, followed by 81 experimental trials, and took ± 1 h.

14 *Results*

15 *Trial-exclusion criteria*

16 Trials were discarded when horizontal gaze deviation during the retention interval exceeded
17 the maximum displacement of the central gradient (5.1%). Due to a technical issue, manual
18 responses and condition were not logged for some trials; these were excluded (2.2%). No
19 participants were excluded. In total, 2,254 trials remained for further analysis.

20 *Behavioral results*

21 For regular trials, accuracy was 73.3% ($SE = 1.6$), and mean correct RT was 2.3 s ($SE = 0.2$).
22 For catch trials, accuracy was 68.5% ($SE = 3.8$), and mean correct RT was 1.0 s ($SE = 0.1$).

23 *Eye-movement results*

24 As in Exp. 1, we analyzed gaze deviation in the untrimmed data (excluding catch trials and

1 trials with logging errors). We again found that the eyes were briefly captured by the memory-
2 match probe at the start of the retention interval (240 - 650 ms; Figure 2b,d). Most gaze errors
3 were directed the toward memory-match probe (4.9%); the eyes rarely went to the non-matching
4 probe (1.0%).

5 *Pupil-size results*

6 Figure 3b shows pupil size over time as a function of Probe Brightness (excluding catch trials
7 and trials with logging errors). The results were very similar to those of Exp. 1. Crucially, we
8 again found that the pupil was larger when the probe appeared on a bright, compared to a dark,
9 background. This effect was reliable from 810 - 1220 ms (criterion: $t > 2$ for at least 200 ms).

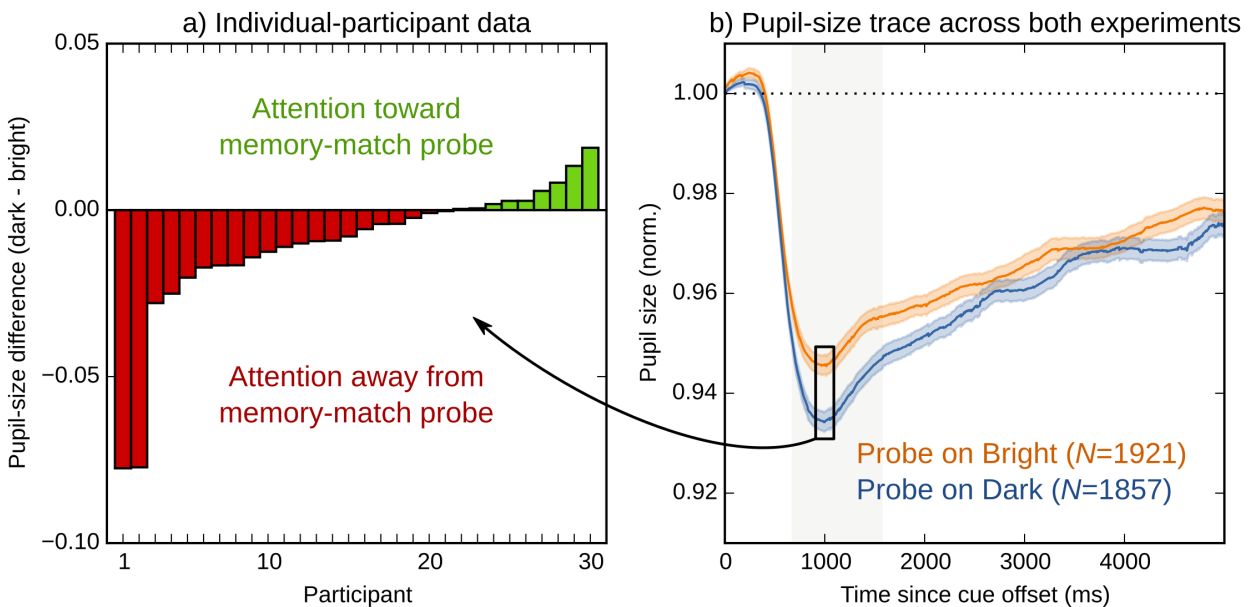
10 *Discussion*

11 Exp. 2 replicated the key results of Exp. 1. We again found that, at the start of the retention
12 interval, the eyes were captured by the probe that matched the content of visual working memory
13 (memory-match probe). However, again, we found no evidence for a sustained bias of attention
14 toward the memory-match probe. Rather, we observed the opposite pattern: When the memory-
15 match probe was presented on a bright background, the pupil was larger than when it was
16 presented on a dark background.

17 *Crossexperimental analysis*

18 Because Exp. 1 and 2 were similar in methods and results, we performed a crossexperimental
19 analysis on the combined data. To test how reliable the attention bias away from the memory-
20 match probe was when considering both experiments together, we determined, per participant, the
21 mean difference in pupil size between Probe-on-Dark and Probe-on-Bright trials in the 950 - 1050
22 ms interval. The results are not crucially dependent on the exact interval; however, because of the
23 initial pupillary constriction, we could not meaningfully analyze pupil size in the period during
24 which the eyes were sometimes captured by the memory-match probe. (This may explain why we
25 did not observe any attentional capture in the pupil-size results; we return to this point in the

1 discussion.) As shown in Figure 4a, there was a clear tendency for the pupil to be larger on Probe-
 2 on-Bright, compared to Probe-on-Dark, trials.



3
4
5
6 **Figure 4.** Results from crossexperimental analyses. a) The effect of Probe Brightness on pupil size for
 7 individual participants. A positive value (green) indicates that the pupil was larger when the memory-match
 8 probe appeared on a dark, compared to a bright, background. b) Pupil size over time as a function of Probe
 9 Brightness (Probe-on-Bright, Probe-on-Dark). The box and arrow indicate the 950-1050 ms interval on which
 10 the individual-participant data (a) are based. Gray shadings indicate a reliable effect of Probe Brightness.
 11 Error bands indicate standard errors.

12 Next, we used default one-sided Bayesian paired-samples t-tests (Rouder, Speckman, Sun,
 13 Morey, & Iverson, 2009) to test which model was best supported by the data: an *Attention-*
 14 *Toward* (the memory-match probe) model, in which the pupil is largest for Probe-on-Dark trials;
 15 a *No-Attention-Bias* model, in which Probe Brightness has no effect on pupil size; or an *Attention-*
 16 *Away* (from the memory-match probe) model, in which the pupil is largest for Probe-on-Bright
 17 trials.

18 First we compared the Attention-Toward and No-Attention-Bias models. This showed strong
 19 evidence in favor of the No-Attention-Bias model ($BF = 16.8$), suggesting that the lack of an

1 effect in the predicted direction was not due to insufficient statistical power. Next we compared
2 the Attention-Away and No-Attention-Bias models. This showed moderate evidence in favor of
3 the Attention-Away model ($BF = 8.7$). (For reference, a classical one-sided paired-samples t-test
4 also revealed an effect of Probe Brightness: $t(29) = 2.7, p = .005$)

5 When analyzing pupil size over time, using the data from both experiments, the pupil was
6 larger when the probe appeared on a bright, compared to a dark, background. This effect was
7 reliable from 680 - 1570 ms (criterion: $t > 2$ for at least 200 ms; Figure 4b).

8 In summary, a Bayesian analysis revealed moderate evidence that, across the two
9 experiments, there was an attention bias away from, rather than toward, the probe that matched
10 the contents of visual working memory.

11 Discussion

12 Here we report two experiments in which we tested the hypothesis that there is a sustained
13 bias of visual attention toward stimuli that match the contents of visual working memory
14 (memory-match stimuli). We found that, despite instructions to maintain central fixation, the eyes
15 were often captured by memory-match stimuli at the start of the retention interval (Figure 2),
16 consistent with previous studies (Hollingworth et al., 2013; Hollingworth, Richard, & Luck, 2008;
17 Mannan et al., 2010; Olivers et al., 2006; Silvis & Van der Stigchel, 2014; Wong & Peterson,
18 2011). However, this initial bias did not result in a sustained shift of attention as measured
19 through pupillometry (Figure 3 and Figure 4); rather, later in time, attention appeared to be biased
20 away from memory-match stimuli.

21 Our results speak against single-state models according to which visual-working memory is a
22 uniform attentional template: These models would predict a sustained attention bias toward
23 memory-match stimuli. Rather, our results are consistent with recent models according to which
24 working-memory items can be in different states (Olivers, Peters, Houtkamp, & Roelfsema, 2011;
25 Zokaei, Ning, Manohar, Feredoes, & Husain, 2014b): prioritized or accessory. An item is
26 *prioritized* when it is behaviorally relevant; there can only be one prioritized item at a time. An
27 item is *accessory* when it is not directly relevant, yet relevant enough to be remembered; there can

1 be several accessory items at a time.

2 The difference between prioritized and accessory working-memory states was demonstrated
3 in a compelling study by Zokaei, Manohar, Husain, and Feredoes (2014a, Exp. 1). In their
4 experiment, participants remembered the motion direction of two moving stimuli, one red and one
5 green. Next, a red or green cue was shown, and participants indicated the location of the
6 corresponding memorized stimulus; presumably, this caused the cued item to become prioritized
7 (because it was immediately relevant), and the uncued item to become accessory. Next,
8 transcranial magnetic stimulation (TMS; either high or low intensity) was applied over brain area
9 MT+, thus disrupting brain activity in the region that encodes motion direction. Finally,
10 participants saw a red or green moving test stimulus, and matched the motion direction of the test
11 stimulus to the corresponding memorized stimulus. Zokaei and colleagues (2014a) found that
12 high-intensity TMS reduced working-memory precision, but—crucially—only for the prioritized
13 (cued) item. This suggests that prioritized working-memory items are represented in visual
14 cortices (area MT+ in this case), while accessory items are not.

15 Following the idea that working memory guides attention by modulating baseline activity in
16 visual cortices (e.g., Chelazzi et al., 1993), the results of Zokaei and colleagues (2014a) suggest
17 that only prioritized items should guide attention. This was confirmed by Van Moorselaar,
18 Theeuwes, and Olivers (2014, Exp. 4), who used a design similar to that used by Olivers and
19 colleagues (2006, see Introduction) with the important difference that participants kept two colors
20 in memory, rather than one. Both colors were tested on every trial, but an arrow cue indicated
21 which color was tested first; the cued item thus became prioritized (what comes first is most
22 important), and the uncued item became accessory. Next, participants performed a visual-search
23 task. Response times on the visual-search task increased when there was a memory-match
24 distractor, suggesting that memory-match distractors captured attention (replicating Olivers et al.,
25 2006). But, crucially, this only happened for distractors that matched the prioritized (cued) item;
26 distractors that matched the accessory item did not attract attention more than did neutral
27 distractors. This suggests that prioritized items guide attention, while accessory items do not.

1 One interpretation of the present results follows a multi-state model of working memory.
2 Only one color needed to be remembered on each trial. Therefore, this color was initially
3 prioritized, and captured attention; this explains why the memory-match probe captured the eyes
4 at the start of the retention interval (Figure 2). However, the color of the memory-match probe
5 was easily confused with the to-be-remembered color, because both were different shades of the
6 same color category. To minimize confusion, participants may have put the to-be-remembered color
7 in an accessory state, and strategically avoided attending toward the memory-match probe; this
8 could explain the attention bias away from the memory-match probe that emerged later in the
9 retention interval, as measured through pupillometry (Figure 3).

10 This interpretation is reminiscent of a study by Sawaki and Luck (2011), who measured
11 event-related potentials (ERP) in a design similar to ours. In their experiment, participants
12 remembered the orientation of a colored rectangle. In the retention interval, two task-irrelevant
13 probes were presented, one of which matched the color of the memorized rectangle. Crucially, the
14 memory-match probe evoked a distractor positivity, an ERP component that is believed to index
15 suppression of attention (Hickey, Di Lollo, & McDonald, 2009). Sawaki and Luck (2011)
16 interpreted this as evidence for a strategic suppression of the memory-match probe.

17 Another interpretation of the present results and those of Sawaki and Luck (2011) is in terms
18 of inhibition of return (IOR). When attention is captured by a salient stimulus, such as a bright
19 flash or sudden movement, detection and discrimination of that stimulus initially improves:
20 attentional facilitation. However, facilitation lasts only briefly, and is followed by a period of
21 inhibition (of return), during which detection and discrimination are impaired (Posner & Cohen,
22 1984). IOR is often interpreted as a been-there-done-that mechanism (Klein, 2000): A stimulus
23 that captured attention, but turned out to be irrelevant, is inhibited so that it does not capture
24 attention again. We have previously shown that IOR is reflected in pupil size as a relative dilation
25 when a bright, compared to a dark, stimulus is inhibited (Mathôt et al., 2014). Therefore, in the
26 present study, the attention bias away from the memory-match-probe may have reflected IOR;
27 that is, it may have been a natural consequence of memory-driven attentional capture, rather than

1 strategic inhibition.

2 We have used a new pupillometric technique, which is based on the assumption that the
3 pupil is larger when you attend to dark, compared to bright, stimuli. But is this logic valid? And is
4 this technique sufficiently reliable? With respect to validity, we and others have systematically
5 found that the pupillary light response, when combined with a bright/ dark manipulation,
6 measures various forms of visual attention (reviewed in Mathôt & Van der Stigchel, 2015):
7 voluntary (Binda & Murray, 2015; Binda et al., 2013; Mathôt et al., 2013; Naber et al., 2013),
8 involuntary (Mathôt et al., 2014), presaccadic (Mathôt, van der Linden, Grainger, & Vitu, 2015;
9 see also Ebitz, Pearson, & Platt, 2014), and feature-based attention (Binda, Pereverzeva, &
10 Murray, 2014). With respect to reliability, we have previously shown that manual responses and
11 the pupillary light response are about equally sensitive measures of attention (Mathôt et al.,
12 2013). This high sensitivity is corroborated by our ongoing work on a pupillometric method to
13 decode the focus of attention, which reaches over 90% accuracy on single trials (Mathôt, Melmi,
14 Van der Linden, & Van der Stigchel, 2015). Taken together, the pupillary light response seems to
15 be a valid and reliable measure of visual attention.

16 A legitimate question is why pupil size did not show attentional capture toward the memory-
17 match probe, whereas eye movements did. In part, this is due to selection: The eye-movement
18 results are based on the full data, including trials with gaze errors, whereas the pupil-size results
19 are based on the trimmed data, excluding trials with gaze errors. Therefore, pupil size may not
20 have shown attentional capture, because trials on which this occurred most strongly were
21 excluded from the analysis. In addition, the pronounced pupillary constriction at the start of the
22 retention interval may have masked any remaining effects of attentional capture on pupil size,
23 which we would expect to emerge around the same time (400-800 ms, cf. Mathôt et al., 2014).
24 Therefore, the dissociation between eye-movement and pupil-size results is likely skin-deep—and
25 certainly difficult to interpret—and we prefer to treat both sources as complementary. However, we
26 acknowledge that we do not fully understand how attentional capture as measured through eye-
27 movements relates to inhibition as measured through pupillometry; some caution is therefore

1 warranted.

2 In summary, we have used pupillometry and eye movements to test whether and when
3 attention is biased toward stimuli that match the contents of visual working memory (memory-
4 match stimuli). We found that the eyes were drawn toward memory-match stimuli at the start of
5 the retention interval, but that there was no sustained attention bias toward memory-match
6 stimuli; if anything, attention was biased away from them (cf. Sawaki & Luck, 2011). We have
7 offered two interpretations of our results: Following multi-state models of working memory
8 (Olivers et al., 2011; Zokaei et al., 2014b), participants may have avoided attention from being
9 continuously drawn toward memory-match stimuli by putting the memorized color in an
10 accessory working-memory state; alternatively, the attention bias away from the memory-match
11 probe may have reflected inhibition of return. Finally, we suggest that pupillometry, especially
12 when used with a bright/ dark manipulation, is a promising way to unobtrusively track attention
13 over time.

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Competing financial interests

The authors declare no competing financial interests.

Author contributions

EH collected the data. SM and EH analyzed the data. SM wrote the first draft of the manuscript. All authors contributed to the design of the experiment, and revision of the manuscript.

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