

FOCUS ARTICLE

Revealing visual working memory operations with pupillometry: Encoding, maintenance, and prioritization

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Abstract

Pupillary dynamics reflect effects of distinct and important operations of visual working memory: encoding, maintenance, and prioritization. Here, we review how pupil size predicts memory performance and how it provides novel insights into the mechanisms of each operation. Visual information must first be encoded into working memory with sufficient precision. The depth of this encoding process couples to arousal-linked baseline pupil size as well as a pupil constriction response before and after stimulus onset, respectively. Subsequently, the encoded information is maintained over time to ensure it is not lost. Pupil dilation reflects the effortful maintenance of information, wherein storing more items is accompanied by larger dilations. Lastly, the most task-relevant information is prioritized to guide upcoming behavior, which is reflected in yet another dilatory component. Moreover, activated content in memory can be pupillometrically probed directly by tagging visual information with distinct luminance levels. Through this luminance-tagging mechanism, pupil light responses reveal whether dark or bright items receive more attention during encoding and prioritization. Together, conceptualizing pupil responses as a sum of distinct components over time reveals insights into operations of visual working memory. From this viewpoint, pupillometry is a promising avenue to study the most vital operations through which visual working memory *works*.

This article is categorized under:

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encoding, maintenance, prioritization, pupillometry, visual working memory

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1 | INTRODUCTION

Visual working memory (VWM) enables us to temporarily maintain and manipulate visual information, which is vital for everyday functioning. Imagine you are conducting a simple chemistry experiment: You need to combine a red and blue substance. Glancing at your chemistry book with instructions, you create an internal representation of the two colored substances; this process is also known as *encoding*. You then walk over to the cabinet to retrieve the substances, which requires you to *maintain* these internal representations. The blue substance should be added to the test tube first, and you therefore *prioritize* this representation to help you find it in the cabinet. This example illustrates how VWM employs different operations to guide behavior: encoding, maintenance, and prioritization (Figure 1; Awh et al., 2006; Baddeley, 1992a; Mance & Vogel, 2013; Olivers et al., 2011; Souza & Oberauer, 2016; van Ede, 2020; van Ede & Nobre, 2023; Woodman & Vogel, 2005).

Each operation serves to accomplish a specific goal. Encoding can be defined as creating an internal representation of (attended) information from the environment (i.e., transferring the colored substances from the book to your mind; Awh et al., 2006; Baddeley, 1992a; Woodman & Vogel, 2005). Subsequently, this internal representation has to be maintained to prevent losing the information (i.e., remembering the substances when walking to the cabinet). A fundamental function of (V)WM is storing past information to guide future behavior (Baddeley, 1992b). This is effectuated by selectively prioritizing the most task-relevant content held internally in (V)WM (i.e., trying to find the blue substance first). Such internal prioritization selectively transforms maintained material (e.g., by reinvigorating relevant and/or inhibiting irrelevant material, action planning, reducing load, etc.) to prepare one for efficient upcoming behavior (Olivers et al., 2011; Olivers & Roelfsema, 2020; Souza & Oberauer, 2016; van Ede, 2020; van Ede & Nobre, 2023). Whilst the above operations are naturally related, their underlying cognitive mechanisms likely differ (Awh et al., 2006).

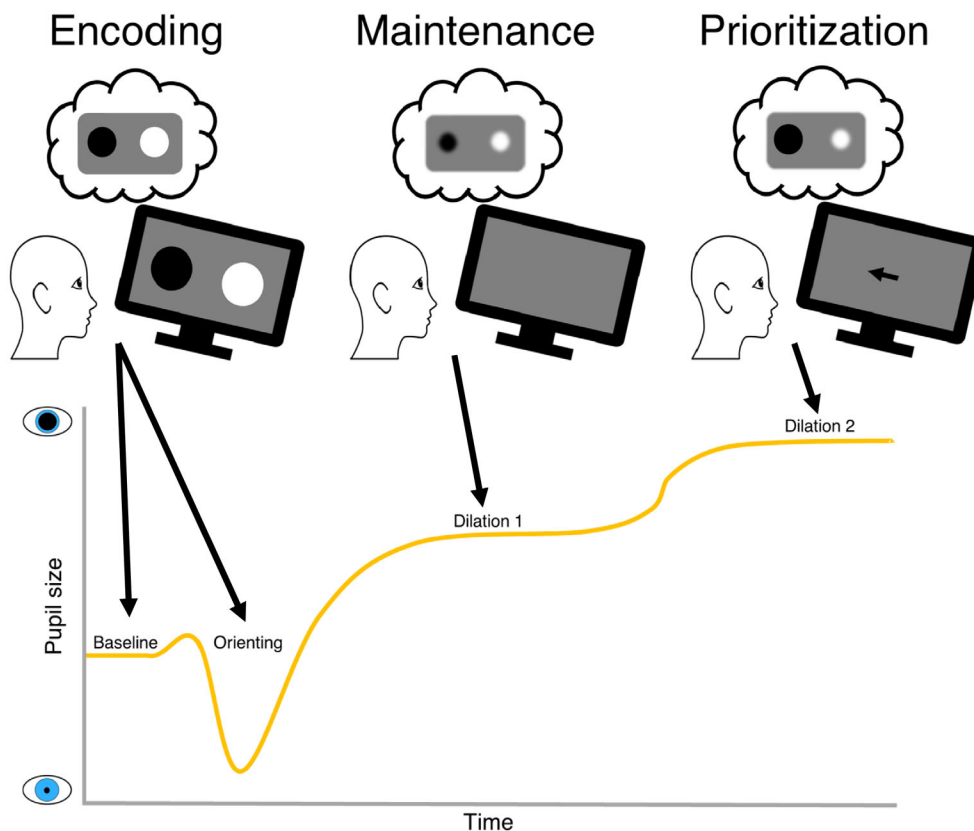


FIGURE 1 The upper part of the figure shows a schematic overview of the different VWM stages. During encoding, information is committed to memory. Afterward, the information needs to be maintained. Lastly, prioritizing relevant information guides upcoming behavior. The lower part of the figure schematically shows pupil size over time and highlights the important signal components. Baseline pupil size and the pupil orienting response index how much is encoded. The first dilatory response reflects the effort associated with maintaining information. Prioritizing the most relevant information also elicits a dilation. The upper procedure is based on Hustá et al. (2019).

Although behavioral studies have provided great insights into these distinct operations, it is difficult to precisely disentangle their underlying cognitive mechanisms. For example, in many tasks, only a single response (e.g., a button press or reporting a memorized color on a color wheel) summarizes the outcome of all these cognitive processes in a given trial. This prevents one from explicitly determining whether VWM use differs between two experimental conditions in terms of encoding, maintenance, or prioritization. To overcome this critical limitation, we here propose that pupillometric signal components capture attentional processes during paramount operations of VWM use. Therefore, pupil size allows for the study of the cognitive processes underlying each operation.

The lower part of Figure 1 shows a schematic overview of how the pupil changes size over time during a VWM task. Before the to-be-encoded items are presented, the baseline size of the pupil is measured. Shortly after the presentation of the memory stimuli, the pupil briefly dilates and subsequently constricts strongly, which together is referred to as the pupil orienting response (Strauch, Wang, et al., 2022; C.-A. Wang & Munoz, 2015). Baseline pupil size and the pupil orienting response both reflect encoding (Blom et al., 2016; Galeano-Keiner et al., 2023; Koevoet, Naber, et al., 2023; Starc et al., 2017). Following encoding, the information needs to be maintained, which elicits a pupil dilation (Beatty, 1982; Kahneman, 1973; Robison & Unsworth, 2019). When a specific piece of memorized material is prioritized, an additional pupil dilation can be observed (Robison et al., 2023; Unsworth & Robison, 2018). In sum, different pupillary signal components emerge over time and each of these provides insights into distinct operations of VWM. Throughout this review, we discuss these putative links between pupillary response components and VWM operations. We also incorporate findings from studies exploiting the attentional modulation of the low-level pupil light response (PLR) to further uncover the inner workings of VWM.

2 | ENCODING

In order to ultimately use information in VWM to guide future behavior, visual information must first of all be encoded (Awh et al., 2006; Baddeley, 1992a; Woodman & Vogel, 2005, see Figure 1). Committing visual information to VWM is tightly linked to the processing of external target stimuli, which is in turn driven by arousal and attentional processes. As such, arousal and attention determine how well visual items are encoded into working memory. First, in an optimal arousal state, wherein one is neither under- nor over-aroused, stimulus processing is most effective (Aston-Jones & Cohen, 2005b; van den Brink et al., 2016). Second, attended information is encoded more deeply than unattended information (Awh et al., 2006; Gazzaley et al., 2008; Griffin & Nobre, 2003).

Baseline pupil size reveals fluctuations in arousal as this pupillary signal component is indicative of tonic locus coeruleus (LC) activity (Aston-Jones & Cohen, 2005b; Gilzenrat et al., 2010; Jepma & Nieuwenhuis, 2011; Sirois & Brisson, 2014). LC is a brainstem nucleus that projects noradrenaline throughout the brain (Aston-Jones & Cohen, 2005b; Schwarz et al., 2015). Tonic LC activity is longlasting and firing patterns unfold over time slowly, revealing one's "baseline" arousal level at a given time. In turn, it is plausible that baseline pupil size predicts upcoming VWM encoding. The adaptive gain theory and the Yerkes-Dodson curve posit that the level of arousal and task performance follow an inverted-U relationship (Figure 2; Aston-Jones & Cohen, 2005b; Teigen, 1994; Yerkes & Dodson, 1908). More specifically, the adaptive gain theory states that very low and very high tonic LC firing rates—and thus small and large baseline pupil sizes—are associated with drowsiness and overarousal, respectively. Intermediate tonic LC firing rates and baseline pupil sizes should thus be accompanied with optimal task performance. Therefore in relatively simple tasks, the general arousal levels are somewhere "left" on the inverted-U, and relatively larger baseline pupils should enhance performance (Figure 2). In contrast, whenever a task is more demanding arousal levels shift to the "right" side of the inverted-U. Here, the prediction flips: Smaller baseline pupils should be predictive of better performance. Indeed in relatively difficult tasks, smaller baseline pupil sizes preceding the onset of to-be-encoded colors predict more precise recall of colors several seconds later (Galeano-Keiner et al., 2023; Koevoet, Naber, et al., 2023). Moreover, pupil sizes preceding stimulus onset do not only predict how precisely objects will be encoded, but also how many items will be encoded (Koevoet, Naber, et al., 2023, note that Robison and Unsworth (2019) report this effect only in 1 of 3 experiments).¹ Moving over to the "left" side of the curve, Starc et al. (2017) let participants perform a simple task wherein only a single location had to be retained. Here, larger rather than smaller baseline pupil sizes were associated with more precise reports. Mechanistically, variations in baseline pupil size and performance result mainly from spontaneous fluctuations of tonic arousal rather than from external factors (i.e., the amount of incoming light/visual information; Mathôt et al., 2023). These findings show that arousal, as indexed by baseline pupil size, lays the foundation for upcoming encoding following a pattern mediated by task difficulty and arousal levels.

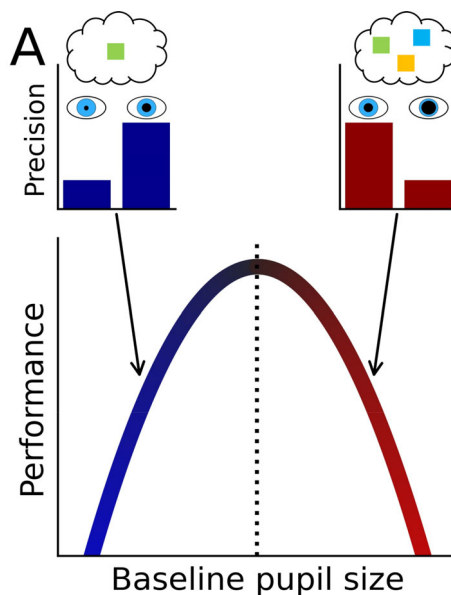


FIGURE 2 Schematic overview of how baseline pupil size predicts encoding in VWM tasks. Relatively simple tasks may lead to boredom and thus under-arousal (blue, based on Starc et al. (2017)). During a general state of under-arousal, spontaneous increases in arousal benefit VWM encoding—wherein larger baseline pupil sizes predict more precise VWM encoding. In contrast, whenever one is highly engaged with a more difficult task, this can cause over-arousal (red, based on Koevoet, Naber, et al. (2023)). In this state, spontaneous decreases in arousal benefit upcoming VWM encoding. Here, smaller baseline pupil sizes index more precise encoding into VWM.

Besides arousal, the degree of attention for the to-be-encoded items is another distinct aspect that affects encoding (Awh et al., 2006; Griffin & Nobre, 2003). Following baseline and upon the presentation of a visual stimulus, the pupil first briefly dilates for around 220 ms and subsequently constricts (i.e., becomes smaller) up until ~ 700 – 1000 ms afterward (see Figure 1; Lynn, 2013; Nieuwenhuis et al., 2011; Sokolov, 1963; Strauch, Wang, et al., 2022; Wang & Munoz, 2015). Many previous studies have referred to the fast transient dilation as the pupil orienting response, but the later constriction notably captures many effects linked to attentional orienting (see Strauch, Wang, et al., 2022). Here, we consider both the initial dilation as well as the later constriction as parts of the pupil orienting response. Single unit recordings in nonhuman primates show that this pupil response is mediated by a superior colliculus-centered circuit including frontal eye fields and basal ganglia (Strauch, Wang, et al., 2022; Wang & Munoz, 2015). In line with this, these brain areas are known to directly contribute to overt and covert attentional orienting toward incoming visual input (Allen et al., 2021; Petersen & Posner, 2012; Schall, 2004; Wardak et al., 2006). The amplitude of the pupil orienting constriction following stimulus onset scales with the relevance (salience) of visual changes, and has therefore been proposed to reflect the *depth of sensory processing* (Barbur & Thomson, 1987; Binda & Gamlin, 2017; Naber et al., 2018; Naber, Frässle, et al., 2013; Strauch, Wang, et al., 2022). Put differently, the pupil orienting constriction amplitude reveals how strongly attention is oriented toward incoming visual input. Building on this notion, we recently showed that the pupil orienting response also reflects the *depth of encoding* into VWM. Specifically, pupil orienting constrictions predicted not only how *much*, but also how *precisely* information was encoded into VWM (Figure 3a; Koevoet, Naber, et al., 2023), where stronger constriction amplitudes accompanied better VWM performance in terms of quantity and quality.

Pupil light responses (PLRs) provide further insights into VWM encoding. The PLR entails pupil constrictions to bright stimuli and dilations to dark stimuli. The neural substrates mediating the PLR are well understood, and include pretectal olivary nucleus, Edinger-Westphal nucleus and ciliary ganglion (for a full overview see Loewenfeld, 1958). Originally, the PLR was thought of as a low-level reflex that regulates the amount of light landing on the retina to optimize visual processing. However, more recently the PLR has been shown to be modulated by attentional processes, likely mediated through neural connections between cortical regions involved in attention regulation and subcortical regions involved in pupil size control (such as superior colliculus and frontal eye fields; Joshi & Gold, 2020; Mathôt & Van der Stigchel, 2015; Strauch, Wang, et al., 2022). To illustrate, pupil size adjusts to the subjectively perceived brightness of a (covertly) attended stimulus—even when the overall brightness on the retina remains constant (Binda et al., 2014; Binda & Gamlin, 2017; Mathôt et al., 2013; Mathôt & Van der Stigchel, 2015; Naber et al., 2011;

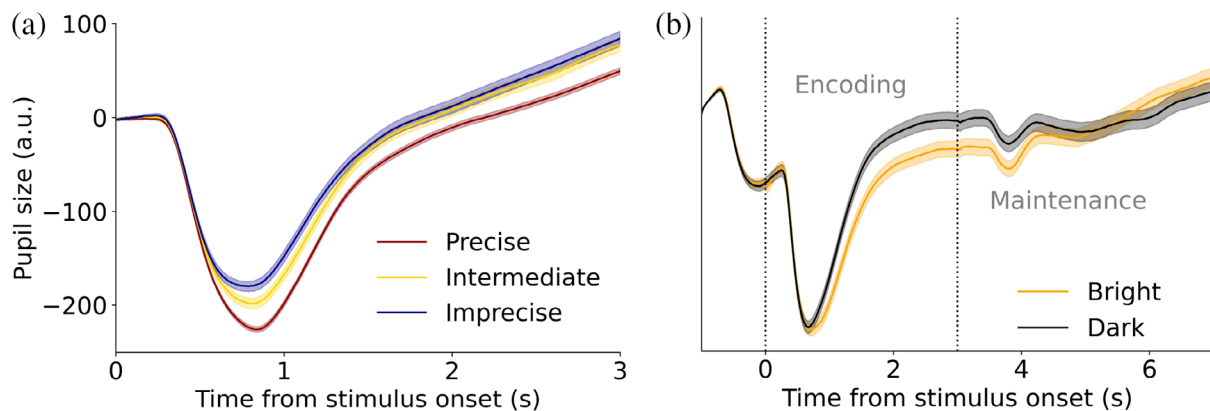


FIGURE 3 (a) Pupil constrictions upon stimulus onset are more pronounced whenever items are encoded more precisely. (b) The pupil light response uncovers which item (bright or dark) is encoded. This effect dissipates when items are maintained (and not physically presented anymore). (a,b) Vertical axes are shared. Transparent patches reflect standard errors of the mean. Data from Koevoet, Naber, et al. (2023) and Zhou et al. (2022), and Blom et al. (2016), respectively.

Naber, Alvarez, et al., 2013). In other words, the pupil constricts whenever a bright portion of the visual field is covertly attended, and vice versa, whenever a dark portion of the visual field attended, the pupil dilates. This phenomenon allows so-called pupil luminance-tagging (Mathôt & Van der Stigchel, 2015; Naber, Alvarez, et al., 2013), in which distinct stimuli receive distinct luminance levels (i.e., bright and dark). Whenever one of these stimuli is attended, its luminance is more strongly reflected in the pupil responses—this same principle is used in pupil flicker tagging studies (e.g., Naber et al., 2018; Naber, Alvarez, & Nakayama, 2013). This allows the pupil to reliably track the focus of covert attention (Binda et al., 2014; Mathôt et al., 2013; Mathôt et al., 2016; Mathôt & Van der Stigchel, 2015; Naber, Alvarez, et al., 2013; Strauch, Romein, et al., 2022). Luminance-tagging can be used to determine which items are encoded into VWM: Blom et al. (2016) observed stronger pupil constrictions whenever bright items are encoded in comparison to whenever dark items are encoded (Figure 3b; also see Hustá et al., 2019). Moreover, the strength of this modulation on the constriction response predicts the accuracy on the VWM task across participants (i.e., participants with stronger PLR modulations perform better at the VWM task; Blom et al., 2016). These results further bolster the notion that stimulus-evoked pupil responses reflect the *depth of encoding*; this is even extended by the possibility to track what is encoded using the PLR (i.e., bright vs. dark).

Distinct parts of the pupillary signal shed light on disparate aspects that drive encoding. Tonic fluctuations in arousal, as captured by baseline pupil size, lay the foundation for the encoding in the upcoming trial. Subsequently, pupil constrictions upon stimulus onset directly inform about how strongly attention is deployed during stimulus encoding. Moreover, pupil size even reveals *what* is encoded through modulations of the PLR. Together, the pupil tracks both tonic arousal and attentional orienting in real time which together reveal how much, how precise and what is encoded into VWM.

3 | MAINTENANCE

Both during and after stimulus encoding, the internal and fleeting representations require maintenance to prevent information loss. Maintaining information typically requires effort, especially when storing multiple representations (Figure 4). The relatively late pupil dilation component peaks around 2–3 s after stimulus onset and links to the degree of mental effort exerted during (V)WM maintenance (Beatty, 1982; Kahneman, 1973; Kahneman & Beatty, 1966; Sirois & Brisson, 2014; van der Wel & van Steenbergen, 2018). Neurophysiological recordings in animals and human imaging studies indicate that pupillary dilations are driven by phasic activity in LC, which projects noradrenaline throughout the brain (Alnæs et al., 2014; Aston-Jones & Cohen, 2005b; Joshi & Gold, 2020; Murphy et al., 2014; Schwarz et al., 2015; Strauch, Wang, et al., 2022). In contrast to long-lasting, slowly unfolding tonic LC firing patterns, phasic LC responses are faster, transient and generally occur in response to external, internal or cognitive events (e.g., Aston-Jones & Cohen, 2005a). Such phasic LC firing is regulated by anterior cingulate cortex, and possibly by orbitofrontal cortex (Arnsten & Goldman-Rakic, 1984; Kim & Lee, 2003; Luppi et al., 1995). Phasic LC activity, and thus

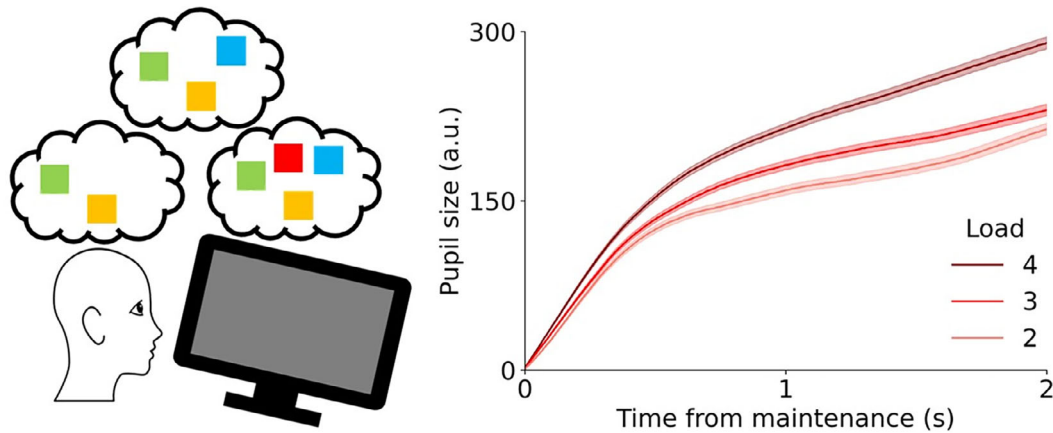


FIGURE 4 Maintaining more representations is increasingly effortful leading to enhanced pupil dilation. Transparent patches reflect standard errors of the mean. Data from Zhou et al. (2022).

BOX 1 Differences between pupil dilation and contralateral delay activity

Contralateral delay activity (CDA), as measured with electroencephalography (EEG), is evoked by selectively encoding only items presented on one side of the visual field while ignoring items on the other side. This leads to enhanced contralateral activity for the attended items compared with the non-attended hemifield. The CDA is then calculated by calculating the difference in activity between hemispheres (Luria et al., 2016). Both the CDA and effort-related pupil dilation objectively index how much is maintained in (V)WM (Figure 4; Luria et al., 2016; Robison & Unsworth, 2019). While these measures seem similar upon first glance, they differ in multiple ways. Whereas the CDA has been argued to exclusively measure VWM load (see Hakim et al., 2019), pupil dilation reflects mental effort more generally and thus captures a multitude of other (cognitively) demanding processes such as motor planning (Richer & Beatty, 1985; Strauch, Wang, et al., 2022). This makes pupil dilation a more flexible method, but also introduces potential confounds that should be controlled for when investigating VWM. More practically, the CDA is inherently based on space (i.e., subtracting ipsilateral from contralateral activity), while pupil dilation is more flexible in this regard since effort is measured regardless of space. In terms of design, pupil dilation benefits from “slow” and relatively long trials (Mathôt & Vilotjević, 2022; Strauch, Wang, et al., 2022), while EEG experiments include a higher number of trials more quickly. Although the number of trials is generally lower in pupillometry experiments, the signal-to-noise ratio is considerably higher than in EEG studies. This allows for linking pupillary dynamics to behavior on a trial-by-trial basis—effectively capturing variability of behavioral outcomes (e.g., Koevoet, Naber, et al., 2023).

pupillary dilation, sensitively index how much mental effort is exerted through two potential neural mechanisms. First, phasic LC firing enhances neural gain during attentional alerting, in turn leading to the engagement of attentional networks (Corbetta & Shulman, 2002; Posner et al., 2006). Second, the noradrenergic projections from LC are thought to orchestrate and coordinate activity within and between neural networks/populations, allowing for flexible switching and coordinated recruitment of brain areas to subserve behavior (Dahl et al., 2022; Poe et al., 2020; Wainstein et al., 2022).

Robison and Unsworth (2019) illustrate the link between pupil dilation during VWM maintenance and mental effort elegantly: Participants memorized six colors and subsequently reported each color. Here, the pupil dilates more during “good” trials in which four or more colors were reported correctly, when compared with “poor” trials in which only one or two correct colors were recalled. Thus, pupil dilation indexes the amount of stored information through the exerted effort during maintenance. Thus, akin to neural measures such as contralateral delay activity (Box 1; Luria et al., 2016), effort-related pupil dilations during maintenance index the amount of stored information in (V)WM (Beatty, 1982; Kahneman, 1973; Kahneman & Beatty, 1966; Robison & Unsworth, 2019; Zhou et al., 2022). This effort

effect allows to investigate individual differences in capacity because the dilatory response increases asymptotically with additional load until it approaches one's VWM limit (Box 2; Ahern & Beatty, 1979; Kahneman, 1973; Unsworth & Robison, 2015, 2017b, 2018). Whenever task demands become too high, observers experience "overload" and give up on the task. Giving up is accompanied by drops in pupillary dilation indicating reduced exerted effort (Granholm et al., 1996; Kahneman, 1973), which is in line with inverted-U patterns in frontal and parietal activity with increased task load (Kosachenko et al., 2023; Leung et al., 2004; Linden et al., 2003) (also see Ma et al., 2014). Such pupillary dilation effects during maintenance may be informative regarding the format of VWM representations (i.e., slots (Luck & Vogel, 1997, 2013; Zhang & Luck, 2008) vs. resources accounts (Bays & Husain, 2008; Ma et al., 2014)). Although direct studies into this issue remain scarce, some work has provided indirect indications into this debate without strong support for either account (see Kosachenko et al., 2023; Kursawe & Zimmer, 2015; Zhou et al., 2022). Targeted studies are necessary to reveal how pupillometry may inform about the format of VWM representations.

Pupil dilation during the VWM maintenance phase may also reflect the precision of the maintained material although evidence supporting this has thus far been mixed. Typically, precision estimates depend on reproducing VWM content through continuous reports; for example, by using a color wheel or recreating a memorized orientation (e.g., van Ede et al., 2019; Zhang & Luck, 2008; Zhou et al., 2022). Counter-intuitively, pupil dilation decreases in trials with relatively precise answers compared to trials with imprecise answers (Galeano-Keiner et al., 2023). Another study reports no reliable effects of pupil size on precision during maintenance in a spatial working memory task (Starc et al., 2017). In sum, convincing evidence exists for a link between pupil dilation and the number of representations during maintenance, but less evidence exists for a link between pupil dilation and the precision of stored

BOX 2 Pupillary dynamics predict individual differences in VWM capacity

The capacity of VWM is highly limited. Many studies have focused on determining how much content can be stored simultaneously (and the format in which representations are stored; Bays et al., 2009; Bays & Husain, 2008; Luck & Vogel, 1997; Van der Stigchel, 2020; Zhang & Luck, 2008). Individual differences in VWM capacity correlate with fluid intelligence, attention control and preparatory oculomotor control, indicating a link between VWM and everyday functioning (Fukuda et al., 2010; Oberauer et al., 2005; Robison et al., 2023; Unsworth et al., 2023). Pupillary dynamics have shed light on the neurocognitive underpinnings of VWM capacity by studying individual differences (Robison et al., 2023; Robison & Brewer, 2020; Robison & Unsworth, 2019; Unsworth & Miller, 2021; Unsworth & Robison, 2018, 2020). Such studies show that individuals with a more stable baseline (i.e., pretrial) pupil size across trials, and thus stable levels of arousal throughout the task, tend to have larger VWM capacities (Robison & Unsworth, 2019; Unsworth & Robison, 2015, 2017a). The detrimental effects of a highly variable baseline pupil size are in line with the notion that neurodevelopmental disorders (e.g., attention-deficit hyperactivity disorder and autism spectrum disorders) are characterized by inconsistent neural signaling, leading to attentional and working memory deficits (Falahpour et al., 2016; Koevoet, Deschamps, et al., 2023; MacDonald et al., 2006; Wainstein et al., 2017; Wainstein et al., 2022; Wang et al., 2018). Note that another line of work initially suggested that individuals with larger resting-state baseline pupil size (i.e., absolute size during fixation) scored higher in fluid intelligence (Tsukahara et al., 2016; Tsukahara & Engle, 2021a, 2021b). However, no other lab has been able to replicate this finding – even when carefully considering lighting conditions (Coors et al., 2022; Robison & Campbell, 2023; Ruuskanen et al., 2023; Unsworth et al., 2023; Unsworth & Miller, 2021). Moreover, there seems to be no relationship between resting-state baseline pupil size and VWM capacity (Robison & Campbell, 2023; Ruuskanen et al., 2023). From this, it seems that individual differences in absolute pupil size do not drive different forms of cognition, including VWM functioning. As for pupil dilations, high VWM capacity individuals show enhanced pupillary dilations during maintenance, reflecting an increase of exerted effort during the task (Robison & Brewer, 2020; Unsworth & Robison, 2015). Through its reflection of mental effort instead of objective load *per se*, pupil dilation reveals a richer picture of how much effort an individual needs to exert to complete a task (Ahern & Beatty, 1979; Beatty, 1982; Kahneman, 1973). Together, pupillometry informs about individual differences in cognitive capabilities, such as VWM capacity. Through such a link, pupillometry holds promise to potentially improve the diagnosis of neurodevelopmental disorders in the future.

representations (note that the quantity and quality of VWM representations are difficult or even impossible to disentangle fully, see Ma et al., 2014; Schneegans et al., 2020; Schurgin et al., 2020; van den Berg et al., 2012; Williams et al., 2022). Existing pupillometric studies inferred precision from the response provided at the end of trial. Instead, future work should specifically manipulate the precision of VWM representations—possibly through cues indicating the required precision of memory reports—to more clearly determine if and how pupil dilation captures the quality of stored material.

The successful luminance-tagging of external items during encoding may also be possible during internal maintenance. Pupil size is modulated by semantic and illusory brightness (Laeng & Sulutvedt, 2014). As such, seeing pictures of a sun or words associated with brightness constricts the pupil, while seeing pictures of a night sky or words associated with darkness dilates the pupil (Binda et al., 2013; Mathôt et al., 2017; Naber & Nakayama, 2013). The brightness of internal representations therefore modulates the PLR beyond physical brightness alone (Laeng & Sulutvedt, 2014). This inspired the intriguing idea that the PLR might reveal *what* is stored during VWM maintenance. However, Blom et al. (2016) did not find evidence for a modulation of pupil size dependent on the brightness of the maintained item. Thus, unlike for the operation of encoding (also see Prioritization), the PLR cannot reveal which representations are maintained in VWM.

We present two potential neural mechanisms that can account for this observation. First, it is possible that cognitive modulations of the PLR mainly reflect visual processes and storage in early visual cortex. However, VWM relies on many more brain areas than only early visual cortex: most of nonhuman primate and human neocortex seems to be involved, with each area playing a different role in (V)WM storage (Christophel et al., 2017). It is thus possible that representations were stored outside early visual areas, explaining why pupil size did not reflect the brightness of VWM content throughout the entire maintenance interval. Second, it is possible that the observed pattern may indicate an ‘activity silent’ state of storing information when it is not yet necessary to guide behavior (Christophel et al., 2017; Stokes, 2015; Stokes et al., 2020). The dynamic coding framework dictates that information is not necessarily stored through continuous neural activity during maintenance. Instead, information is transformed into activity-silent states through short-term synaptic connections that are only “re-activated” when needed (Rose, 2020; Stokes, 2015; Stokes et al., 2013, 2020; Wolff et al., 2017). Potentially, pupil size does not reflect these dormant VWM representations, but only reflects actively attended items (see Section 4). This could explain why the brightness of unattended VWM content cannot be revealed during the entire maintenance interval. The results from Fabius et al. (2017) may complement this proposition: In this study, observers either memorized the location or the orientation of gratings for a relatively long duration (8 s). The orientation was always presented centrally on a gray background. In contrast, location was encoded on a dark or bright background, meaning that only space but not the items themselves were luminance-tagged, allowing the PLR-based tracking of the allocation of spatial covert attention during the task (Binda et al., 2014; Mathôt et al., 2013). Indeed, only when encoding an item’s location (not orientation), its background’s brightness tagged the pupil, although the effect dissipated a few seconds later during maintenance (as in Blom et al., 2016). Crucially, approximately 3 s before the observer is tested on the memory of the spatial location, the pupil starts to reflect the brightness of the background surrounding the memorized location again. Here, the re-emergence of the PLR effect possibly reflects the re-activation of a formerly activity-silent representation and, again, nicely fits with the dynamic coding framework (Stokes et al., 2015). Nonetheless, the proposed contributing neural mechanisms remain speculative and require further investigation.

4 | PRIORITIZATION

VWM allows for the use of past information to guide future behavior. A crucial aspect of this utility concerns the prioritization of the relevant parts of stored content to prepare for action (Heuer et al., 2020; Olivers & Van der Stigchel, 2020; Souza & Oberauer, 2016; van Ede, 2020; van Ede & Nobre, 2023). Prioritizing relevant material in VWM facilitates upcoming task performance, leading to faster and more accurate responses (Oberauer, 2019; Olivers et al., 2011; Olivers & Roelfsema, 2020; Souza & Oberauer, 2016; van Ede, 2020). Retro-cues, which cue a particular piece of information that is maintained in VWM, offer an elegant way to study internal prioritization (Figure 5; Souza & Oberauer, 2016; van Ede & Nobre, 2023). Combining retro-cues with the PLR has provided intriguing insights into this internal prioritization process. Unsworth and Robison (2017c) used luminance-tagging (black and white backgrounds) to track covert attention in combination with retro-cues to investigate prioritization. Here, pupil size indicates that the retro-cued side is attended prior to the probe/response screen. If the cue points to the location of an item that

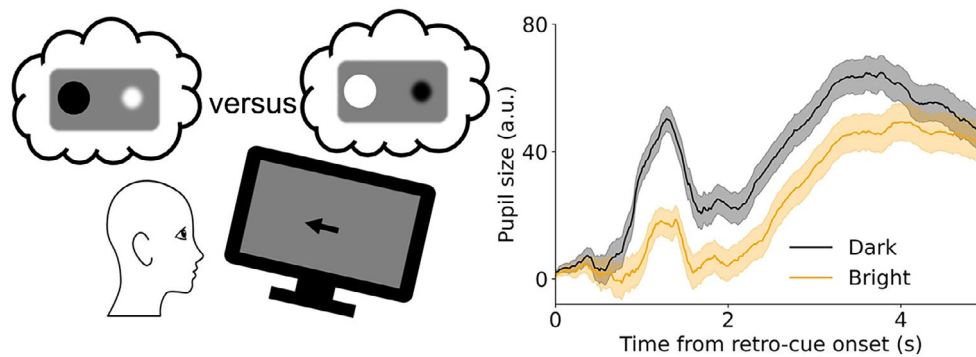


FIGURE 5 Schematic overview of prioritizing a bright or dark memorized item on the left. The right shows pupil responses to a retro-cue when internally prioritizing a bright or dark stimulus. Note that the small constriction around 2000 ms after cue onset is likely caused by the offset of the cue. Transparent patches reflect standard errors of the mean. Data from Hustá et al. (2019).

was located at a bright background, the cue triggers a relative pupil constriction, likely due to the reactivation of the internally-stored luminance property of the item's background.

More recently, pupillometric studies further investigated the internal prioritization process through luminance-tagging a memorized item itself rather than an external background (Hustá et al., 2019; Zokaei et al., 2019). Hustá et al. (2019) investigated effects of retroactive spatial cues during the maintenance of dark and bright items. Strikingly, the pupil indeed dilated more whenever a dark item was cued as compared to the cueing of a bright item (Figure 5). This vindicates the notion that pupil size indexes what is internally prioritized based on its brightness. Similar effects were reported using auditory retro-cues, an effect which persisted even when brightness was irrelevant to the task (Zokaei et al., 2019). Moreover, retro-cueing items by means of inducing temporal expectations of which item would be probed (as in van Ede et al., 2017) also induced this PLR prioritization effect. To further establish that the PLR modulation reflects the internal prioritization effect, the extent of the PLR modulation predicts the precision of VWM reports between participants across three experiments (Zokaei et al., 2019). Together, these findings show how the pupil reveals the content of *what* is internally prioritized, and that the degree to which items are internally attended affects subsequent behavior.

Beyond the insights that the PLR provides into the internal prioritization process (Hustá et al., 2019; Unsworth & Robison, 2017c; Zokaei et al., 2019), prioritizing material in VWM also evokes an effort/alerting related dilatory pupil response more generally (Figure 1; Robison et al., 2023; Unsworth & Robison, 2018)—likely mediated by phasic LC firing as during pupil dilations during maintenance. We speculate that not only the extent of the prioritization-evoked PLR is linked to performance (Zokaei et al., 2019), but that this more general dilatory response also predicts subsequent behavior in terms of accuracy, speed and precision. However, a direct link between this dilation response indicative of prioritization and behavior remains to be investigated.

5 | CONCLUSION

Working memory is essential for flexible and intelligent behavior. VWM effectuates much of its vital functioning through three key cognitive operations: encoding, maintenance, and prioritization. We here presented the idea that each of these operations is represented by different pupillary response components (Figure 1). While the *depth of encoding* is indexed by pupil orienting constrictions and baseline pupil size (Galeano-Keiner et al., 2023; Koevoet, Naber, et al., 2023), the *maintenance* of material is reflected by pupillary dilations (Beatty, 1982; Kahneman, 1973; Robison & Unsworth, 2019; Strauch, Wang, et al., 2022; Zhou et al., 2022). The *prioritization* of material is also accompanied by a pupil dilation response (Robison et al., 2023; Unsworth & Robison, 2018), but the direct link to behavior remains to be investigated. Beyond these more general pupil responses, the PLR provides even more finely grained item-specific insights into VWM operations. If items are of differential brightness, the PLR reveals which item is attended during encoding and prioritization (Hustá et al., 2019; Unsworth & Robison, 2017c; Zokaei et al., 2019).

Overcoming the inherent limitations of purely behavioral measures, the pupil equips researchers with the necessary tools to investigate the distinct cognitive processes underlying VWM operations. This allows for studying these

operations in isolation as well as understanding their interactions. Here we have reviewed findings that show that pupillometry has provided unique insights into longstanding debates (e.g., slots vs. resources), and continues to contribute to recent advancements in the field of VWM (e.g., the dynamic coding framework). To conclude, pupil size is a powerful tool to illuminate the most vital operations through which VWM works.

AUTHOR CONTRIBUTIONS

Damian Koevoet: Conceptualization (equal); formal analysis (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Christoph Strauch:** Conceptualization (equal); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Stefan Van der Stigchel:** Funding acquisition (lead); supervision (supporting); writing – review and editing (supporting). **Sebastiaan Mathôt:** Data curation (lead); writing – review and editing (supporting). **Marnix Naber:** Conceptualization (equal); supervision (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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ENDNOTE

¹ Note that accumulating work questions the distinction between the quantity and quality of VWM representations as proposed by Zhang and Luck (2008). According to most contemporary views, VWM representations are captured only by their quality/precision and psychophysical similarities (e.g. similar colors are more difficult to remember than distinct ones) (Ma et al., 2014; Schneegans et al., 2020; Schurgin et al., 2020; van den Berg et al., 2012; Williams et al., 2022). Here, we employ the terms quantity and quality free from potential theoretical implications and base our use solely on manipulations/outcome measures. Specifically, we refer to quantity when set sizes were manipulated. Whenever continuous errors were of interest, we refer to quality.

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