University of Groningen

The Pupillary Light Response Reflects Visual Working Memory Content

Husta, Cecilia; Dalmaijer, Edwin; Belopolsky, Artem; Mathot, Sebastiaan

Published in:
JOURNAL OF EXPERIMENTAL PSYCHOLOGY-HUMAN PERCEPTION AND PERFORMANCE

DOI:
10.1037/xhp0000689

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2019

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Husta, C., Dalmaijer, E., Belopolsky, A., & Mathot, S. (2019). The Pupillary Light Response Reflects Visual Working Memory Content. *JOURNAL OF EXPERIMENTAL PSYCHOLOGY-HUMAN PERCEPTION AND PERFORMANCE*, *45*(11), 1522-1528. https://doi.org/10.1037/xhp0000689

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the “Taverne” license. More information can be found on the University of Groningen website: https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment.

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Download date: 03-03-2024

American Psychological Association

Journal of Experimental Psychology:
Human Perception and Performance

© 2019 American Psychological Association
ISSN: 0096-1523

2019, Vol. 45, No. 11, 1522–1528
http://dx.doi.org/10.1037/xhp0000689

The Pupillary Light Response Reflects Visual Working Memory Content

Cecília Hustá
University of Groningen

Edwin Dalmaijer
University of Cambridge

Artem Belopolsky
VU University Amsterdam

Sebastiaan Mathôt
University of Groningen

Recent studies have shown that the pupillary light response (PLR) is modulated by higher cognitive functions, presumably through activity in visual sensory brain areas. Here we use the PLR to test the involvement of sensory areas in visual working memory (VWM). In two experiments, participants memorized either bright or dark stimuli. We found that pupils were smaller when a prestimulus cue indicated that a bright stimulus should be memorized; this reflects a covert shift of attention during encoding of items into VWM. Crucially, we obtained the same result with a poststimulus cue, which shows that internal shifts of attention within VWM affect pupil size as well. Strikingly, the effect of VWM content on pupil size was most pronounced immediately after the poststimulus cue, and then dissipated. This suggests that a shift of attention within VWM momentarily activates an "active" memory representation, but that this representation quickly transforms into a "hidden" state that does not rely on sensory areas.

Public Significance Statement

In this study, we show that actively processing brightness-related information in visual working memory is reflected in the pupillary light response, such that processing dark information results in larger pupils than processing light information. This suggests that this active processing relies on sensory areas, but as this representation transforms into a "hidden" state the involvement of these regions diminishes.

Keywords: pupillometry, pupil light response, visual working memory

Supplemental materials: http://dx.doi.org/10.1037/xhp0000689.supp

Traditionally, the pupillary light response (PLR) was considered a reflex in response to changes in environmental brightness. However, recent studies have demonstrated that the PLR is modulated by higher-level cognition (reviewed in Binda & Murray, 2015; Mathôt, 2018). Such effects likely occur when higher-level cognition affects activity in visual sensory brain areas, which is subsequently "read out" by the pupils.

For example, in several studies, participants were presented with both a dark and a bright stimulus, and were subsequently cued to attend to either one of these without shifting their gaze (i.e., covert attention). Attending to the bright stimulus resulted in smaller pupils than attending to the dark stimulus (Binda, Pereverzeva, & Murray, 2013; Mathôt, van der Linden, Grainger, & Vitu, 2013; Naber, Alvarez, & Nakayama, 2013; Unsworth & Robison, 2017). Single-cell-recording studies have linked this effect to the frontal eye fields (FEF), a part of the frontal cortex that is associated with covert visual attention. Microstimulation of FEF results in increased covert attention to a specific part of the visual field (Moore & Fallah, 2001). Crucially, if the stimulated region corresponds to the location where a bright stimulus appears, the pupil constricts more strongly than if the stimulus appears at a different, unstimulated location (Ebitz & Moore, 2017). A similar effect has been reported for microstimulation of the superior colliculus (SC), a midbrain region that is similarly associated with visual attention (Wang & Munoz, 2018). Taken together, both behavioral and neurophysiological studies have shown that covert visual attention enhances the PLR.

A PLR can even be elicited without the physical presence of bright or dark stimuli. In studies of mental imagery, participants

---

Cecília Hustá, Faculty of Science and Engineering and Department of Experimental Psychology, University of Groningen; Edwin Dalmaijer, MRC Cognition and Brain Sciences Unit, University of Cambridge; Artem Belopolsky, Department of Experimental and Applied Psychology, VU University Amsterdam; Sebastiaan Mathôt, Department of Experimental Psychology, University of Groningen.

Participant data, experimental scripts, and analysis scripts are available from https://osf.io/ejxfa/.

Correspondence concerning this article should be addressed to Sebastiaan Mathôt, Department of Experimental Psychology, University of Groningen, Grote Kruisstraat 2/1, 9712 TS Groningen, the Netherlands. E-mail: s.mathot@cogsci.nl

were instructed to imagine stimuli that had previously been presented with varying brightness levels. The size of the pupil varied depending on the imagined brightness, with brighter objects resulting in smaller pupils (Laeng & Sulutvedt, 2014). This effect was replicated with mental imagery of real-life scenarios: Imagery of scenes such as "a sunny sky" resulted in smaller pupils than imagery of scenes such as "a dark room" (Laeng & Sulutvedt, 2014). These results are consistent with the finding that similar visual sensory areas are active during perception and mental imagery of visual objects (Ganis, Thompson, & Kosslyn, 2004). Presumably, the activity in visual sensory areas that is elicited by mental imagery subsequently affects pupil size.

According to many theoretical frameworks, mental imagery is highly related to visual working memory (VWM). VWM is a system with limited storage capacity that holds visual information ready for immediate use. VWM consists of encoding and maintenance. During encoding, visual stimuli are visible and a VWM representation is created (Bundesen, 1990; Dalmaijer, Manohar, & Husain, 2018). During maintenance, stimuli are no longer visible, and their VWM representations therefore need to be rehearsed so that they can be used later (Zokaei, Heider, & Husain, 2014). Analogous to mental imagery, maintenance of stimuli in VWM activates visual sensory areas (Yi, Turk-Browne, Chun, & Johnson, 2008). However, there are also clear differences between mental imagery and VWM; specifically, VWM generally retains a memory of items that were just seen, whereas mental imagery refers to a mental picture of something that was retrieved from long-term memory, or even of something that is purely the product of one's imagination. Nevertheless, there are clear similarities between mental imagery and VWM, and this leads to the prediction that maintaining bright stimuli in VWM should lead to pupil constriction.

However, the only study so far that investigated this question reported that maintaining bright or dark stimuli in VWM did not affect the PLR (Blom, Mathôt, Olivers, & Van der Stigchel, 2016). Blom and colleagues (2016) cued participants to memorize either bright or dark objects. In different experiments, participants memorized the shape, orientation, or exact brightness level of the stimuli. Pupil size was significantly smaller when participants were encoding the bright as compared to the dark stimuli. However, this effect faded approximately one second after the stimuli disappeared from the screen. This led Blom and colleagues (2016) to conclude that the PLR reflects VWM content during encoding, but not during maintenance. Phrased differently, the authors concluded that keeping bright or dark objects in VWM does not affect pupil size.

However, there are several alternative explanations for the results of Blom and colleagues (2016) that warrant a reinvestigation of this crucial question. Notably, in their experiments, participants were presented with a cue before (rather than after) the presentation of the brightness-related stimuli, and this cue indicated whether only the bright or only the dark stimuli needed to be memorized. Therefore, participants covertly shifted their attention to either the bright or the dark stimuli while these were actually present on the screen, leading to differences in pupil size (cf. Binda et al., 2013; Mathôt et al., 2013). Crucially, because this pupil-size difference persisted into the maintenance period, it was not clear whether any pupil-size differences during maintenance were due to VWM per se, or merely reflected a carry-over effect from the encoding phase (as Blom and colleagues concluded).

The question of whether brightness-related content in VWM affects pupil size is important, because, if so, this would strongly suggest that VWM relies on sensory brain areas—currently a hotly debated topic (Gayet, Paffen, & Van der Stigchel, 2018; Xu, 2017). Therefore, to firmly establish whether keeping bright or dark stimuli in VWM affects pupil size, we designed a paradigm that allowed us to distinguish any effects due to VWM encoding from effects due to VWM maintenance.

In Experiment 1, we first replicated the effect of covert visual attention on the PLR (Binda et al., 2013; Blom et al., 2016; Mathôt et al., 2013; Unsworth & Robison, 2017). As shown in many earlier studies, we expected that directing covert attention to dark or bright stimuli during VWM encoding would be reflected in the PLR. Crucially, we then introduced a retro-cue to investigate the relationship between VWM maintenance and the PLR (cf. Belopolsky & Theeuwes, 2011). In this condition, participants were instructed to first encode both bright and dark stimuli, so that the encoding phase was identical in all trials. Subsequently, participants dropped one stimulus from VWM when the retro-cue was presented, leaving either only bright or only dark stimuli for maintenance in VWM. We predicted that maintaining bright stimuli would result in smaller pupils as compared to maintaining dark stimuli.

In Experiment 2, we replicated the key results of Experiment 1. In addition, we investigated whether the extent to which the PLR reflects VWM content depends on memory load; specifically, single-item-template theories posit that only a single item in VWM can be in a prioritized state, and that only this item is represented in visual sensory areas (Folk & Anderson, 2010; Houtkamp & Roelfsema, 2009; Oberauer, 2002; Olivers, Peters, Houtkamp, & Roelfsema, 2011; Zokaei, Manohar, Husain, & Feredoes, 2014). These theories are largely based on studies investigating whether visual attention is guided by the contents of visual working memory (e.g., Frătescu, Van Moorselaar, & Mathôt, 2019; van Moorselaar, Theeuwes, & Olivers, 2014). However, when applied to the present paradigm, single-item-template theories would predict that the effect of VWM content on the PLR is reduced, or even absent (van Moorselaar et al., 2014), when more than one item is maintained in VWM.

To foresee the results, we found that the content of VWM indeed affects the PLR: Pupil size is smaller when participants maintain a bright item, as compared to a dark item. We did not find a compelling dissociation between a memory load of one or two items.

Experiment 1

Method

Participant data, experimental scripts, and analysis scripts are available from https://osf.io/ejxfa/.

Participants. We recruited 30 first-year psychology students from the University of Groningen, who participated for course credit. We based our sample size ($N = 30$) on a previous study (Mathôt, Grainger, & Strijkers, 2017) that used a similar analysis and similarly investigated a cognitive effect on the PLR. All participants had normal or corrected to normal vision, except for 2 participants, who were able to participate without their glasses. The age of the participants ranged between 18 and 54 ($M = 21$, $SD = 6.47$), and 23 participants were females, 6 were males, and one identified as a different gender. Both experiments were approved by the local ethics review board of the Department of Psychology of the University of Groningen (17370-S-NE).

Apparatus. Participants' eye movements and pupil sizes were recorded with an Eyelink 1000 (SR Research, Mississauga, Ontario, Canada), and the data was sampled at 1000 Hz. We recorded the right pupil. The experiment took place in a dark room and participants placed their head in a chin rest. The task was designed with OpenSesame 3.2.0 (Mathôt, Schreij, & Theeuwes, 2012), using PyGaze for eye tracking (Dalmaijer, Mathôt, & Van der Stigchel, 2014). The stimuli were presented on a monitor with an LCD display with a 60 Hz refresh rate and a resolution of 1920 × 1080.

Procedure and stimuli. Before the experiment, the eye tracker was calibrated with a five-point calibration procedure. Next, on each trial, participants memorized a particular brightness level of black and white circles that appeared on a gray background (62 cd/m^2). Participants were instructed to keep their eyes focused on a central black fixation dot (2 cd/m^2) at all times. There were 10 practice trials. Next, there were 16 blocks of 16 trials. The order of conditions was fully randomized within blocks.

In the Pre-Cue condition, participants were initially presented with a cue (an arrow pointing to the left or right) indicating whether the stimulus on the left or right would be task relevant. Subsequently, two stimuli appeared (one black and one white circle), one of which they had to encode. This was followed by a 4-s retention interval. During the response phase, participants were presented with a circle of the same or a similar brightness as the one they had memorized. Participants had to report whether the brightness of this circle was the same as, or different from, the one they had memorized. The Retro-Cue condition was almost identical to the Pre-Cue one; however, the order of the cue and target was reversed. (For durations of individual phases of the trial, see Figures 1a and 1c).

The targets for the bright and dark trials were randomly selected from a range of possible brightness levels. The bright range extended from 88 cd/m^2 to 96 cd/m^2, and the dark range extended from 11 cd/m^2 to 19 cd/m^2. A "different" response stimulus was brighter on some trials and darker on others. The size of this difference was controlled by a Quest adaptive procedure (Watson & Pelli, 1983). It was implemented to control for participants' accuracies, holding them constant at 75% for dark and bright stimuli separately.

After participants completed the task, they were asked about the strategies they used throughout the experiment (see online supplemental materials).

Exclusion criteria. For both conditions, trials in which the pupil during the baseline period (see Results) was smaller than 2.1 mm in diameter or greater than 6.8 mm in diameter ($N(\text{trial}) = 6$) were excluded (as values above these were clear outliers based on a visual inspection of the pupil-baseline histogram). Additionally, in the Pre-Cue condition, trials were excluded if participants' horizontal gaze position deviated from the central band (between the targets) position during the presentation of the encode screen ($N(\text{trial}) = 522$). No such exclusion criterion was used for the Retro-Cue condition, because participants did not know which stimulus was the target during the presentation of the encode screen, and eye movements could therefore not be systematically biased toward the to-be-memorized stimulus.

Results

Pupil size was baseline corrected by subtracting mean pupil size during the 3–4-s interval, just before the start of the crucial period (Mathôt, Fabius, Van Heusden, & Van der Stigchel, 2018). We conducted a linear mixed effects analysis (LME) on all trials (correct and incorrect; analyzing only correct trials did not qualitatively change the results) with Pupil Size as the dependent measure, and two fixed effects, each containing two levels (Brightness: Bright and Dark; Condition: Pre-Cue and Retro-Cue), and their interaction. We included by-participant random intercepts and slopes for all fixed effects (including the interaction). This analysis was conducted for each 10-ms time window separately; that is, separate models were fitted with mean pupil size for each 10-ms time window as a dependent measure. We considered effects significant if $t > 1.96$ (cf. Mathôt, Dalmaijer, Grainger, & Van der Stigchel, 2014; Mathôt et al., 2013), although we emphasize overall patterns and effect sizes rather than significance of individual data points. There was a significant interaction between Brightness (Bright; Dark) and Condition (Pre-Cue; Retro-Cue) between 4800 ms and 6090 ms. Therefore, we also performed two separate LMEs for the two conditions (also run with all trials).

For the Pre-Cue condition, there was a significant effect of Brightness from 4700 ms to 7390 ms, meaning that the pupil difference appeared during encoding of the brightness-related stimuli and briefly persisted into the maintenance phase (Figure 1a). Twenty-five participants (out of 30) showed an effect in the expected direction (Figure 1b). In general, this means that when participants covertly attended to the white circles on the encode screen, their pupils were smaller than when they attended to the black circles.

In the Retro-Cue condition, there was an effect of Brightness from 4900 ms until 7590 ms (Figure 1c), directly corresponding to the maintenance phase. The effect occurred in the expected direction for 25 participants (out of 30; Figure 1d). This indicates that VWM content is reflected in the PLR not only during encoding but also during maintenance. Phrased differently, shifting attention within VWM representations (that are brightness-related) is reflected in pupil size, such that internally shifting attention toward bright stimuli elicits smaller pupils than internally shifting attention toward dark stimuli.

The accuracies between the Pre-Cue and Retro-Cue conditions were kept similar, although not perfectly identical, by a Quest adaptive procedure (Watson & Pelli, 1983). In the Pre-Cue condition, the mean accuracy was 75% for bright trials and 74% for dark trials. In the Retro-Cue condition, the mean accuracy was 71% for bright and 69% for dark trials. Therefore, it is unlikely that effects on pupil size were driven by differences in accuracy between conditions.

Discussion

In Experiment 1, we examined whether visual working memory (VWM) content is reflected in the pupillary light response (PLR).

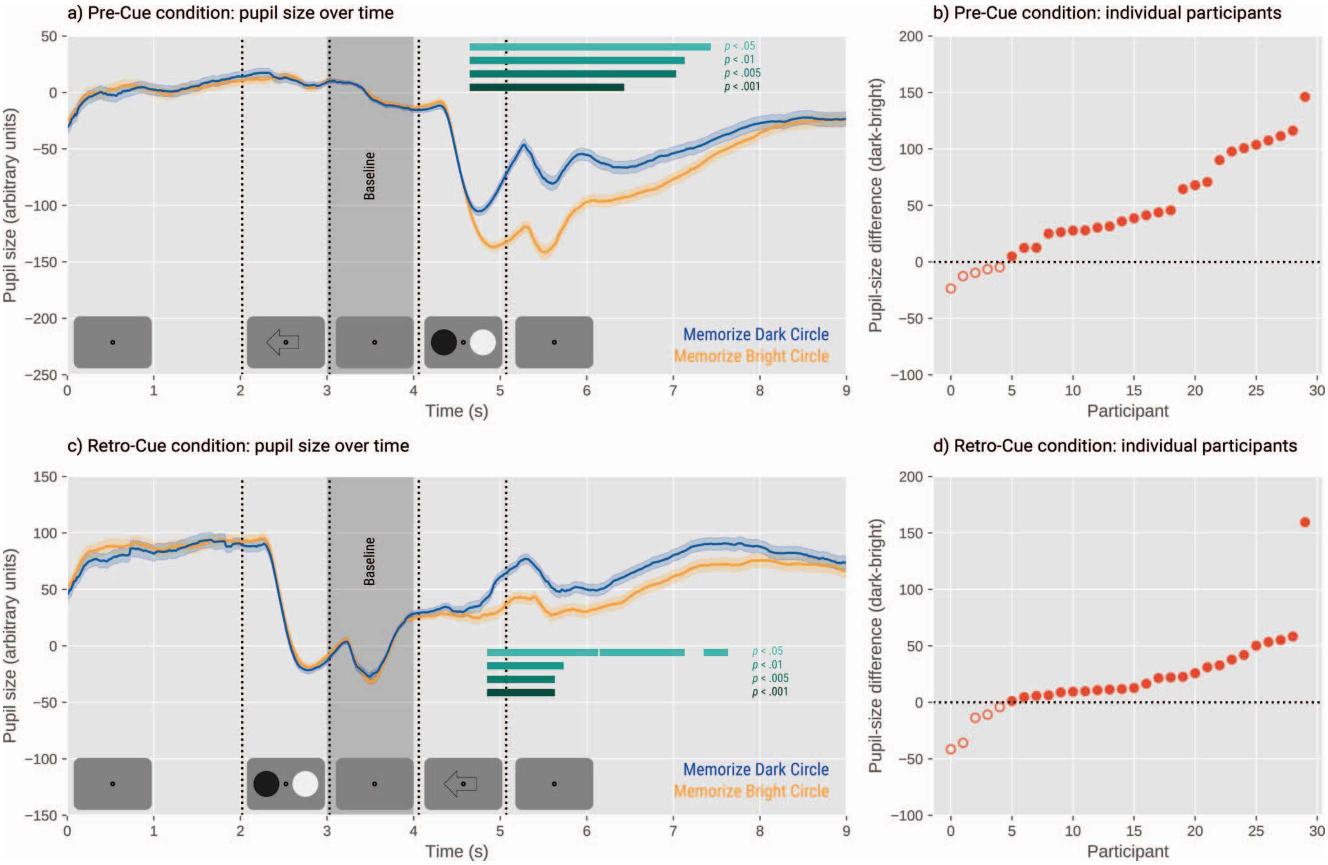


Figure 1. Results of Experiment 1. a) This figure shows average pupil size for all participants through the progression of all Pre-Cue trials. The orange line represents average pupil size when bright stimuli are the targets and the blue line when dark stimuli are the targets. The shaded error bands represent the grand standard error (i.e., across individual trials). The green horizontal bars indicate the periods during which there was a reliable effect of Brightness, separately for the Post-Cue and Pre-Cue conditions (see main text for details). b) Shows the average effects of individual participants in the Pre-Cue condition between 4.5 s and 6.5 s calculated by subtracting the mean pupil size for bright trials from dark trials. c) Shows averaged pupil size for all participants through the progression of all Retro-Cue trials. d) Shows the average effects of individual participants in the Retro-Cue condition calculated in the same way as for the Pre-Cue condition. See the online article for the color version of this figure.

Specifically, we wanted to know whether maintaining bright stimuli in VWM is associated with smaller pupils than maintaining dark stimuli. We showed that VWM content is reflected in the PLR during both encoding and when actively processing the content during VWM maintenance (i.e., when dropping one item after a retro-cue). Consistent with previous studies (Binda et al., 2013; Laeng & Sulutvedt, 2014; Mathôt et al., 2013), this shows that the PLR, which was previously thought of as a simple reflex, is controlled by higher cognitive processes, such as working memory.

Experiment 2

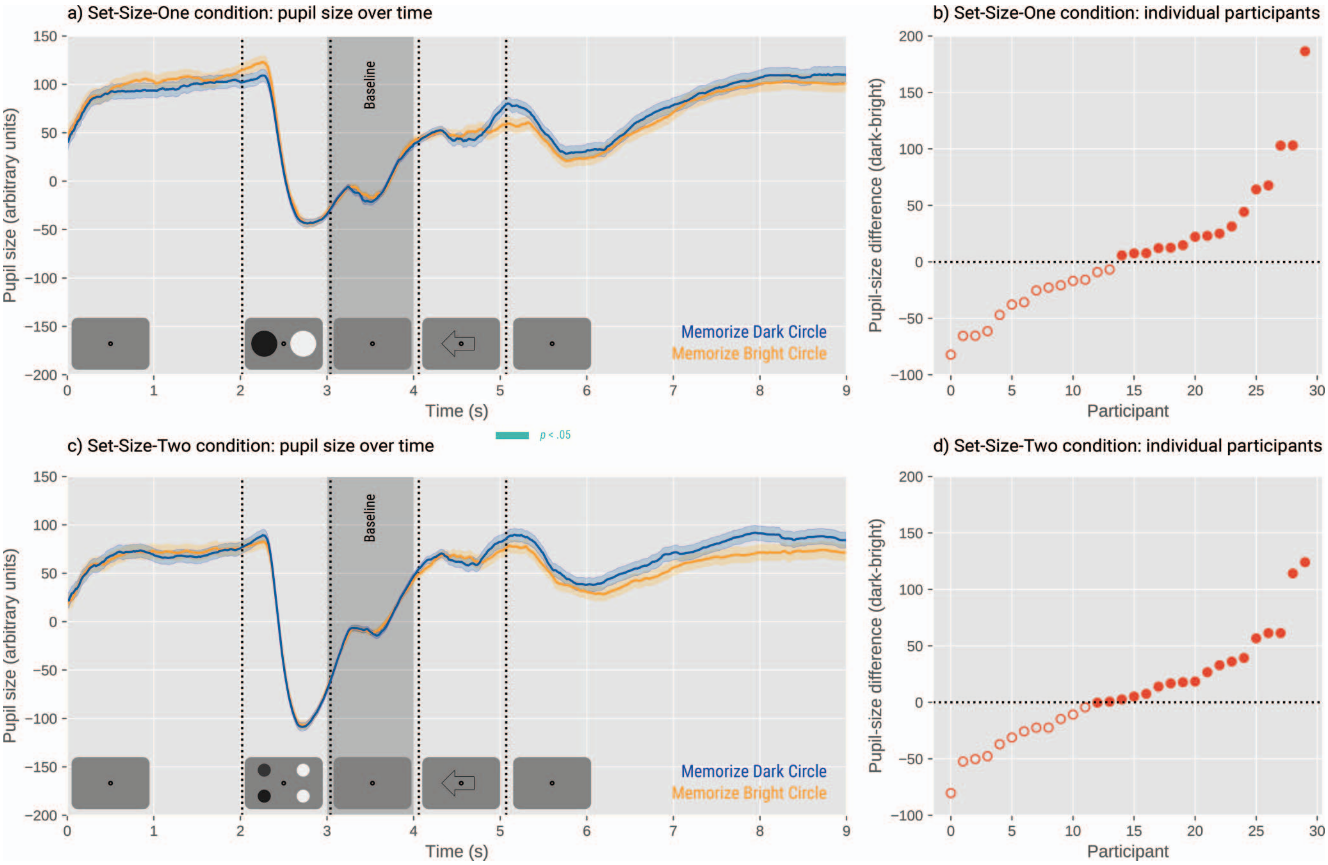
Method

The methods were similar to those of Experiment 1, and only differences are described below.

Participants. Thirty new participants were recruited. The age of the participants ranged between 18 and 34 ($M = 21.03$, $SD = 3.00$), and 19 were females and 11 were males.

Procedure and stimuli. The goal of the task was again to remember brightness level of black and white stimuli, but the number of stimuli now varied (within blocks). There were 16 practice trials. Next, there were 14 blocks of experimental trials.

The sequence of both conditions was the same as in the Retro-Cue condition in Experiment 1. The Retro-Cue condition from Experiment 1 was identical to the Set-Size-One condition from Experiment 2, in which participants maintained one stimulus (Figure 2a). In the Set-Size-Two condition, participants maintained two stimuli, after four circles were presented on the encode screen (Figure 2c). The subsequent arrow indicated whether the stimuli on the right or left were task relevant, and two circles were presented on the response screen. On “different” trials, the brightness of only one of the circles changed to


a) Set-Size-One condition: pupil size over time

b) Set-Size-One condition: individual participants

c) Set-Size-Two condition: pupil size over time

d) Set-Size-Two condition: individual participants

Figure 2. Results of Experiment 2. a) This figure shows average pupil size for all participants through the progression of all Set-Size-One trials. The orange line represents average pupil size when bright stimuli are the targets and the blue line when dark stimuli are the targets. The shaded error bars represent the grand standard error (i.e., across individual trials). The green horizontal bar indicates the period during which there was a reliable effect of Brightness on pupil size across the two Set-Size conditions (see main text for details). b) Shows the average effects of individual participants in the Set-Size-One condition between 4.5 s and 6.5 s calculated by subtracting the summed pupil size for bright trials from dark trials. c) Shows averaged pupil size for all participants through the progression of all Set-Size-Two trials. d) Shows the average effects of individual participants in the Set-Size-Two condition calculated in the same way as for the Set-Size-One condition. See the online article for the color version of this figure.

ensure that participants remembered the brightness of both circles.

The targets for the bright and dark trials were again selected from a specified brightness range. There were two bright ranges (very bright: 101 cd/m^2–113 cd/m^2; somewhat bright: 83 cd/m^2–92 cd/m^2) and two dark ranges (somewhat dark: 23 cd/m^2–32 cd/m^2; very dark: 2 cd/m^2–13 cd/m^2). How a stimulus changed on "different" trials depended on the brightness range it was selected from: Very bright and somewhat dark always changed to a darker stimulus; somewhat bright and very dark always changed to a lighter stimulus. When four circles were presented on the screen, they were all selected from different brightness ranges, to ensure sufficient variance in the brightness levels. The size of the brightness difference was controlled by a Quest adaptive procedure (Watson & Pelli, 1983). It was implemented to control for the participants' accuracies, holding them constant at 75%, and it controlled for the accuracy separately in the four conditions (Set-Size-One Bright, Set-Size-One Dark, Set-Size-Two Bright, and Set-Size-Two Dark).

Exclusion criteria. Trials on which the pupil size at baseline was lower than 2.1 mm or higher than 6.8 mm in diameter (N(trial) = 9) were again excluded.

Results

A similar LME analysis was performed as for Experiment 1, using Brightness (Bright and Dark) and Memory Load (Set-Size-One and Set-Size-Two) as fixed effects. This analysis revealed no interaction between Memory Load and Brightness after the presentation of the retro-cue. This means that the effect of brightness on the PLR did not notably differ between the two memory-load conditions, in turn suggesting that the effect of brightness-related VWM content on the PLR does not crucially depend on the priority status of the items in VWM.

Since we did not find a significant interaction, we created a model with only the main effect of Brightness. (We could not meaningfully analyze the main effect of Memory Load in this analysis, because the memory array was shown before the baseline period. However, the main effect of Memory Load was not of primary interest here; Kahneman & Beatty, 1966). Crucially, we found that participants' pupils were smaller when maintaining bright stimuli, as compared to dark stimuli, at the beginning of the maintenance phase from 5000 ms to 5300 ms. Numerically, this effect was slightly more pronounced in the Set-Size-One condition (Figure 2a) than in the Set-Size-Two condition (Figure 2c), although (as noted above) there was no reliable interaction between Memory Load and Brightness, and we therefore did not analyze the conditions separately.

The accuracies of all conditions were close to 75% due to interleaved Quest adaptive procedures (Watson & Pelli, 1983). However, this procedure was slightly less effective in the Set-Size-One condition, where mean accuracy for the bright trials was 69% and 68% for the dark trials. In the Set-Size-Two condition, the accuracy was 74% for the bright and 71% for the dark trials. Importantly, however, accuracies for the Brightness conditions (if not for Memory Load) were highly similar, indicating the accuracy differences do not account for the effect of Brightness.

Discussion

The results of Experiment 2 support our conclusions from Experiment 1 that the VWM content is reflected in the PLR not only during encoding but also during maintenance, especially while actively processing the content. This indicates that when people shift attention within their VWM representations (that are brightness-related), these internal shifts are reflected in their pupil size such that rehearsing bright stimuli elicits smaller pupils than rehearsing dark stimuli. However, we did not find a compelling dissociation between maintenance of one or two brightness-related stimuli. Such a dissociation would be predicted by strong single-item-template theories, which hold that there can be only one active item in VWM at a time (Olivers et al., 2011). We found qualitatively similar effects on pupil size with a memory load of two items, as compared to one item. Overall, our results suggest that whether a VWM item is in an active or "silent" state depends strongly on time, and at most weakly on memory load.

General Discussion

In two experiments, we examined whether visual working memory (VWM) content is reflected in the pupillary light response (PLR). Overall, we showed that VWM content is reflected in the PLR both during encoding (i.e., when covertly attending the to-be-encoded items) and while actively processing the content during maintenance. This shows that PLR is controlled by higher cognitive processes, which confirms that the PLR is more than just a simple reflex (Binda et al., 2013; Laeng & Sulutvedt, 2014; Mathôt et al., 2013). Our results further suggest that VWM involves sensory representations, presumably in the visual cortex (Yi et al., 2008), which subsequently trigger pupil responses.

A striking aspect of our results is the time course (in the Retro-Cue condition of Experiment 1, and Experiment 2). The content of VWM affected pupil size most strongly briefly after the presentation of the retro-cue, rather than throughout the entire retention interval. This did not appear to be driven by increased noise with increasing time since the baseline period, because we observed a clear "bump" in the effect of VWM content on pupil size immediately following the presentation of the retro-cue (around the 5.5-s mark in Figures 1 and 2). This was unexpected, considering that we anticipated that the effect on pupil size reflected maintenance of different brightness levels, which should occur during the entire retention interval. However, this time course is consistent with recent studies showing that VWM maintenance is not accompanied by sustained activity in visual sensory brain areas, but rather that such activity is periodical or transient (Rose et al., 2016; Sprague, Ester, & Serences, 2016; Sreenivasan, Curtis, & D'Esposito, 2014; Stokes, 2015; Wolff, Jochim, Akyürek, & Stokes, 2017). Our finding that pupil size reflects VWM content only briefly may reflect a transition from an "active" state (which is reflected in pupil size) to a "hidden" state (which is not reflected in pupil size). This provides unique new support for the notion of hidden VWM states, which has so far come primarily from decoding analyses in brain imaging; however, decoding studies provide inconclusive evidence for hidden states, because simulations indicate that re-emerging stimulus decodability in neuroimaging data could also reflect sustained neural activity (Schneegans & Bays, 2017).

The finding that VWM content affects pupil size only briefly, rather than throughout the entire retention period, further suggests that this effect is not purely driven by mental imagery, because a recent study suggests that mental imagery of bright or dark objects affects pupil size in a sustained fashion (although a detailed time course analysis was not provided; Laeng & Sulutvedt, 2014).

So why is pupil size affected by the content of VWM and other cognitive factors? Possibly, the effect of higher cognitive functions on pupil size are preparatory mechanisms that optimize pupil size in anticipation of an environmental change in brightness (Mathôt, van der Linden, Grainger, & Vitu, 2015). For example, if you are in the dark and think about turning on a lamp, it is likely that you are going to do this soon. Therefore, it might be beneficial for your pupils to constrict before a sudden change of luminance impairs your vision.

References

Belopolsky, A. V., & Theeuwes, J. (2011). Selection within visual memory representations activates the oculomotor system. *Neuropsychologia, 49,* 1605–1610. http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.045

Binda, P., & Murray, S. O. (2015). Keeping a large-pupilled eye on high-level visual processing. *Trends in Cognitive Sciences, 19,* 1–3. http://dx.doi.org/10.1016/j.tics.2014.11.002

Binda, P., Pereverzeva, M., & Murray, S. O. (2013). Pupil constrictions to photographs of the sun. *Journal of Vision, 13*(6), 8. http://dx.doi.org/10.1167/13.6.8

Blom, T., Mathôt, S., Olivers, C. N. L., & Van der Stigchel, S. (2016). The pupillary light response reflects encoding, but not maintenance, in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance, 42,* 1716–1723. http://dx.doi.org/10.1037/xhp0000252

Bundesen, C. (1990). A theory of visual attention. *Psychological Review, 97,* 523–547. http://dx.doi.org/10.1037/0033-295X.97.4.523

Dalmaijer, E. S., Manohar, S. G., & Husain, M. (2018). *Parallel encoding of information into visual short-term memory*. Advance online publication. http://dx.doi.org/10.1101/398990

Dalmaijer, E. S., Mathôt, S., & Van der Stigchel, S. (2014). PyGaze: An open-source, cross-platform toolbox for minimal-effort programming of eyetracking experiments. *Behavior Research Methods, 46,* 913–921. http://dx.doi.org/10.3758/s13428-013-0422-2

Ebitz, R. B., & Moore, T. (2017). Selective modulation of the pupil light reflex by microstimulation of prefrontal cortex. *The Journal of Neuroscience, 37,* 5008–5018. http://dx.doi.org/10.1523/JNEUROSCI.2433-16.2017

Folk, C. L., & Anderson, B. A. (2010). Target-uncertainty effects in attentional capture: Color-singleton set or multiple attentional control settings? *Psychonomic Bulletin & Review, 17,* 421–426. http://dx.doi.org/10.3758/PBR.17.3.421

Frătescu, M., Van Moorselaar, D., & Mathôt, S. (2019). Can you have multiple attentional templates? Large-scale replications of Van Moorselaar, Theeuwes, and Olivers (2014) and Hollingworth and Beck (2016). *Attention, Perception, & Psychophysics*. Advance online publication. http://dx.doi.org/10.3758/s13414-019-01791-8

Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research, 20,* 226–241. http://dx.doi.org/10.1016/j.cogbrainres.2004.02.012

Gayet, S., Paffen, C. L. E., & Van der Stigchel, S. (2018). Visual working memory storage recruits sensory processing areas. *Trends in Cognitive Sciences, 22,* 189–190. http://dx.doi.org/10.1016/j.tics.2017.09.011

Houtkamp, R., & Roelfsema, P. R. (2009). Matching of visual input to only one item at any one time. *Psychological Research, 73,* 317–326. http://dx.doi.org/10.1007/s00426-008-0157-3

Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science, 154,* 1583–1585. http://dx.doi.org/10.1126/science.154.3756.1583

Laeng, B., & Sulutvedt, U. (2014). The eye pupil adjusts to imaginary light. *Psychological Science, 25,* 188–197. http://dx.doi.org/10.1177/0956797613503556

Mathôt, S. (2018). Pupillometry: Psychology, physiology, and function. *Journal of Cognition, 1,* 1–23.

Mathôt, S., Dalmaijer, E., Grainger, J., & Van der Stigchel, S. (2014). The pupillary light response reflects exogenous attention and inhibition of return. *Journal of Vision, 14*(14), 7. http://dx.doi.org/10.1167/14.14.7

Mathôt, S., Fabius, J., Van Heusden, E., & Van der Stigchel, S. (2018). Safe and sensible preprocessing and baseline correction of pupil-size data. *Behavior Research Methods, 50,* 94–106. http://dx.doi.org/10.3758/s13428-017-1007-2

Mathôt, S., Grainger, J., & Strijkers, K. (2017). Pupillary responses to words that convey a sense of brightness or darkness. *Psychological Science, 28,* 1116–1124. http://dx.doi.org/10.1177/0956797617702699

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods, 44,* 314–324. http://dx.doi.org/10.3758/s13428-011-0168-7

Mathôt, S., van der Linden, L., Grainger, J., & Vitu, F. (2013). The pupillary light response reveals the focus of covert visual attention. *PLoS ONE, 8,* e78168. http://dx.doi.org/10.1371/journal.pone.0078168

Mathôt, S., van der Linden, L., Grainger, J., & Vitu, F. (2015). The pupillary light response reflects eye-movement preparation. *Journal of Experimental Psychology: Human Perception and Performance, 41,* 28–35. http://dx.doi.org/10.1037/a0038653

Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences of the United States of America, 98,* 1273–1276. http://dx.doi.org/10.1073/pnas.98.3.1273

Naber, M., Alvarez, G. A., & Nakayama, K. (2013). Tracking the allocation of attention using human pupillary oscillations. *Frontiers in Psychology, 4,* 919. http://dx.doi.org/10.3389/fpsyg.2013.00919

Oberauer, K. (2002). Access to information in working memory: Exploring the focus of attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28,* 411–421. http://dx.doi.org/10.1037/0278-7393.28.3.411

Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences, 15,* 327–334. http://dx.doi.org/10.1016/j.tics.2011.05.004

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science, 354,* 1136–1139. http://dx.doi.org/10.1126/science.aah7011

Schneegans, S., & Bays, P. M. (2017). Restoration of fMRI decodability does not imply latent working memory states. *Journal of Cognitive Neuroscience, 29,* 1977–1994. http://dx.doi.org/10.1162/jocn_a_01180

Sprague, T. C., Ester, E. F., & Serences, J. T. (2016). Restoring latent visual working memory representations in human cortex. *Neuron, 91,* 694–707. http://dx.doi.org/10.1016/j.neuron.2016.07.006

Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in Cognitive Sciences, 18,* 82–89. http://dx.doi.org/10.1016/j.tics.2013.12.001

Stokes, M. G. (2015). "Activity-silent" working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences, 19,* 394–405. http://dx.doi.org/10.1016/j.tics.2015.05.004

Unsworth, N., & Robison, M. K. (2017). Pupillary correlates of covert shifts of attention during working memory maintenance. *Attention, Perception, & Psychophysics, 79,* 782–795. http://dx.doi.org/10.3758/s13414-016-1272-7

van Moorselaar, D., Theeuwes, J., & Olivers, C. N. L. (2014). In competition for the attentional template: Can multiple items within visual working memory guide attention? *Journal of Experimental Psychology: Human Perception and Performance, 40,* 1450–1464. http://dx.doi.org/10.1037/a0036229

Wang, C. A., & Munoz, D. P. (2018). Neural basis of location-specific pupil luminance modulation. *Proceedings of the National Academy of Sciences, 115,* 10446–10451. http://dx.doi.org/10.1073/pnas.1809668115

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33,* 113–120. http://dx.doi.org/10.3758/BF03202828

Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience, 20,* 864–871. http://dx.doi.org/10.1038/nn.4546

Xu, Y. (2017). Reevaluating the sensory account of visual working memory storage. *Trends in Cognitive Sciences, 21,* 794–815. http://dx.doi.org/10.1016/j.tics.2017.06.013

Yi, D.-J., Turk-Browne, N. B., Chun, M. M., & Johnson, M. K. (2008). When a thought equals a look: Refreshing enhances perceptual memory. *Journal of Cognitive Neuroscience, 20,* 1371–1380. http://dx.doi.org/10.1162/jocn.2008.20094

Zokaei, N., Heider, M., & Husain, M. (2014). Attention is required for maintenance of feature binding in visual working memory. *Quarterly Journal of Experimental Psychology, 67,* 1191–1213. http://dx.doi.org/10.1080/17470218.2013.852232

Zokaei, N., Manohar, S., Husain, M., & Feredoes, E. (2014). Causal evidence for a privileged working memory state in early visual cortex. *The Journal of Neuroscience, 34,* 158–162. http://dx.doi.org/10.1523/JNEUROSCI.2899-13.2014

Received February 13, 2019
Revision received June 29, 2019
Accepted July 8, 2019 ■