The pupillary light response reflects encoding, but not maintenance, in visual working memory

[1]Tessel Blom, [2]Sebastiaan Mathôt, [3]Christian N.L. Olivers, [1]Stefan Van der Stigchel

[1]Department of Experimental Psychology, Helmholtz Institute, Utrecht University, Utrecht, The Netherlands

[2]Aix-Marseille University, CNRS, LPC UMR 7290, Marseille, France

[3]Department of Cognitive Psychology, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

Abstract

The pupillary light response has been shown not to be a purely reflexive mechanism, but to be sensitive to higher order perceptual processes, such as covert visual attention. In the present study we examined whether the pupillary light response is modulated by stimuli which are not physically present, but maintained in visual working memory. In all conditions, displays contained both bright and dark stimuli. Participants were instructed to covertly attend and encode either the bright or the dark stimuli, which then had to be maintained in visual working memory for a subsequent change-detection task. The pupil was smaller in response to encoding bright stimuli compared to dark stimuli. However, this effect did not sustain during the maintenance phase. This was the case even when brightness was directly relevant for the working memory task. These results reveal that the encoding of task-relevant and physically present information in visual working memory is reflected in the pupil. In contrast, the pupil is not sensitive to the maintenance of task-relevant, but no longer visible stimuli. One interpretation of our results is that the pupil optimizes its size for perception of stimuli during encoding; however, once stimuli are no longer visible (during maintenance), an "optimal" pupil size no longer serves a purpose, and the pupil may therefore cease to reflect the brightness of the memorized stimuli.

Keywords: pupillometry, visual working memory, encoding, maintenance

Introduction

Traditionally, the pupillary light response (PLR) has been thought to respond to the amount of light entering the eye (Loewenfeld & Lowenstein, 1993). However, recent studies have shown that the PLR is not just a reflexive process, but is also affected by cognitive factors (as reviewed in Mathôt & Van der Stigchel, 2015). For instance, stimuli that subjectively appear bright (e.g. the sun) trigger a constriction of the pupil compared to equiluminant stimuli that appear less bright (e.g. an indoor scene; Binda, Pereverzeva, & Murray, 2013a; Laeng & Endestad, 2012; Naber & Nakayama, 2013). Furthermore, the PLR has been shown to reflect the percept rather than the actual stimulus during episodes of binocular rivalry; that is, when a bright stimulus is presented to one eye, and a dark stimulus to the other eye, the pupil constricts when the brighter stimulus dominates awareness (Naber, Frässle, & Einhäuser, 2011).

Moreover, a recent study by Laeng and Sulutvedt (2014) suggests that the PLR is sensitive to mental imagery. Participants were first presented with a triangle that varied in luminance. Next, while the display remained blank, participants were asked to imagine the same triangle. Results showed that the pupil dilated or constricted in response to, respectively, dark and bright imagined objects. This finding was confirmed in a subsequent experiment, in which participants had to imagine familiar scenarios, instead of triangles, whilst looking at a blank screen.

In the present study, we examined the PLR when stimuli were not physically present, but were kept in visual working memory (VWM). Given that the PLR appears sensitive to higher-order perceptual representations, we wondered whether it is also sensitive to remembered stimuli, rather than actual stimuli. VWM refers to the temporary storage and manipulation of visual information (Baddeley, 1992; Blankenship, 1938; Smith & Jonides, 1997). Theories of VWM generally distinguish between an encoding phase and a maintenance phase. Encoding occurs when a to-be-remembered object is selected in order to store its features. Maintenance happens when the object is no longer visible and its features have to be mentally rehearsed in order to not be forgotten (Cohen, Sreenivasan, & D'Esposito, 2014; Woodman & Vogel, 2005). Encoding and maintenance processes in VWM have been claimed to be two distinct processes (Baddeley, 1992; Woodman & Vogel, 2005). Here we assessed whether the PLR differentially responds to these stages, or is sensitive to both of them. For this purpose, participants were first presented with a cue indicating which of two types of stimuli they had to encode and maintain: dark or bright stimuli. This was then followed by a retention interval, in which participants were required to maintain the stimuli in VWM for a subsequent change-detection task.

If the PLR only reflects the interaction with the actual stimulus, the pupil should be smaller for the brighter stimuli during the encoding phase when the stimuli are presented on the screen. But if the PLR also reflects the content of VWM, this difference in pupil size should persist during the retention interval when the stimuli have to be maintained. To make a distinction between the encoding and the maintenance phase, we included a control condition in which the stimuli only had to be encoded, but did not have to be maintained. In the control condition, participants were presented with the same dark and bright stimuli, but had to indicate whether a target, which was presented before the stimulus array, was present. Here the response was given after a time period that matched the retention interval in the memory condition. Any maintenance-related effects on the pupil in the memory condition should thus arise after the encoding phase as indicated by the control condition.

Experiment 1

In Experiment 1, we examine modulations of the PLR by stimuli which are not physically present, but are kept in visual working memory (VWM). With the inclusion of the control (Attention) condition, we can distinguish the PLR induced by the interaction with the actual stimulus during the encoding phase from the PLR during the maintenance phase. If the content of VWM is reflected in the PLR, the pupil should be smaller for brighter stimuli during the retention interval in the experimental condition than in the control condition, in which merely the presence, rather than the characteristics, of the stimulus had to be maintained.

Methods

Materials

Participant data, and experimental and analyses scripts, are available from: https://bitbucket.org/smathot/p0014.3-pupil-size-and-working-memory-same-different/.

Participants

Fifteen observers (eight female) participated in Experiment 1. Participants were recruited from Utrecht University. All participants were between 18 and 23 years of age and reported normal or corrected-to-normal vision. All participants signed informed consent before participating and received monetary compensation.

Apparatus and Software

The left eye was recorded with an Eyelink 1000 (SR Research, Mississauga, Canada, ON), a video-based eye tracker sampling at 1000 Hz. Stimuli were presented on a 24-inch LG 24MB65PM monitor (1920x1200 px, 60 Hz). Stimulus presentation was controlled with OpenSesame (Mathôt, Schreij, & Theeuwes, 2012) and PsychoPy (Peirce, 2007). A chin rest was used to fixate the participant's head relative to the camera.

Procedure and Stimuli

Before each experiment, a 9-point eye-tracker calibration was performed. Before each trial, a 1-point drift check was completed. Participants were instructed to keep their gaze at the central fixation point throughout the entire trial. All experiments consisted of a Visual-Working-memory condition and an Attention condition, which were blocked and switched halfway the experiment. The order of the conditions was counterbalanced between participants. The trial sequences are depicted in Figure 1.

In the *Visual-Working-memory (VWM) condition*, participants remembered targets and performed a change-detection task after a retention interval. The targets were part of a memory array. The memory array consisted of four red (4.2˚, 28.7 cd/m^2) and four green (4.2˚, 45.9 cd/m^2) placeholders, which were arranged in a circle with an eccentricity of 6.5˚ around the fixation point. The bright and dark targets were always presented in alternation (bright, dark, bright, dark, etc.), and equally spaced in a ring around the central fixation point. Observers were instructed to remember the shapes inside a specific placeholder color, either red or green, as indicated by a red or a green cue (1.2˚). The number of trials in which one placeholder color contained dark shapes and the other placeholder color contained bright shapes was the same. This varied randomly from trial to trial, but was fixed per trial. Thus, on a particular trial, observers would either be remembering all dark or all bright shapes. We used a color cue, instead of directly instructing participants to remember the bright or black stimuli, to de-emphasize brightness in the task instructions. The shapes that had to be remembered consisted of eight different, basic figures: a pentagon, triangle, star, rhombus, square, cross, circle and quatrefoil. All shapes were matched on surface area. The bright shapes had a luminance of 98.0 cd/m^2 and the dark shapes had a luminance of 0.13 cd/m^2. The memory array was followed by a retention interval of 4000 ms. During the retention interval, participants kept the targets in memory for the following change-detection task. In the subsequent change-detection task, participants indicated whether all the targets were the same (left arrow key) or if one of the targets had changed (right arrow key). In 50% of the trials all targets were the same as during the encoding phase. The trial ended once the participant had responded.

The color of the targets, the color of the placeholders, and same or different in the change-detection task were randomized within blocks. The VWM condition consisted of 96 experimental trials (6 blocks) preceded by 16 practice trials.

In the *Attention (ATT) condition*, participants searched for one specific element within a search array. The ATT condition was a control for the VWM condition, because the same stimuli only had to be encoded and not maintained in memory. The search array in the ATT condition was the same as the memory array in the VWM condition and was preceded by the presentation of the to-be-searched target. The target (2.5˚) was presented in the grey color of the background on either a red or a green placeholder (4.2˚) for 1000 ms. The color of the placeholder indicated within which figures of the search array the target had to be searched. The search array was presented for 3000 ms and followed by a retention interval of 4000 ms. During the retention interval, participants withheld their response to the presence of the target. Therefore, the trial progression of the ATT condition was similar to that of the VWM condition. The response was given during the second presentation of the target after the retention interval. The trial ended once the participant had indicated if the target had been present (left arrow key) or absent (right arrow key).

The color of the targets, the color of the placeholders, and the presence or absence of the target in the search array were randomized within blocks. The ATT condition consisted of 96 experimental trials (6 blocks) preceded by 16 practice trials.

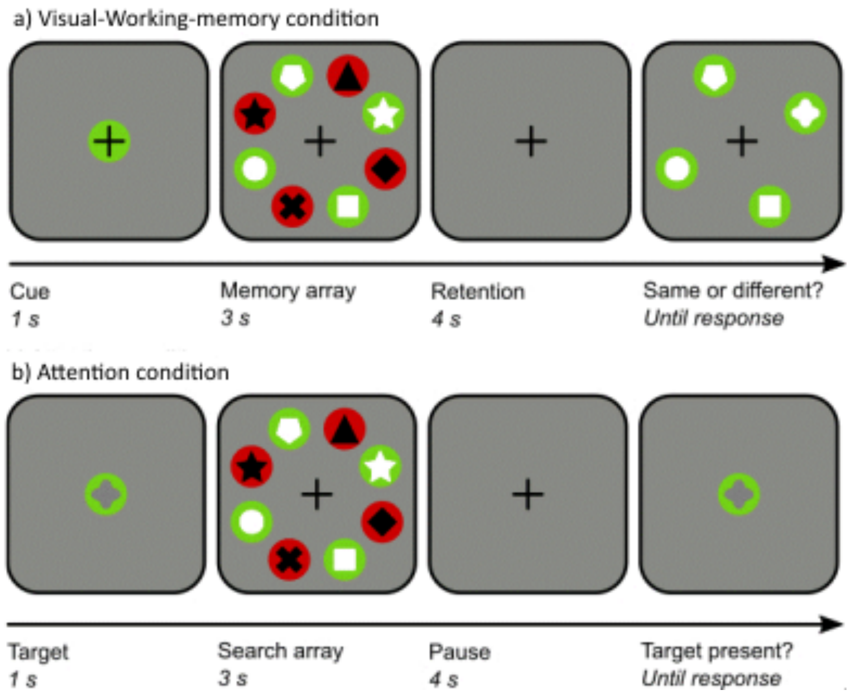

Figure 1*. The trial sequence as presented in a) the VWM condition and b) the ATT condition. In the VWM condition participants were instructed to remember the shapes presented in the cued color. In the ATT condition participants had to search for the target.*

Data Analysis

Significance and trial-exclusion criteria

For the linear mixed-effects (LME) analyses we used t>2, which is comparable to p<0.05 (Baayen, Davidson, & Bates, 2008). However, explicit p values have been omitted due to recent concerns about p value estimation for LME models. For the pupil-trace analysis, only sequences of at least 200 ms for which t>2 were considered to be significant (Mathôt, Van der Linden, Grainger, & Vitu, 2013). Our analysis is similar to previous studies investigating modulations of the PLR (e.g. Mathôt, Dalmaijer, Grainger, & Van der Stigchel, 2014). Trials were excluded when, at any point after cue onset and before the response, participants fixated more than 2.4°[1] in a radius from the fixation dot. No other filtering criteria were applied.

Pupil-Trace Analyses

We analyzed pupil surface throughout the trial relative to a baseline period of 100 ms prior to the cue onset (cf. Mathôt et al., 2013). Cubic-spline interpolation was used for the reconstruction of blinks (Mathôt, 2013). To test for effects of Target Brightness (Dark, Bright) in each Condition (Visual-Working-memory, Attention), we conducted an LME with Target Brightness as fixed effect for each condition separately. Periods during which there was a significant pupil effect were based on these models. To test whether the effect of Target Brightness differed between conditions, we conducted an LME with Target Brightness, Condition, and their interaction as fixed effects. In all cases, models included by-participant random intercepts and slopes for all fixed effects, used pupil size as dependent measure, and were conducted for each 10 ms window separately.

As can be seen in Figure 2, both the presentation of the cue and the search display triggered a pupillary constriction; these are visual responses to a change of visual input. In addition, there was a slow dilation throughout the trial reflecting steadily increasing arousal. This pupil dilation relative to the start of the trial is non-informative since it only indicates that the participant paid attention, but does not provide us with information about the content of VWM (Mathôt, Dalmaijer, Grainger, & Van der Stigchel, 2014). Therefore, we focus

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1 A stricter criterion of e.g. a 1.2° threshold did not substantially change the results of the experiments.

on a constriction of the pupil on Target-Color-Bright compared to Target-Color-Dark trials, which from here on will be referred to as the pupil effect. Phrased differently, we restrict our analyses to differences between conditions.

Results and Discussion

No participants were excluded and after selection, 2524 trials (87.6%) were entered into the analyses.

Behavioral Data

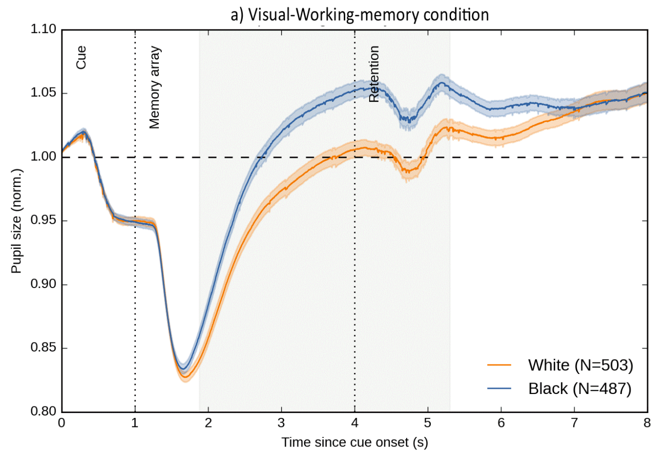
In the VWM condition, the mean accuracy was 83% (SD 9%). In the ATT condition, the mean accuracy was 99% (SD 1%).

A paired-samples t-test showed no significant difference in accuracy between bright and dark targets in the ATT condition ($t(14)=.225$, $p=.825$), nor in the VWM condition ($t(14)=.245$, $p=.81$).

Pupil traces

The pupil responses for the VWM and ATT condition are shown in Figure 2. In the VWM condition, there was a significant pupil effect, such that the pupil was smaller for bright targets than dark targets, between 1880 – 5299 ms (that is, all LMEs conducted within this window yielded a reliable effect of Target Brightness). In the ATT condition, the same pupil effect was evident during the interval 1760 – 4019, with the exception of a brief period between 3339 and 3350 ms. There was no interaction between Condition and Target

Brightness (that is, LMEs did not yield a reliable Target Brightness by Condition interaction for at least 200 consecutive milliseconds).



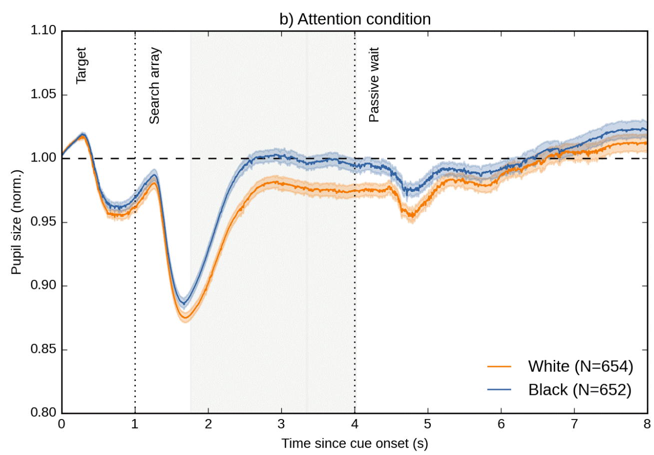


Figure 2*. Pupil size as a function of Stimulus Color and time since cue onset for a) the VWM condition and b) the ATT condition. The orange line portrays pupil size for Bright Stimuli and the blue line for Dark Stimuli. Error shadings indicate standard errors. Data reflects the unsmoothed grand mean signal.*

The results of Experiment 1 show that the pupil is smaller when bright rather than dark stimuli are encoded into working memory; however, this effect dissipates during VWM maintenance and is no longer present during the final part of the delay period. Although the pupil effect qualitatively persists for some time during VWM maintenance, this is likely a lingering response stemming from encoding; that is, it takes some time for the pupil effect to disappear. This interpretation is supported by the observation that the pupillary results of the VWM condition are similar to those of the ATT condition: in the ATT condition participants had to remember the presence of the target, not the visual objects. Since there is also still a pupil effect at the start of the retention interval in the ATT condition, this effect cannot be explained by the content of VWM but is probably the aftermath of the encoding phase.

In Experiment 1, the stimuli were all canonical figures and hence the stimuli were probably easy to verbalize. Therefore, the loss of the pupil effect during the maintenance phase could possibly be explained by the verbalization of the stimuli. In order for stimuli to be stored in VWM, they should not be verbalized. Within working memory, the phonological loop and the visuospatial sketchpad entail two different systems (Baddeley, 2003). If a stimulus is therefore verbalized, it will not be maintained in VWM. In Experiment 2 we tried to avoid the verbalization of stimuli.

Experiment 2

In Experiment 2 we used stimuli that were harder to verbalize. The task-relevant stimulus' feature for the change-detection task was no longer the shape, as in Experiment 1, but the orientation of a single shape. The orientation of the stimuli only slightly varied, which makes verbalization harder, and hence we tried to ensure that visual (as opposed to verbal) working memory was used. The rest of the design stayed the same.

Methods

Participants

Sixteen new observers (eleven female) participated in Experiment 2.

Procedure and Stimuli

In Experiment 2, the stimuli were squares that had been rotated in 11.25° steps, making a total of eight possible stimuli. Furthermore, to keep overall accuracy at around the same level as in Experiment 1, the memory array contained six instead of eight stimuli. Therefore, three stimuli had to be kept in VWM in the VWM condition. The memory and search array for Experiment 2 can be found in Figure 3.

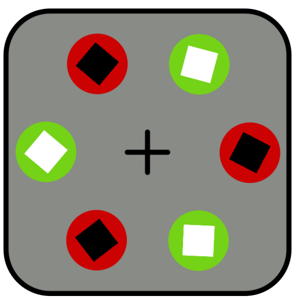


Figure 3. *The memory array as presented in the VWM condition and the search array as presented in the ATT condition consisted of a total of six squares that had been rotated in 11.25° steps.*

Results and Discussion

No participants were excluded. After selection (using the same criteria as for Experiment 1), 2320 trials (75.5%) were entered into the analyses.

Behavioral Data

In the VWM condition the mean accuracy was 66% (SD 7%). In the ATT condition the mean accuracy was 73% (SD 8%).

A paired-samples t-test showed no significant difference in accuracy between bright and dark targets in the ATT condition ($t(15)=.554$, $p=.588$), nor in the VWM condition ($t(15)=.990$, $p=.338$).

Pupil traces

The results are qualitatively similar to those of Experiment 1. There was no significant effect of Target Brightness in the VWM condition. In the ATT condition there was a brief interval (2220-2419 ms) showing a significant effect of Target Brightness as shown in Figure 4. There was no interaction between Condition and Target Brightness.

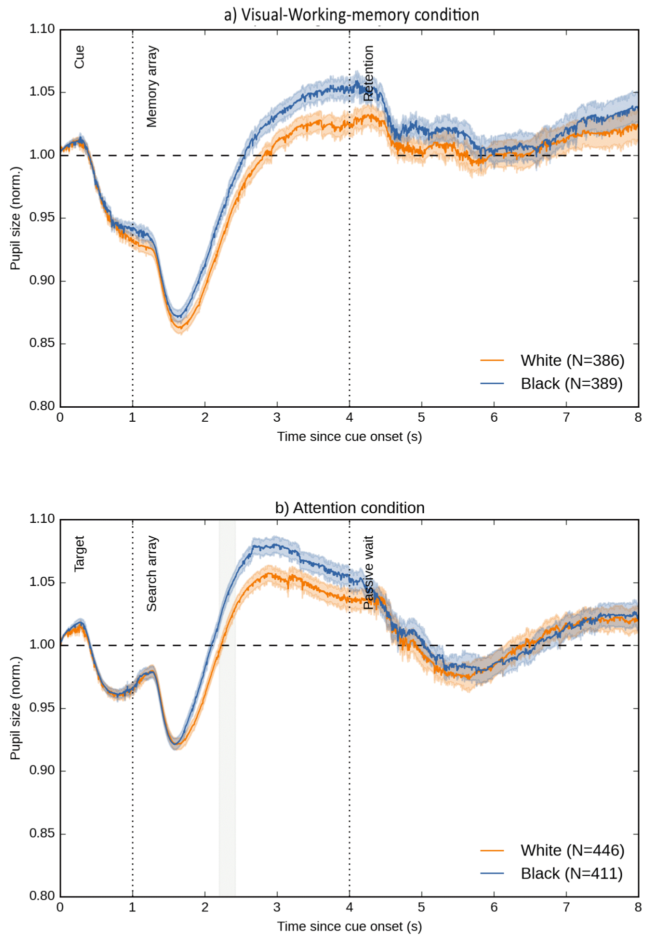


Figure 4*. Pupil size as a function of Stimulus Color and time since cue onset for a) the VWM condition and b) the ATT condition in Experiment 2. The orange line portrays pupil size for Bright Stimuli and the blue line for Dark Stimuli. Error shadings indicate standard errors. Data reflects the unsmoothed grand mean signal.*

In Experiment 2, we found no significant effect of Stimulus Brightness on the PLR in the VWM condition. Since there was also no pupil effect during the encoding phase, it is possible that the low amount of valid trials, especially in the VWM condition, left us with less statistical power to detect differences. But since the pupil traces of Experiment 2 resemble the pupil traces of Experiment 1, we tentatively conclude that it was not the verbalization of the stimuli that prevented a pupil effect during the maintenance phase. In Experiment 3 we examined the possibility that luminance has to be the task-relevant feature in order to evoke a PLR during the maintenance phase.

Experiment 3

In both Experiment 1 and 2, the brightness of the stimuli was not the task-relevant feature. Participants had to perform a change-detection task regarding the shape or orientation of the items and not their brightness. It has been suggested that VWM only stores those visual features that are relevant for subsequent behavior (Dehaene, Kerszberg, & Changeux, 1998). Since the brightness was irrelevant for subsequent behavior, it is possible that the brightness information was lost shortly after encoding and, with that loss, the pupil effect. In Experiment 3, the experimental design was adapted such that we used stimuli of different luminances. The participant's task was now to remember the specific luminance, rather than the shape or orientation.

Methods

Participants

Sixteen new observers (twelve female, 1 author [TB]) participated in Experiment 3.

Procedure and Stimuli

In Experiment 3, the change-detection task involved the luminance of the stimuli. The memory and search array consisted of four circular stimuli. Two of these were more-or-less white (the bright targets), but differed slightly in their exact brightness; the other two were more-or-less black (the dark targets), but also differed slightly in brightness. There were three possible variations of white, two of which were randomly selected on each trial. Similarly, there were three possible variations of black, two of which were selected on each trial. In the VWM condition, participants had to keep the luminance of two stimuli in VWM and perform a change-detection task where in 50% of the trials one of the luminances had changed. The memory and search array for Experiment 3 are shown in Figure 5.

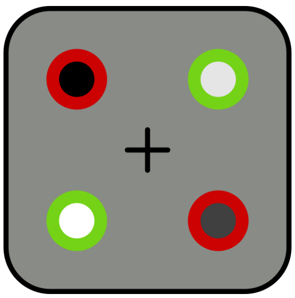


Figure 5. *The memory array as presented in the VWM condition and the search array as presented in the ATT condition consisting of four circles with two white and two black circles.*

Results and Discussion

No participants were excluded and after selection, 2411 trials (78.4%) were entered into the analyses.

Behavioral Data

In the VWM condition the mean accuracy was 79% (SD 5%). In the ATT condition the mean accuracy was 74% (SD 10%).

A paired-samples t-test showed a significant difference in accuracy for bright (M=.75, SD=.055) and dark (M=.82, SD=.072) targets in the VWM condition ($t(15)=3.594$, $p=.003$), and a significant difference in accuracy for bright (M=.69, SD=.12) and dark (M=.8, SD=.12) targets in the ATT condition ($t(15)=3.377$, $p=.004$). However, given the close similarity of the pupillary results of Experiments 3 (see below) to those of Experiments 1 and 2, we believe that the difference in accuracy for bright and dark targets did not strongly affect pupillary responses.

Pupil traces

Figure 6 shows the pupil responses for the VWM condition and the ATT condition. In the VWM condition a significant pupil effect was found between 1880 – 4799 ms and 4820 – 5069 ms and in the ATT condition between 310 – 4659 ms and 6180 – 6569 ms. In the ATT condition, the pupil effect already emerged when the target was presented, because the target contained a luminance to which the PLR responded (this was not the case in Experiments 1 and 2). This induced a strong interaction between Condition and Stimulus Color. Crucially, this interaction was driven by the first 2 or 3 seconds during encoding, and fully disappeared before the retention interval (4 – 8 s); again, we found no difference (i.e. no Target-Brightness by Condition interaction) between the VWM and ATT conditions during this interval.

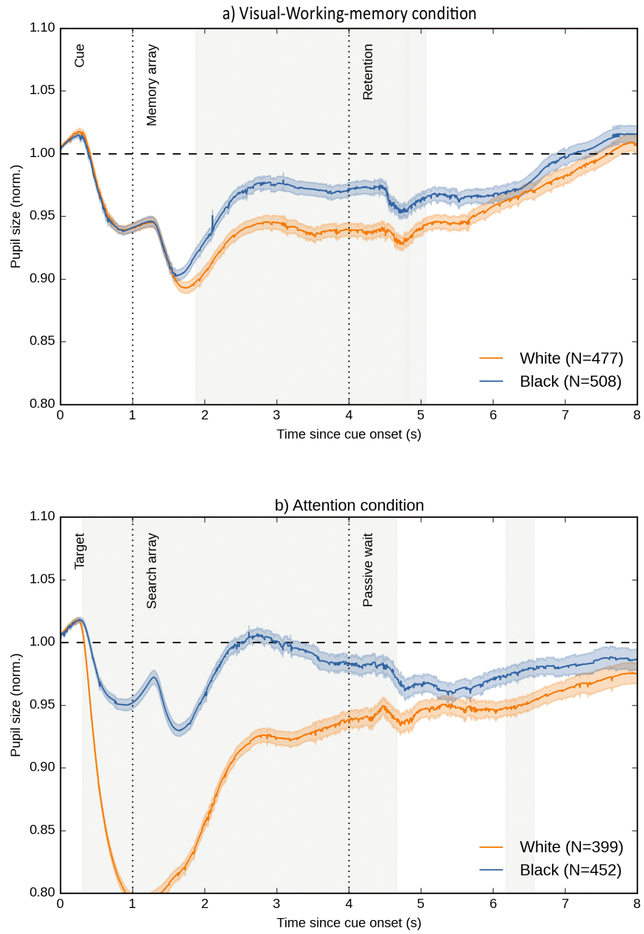


Figure 6*. Pupil size as a function of Stimulus Color and time since cue onset for a) the VWM condition and b) the ATT condition in Experiment 3. The orange line portrays pupil size for Bright Stimuli and the blue line for Dark Stimuli. Error shadings indicate standard errors. Data reflects the unsmoothed grand mean signal.*

In Experiment 3, we again found that the pupil is smaller when bright, compared to dark, stimuli are encoded into working memory, but that this effect dissipates during VWM maintenance. We conclude that the content of VWM is not reflected in the PLR.

Crossexperimental Analyses

Relationship between the pupil effect and behavioral performance

We assume that the pupil effect during encoding reflects how well stimuli are encoded into visual working memory. If so, then participants who show a strong pupil effect should also do well on the change-detection task. To test this, we determined the following per-participant measures: accuracy on the change-detection task and the pupil effect during the last 100 ms of the encoding interval in the VWM condition (during which the overall pupil effect was largest). The three experiments differ in their overall accuracy and pupil effect, which could drive a correlation between both measures. To account for this, we conducted a multiple linear regression with Pupil Size as dependent measure, and Accuracy and Experiment as predictors. This analysis showed a clear relationship between Accuracy and Pupil Size ($t(43) = 2.8$, $p = .028$; Figure 7), which was not (fully) driven by overall differences between our three experiments. This confirms our assumption that the pupil effect during encoding reflects encoding of information into visual working memory.

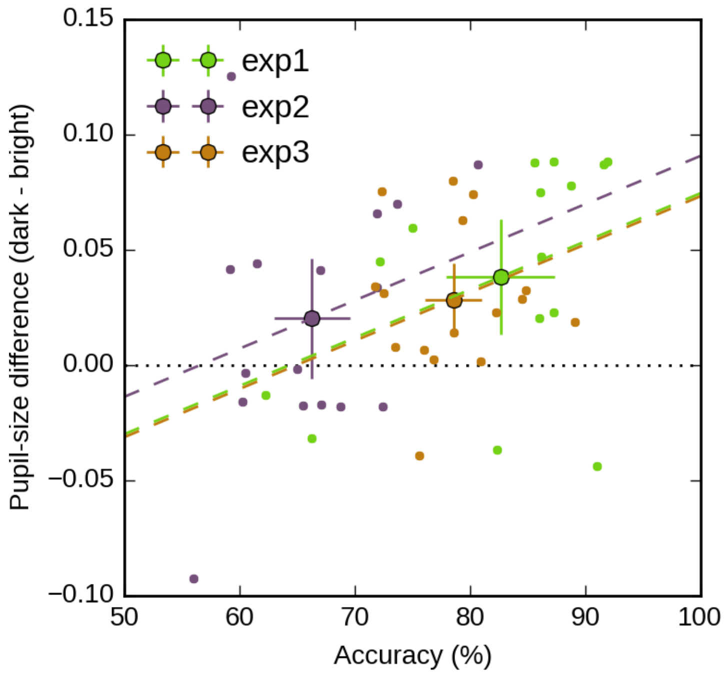


***Figure** 7. Accuracy on the change-detection task predicts the pupil effect during the last 100 ms of the encoding interval of the VWM condition. Small dots indicate individual participants. Large dots indicate experiment means, with 95% confidence intervals. Colored lines indicate estimated regression slopes for the three experiments. (Estimates are parallel because our analysis did not include an Experiment by Accuracy interaction.)*

Bayesian analysis

Visual inspection of the results of Experiments 1 (Figure 2), 2 (Figure 4), and 3 (Figure 6) reveals two key points: In the VWM condition, the pupil effect builds up during the encoding interval, and dissipates during the maintenance interval; the time course of the pupil effect is similar between the VWM and ATT conditions (although overall pupil size differs somewhat). This suggests that encoding bright or dark stimuli affects pupil size, but maintaining these stimuli in working memory does not. To quantify the evidence for this conclusion, we conducted a Bayesian analysis using the following logic.

If maintaining bright/dark stimuli in working memory has no effect on pupil size, then the pupil effect in the VWM condition should be short-lived, and thus similar to the ATT condition. Therefore, the pupil effect should be the same during the last 100 ms of the maintenance interval in the VWM condition (7.9 – 8.0 s), and the last 100 ms of the passive-wait interval in the ATT condition (7.9 – 8.0 s). To test this, we determined the per-participant pupil effect during these two intervals, and compared them using a Bayesian paired-samples T-test. This revealed moderate evidence against a difference (Bf = 0.169); that is, at the end of the trial, there is no difference in pupil effect between the VWM and ATT conditions.

In summary, a Bayesian analysis confirms that our results best fit a model in which pupil size is driven by the brightness of stimuli during encoding, but not maintenance, of visual working memory.

General Discussion

In the present set of experiments, we examined whether the content of VWM is reflected in the pupillary light response (PLR). Because the PLR has been shown to be sensitive to higher order perceptual representations (Binda et al., 2013b; Laeng & Endestad, 2012; Naber & Nakayama, 2013), we examined modulations of the PLR by stimuli which were not physically present, but had to be kept in VWM. Participants covertly attended and encoded bright and dark stimuli, which had to be maintained in VWM for a subsequent change-detection task. As expected, the pupil was smaller when the bright stimuli had to be encoded compared to when the dark stimuli had to be encoded. This indicates that the encoding of information into visual working memory is reflected in the PLR. Interestingly, we observed a correlation between the accuracy on the change-detection task and the difference in pupil size between bright stimulus trials and dark stimulus trails during the encoding phase, where a larger pupil effect correlated with a higher accuracy. Many researchers have shown that an item must first be attended before it can be encoded into VWM (e.g. Mack & Rock, 1998) and since it has been previously suggested that the PLR can be used to track the focus of attention (Mathôt et al., 2014, 2013), our results are in line with these findings.

We further assessed whether the PLR differentially responds to encoding and maintenance of visual information. The pupil effect that emerged during the encoding phase did not sustain during the maintenance phase. This was consistent across all three experiments: whether it was the shape (Experiment 1), orientation (Experiment 2), or luminance (Experiment 3) of the stimulus that was relevant for subsequent behaviour, the maintenance of the stimuli was not reflected in the PLR. A subsequent Bayesian analysis showed that pupil size was likely driven by the brightness of stimuli during encoding, but not maintenance, of visual working memory. We therefore conclude that the content of VWM is not reflected in the PLR.

Because the relation between working memory encoding and the PLR is strictly correlational, it cannot be determined whether the observed effect on the PLR is caused by the encoding in VWM or whether being encoded into VWM is the result of a modulation of the PLR. Indeed, when considering a possible explanation for the PRL modulation, it becomes evident that the PLR is not simply an epiphenomenon of encoding information in VWM. As the optimal size of the pupil depends on how much light is available, we argue that the observed effects on the pupillary light response may serve to optimize the pupil size specifically for objects that need to be encoded in VWM. The pupil size is therefore tuned to the brightness of the to-be-encoded information, making the link between the pupillary light response and memory encoding beneficial. However, once stimuli are no longer visible (during maintenance), an "optimal" pupil size no longer serves a purpose, and the pupil may therefore cease to reflect the brightness of the memorized stimuli.

At first sight, the present paradigm is quite similar to paradigms used to investigate mental imagery: both during imagery and during the maintenance of an object in visual working memory, the relevant object is not present on the screen and is only represented internally. Indeed, the two processes have been found to be related: Keogh and Pearson (2011) found that performance in visual working memory can predict the strength of mental imagery as assessed with binocular rivalry. Furthermore, individuals with strong mental imagery seem to use mental imagery as a mnemonic strategy for visual working memory tasks (Keogh & Pearson, 2014). The present findings suggest a possible dissociation between mental imagery and visual working memory with respect to the effect on the PRL: whereas the PLR does appears to reflect the content of mental imagery (Laeng & Sulutvedt, 2014), the PLR is not modulated by the content of visual working memory. There are, however, many possible reasons for this difference. First, it might be that the timing of the two processes is different. The present interval was relatively short (i.e. 4 seconds), whereas mental imagery is generally assessed using longer intervals (e.g., Laeng & Sulutvedt, 2014; Keogh & Pearson, 2014). Although there was no such hint in our data, it could be that the effects of visual memory only become apparent with a longer interval. Second, it might be that the internal operations differ in the amount of mental effort that is required: whereas visual memory does not require any computations on the internal representation, mental imagery is perhaps a more active process, requiring additional mental resources. Whatever the explanation, our results are reminiscent of the findings by Binda and colleagues (2014) who showed that knowledge that a task-relevant bright stimulus will appear was found be insufficient to cause pupil constriction, which only occurs when the stimulus is displayed and it is attended. Future studies could compare the effects of maintenance in visual working memory and imagery on the pupillary light response to directly investigate this apparent dissociation.

To conclude, the present set of experiments showed that encoding information into VWM is reflected in the PLR: The encoding of a bright stimulus leads to a pupil constriction compared to the encoding of a dark stimulus. The maintenance of said stimuli in VWM is however not reflected in the PLR. Our results therefore suggest that the pupil size is tuned to the brightness of the to-be-encoded information, allowing for an optimal encoding of visual information.

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