

Pupil size reflects the focus of feature-based attention

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Binda P, Pereverzeva M, Murray SO. Pupil size reflects the focus of feature-based attention. *J Neurophysiol* 112: 3046–3052, 2014. First published September 17, 2014; doi:10.1152/jn.00502.2014.—We measured pupil size in adult human subjects while they selectively attended to one of two surfaces, bright and dark, defined by coherently moving dots. The two surfaces were presented at the same location; therefore, subjects could select the cued surface only on the basis of its features. With no luminance change in the stimulus, we find that pupil size was smaller when the bright surface was attended and larger when the dark surface was attended: an effect of feature-based (or surface-based) attention. With the same surfaces at nonoverlapping locations, we find a similar effect of spatial attention. The pupil size modulation cannot be accounted for by differences in eye position and by other variables known to affect pupil size such as task difficulty, accommodation, or the mere anticipation (imagery) of bright/dark stimuli. We conclude that pupil size reflects not just luminance or cognitive state, but the interaction between the two: it reflects which luminance level in the visual scene is relevant for the task at hand.

attentional modulation of visual responses; feature-based attention; motion-defined surfaces; spatial attention

ATTENTION PRIORITIZES PROCESSING of some sensory signals over others, and attentional selection can follow different strategies. One strategy is to focus attention at particular spatial locations. Some authors have suggested that shifts of spatial attention are tightly linked to eye movements (Corbetta 1998; Kowler et al. 1995; Moore and Fallah 2004), so much that the two may rely on the same neural circuits (Kustov and Robinson 1996; Rizzolatti et al. 1994), although there is evidence against this (Gregoriou et al. 2012; Ignashchenkova et al. 2004; Juan et al. 2004). However, attention can also be deployed based on nonspatial criteria, as in “global feature-based attention” (Martinez-Trujillo and Treue 2004; Saenz et al. 2002; Serences and Boynton 2007; Treue and Martinez Trujillo 1999) or “surface/object-based attention” (Ernst et al. 2013; He and Nakayama 1995; O’Craven et al. 1997; Valdes-Sosa et al. 2000; Wannig et al. 2007). Being spatially distributed, this type of attention is fundamentally distinct from eye movements, and its control likely depends on separate neural circuits (Greenberg et al. 2010; Maunsell and Treue 2006; Runeson et al. 2013), although different types of attention may ultimately affect visual responses through similar mechanisms (Maunsell and Treue 2006; McAdams and Maunsell 1999; Reynolds and Chelazzi 2004).

Recently, we showed that covert spatial attention affects pupil diameter; when attention is directed to a brighter region of an image, the pupil constricts relative to when attention is directed to a darker region (Binda et al. 2013a). Thus pupil size

not only adjusts to ambient luminance (the pupillary light reflex) and dilates with cognitive effort (Kahneman and Beatty 1966), two long-known effects, but it also indexes the location of attention in the visual scene. Confirming our findings, others emphasized the link between attentional modulations of pupil size and changes in eye position (Mathôt et al. 2013) and suggested the two “movements” of the eye to be part of the same orienting response (Wang et al. 2012). We reasoned that if the effects of spatial attention on pupil size were indeed a by-product of the links between control systems for the pupil and eye movements, no pupil change would occur if attention were allocated according to a nonspatial strategy, i.e., with feature-based attention (when targets and distracters are spatially overlapping).

In addition, we reasoned that manipulating the spatial separation between target and distracter stimuli could also allow for a distinction between two broad classes of neural models implementing the effect of attention on pupil size. Pupillary light responses are largely explained by activity in the olivary pretectal nucleus (OPN) nucleus (Gamlin et al. 1995; Loewenfeld 1993), which represents light level with very large receptive fields (Clarke et al. 2003b). One possibility is that attention enhances activity in some of these cells (e.g., those representing the left vs. right hemifield), leading to smaller pupils when the brighter region (hemifield) is attended. Clearly, this mechanism will not predict any attentional modulation for stimuli that are not segregated in space. However, in a second model, the pupillary light response depends on both OPN activity and a cortical representation of light or brightness. This model is compatible with an effect of feature-based attention on pupil size; like most visual cortical signals, the cortical representation of light should be enhanced by attention, no matter whether the bright target is selected on the basis of its spatial location or its features.

Therefore, showing an effect of feature-based attention on pupil size would strongly support the hypothesis that pupillometry provides an indirect index of visual cortical processing, which is foundational to the growing body of literature that proposes pupillometry as a noninvasive index of perceptual and cognitive states (Hartmann and Fischer 2014; Laeng and Endestad 2012; Laeng and Sulutvedt 2014; Stoll et al. 2013), useful even in research with children and special populations (Blaser et al. 2014).

METHODS

A total of 12 subjects (11 naive, 5 females, age range 19–43 yr), with normal or corrected-to-normal vision, gave informed consent to participate in the experiments approved by the University of Washington Human Subjects Institutional Review Board and in line with the Declaration of Helsinki. Six subjects participated in *experiments*

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1–3 (which may be thought of as 3 blocked conditions of a single experiment); the other six took part in *experiment 4*.

Subjects viewed a 35 × 28-cm calibrated CRT monitor from a distance of 81 cm, with head position stabilized by a chin rest. Displays were generated in Matlab (The MathWorks) using the Psychophysics Toolbox (Brainard 1997; Pelli 1997). Pupil diameter and two-dimensional eye position were measured monocularly with a video-based eye tracker (ASL Eyetrack 6; remote sensor mounted below the monitor). A standard 9-point calibration was run at the beginning of each 45-min-long session.

Stimuli consisted of motion-defined surfaces presented against a gray background (60.3 cd/m²). There were two types of surfaces: a dark surface composed of black dots (0.6 cd/m²) and a bright surface of white dots (110.1 cd/m²). On a given trial, one surface (*experiment 1*) or both surfaces (*experiments 2–4*) were displayed (see Fig. 1). Each was defined by 200 dots (0.25-deg diameter) that moved within a 5 × 5-deg aperture in clockwise or counterclockwise direction (white and black dots always moved in opposite directions). Dots located within the inscribed circle moved with 100% coherence (200-ms lifetime) at 120 deg/s angular speed (except for short speed-increment events, see below), whereas those at the four corners of the square moved randomly (preliminary observations indicated that this made speed-increment events in the central circular area harder to detect) and the central 1 deg was masked to facilitate fixation maintenance.

In all experiments, trials began with a fixation spot (a 0.25-deg red dot) shown at screen center; after 2 s, a symbolic cue (0.75-deg red letter) replaced the fixation spot; “W” cued the bright surface, and “D” cued the dark surface. Cue onset and offset (2 and 8 s into the trial) were kept constant across experiments, and we varied the time of surface presentations and their spatial configuration (Fig. 1). In *experiment 1*, only the cued surface was presented, at the center of the screen. In *experiments 2–4*, the two surfaces were simultaneously presented so that the overall luminance of the display remained

constant. In *experiment 2* and *4*, both surfaces were presented centrally. In *experiment 3*, the bright and the dark surfaces were centered at 5-deg eccentricity in the left and right hemifields. The design of these experiments may be likened to the “event-related” approach of electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) experiments, in that it allows for following the dynamics of pupillary responses after the presentation of light stimuli and attentional cues; this stands in contrast to the design adopted by others, where luminance is continuously modulated (Naber et al. 2013), as in “steady-stated” approaches.

Subjects were asked to refrain from blinking at all times, except during the 2-s intertrial interval (ITI) marked by cue offset, and to maintain their gaze on the fixation mark. Their task was to count (and report during the ITI) the number of brief (100 ms) speed increments that occurred on the cued surface, ignoring speed increments in the uncued surface (if present). Acoustic feedback was given during the ITI. In *experiments 1–3*, the number of speed increments varied between 1 and 3. The magnitude of speed increments was staircased to ensure equal performance across conditions and over testing time. Average performance when the dark and the bright surfaces were cued was 81 ± 2% and 84 ± 3% for *experiment 1*, 83 ± 2% and 80 ± 3% for *experiment 2*, and 78 ± 1% and 80 ± 1% for *experiment 3*. For *experiment 4*, speed increments varied between 0 and 1 (accounting for the shorter stimulus duration), and we fixed task difficulty with a preliminary session (100 trials); the percentage correct in the experimental sessions was 72 ± 3% and 72 ± 4%. Performance levels in the two cueing conditions were statistically indistinguishable in all experiments (paired *t*-test, *df*: 5, *t* < 1 and *P* > 0.2 in all cases). The speed increment values that allowed for these matched performance levels (percentages of base speed for the darker and brighter surfaces, ±SE across subjects) were 86 ± 5% and 104 ± 5% for *experiment 1*, 122 ± 11% and 166 ± 18% for *experiment 2*, 121 ± 8% and 147 ± 6% for *experiment 3*, and 64 ± 13% and 76 ± 18% for *experiment 4*. This means that the motion of the bright surface was originally more

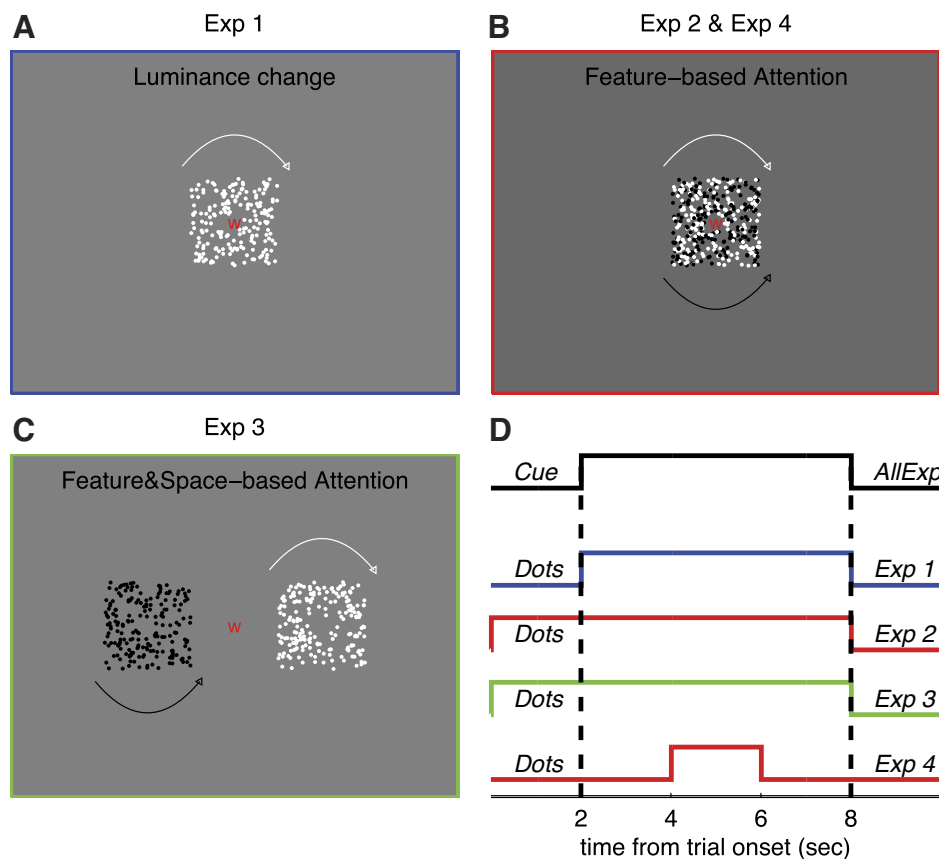


Fig. 1. Spatial arrangement and time courses of stimulation. A–C: approximately in scale representation of the display in *experiments 1–4*. Subjects maintained fixation on a dot at the center of the screen and reported speed increments in 1 of the 2 surfaces (defined by coherently rotating dots) as indicated by a symbolic cue (the letter “W” or “D”). D: presentation times of the cue (black line) and the moving dot surfaces (colored lines, relevant experiment indicated at right of each line). Exp, experiment.

difficult to judge than that of the dark surface. Considering the pupil-dilating effect of cognitive effort, one might take this to predict larger pupil size when the bright surface was cued (the opposite of our results); however, we note that any such difference in effort should have been abolished by matching percent correct, and hence difficulty level. Finally, also note that the number of speed increments was always matched across conditions, ensuring that the salience of the stimuli (potentially driving bottom-up shifts of attention) was the same irrespectively of which surface was cued. Specifically, we used a pseudorandomized schedule so that each sequence of speed changes (1, 2, or 3 for *experiments 1–3* and 0 or 1 for *experiment 4*) was presented the same number of times across conditions (attend to bright/dark, rotating clockwise and counterclockwise).

Data analyses. Eye tracking data were acquired at 120 Hz (pupil diameter was measured with a resolution of 0.05 mm); individual samples where eye position took unrealistic values (locations outside the screen monitor, mostly due to blinks) were treated as signal losses. The average horizontal gaze position in the first 50 ms of each trial was subtracted from samples acquired across the rest of the trial. Only for *experiment 3*, trials were excluded if any horizontal eye-position sample during the stimulus presentation window (2–8 s into the trial) deviated by more than 2 deg toward the attended stimulus (excluded trials: $4.92 \pm 2.3\%$). For all other experiments, a statistical analysis showed that the distribution of horizontal and vertical eye position was indistinguishable across attention conditions (all P values >0.05 , uncorrected). For this analysis, the average horizontal and vertical eye position (deviation from baseline) during the stimulus presentation window (same temporal intervals used to compare pupil size values, see Figs. 2D and 3B) was computed for each subject, separately for the “attend to bright” and “attend to dark” condition, and the two conditions were compared with a series of paired t -tests, none of which reached statistical significance (all uncorrected P values >0.05).

The average pupil diameter in the 500 ms preceding cue onset was subtracted from samples acquired across the full trial; the resulting pupil change time courses were binned in steps of 50 ms. These were averaged across trials (at least 30 per subject and condition), and the difference between the average time-courses was computed. A t -test was run on pupil-difference values from the six subjects in each of the 50-ms time bins; the first bin of a pair with significant values estimated the average latency of the effect relative to cue onset.

RESULTS

We measured pupil size while subjects maintained fixation and two sets of dots, black and white, rotating in opposite directions, defined two perceptually segregated surfaces: dark and bright. A symbolic cue indicated which surface was to be selectively attended, and subjects reported the number of subtle speed increments in the cued surface.

Figure 2, A–C, presents the results from *experiments 1–3*, run on the first set of 6 subjects. In baseline *experiment 1* (Fig. 2A), only the cued surface was presented on a given trial, centered at fixation (see Fig. 1A), producing a change of the overall display luminance. As expected, pupil size was smaller during the presentation of the brighter vs. the darker surface (gray vs. black curve). Pupil change traces are complex, probably reflecting the multiplicity of factors influencing pupil size: among others, the transient constriction at the onset of stimuli defined by motion, contrast, color (e.g., Barbur et al. 1992), and the progressive dilation with perceptual decisions and cognitive effort (e.g., Einhauser et al. 2008; Kahneman and Beatty 1966), as involved by our behavioral task. However, the pupil difference time course (blue curve) has a much simpler shape. A significant difference arises 350–400 ms after cue/

surface onset (blue vertical line) and remains sustained until the beginning of the ITI, marked by cue/surface offset. Data acquired beyond this point must be interpreted with caution because blinks and button presses were allowed in this interval and likely contaminated recordings; these might be responsible for the transient dilation that was consistently observed in the ITI.

Figure 2B shows the results of *experiment 2*, in which both surfaces were presented on each trial, at the same central location (see Fig. 1B), and subjects selectively attended to the brighter (gray curve) or the darker one (black curve). Because the pattern of stimulation was identical across trials and overall luminance always constant, no pupillary light response is expected. However, we find that directing attention to one of the two surfaces was sufficient to induce a consistent and sustained pupil size difference (red curve). The two surfaces were displayed at the start of the trial, but a significant pupil size difference emerged only after the cue presentation: the first significant data point is between 1.300 and 1.350 s after cue onset (red vertical line). The bar plot in Fig. 2D shows the average pupil difference over the cueing interval (2–8 s from trial onset). The pupil modulation produced by shifting attention from the darker to the brighter surface (red bar, *experiment 2*) is significant [1-sample t -test, t : 2.81, df : 5, false discovery rate (FDR)-corrected $P = 0.04$; note that a 1-sample t -test on the pupil difference between the 2 conditions is equivalent to a paired t -test on the pupil values observed in the 2 conditions], and it is about 33% of that induced by the physical alternation between the two surfaces (blue bar, *experiment 1*).

In *experiment 3*, the same two surfaces were simultaneously presented on each trial, but they were displayed at nonoverlapping locations (see Fig. 1C). The cued surface (brighter vs. darker) could therefore be selected on the basis of both its features and its spatial location. Again, attending to the brighter vs. darker surface resulted in systematically different pupil size (Fig. 2D, 1-sample t -test, t : 2.76, df : 5, FDR-corrected $P = 0.04$), with the effect starting at about 800–850 ms after cue onset (Fig. 2C, green vertical line). A 2×2 repeated-measures ANOVA compared the average pupil change values when subjects attended to the darker vs. brighter surface (factor 1) in *experiments 2* vs. *experiment 3* (factor 2). The two factors did not interact [$F(1,5)$: 4.51, $P = 0.09$], implying that the effect of attention is not significantly different in experiments 3 and 2. Although lack of statistical power might explain the nonsignificant two-tailed test, the data are clearly sufficient to exclude the a priori most likely possibility, that the effect of space- and feature-based attention combined (*experiment 3*) is larger than the effect of feature-based attention alone (*experiment 2*). Across the two experiments, the main effect of attention is significant [$F(1,5)$: 10.13, $P < 0.05$], i.e., pupil size was consistently smaller when subjects attended to the brighter vs. darker surface, across experiments. Moreover, there is a significant main effect of experiment [$F(1,5)$: 15.90, $P < 0.05$]; irrespectively of the attended surface, pupil size was larger in *experiment 2* than in *experiment 3* (compare the average y -position of the gray and black curves between Fig. 2, B and C). Crucially, differences in task performance cannot explain the larger pupil size values observed when subjects attended to the darker vs. brighter surface and overall in *experiment 2* vs. *experiment 3* task, because performance was strictly matched both across conditions and across experiments [2×2 ANOVA

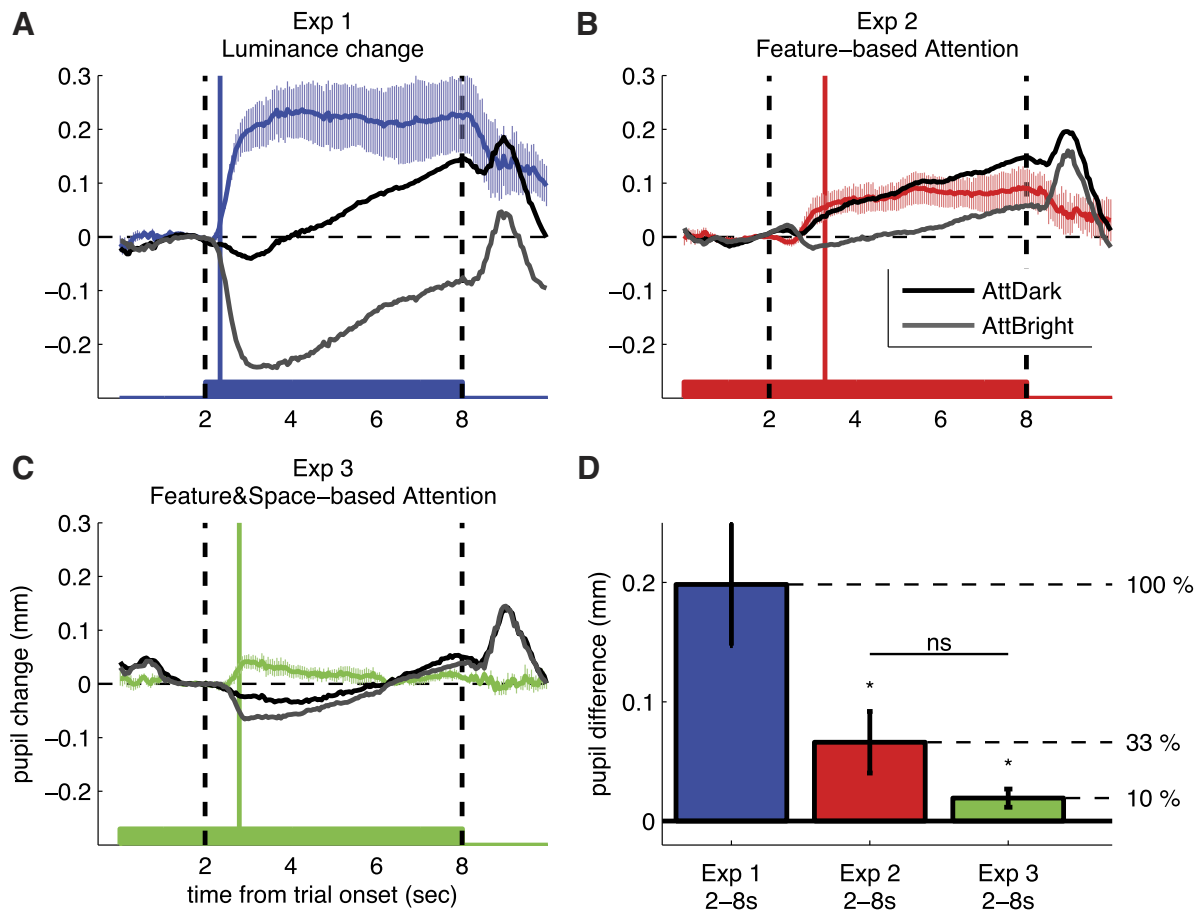


Fig. 2. Results from *experiments 1–3*. *A–C*: “pupil change” time courses for trials where the dark (black, AttDark) or the bright (gray, AttBright) surface was attended, computed by subtracting from each trace the mean pupil diameter in the 0.5-s preceding cue onset and then averaging traces across trials ($n = 6$). Colored curves give the difference between the 2 pupil change time courses, with shades indicating SE across subjects. The vertical colored line indicates the first time bin where the pupil difference is significant. Vertical dashed lines and the stair plot at the *bottom* of each panel give the onset and offset of the cue and the surfaces, respectively. *D*: average pupil difference in a 2- to 8-s interval, with SE across subjects. * $P < 0.05$, statistical significance; $P > 0.05$, not significant (ns); P values false discovery rate (FDR) corrected for multiple comparisons. Brighter and darker thin bars (see legend) give the pupil difference value computed after splitting trials where the behavioral response was/was not correct.

with the same factors as above; main effect of attention: $F(1,5)$: 0.01, $P > 0.1$, main effect of experiment: $F(1,5)$: 1.94, $P > 0.1$, interaction: $F(1,5)$: 2.65, $P > 0.1$].

In *experiment 4* (run on a separate set of 6 subjects), the spatial layout of stimulation was the same as in *experiment 2*, but the bright and dark surfaces were only presented for a 2-s interval, preceded and followed by two intervals where the cue alone was shown. In this way we aimed to exclude two alternative interpretations of the attentional pupil modulation shown in *experiments 2 and 3*: that the pupil change is explained by the cue itself (i.e., by the slightly different luminance profiles of the letters W and D) and that it is induced by the mere mental act of focusing on bright/dark (Laeng and Sulutvedt 2014). Both hypotheses predict a significant pupil size difference in the prestimulus interval where the cue alone was shown, allowing subjects to anticipate the brightness of the to-be-attended surface. However, Fig. 3*A* shows that a pupil size difference emerged only after the surfaces were presented (first significant time point: 2.850–2.900 s after cue onset, i.e., 850–900 ms after stimulus onset) and rapidly returned to baseline on disappearance of the surfaces (even though the cue remained on). Figure 3*B* compares the average pupil difference in two 1-s-long intervals: at the end of the cue-only interval and

at the end of the cue + surfaces interval (analyzing the second half of the cueing and stimulus intervals accounted for the latency of pupillary responses). The pupil size difference was significant only when both the cue and the surfaces were present (1-sample t -test, t : 4.22, df : 5, FDR-corrected $P = 0.02$), not during the prestimulus cueing interval (1-sample t -test, t : -0.54 , df : 5, FDR-corrected $P = 0.61$), with a significant difference between the two intervals (paired t -test, t : 2.71, df : 5, $P < 0.05$).

DISCUSSION

We found that focusing attention on a bright vs. dark stimulus is accompanied by a pupil size change of up to 33% of the change produced by the physical alternation between the same bright and dark stimuli. Similar pupil size modulations are observed when attentional selection can avail of the spatial location of the stimuli (replicating our previous report, Binda et al. 2013a) or when it must be based on their features only. This strongly suggests that the observed attentional modulations are not easily explained as a by-product of actual or suppressed eye movements, which likely accompany shifts of spatial attention (Mathôt et al. 2013; Wang et al. 2012).

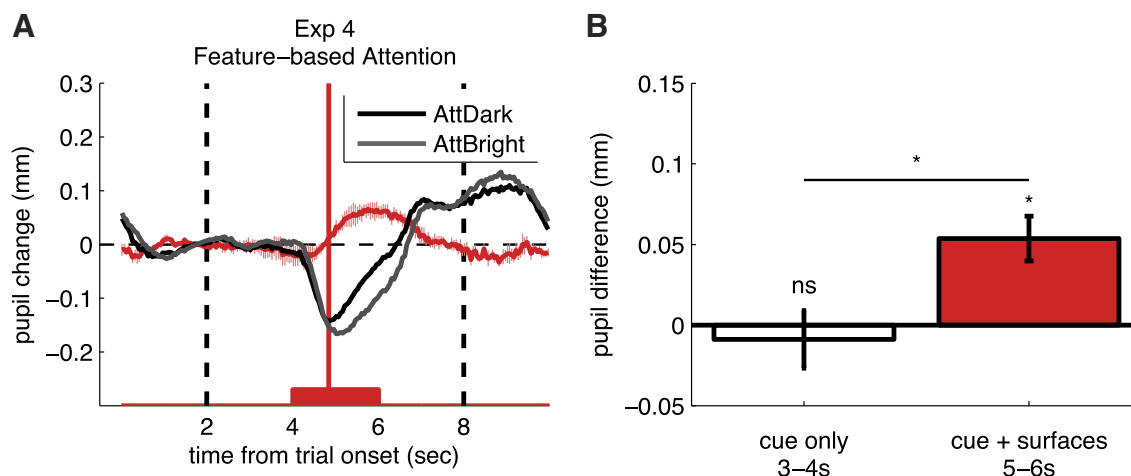


Fig. 3. Results from *experiment 4*. *A*: pupil change and pupil difference time courses, averaged across subjects ($n = 6$); same format as in Fig. 2*A*. *B*: average pupil difference (with SE across subjects) in 2 intervals: before the surface presentations (3–4 s into the trial) and after the surface presentations (5–6 s into the trial). * $P < 0.05$, statistical significance; $P > 0.05$, ns; P values FDR corrected for multiple comparisons.

The feature-based effect we observed in the present study also provides insight into the neural circuitry mediating the attentional modulations on pupil size. Pupillary light responses depend on activity in the subcortical OPN nucleus, which represents light level in very large receptive fields (Gamlin and Clarke 1995; Loewenfeld 1993). Attention could enhance activity in some of these cells, leading to smaller pupils when the brighter region is attended. However, this mechanism would not easily predict any attentional modulation for stimuli that are not spatially segregated (due to the large OPN receptive fields). In an alternative model, pupillary light responses may also depend on a cortical representation of light level (or brightness). This model is supported by evidence showing that pupillary light responses are modulated by factors thought to involve cortical processing, such as interocular competition (Barany and Hallden 1948; Kimura et al. 2014; Lorber et al. 1965; Naber et al. 2011; Richards 1966) or saccadic suppression (Lorber et al. 1965; Zuber et al. 1966), and that pupillary constrictions can be evoked by the mere illusion of brightness (Laeng and Endestad 2012) or by the context usually accompanying bright light, as in pictures of the sun (Binda et al. 2013b; Naber and Nakayama 2013). This model can account for the present results, suggesting that pupillary light responses integrate OPN signals with cortical signals representing light level, which, like most visual cortical signals (Carrasco 2011; Reynolds and Chelazzi 2004), are likely enhanced by selective spatial or feature-based attention.

This effect of attention on pupil size occurs at the earliest possible stage in the visual system, the point where light enters the eye, and changes of pupil size are known to impact on basic visual functions: visual sensitivity (Campbell and Woodhouse 1975; Woodhouse 1975; Woodhouse and Campbell 1975), visual acuity (Campbell and Gregory 1960; Laughlin 1992; Westheimer 1964), and depth of field (Charman and Whitefoot 1977; Marcos et al. 1999). It may therefore be natural to propose a functional role for these attentional modulations of pupil size. However, one should bear in mind that aperture changes spanning the full mechanical range of the human pupil have minute consequences on vision, let alone the tenth-of-millimeter changes induced by attention. Thus we believe that the importance of these attentional modulations of pupil size

lies more in their theoretical implications and practical applications than in their consequences on vision. Specifically, these modulations show that pupil size can be used as a tool to probe visual cortical processing, being an easily accessible, objective, quantitative, and time-varying parameter that can track complex perceptual and cognitive constructs, of which attention is an example, provided that luminance differences are present across the visual scene. Importantly, this index can be obtained without interfering with behavior; for example, measuring pupil size does not interfere with the deployment of attention itself, contrary to many attentional indexes based on behavioral performance (e.g., double-task or invalid cueing designs). We measure a sustained effect of attention, which was approximately constant over the entire task interval. However, recent studies reveal systematic variations of attentional effects over time (Fiebelkorn et al. 2011). Although these oscillations might have been detectable at the level of the pupil, they were likely masked by the structure of the task chosen for our experiments, where the task-relevant speed changes occurred in pseudorandom number and at random times during the task interval (with number and detectability strictly matched across conditions).

The literature on attentional modulations of cortical responses suggests that the effects of spatial and feature-based attention are additive (Runeson et al. 2013; Treue and Martinez Trujillo 1999), which would incorrectly predict a larger pupil size modulation when both can select the cued surface (*experiment 3*) vs. feature-based attention alone (*experiment 2*; the observed trend was in fact opposite). However, in our experiments, the spatial segregation of the stimuli covaried with their eccentricity, and the latter might be more directly responsible for the observed pattern of results. The effect of attention to bright/dark on pupil size is likely to scale with the strength of the bright/dark stimuli, as suggested by our previous results (Binda et al. 2013a) and directly shown in our most recent work (Binda P and Murray SO, unpublished observations). More eccentric stimuli (*experiment 3* vs. *experiment 2*) will evoke weaker pupillary light responses (Clarke et al. 2003a), explaining the smaller attentional modulation of pupil size in *experiment 3* vs. *experiment 2*. There are other aspects of our results that could be accounted for by this model. The random dot stimuli used here are a less powerful pupillary drive than

the bright/dark disks or gratings used in our previous report: when presented in fovea, they evoke smaller pupil changes (compare Fig. 2A in the present article and Fig. 1C in Binda et al. 2013a). If attentional modulations scale with stimulus strength, then we can also account for the effect of spatial attention shown in the present study (10%) being smaller than that found in our previous study (about 30%). Finally, inspection of Fig. 2 suggests that the effect of attention is evident on the “attend to bright” traces (gray), whereas there is little variation across experiments of the “attend to dark” traces (black). This is consistent with our previous findings of a smaller attentional modulation of the pupillary dark vs. light response (Binda et al. 2013a) and can be expected from the smaller pupil size changes evoked by dark vs. light stimulation (Loewenfeld 1993).

However, it is important to acknowledge that the individual traces are complex, likely affected by a multiplicity of variables. For this reason, like in our previous report (Binda et al. 2013a), we quantified the effect of attention by taking the difference of pupil size traces between conditions, i.e., the difference across trials where the brighter vs. darker of two surfaces is cued. This effect cannot be explained by other factors known to affect pupil size. First, a pupil size difference can be expected if eye position is biased toward the cued stimulus (Clarke et al. 2003a). This was a concern in *experiment 3* and in our previous experiments, and was addressed by strictly controlling eye movements (for details see METHODS and Binda et al. 2013a). However, eye position biases cannot explain the pupil size modulations in *experiments 2* and *4*, given that bright and dark surfaces occupied overlapping regions and were defined by limited-lifetime motion; the analysis of eye position for *experiments 2* and *4* further excluded the possibility of such biases. Second, differences in accommodation state can cause pupillary constriction (Bharadwaj et al. 2011; Marg and Morgan 1949), but performance of our challenging behavioral task required subjects to maintain the stimulus plane in sharp focus. Third, pupil diameter is known to increase with cognitive effort (e.g., Kahneman and Beatty 1966); however, task performance was strictly matched across conditions, implying that differences in the “amount of attention” cannot explain our results. Finally, Laeng and Sulutvedt (2014) recently reported that mental imagery of higher/lower luminance levels is sufficient to modulate pupil size. This effect is clearly different from the one we report. When we presented the cue alone, for an interval that gave ample opportunity for the subjects to anticipate the to-be-attended luminance level (*experiment 4*), we found no pupil modulation. Pupil responses to imagery may well have very long dynamics (delays on the order of 10 s cannot be excluded based on the published data), which would make them difficult to detect in the relatively short time frame of our trials. On the contrary, the effect of attention we report has relatively fast dynamics; its latency is variable but only two to three times longer than the pupillary light reflex.

We conclude that pupil size is subject to an attentional modulation, clearly distinct from other known cognitive influences: pupil dilation with increasing “amount of attention” (Kahneman and Beatty 1966) and pupil size changes with imagery (Laeng and Sulutvedt 2014). In both these cases, a pupil change accompanies changes of the subjects’ internal state, irrespectively of the visual stimulation. In contrast, we

show in the present work that pupil size depends on the interaction between the pattern of visual stimulation and the subjects’ behavioral goals. This effect is also quite distinct from previously reported cortical influences on pupil size, including “onset responses” to color or motion transients (Barbur et al. 1992; Young et al. 1993) and pupillary constrictions in response to variations of brightness (Laeng and Endestad 2012) or image content (Binda et al. 2013b; Naber and Nakayama 2013), for in all these cases the pupil modulation does not interact with the actual light levels of the image. In particular, our previous work (Binda et al. 2013b) showed that the pupil constricts more in response to pictures of the sun (contextual cues normally associated to high luminance levels) than with images of matched luminance and low-level features, and that this effect is independent of the location of attention. Moreover, control images included pictures of the moon, implying that the pupillary constriction could not be explained by the effect of focused attention on the most salient bright elements, the sun and the moon arguably being of similar salience.

Conclusion. Pupil size reflects which luminance level in the visual scene is most relevant for the task at hand, providing a simple and robust means to keep track of what is attended, be it spatial regions or features.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

P.B., M.P., and S.O.M. conception and design of research; P.B. performed experiments; P.B. analyzed data; P.B. and S.O.M. interpreted results of experiments; P.B. prepared figures; P.B. drafted manuscript; P.B. and S.O.M. edited and revised manuscript; P.B., M.P., and S.O.M. approved final version of manuscript.

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