BRIEF REPORT

Individual differences in the allocation of attention to items in working memory: Evidence from pupillometry

Nash Unsworth · Matthew K. Robison

Abstract We utilized pupillary responses as an online measure of attentional allocation and fluctuations in attention in order to better examine both how attention is allocated to items in working memory (WM) and individual differences therein. We found that the pupillary response during a delay was modulated by the number of items to be held in memory, reaching asymptote close to capacity limits. Furthermore, we found that during the delay, how individuals allocated attention to items in WM depended on the number of items to be held, as well as on an individual's capacity. Finally, we found that pretrial pupil diameter distinguished correct and error responses and that individuals with more variability in pretrial pupil diameter had lower behavioral capacity estimates. These results suggest that individual differences in WM are due both to differences in the amount of attention that can be allocated to maintain items in WM and to differences in fluctuations in attention control across trials.

Keywords Individual differences · Memory capacity · Working memory

Working memory (WM) is a system responsible for the active maintenance and online manipulation of information over short intervals. An important aspect of WM is that it is thought to be capacity limited, such that only four or so items can be actively maintained (Cowan, 2001). Theoretically, the capacity limit arises because only four or so items can be individuated and maintained through the continued allocation of attention (Craik & Levy, 1976). As such, the ability to actively maintain items in WM is critically dependent on the ability to allocate attention to items within WM. If attention is captured

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by distracting internal or external information, the representations will not be maintained, and performance will suffer. In terms of individual differences in WM, recent work has suggested that individuals differ in both the number of items that can be maintained (Cowan et al., 2005; Unsworth, Fukuda, Awh, & Vogel, 2014; Vogel & Machizawa, 2004) and the ability to control attention to prevent attentional capture (Engle & Kane, 2004; Unsworth et al., 2014; Vogel, McCollough, & Machizawa, 2005). Thus, individual differences in the capacity of WM should partially come down to differences in the amount of attention that can be allocated to items, as well as in the ability to control attention and prevent fluctuations in attention.

Despite this initial evidence, little work has actually examined how individuals differ in their ability to allocate attention to items in WM. In particular, it is not known how attention is allocated to items in WM over short delays and how individuals differ in their ability to consistently allocate attention to actively maintain information in WM. In the present study, we suggest that pupil diameter can be used as a means to track attention allocation and task engagement while performing WM tasks. Much prior research has shown that the pupil dilates in response to the cognitive demands of a task (Beatty & Lucero-Wagoner, 2000; Goldinger & Papesh, 2012; Laeng, Sirois, & Gredebäck, 2012). For example, Hess and Polt (1964) demonstrated that the pupils dilated as a function of problem difficulty in a mental multiplication task, with higher peak dilations for the hardest problems. Similarly, Kahneman and Beatty (1966) demonstrated that pupillary dilation increased as more items were required for recall in a standard short-term memory task (see also Peavler, 1974). These effects reflect task-evoked pupillary responses (TEPRs) in which the pupil dilates relative to baseline levels due to increases in cognitive processing load. A number of studies have demonstrated similar TEPRs in a variety of tasks (Beatty & Lucero-Wagoner, 2000). These and other results led

Kahneman (1973) and Beatty (1982) to suggest that TEPRs are reliable and valid psychophysiological markers of cognitive effort or attentional allocation (Alnæs et al., 2014; Daniels, Nichols, Seifert, & Hock, 2012). That is, phasic pupillary responses correspond to the intensive aspect of attention and provide an online indication of the utilization of capacity (Kahneman, 1973; Just & Carpenter, 1993).

In addition to phasic responses providing an index of attentional allocation, research has suggested that baseline pupil diameter provides an index of the locus coeruleus–norepinephrine (LC-NE) neuromodulatory system, which is thought to be important for regulating attentional resources to maintain alertness and task engagement in a variety of situations (Aston-Jones & Cohen, 2005; Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Murphy, Robertson, Balsters, & O'Connell, 2011; Sara, 2009). A great deal of recent research suggests that there is an inverted-U relationship between LC tonic activity and performance on various cognitive tasks, consistent with the Yerkes–Dodson (1908) curve. Specifically, it is assumed that when tonic LC activity is low, individuals are inattentive and nonalert, leading to poor behavioral performance. As tonic LC activity increases to an intermediate range (phasic mode), attention becomes more focused and behavioral performance becomes optimal. However, as tonic LC activity increases further, the individual experiences a more distractible attentional state, leading to task disengagement (tonic mode) and a reduction in behavioral performance. In accord with these ideas, prior research has consistently shown that under conditions of low levels of alertness (or inattention), the baseline pupil diameter is smaller and more variable than when one is alert (Morad, Lemberg, Yofe, & Dagan, 2000). Furthermore, Murphy et al. found an inverted-U relationship between baseline pupil size and performance on an auditory oddball task, such that performance was worse when baseline pupil size was very small or very large, but performance was best at intermediate baseline levels. Likewise, Kristjansson et al. (2009) found that baseline pupil diameter was much smaller on trials preceding very slow reaction times (indicative of lapses of attention) on a vigilance task, relative to trials on which the reaction times were close to the mean. Kristjansson et al. suggested that fluctuations in alertness and attention resulted in variable reaction times and that baseline pupil diameter provides an index of changes in alertness.

The goal of the present study was to use pupillary responses as an online measure of attentional allocation and fluctuations in attention in order to better examine both how attention is allocated to items in WM and

individual differences therein. Specifically, if phasic pupillary dilations provide an online measure of attentional allocation, and capacity limits in WM reflect the number of items that can be maintained through the continued allocation of attention, then we should find that the pupil dilates up to around four items and plateaus as more items are presented. Furthermore, these phasic responses should coincide with an individual's behavioral estimates of capacity, such that the pupil should plateau at a lower level for low-capacity than for high-capacity individuals. Additionally, by using pupillary dilations it should be possible to examine how individuals are allocating attention to items in WM during a delay, and how this potentially changes as a function of the number of items in WM and of individual differences. Finally, using pretrial baseline pupil diameter, it should be possible to examine how fluctuations in attention and alertness impact the ability to maintain items in WM. Theoretically, when arousal is low, less attention would be allocated to the upcoming trial, making it less likely that items could be maintained in WM, even when only a single item had to be maintained. Thus, fluctuations in arousal and attention should be related to performance, as reflected in fluctuations in pretrial pupil diameter.

To examine these issues, we had participants perform a WM change detection task in which the number of items to be maintained varied from one to eight, and participants' pupils were measured continuously throughout the task. The use of pupil diameter should allow us to track task engagement on a trial-by-trial basis (pretrial baseline pupil diameter) and track attention allocation to items maintained in WM during a delay (phasic pupillary responses).

Method

Participants

The participants were 73 undergraduate students recruited from the subject pool at the University of Oregon. We tested participants over two full academic quarters, using the end of the second quarter as our stopping rule for data collection. Participants were between the ages of 18 and 35 and received course credit for their participation. Data from three of the participants were excluded from the analyses because of data collection problems with the eyetracker, leaving a final sample of 70 participants.

Procedure

Participants were tested individually in a dimly lit room. Pupil diameter was continuously recorded binocularly at 120 Hz

using a Tobii T120 eyetracker. Participants were seated 60 cm from the monitor and did not use a chinrest or other immobilization device.[1] Missing data points, blinks, off-screen fixations, saccades, and/or eyetracker malfunctions were removed.

After providing informed consent and calibrating the eyetracker, participants performed the WM task: a change detection task with colored squares. In this task, participants were first presented with a black fixation cross in the middle of the screen on a gray background for 2,000 ms. Next, participants were presented with arrays of one to eight colored squares ($0.65° × 0.65°$) for 250 ms. The arrays were arranged randomly on a neutral gray background, with each color randomly selected from one of seven easily discriminable colors (red, blue, violet, green, yellow, black, or white). The items in the arrays were separated by at least 2° of visual angle, measured from the centers of the squares. The presentation of the arrays was followed by a delay period of 4,000 ms, and finally the test array reappeared with one of the items circled. Participants responded as to whether or not the circled item had changed color. Half of the trials were change trials. Twenty trials of each array size were randomly presented. Two estimates of capacity (K) were estimated for each individual. First, K was estimated, using Cowan's (2001) formula, for each set size and each individual. These values were then averaged to get an estimate of capacity. Second, we estimated the maximum number of items that an individual could hold in WM (Kmax) as the highest K value across all set sizes. This was done because K estimates from small set sizes place an upper limit on the number of items that can be maintained, and thus can underestimate the number of items that can actually be maintained.

Results

Accuracy and K estimates

First, we examined accuracy as a function of set size. As is shown in Fig. 1a, accuracy was high when four or fewer items were present, but steadily decreased with larger set sizes, $F(7, 483) = 85.95$, $MSE = .01$, $p < .01$, partial η^2 (η_p^2) = .56. Likewise, examining estimates of K suggested that K increased as set size increased until about four items, and then

it plateaued, $F(7, 483) = 57.80$, $MSE = 1.10$, $p < .01$, $\eta_p^2 = .46$. Across all individuals, the K estimate was 3.22 ($SD = 1.03$) and the Kmax estimate was 4.60 ($SD = 1.23$), both of which were significantly different from zero (both ts >26, both ps < .01).

Pupil diameter

Next we turn to our primary analyses of interest, examining pupil size. As noted previously, pupil diameter was measured continuously throughout the task. Therefore, both pretrial baseline and phasic responses were examined. Baselines were computed as the average pupil diameter during the last 500 ms of the fixation screen. The phasic responses were baseline-corrected by subtracting out the baseline pupil diameter on a trial-by-trial basis for each participant. During the delay period, the pupil data were averaged into a series of 200-ms time windows for each trial, and each 200-ms window was baseline-corrected.

Set size and time course Our first set of analyses focused on phasic pupil responses as a function of set size throughout the delay period (i.e., when no stimuli were onscreen). The baseline-corrected pupil diameters were submitted to an 8 (set size) × 20 (200-ms bin) repeated measures analysis of variance (ANOVA). The ANOVA yielded a main effect of set size, $F(7, 483) = 20.27$, $MSE = .04$, $p < .01$, $\eta_p^2 = .23$. As is shown in Fig. 2a, pupil diameter increased as set size increased, and then plateaued between four and five items, consistent with the estimate of Kmax. We also found a main effect of bin, $F(19, 1311) = 13.31$, $MSE = .01$, $p < .01$, $\eta_p^2 = .16$. Importantly, there was a significant Set Size × Bin interaction, $F(133, 9177) = 10.03$, $MSE = .001$, $p < .01$, $\eta_p^2 = .13$. As is shown in Fig. 2b, for set sizes 1–3 the pupil demonstrated an initial increase, but then decreased for a time, only to increase again toward the end of the delay period. For set sizes 4–8, however, the pupil dilated early and then generally maintained a constant level for the duration of the delay.

Individual differences Next we examined how individual differences in WM (indexed by K) would be related to differences in pupillary dynamics. Specifically, we did the same analysis as above, but now entered in each individual's K as a covariate in an analysis of covariance. This analysis suggested a significant Set Size × K interaction, $F(7, 476) = 7.60$, $MSE = .04$, $p < .01$, $\eta_p^2 = .10$. In order to illustrate the effects of interest, we present the mean changes in pupil diameter by K, via a quartile split, and with participants classified into three K groups: low (bottom 25 %), mid (middle 50 %), and high (top 25 %). Note, however, that all K analyses treated the variable as continuous, rather than as arbitrary, discrete groups. As can be seen in Fig. 3, low-K individuals' pupil responses peaked at a lower set size than did those of mid- or high-K individuals, and high-K individuals peaked at higher set sizes.

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[0] We ran a small ($N = 10$) control experiment in which a chinrest was used to ensure that all participants' heads were fixed. The results were identical to those reported in the present study, suggesting that the results were not unduly affected by differences in free viewing. Additionally, on half of the trials in this study, participants were told to simply passively view the arrays. During passive trials, the pupil did not dilate during the delay as a function of set size, suggesting that the results were not simply due to sensory responses such as pupillary light reflex.
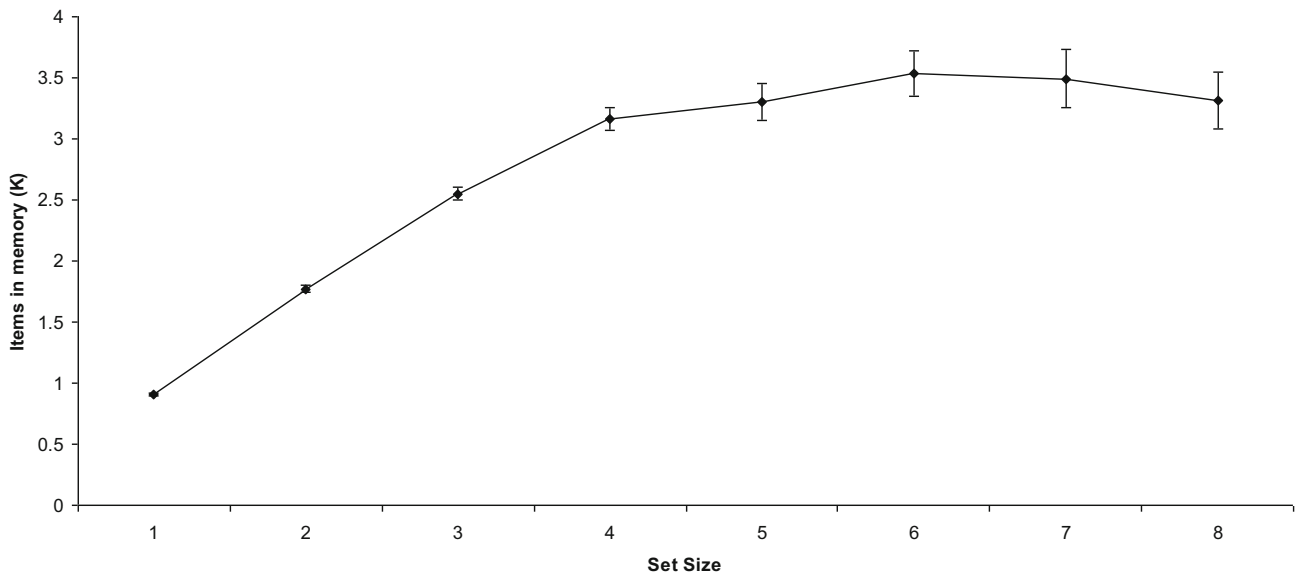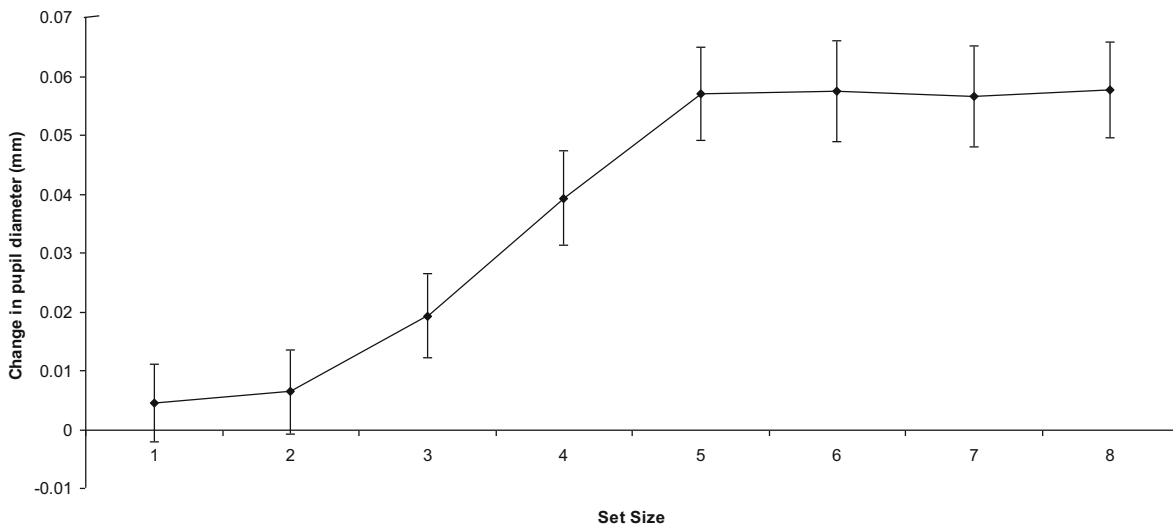
(a)
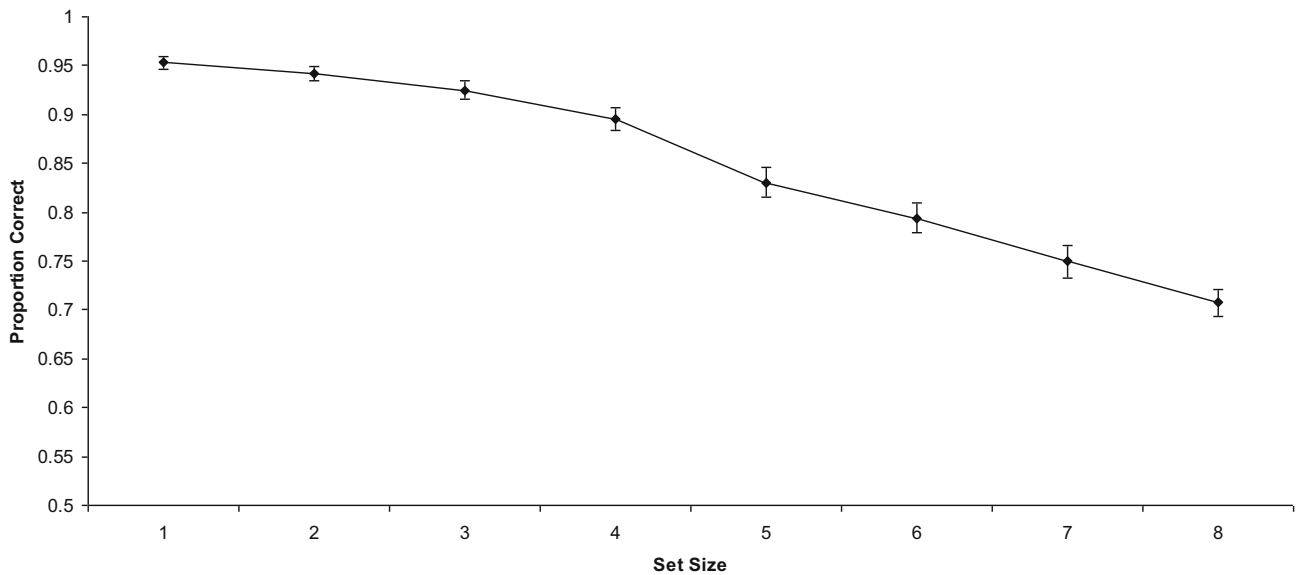
(b)

Fig. 1 (**a**) Proportions correct as a function of set size. (**b**) *K* as a function of set size. Error bars reflect one standard error of the mean

Interestingly, low-*K* individuals demonstrated larger pupil responses at low set sizes (particularly set size 1) than did high-*K* individuals (see also Heitz, Schrock, Payne, & Engle, 2008).

We also observed a significant Set Size × Bin × *K* interaction, $F(133, 9044) = 2.29$, $MSE = .001$, $p < .01$, $\eta_p^2 = .04$. As is shown in Fig. 4, all participants tended to demonstrate a dip

and subsequent rise in pupil diameter for the smallest set sizes (1 and 2). However, for larger set sizes there were marked differences in phasic pupillary dilations for individuals with different levels of *K*. Specifically, as is shown in Fig. 4a, low-*K* individuals' pupils tended to continuously increase throughout the delay. Mid-*K* individuals' pupils (Fig. 4b), however, ramped up early in the delay period, but then began to
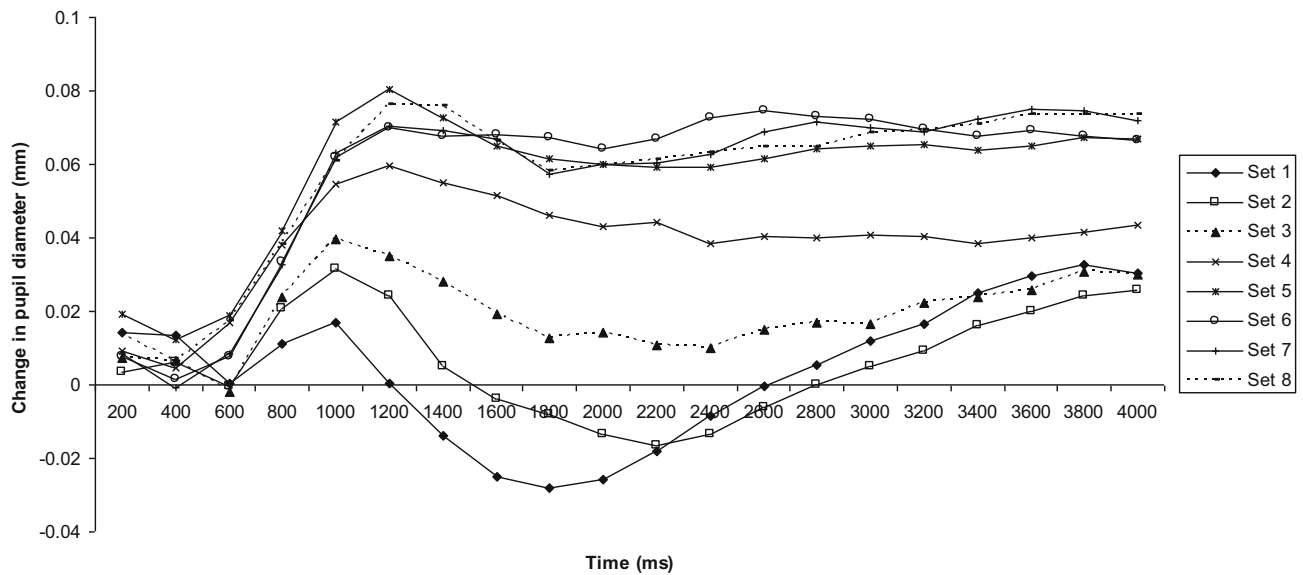
(a)

(b)

Fig. 2 (a) Changes in pupil diameter during the delay as a function of set size. Error bars reflect one standard error of the mean. (b) Changes in pupil diameter as a function of set size and time point during the delay

decrease. Finally, high-K individuals' pupils (Fig. 4c) ramped early in the delay period and maintained that level throughout the delay.

Errors on set sizes 1 and 2 The next set of analyses focused on potential reasons why individuals would make errors at low set sizes. Theoretically, nearly all individuals should be able to maintain one item in WM over the short delay, so why then do participants sometimes make errors at low set sizes?

Prior modeling research has suggested that in order to model errors (and reaction times) at low set sizes, one must incorporate a lapse parameter, whereby errors at low set sizes reflect occasional lapses of attention (e.g., Donkin, Nosofsky, Gold, & Shiffrin, 2013; Rouder et al., 2008). To test this notion, we examined baseline pupil diameters during the fixation screen for correct and error trials for both set size 1 and set size 2. We reasoned that if baseline pupil diameter reflects overall levels of task engagement (Gilzenrat et al., 2010; Murphy et al.,
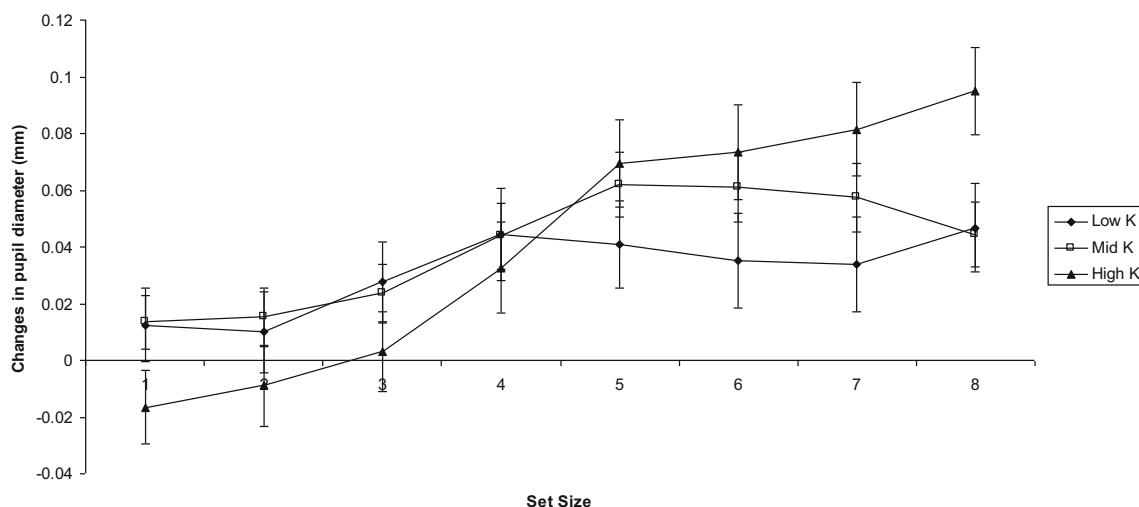
Fig. 3 Changes in pupil diameter during the delay as a function of set size and differences in K. Error bars reflect one standard error of the mean

2011), then on trials where participants are inattentive/nonalert, baseline pupil diameter should be smaller than on trials where participants are attentive/alert. Inattentive trials should be associated with errors, whereas attentive trials should be associated with correct responses. In line with our hypothesis, baseline pupil diameters were smaller on error trials than on correct trials for both set size 1 ($M = 2.73$, $SD = 0.42$, vs. $M = 3.06$, $SD = 0.43$), $t(37) = -7.48$, $p < .01$, $d = 1.21$, and set size 2 ($M = 2.76$, $SD = 0.33$, vs. $M = 3.00$, $SD = 0.33$), $t(37) = -6.48$, $p < .01$, $d = 1.03$. A similar pattern of smaller baseline pupil diameters preceding errors than preceding correct trials was found for all of the other set sizes, as well (all ts > 2.14, all ds > 0.27).

Correlations In our final set of analyses, we examined individual differences in the K estimates of WM capacity and pupillary measures. Specifically, we were interested in whether aspects of both phasic and baseline pupillary responses would predict each individual's K estimate. For the phasic responses, we computed the difference in the change in pupil diameter from set size 1 to set size 8. Higher values indicate a larger change in the phasic response across set sizes and, potentially, higher levels of attentional allocation. For the baseline responses, we computed both the pretrial mean pupil diameter and the coefficient of variation of the pretrial pupil diameter. In this case, the mean pretrial pupil diameter reflects overall task engagement, with larger pupils indicating higher overall levels of task engagement. The coefficient of variation of pretrial pupil diameter, however, reflects fluctuations in task engagement, with higher values indicating more fluctuations in task engagement. Shown in Table 1 are the descriptive statistics and reliability estimates for the measures. Shown in Table 2 are the correlations among the

measures. As can be seen, K correlated with both variability of baseline pupil diameter and the phasic response across set sizes. The overall mean baseline pupil diameter did not correlate with K. To examine these relations in more detail, we submitted all three values to a simultaneous regression predicting the estimates of K. As can be seen in Table 3, both the variability of baseline pupil diameter and the phasic response accounted for unique variance in K, but mean baseline pupil diameter did not. Collectively, variability in baseline pupil diameter and the phasic pupil response accounted for 29 % of the variance in K estimates. These results suggest that individual differences in K are driven, in part, by individual differences in phasic pupillary responses and fluctuations in baseline pupil diameter. This corroborates prior evidence that individual differences in the capacity of WM are partially determined by attention control, and more specifically by fluctuations in attentional states.

Discussion

In the present study, we examined how attention is allocated to items in WM using pupillary responses as an online measure of attention. We found that pupillary dilations during the delay increased and reached an asymptote around four to five items, suggesting a pupillary correlate of WM capacity similar to those found with contralateral delay activity (Vogel & Machizawa, 2004) and the fMRI signal in the intraparietal

Fig. 4 Changes in pupil diameter as a function of time point during the ▶ delay for (**a**) low-K individuals, (**b**) mid-K individuals, and (**c**) high-K individuals
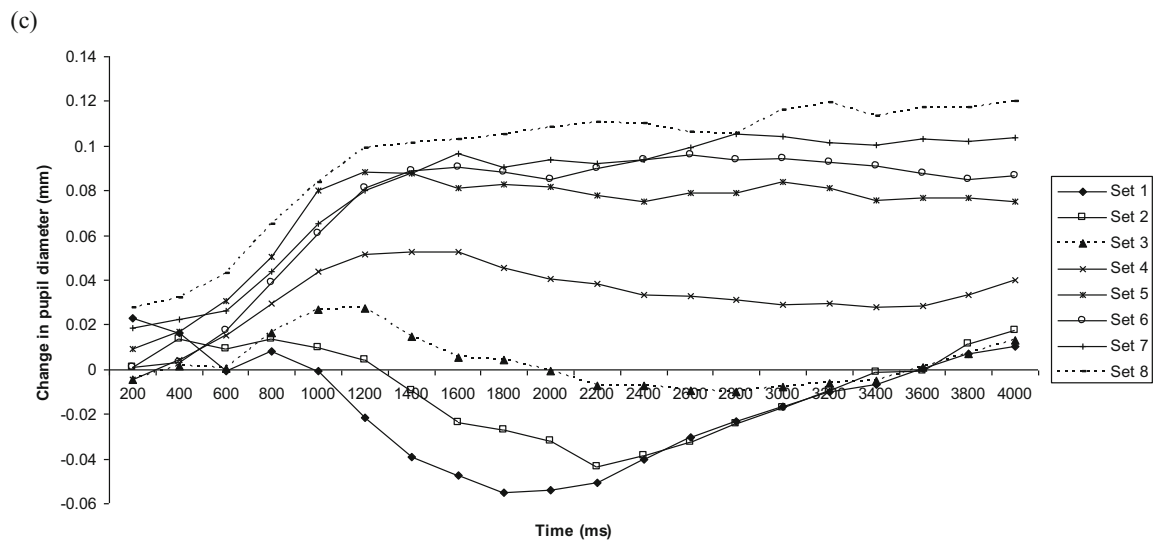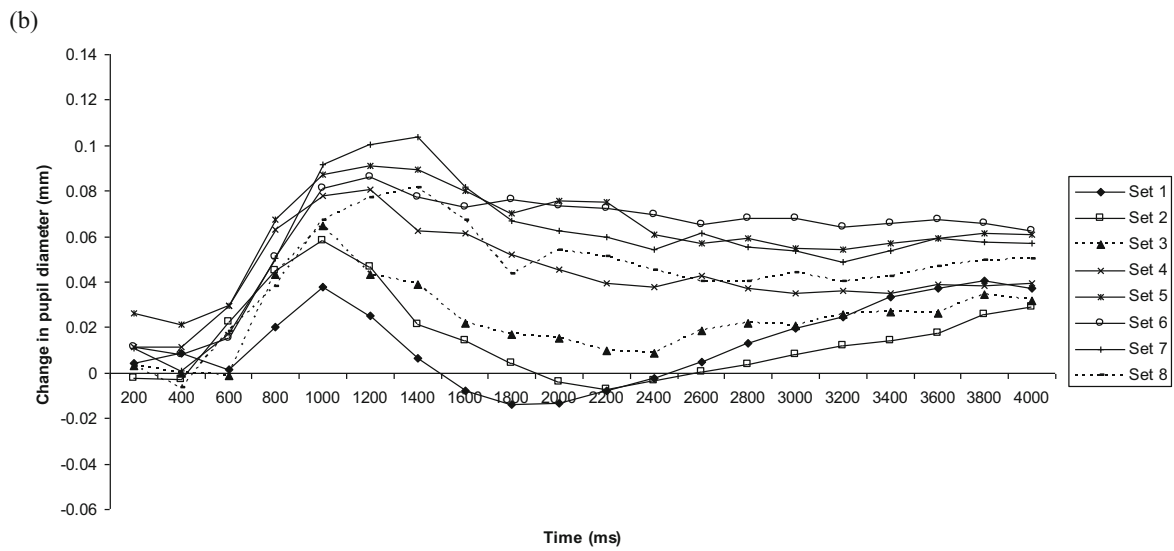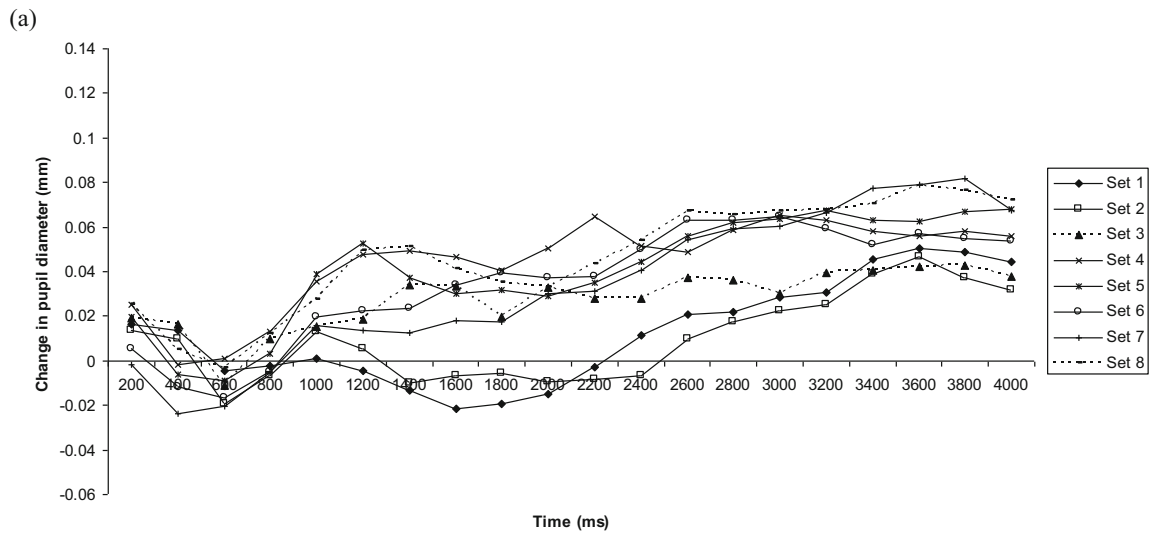
(a)

(b)

(c)

Table 1 Descriptive statistics and reliability estimates for the measures

Measure	M	SD	Skew	Kurtosis	Reliability
K	3.22	1.03	–.15	–1.05	.78
M Baseline	2.79	0.31	.18	–0.43	.98
CoV Baseline	.06	.02	.82	1.35	.89
M Phasic	.05	.07	.85	1.20	.52

CoV = coefficient of variation; reliability for K is based on alpha, and the other reliabilities are split-half.

Table 3 Simultaneous regression predicting K

Variable	B	t	sr²	R²	F
M Baseline	–.03	–0.25	.00		
CoV Baseline	–.34	–3.24**	.11		
M Phasic	.42	3.90**	.16	.29	9.13**

** p < .01.

sulcus (Todd & Marois, 2004). Furthermore, we found that individual differences in estimates of behavioral capacity were related to the pupillary estimates of capacity. In line with prior theorizing, the present results suggest that items in WM are maintained via the continued allocation of attention, and that individual differences in the capacity of WM are partially due to differences in the amount of attention that can be allocated to maintain items in WM (Cowan, 2001; Craik & Levy, 1976; Unsworth & Engle, 2007).

The present results also suggest differences in how attention is allocated to items during the delay as a function of the number of items to be maintained. Specifically, when participants were required to maintain items below their capacity, the pupil initially decreased during the delay and then increased only toward the end of the delay, suggesting that individuals were allocating few attentional resources early on, but as the delay period progressed, attention was needed to potentially maintain or refresh the items (Raye, Johnson, Mitchell, Greene, & Johnson, 2007). When participants were asked to maintain a number of items at or above their capacity, however, the pupil ramped up and peaked early and then tended to maintain that level throughout the delay period, suggesting that attention was being allocated in a more continuous manner to maintain the items in an active state. Importantly, this differed as a function of an individual's capacity. Low-capacity individuals tended to struggle to allocate attention to items in WM above their capacity throughout the delay. Individuals with a capacity closer to the mean, however,

Table 2 Correlations among the measures

	1	2	3	4
1. K	–			
2. M Baseline	.12	–		
3. CoV Baseline	–.35	–.12	–	
4. M Phasic	.43	.25	–.04	–

CoV = coefficient of variation; correlations >.24 are significant at the p < .05 level.

demonstrated an initial ramp up in pupil diameter for items above their capacity, but could not sustain this level of attention throughout the delay. Finally, high-capacity individuals demonstrated a large initial ramp up in attention and were able to maintain a high level of attention throughout the delay. These results suggest that not only are there differences in the amount of attention that can be allocated to items, but there are also differences in how attention can be continuously allocated throughout the delay.

Examining pretrial baseline pupil diameters, the present results suggested that pupil diameter preceding error trials on small set sizes was smaller than the pupil diameter preceding correct trials. This finding is consistent with prior modeling work suggesting that errors on small set sizes could be due to lapses of attention (Donkin et al., 2013; Rouder et al., 2008). Thus, the present study provides direct support for this notion by suggesting that errors on small set sizes (and larger set sizes) are partially due to lower levels of alertness and task engagement (i.e., inattention) just prior to the appearance of the stimulus array. Additionally, in the present study we found that variability in pretrial baseline pupil diameter predicted behavioral estimates of capacity, suggesting that trial-to-trial fluctuations in alertness (or lapses of attention) partially account for individual differences in WM capacity. This finding, coupled with the correlation between the phasic pupillary responses across set sizes, suggests that individual differences in WM are due both to differences in the amount of attention that can be allocated to items (capacity) and to differences in fluctuations in attentional control.

Overall, the present results are consistent with recent research suggesting that pupil diameter provides an index of the LC-NE system (Gilzenrat et al., 2010; Murphy et al., 2011). Given this link between the LC-NE system and pupil diameter, the present results suggest that the LC-NE system is likely involved in the regulation of attention during WM tasks. That is, the LC-NE system is likely important not only in regulating the amount of attention to items in WM, but also in regulating task engagement across trials. Both of these factors seem to be related to individual differences in WM, suggesting a link between LC-NE functioning and individual differences in WM.

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