Testing the Flexibility of Pupillary Working Memory Signals to Visual and Semantic Task Demands

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Data availability

Author contributions

Yueying Dong conceived of the experiment(s), and developed the analysis pipeline. Yun-Chen (Jennifer) Hung revised the experiment and collected stimuli and data. Anastasia Kiyonaga and Tim Brady advised on experimental design. Yun-Chen Hung and Yueying Dong wrote the manuscript, and all authors edited the manuscript.

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Abstract

Working memory (WM) is the ability to temporarily store and flexibly maintain information. Current theories on storage sites suggest that sensory regions involved in perception are also engaged in reflecting WM representations. Recent studies have indicated that this WM representation may be reflected as early as in our pupils. For instance, there are observations on greater pupil dilation during WM maintenance of a dark stimulus compared to bright. Furthermore, this WM pupillary light response (WM-PLR) effect has shown sensitivity to priority cues and heterogeneity across individuals of varying mental imagery strengths. This study aims to understand whether different visual task strategies for WM tasks would also elicit the same pupillary WM signal regardless of individual imagery strengths. Here we show that using a visual detail strategy induces a stronger pupillary WM signal, and a weaker signal when asked to recruit a semantic labeling strategy. These strategy-dependent differences in pupillary responses resemble findings from previous studies, which reported heightened pupillary WM signals in individuals with strong visual imagery. Our study further corroborated this notion that pupillary WM signals are flexible to behavioral goals. Furthermore, these findings demonstrate how early peripheral sensory signals may flexibly maintain and reflect internal representations for later usage.

Introduction

In our daily lives, we often use working memory to represent different details about some scenery that we had previously seen in our brain. Working memory (WM) refers to the cognitive ability of temporary maintenance and manipulation of information (Baddeley, 1992). While early studies on the neural circuitry of WM implicated specific regions such as the prefrontal cortex and the posterior parietal cortex, recent studies point to the sensorimotor recruitment theory as an increasingly favored cognitive model of WM. This theory states that sensory regions recruited for perception are also involved in the temporary retention of that information (D'Esposito & Postle 2015). A review of recent non-human primates and human neuroimaging studies revealed that WM is distributed across different cortical areas in accordance with the modality of the stimulus (Christophel et. al, 2017). For example, fine-grained representations are preserved in early sensory regions like the primary visual cortex, whereas more abstract or verbal information is processed in higher-order areas such as the prefrontal cortex.

Beyond these cortical locations of storage, WM signals have also been detected to be represented as early as the peripheral nervous system, which includes pupils and oculomotor muscles. One of the primary functions of the pupils is to adjust to ambient luminance, and this is controlled by the Pupil Light Response (PLR), where the pupil constricts to bright inputs to the eyes (Mathot et al. 2018). Intriguingly, recent findings suggest that even without perceptual input, pupil size responds to the brightness feature of the WM content, in a way that is analogous to the PLR (Zokaei et al., 2019; Husta et al., 2019; Dong & Kiyonaga 2024;) In these studies, the subjects were asked to simultaneously memorize a dark and a bright stimuli, and then retroactively told which stimuli (dark/ bright) will be subsequently tested. The studies have shown that during memory delay, the pupil dilation is larger when the darker WM item is task-relevant as compared to the bright, despite equivalent sensory input. These findings underscore the flexibility of WM pupillary signals to reflect various behavioral demands. To contrast with the sensory-driven PLR, we will be referring to this WM pupillary response as WM-PLR.

Notably, this WM-PLR signal is a heterogeneous effect that varies across each individual. Intriguingly, Dong & Kiyonaga (2024) found that the WM-PLR signal is also dependent on an individual's visual self-reported imagery strength, assessed via VVIQ. While strong imagers (high VVIQ) would have the largest WM-PLR effect, this effect is absent among weak imagers (low VVIQ). The authors hypothesize that such distinction may potentially be driven by the WM strategy that the subjects adopt: those who reported a higher imagery ability may be more inclined to use using a more visual strategy to complete the task, and those with lower imagery abilities may have more difficulty in constructing mental imagery and thus rely on an abstract WM representation such as semantic or numerical labels.

Nonetheless, no studies have yet tested the hypothesis that Working Memory (WM) pupil response could adapt to represent different task strategies. We suggest that the magnitude of this WM-pupil effect reflects how an item is represented in WM, whether it was visual or semantic. This paper aims to answer the following research question: can working memory pupil response be modulated by task strategy demands? We devised an experiment to see whether the Working Memory (WM)-pupillary effect (i.e. during stimuli maintenance, the bright v.s. dark pupil difference) is sensitive to task demands (Visual v.s. Semantic condition) by retroactively cueing participants to follow either a visual or semantic strategy in a simple matching task. We hypothesize that there should be a greater WM-pupillary effect when people use a visual strategy to maintain some stimuli in their mind, reflecting the flexibility of the pupil in maintaining visual WM representations.

Our experiment highlights a significant difference in the magnitude of WM-PLR trace under a visual or semantic WM task strategy. More specifically, the effect was pronounced when the task required more visual detail, and diminished under more abstract, semantic task demands. These findings affirm the idea that WM representations in early sensory regions can be modulated by task-driven behavioral goals. Moreover, our preliminary results suggest that oculomotor behavior may offer a surprising window into internal cognitive states, providing a non-invasive means to explore how WM is maintained and processed.

Methods

Human subjects

Forty-five healthy adult volunteers with normal or corrected to normal vision gave written informed consent and participated in the experiment. Forty-one participants (20.33 $\pm$ 1.47 years; 34 female) were included in the reported analyses. All participants gave their informed consent in accordance with the protocols approved by the University of California, San Diego Human Research Protections Program. Participants were collected via the SONA platform to conduct the experiment in the Kiyonaga Cognitive Neuroscience Laboratory, and were compensated for their time with extra credit scores for a course. For eye tracking purposes, participants were asked to remove all coverings around their eyes, including makeup and glasses.

Task description

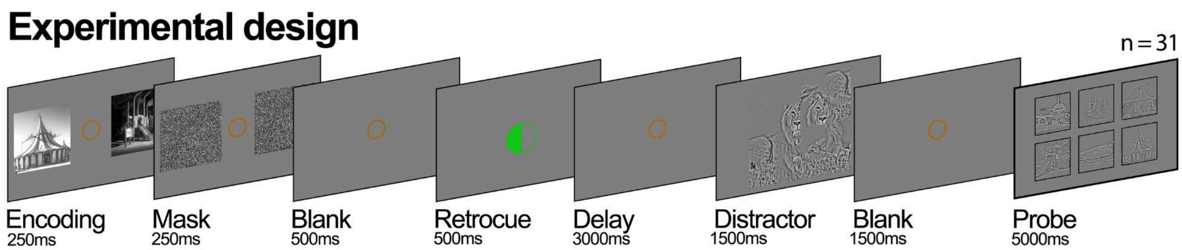

*Fig. 1| **Task design**. An example sequence of events in a visual or semantic trial. In each trial, the participants are asked to remember a two-element array, consisting of one daytime and one nighttime scene. A colored directional cue (i.e., the retrocue) then indicates which item will be tested (left vs. right). The color of the cue signifies the feature to be tested (green = visual, purple = semantic). Following a memory delay, in a visual trial, subjects select the probe that is a cropped portion of the cued image. Alternatively, in a semantic, subjects select the probe matching the semantic category of the cued image.*

Experiment design

To test whether the WM pupillary signal varies to the visual or semantic WM task demands, we manipulated the task relevant feature of the WM items. Similar to the Dong & Kiyonaga (2024), the encoded memory stimuli is a two item-array consisting of a bright and dark item. However, due to the task demands, the stimuli need to have a clear semantic connotation. Therefore we will use naturalistic images that depict day/night time scenes. The stimuli images are drawn randomly from 9 semantic categories (see Stimuli generation for more detail) presented on a horizontal array, counterbalanced order of left and right. Participants were asked to fixate on a center circle throughout the entire trial up to the probe onset.

Next, the retrocue appeared for 500ms and informed the participant whether the left or right item will be relevant for the subsequent memory test . Additionally, the color of the retrocue informed whether the memory test will be visual (green) or semantic (purple). In some trials, participants responded to a distractor text or image (see Distractor for details), presented for 1500 ms and followed by a 1500 ms delay. In the majority of trials, a 3000 ms delay followed the retro-cue, after which the probe array appeared. Participants were then required to select the correct probe image from an array of six. For semantic tests, the correct image is the one that matches the semantic category of the probed image. For visual tests, the correct image is one that exactly matches the cued item. Finally, the subjects selected the matching probe from an array of six images. All subjects went through 216 trials for a total of 60 minutes, and practiced the experiment for 21 trials.

The experiment was presented on Psychopy with a neutral gray background. The pupils are tracked with EyeLink for the entirety of the experiment, and participants can keep their head still by resting their chin on a chin rest. The luminance of the room will be kept at a stable level to avoid confounding variables of light interference with pupillary light response. At the end of the eye tracking experiment, participants will be asked about their task strategies. They will then be asked to fill out the Vividness Of Visual Imagery Questionnaire (VVIQ) to assess mental imagery strength.

Stimuli generation

Twenty natural scenic images for both daytime and nighttime across nine different categories (shopping cart, ferris wheel, circus, house, playground, bench, gas station, schoolbus, airport) were obtained from the World Wide Web. These images were cropped, grayscaled, and matched for luminance across daytime and nighttime scenes. All images were stripped of any salient features such as gas station names or people. The probe images underwent the same processing as the foil images, with the added step of high-pass filtering to suppress brightness features and preserve only contour information.

Probe generation

For each cued and uncued image, we paired it with a foil. In visual trials, foils were randomly selected from images sharing the same semantic label but ranked in the 30th percentile of visual dissimilarity to the original image. In contrast, for semantic trials, foils were chosen from images with a different semantic label but ranked in the 30th percentile of highest visual similarity to the original image. The final image pair was randomly selected, with the foil determined according to the cued condition criteria.

Distractor

To verify that participants were adhering to the cued strategy, we included a distractor task on 30% of the trials. Distractors were either verbal or visual and required a binary judgment. In the verbal distractor condition, participants judged whether a presented word referred to a man-made object. In the visual distractor condition, participants indicated whether the displayed image was scrambled. Answers were recorded by pressing the ‘w’ key for yes and ‘d’ for no. Each image had a corresponding word label, and distractor images were either drawn from the foil category or randomly selected from the THINGS dataset and filtered in the same process as the stimuli.

Data analysis

Data Preprocessing

Data preprocessing included artifact rejection and interpolating any missing data due to blinks from the raw data. Here, we follow the methods described by Kret and Sjak-Shie (2019). This includes looking for outliers within a dilation speed change per trial. We calculated the absolute value of the first derivative by subtracting the current dilation with the preceding dilation sample. Outliers within the speed space are defined as any samples that exceed the threshold, with a small padding added before and after a potential blink. The threshold takes in the median absolute deviation (MAD) from the speed space, multiplied by a constant *n*, and summed with the median dilation speed:

$$MAD = median(|d^{'} - median(d^{'})|)$$

$$Threshold = median(d^{'}) + n * MAD$$

Following outlier removal, we interpolate to smooth over any resulting discontinuities. Interpolation is done by cubic spline interpolation, or linear interpolation if not enough data is available. A second round of thresholding and interpolation is applied to remove artifacts that may remain after initial interpolation failures.

Pupil performance

As our subject of interest is the within subject pupil change during task demand, we analyze the average pupil size after the retro cue onset and before probe onset. In this maintenance and retrieval period, the pupil size should be purely memory driven and not modulated by other confounding variables. We take the average pupil size during the 100ms before the retro cue onset as the baseline pupil size, and baseline correct the pupil in the epoch of interest. Finally, we extract only the trials without distractors as those include a confounding factor to the pupil size. Our analysis did not account for individual variability, and averaged across all subjects for each trial condition.

Results

In our experiment, we examine within subject effects of task demands on the flexibility of working memory (WM) pupillary signatures. Another supplementary analysis by Dong and Kiyonaga (2024) had shown that people with stronger mental imagery elicited a greater WM pupillary response. Based on this previous work, we anticipate to see a greater pupil dilation difference between recalling a bright and dark image for visual detail strategies. This may reflect the level of abstraction at which WM representations are maintained, which likely adapts to task demands. In addition, we expect to see pupil size for maintaining nighttime images to be greater than daytime for the visual detail trials. Here we denote the average pupil change over time in dark when the cued image is a nighttime scene, and bright when the cued image is daytime. The graphs depict this WM pupillary response for the visual detail (green) and semantic (purple) conditions. Shadings indicated $\pm$ SEM.

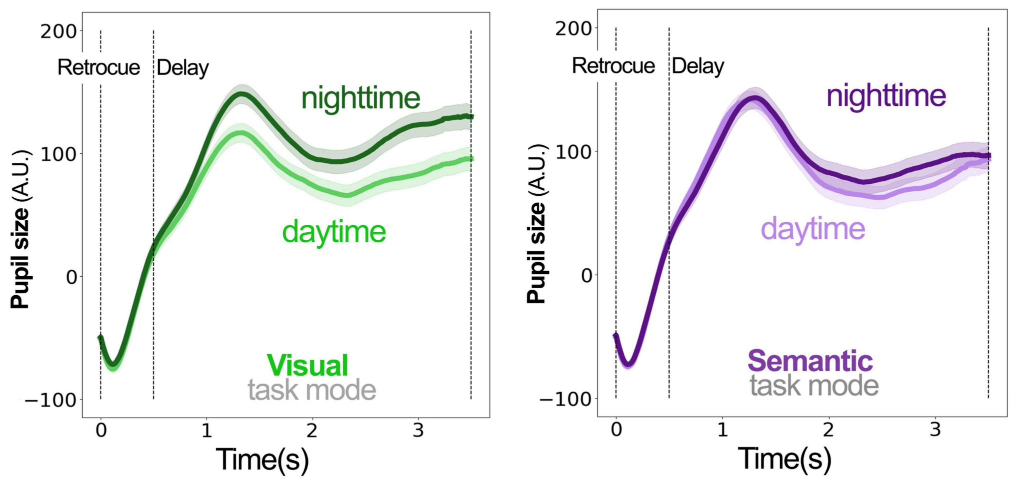

Fig. 2a, b| ***Pupillary signals across time****. Images depict the pupil size averaged over all participants over the time from retro cue offset to probe onset (delay period). Fig. 2a shows a significant difference in average pupil size for nighttime versus daytime. In the semantic trials (Fig. 2b), the pupil size for nighttime and daytime are almost overlapping and have a smaller difference compared to the visual detail condition.*

From Figure 2, we can see that this WM pupillary response is apparent during a visual detail strategy, but absent during a semantic strategy. This finding not only bolsters the idea that our pupils can flexibly adjust similarly to WM in order to guide upcoming behavior, but also that pupillary responses reflect some WM representation during a maintenance period.

Discussion

There has been growing interest in detecting working memory (WM) signals from early peripheral regions, particularly within the field of visual WM. Compared to popular neuroimaging techniques, eye-tracking provides an inexpensive and noninvasive tool to probe the underpinnings of WM. More specifically, researchers have investigated the characteristics of the WM-related pupillary light response through examining how it adapts to factors such as memory priority and the strength of an individual's mental imagery. Our findings reveal that this pupillary signal supports behavior across different task demands and reflects the abstraction level. Furthermore, these findings are consistent with our earlier hypothesis that people with stronger mental imagery may have a greater WM pupillary responses because they may be using a strategy that requires more visual details, while weak imagers do not have this effect due to a more abstract working memory strategy.

While our finding offers novel insights into the pupillary signatures of WM, several methodological hurdles must be considered to accurately interpret the results. It has been known that the pupillary light reflex can be influenced by various factors, including luminance, cognitive effort, and the vividness of mental imagery. Therefore, it is essential to design the experiment in a way that minimizes or eliminates these potential confounds. A key challenge arises from the inherent difference in difficulty between visual detail-based and semantic-based memory strategies; it is generally easier for participants to remember the semantic label of an image, which often becomes the default strategy. This discrepancy introduces a confounding variable, as the tasks are not equally demanding.We attempted to address this imbalance by adjusting the probes (see Methods), though future work can be done on refining this task difficulty matching. Further complications include the limitations of eye-tracking technology, which is sensitive to participant movement and often fails to accurately record pupil size when gaze deviates a certain distance from the center. Finally, in data analysis, determining an appropriate baseline period for pupil size is somewhat subjective as the choice of a very high or very low baseline can significantly impact the interpretation of subsequent pupil changes.

Overall, our paper demonstrated that pupillary signatures of WM exhibit comparable characteristics to that of WM and possess the capacity to flexibly transition between representations. Future work includes looking into how this may reflect for other pupillary responses such as the pupillary near response, where pupil size adjusts to the viewing distance of some scenery. We suggest that there may also be a similar effect to the working memory pupillary light response when the stimulus is no longer perceived. Moreover, coupling pupillary signals with other oculomotor behaviors such as microsaccades can reveal more about how we process visual working memory information. Recent papers have shown that microsaccades reveal how our working memory representations become more generalized and abstract over time. Future analyses could investigate whether microsaccades played a role in offloading cognitive information from our pupils or vice versa to see if participants were truly using a visual detail or abstract memory strategy.

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