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Occipital TMS at phosphene detection threshold captures attention automatically

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ABSTRACT

Strong stimuli may capture attention automatically, suggesting that attentional selection is determined primarily by physical stimulus properties. The mechanisms underlying capture remain controversial, in particular, whether feedforward subcortical processes are its main source. Also, it remains unclear whether only physical stimulus properties determine capture strength. Here, we demonstrate strong capture in the absence of feedforward input to subcortical structures such as the superior colliculus, by using transcranial magnetic stimulation (TMS) over occipital visual cortex as an attention cue. This implies that the feedforward sweep through subcortex is not necessary for capture to occur but rather provides an additional source of capture. Furthermore, seen cues captured attention more strongly than (physically identical) unseen cues, suggesting that the momentary state of the nervous system modulates attentional selection. In summary, we demonstrate the existence of several sources of attentional capture, and that both physical stimulus properties and the state of the nervous system influence capture.

Introduction

Attention dramatically influences how stimuli are processed and perceived. This can be characterized by paradigms in which an attention-capturing stimulus (cue) is presented somewhere in the visual field, followed by a target display (Müller and Rabbitt, 1989; Posner, 1980). Target discrimination is improved when the target appears at the same location as the cue (valid cueing), compared to other locations (invalid cueing). Capture is classically considered as an automatic, reflex-like process that operates rapidly at the expense of being inflexible, primarily dominated by physical stimulus properties (Theeuwes, 1991, 1992; Theeuwes et al., 2006). The present study investigated to what extent physical stimulus properties determine attentional capture. Our findings suggest that automatic capture relies on multiple, both cortical and subcortical neural sources and that moment-to-moment variations in cortical excitability actively modulate capture strength.

A growing body of evidence suggests that despite its speed, automatic attentional capture is highly sensitive and flexible (Eimer and Kiss, 2008; Folk et al., 1992). Some studies reported capture by low-contrast stimuli, even below the threshold for conscious report (McCormick, 1997; Mulckhuyse et al., 2007). Furthermore, brighter stimuli capture attention more strongly than fainter stimuli (Fuller et al., 2009), indicating that capture is not a rigid, all-or-nothing phenomenon, but rather shows gradual scaling properties. Previous studies investigating the relationship between stimulus intensity and capture strength typically used either low or high intensities, rendering any direct comparisons difficult. In this study, we asked whether capture strength can be partly divorced from stimulus properties, and can be driven by variability within the nervous system, even when physical stimulus intensity is held constant. To examine this, we measured the strength of attentional capture when cues were presented at a constant intensity: the detection threshold for conscious report.

Our second aim was to investigate the neural mechanisms supporting conscious and unconscious attentional capture, specifically the extent to which the two rely on distinct neural mechanisms. Fig. 1 depicts the neural structures mediating processing of a visual stimulus (the square) from retina to cortex, i.e., potential loci of attentional capture effects. It has been suggested that unconscious capture principally relies on the fast feedforward subcortical pathway which progresses from the retina through the superior colliculus (and other subcortical structures) before reaching cortex. This 'retinotectal' feedforward pathway is postulated to act as a rapid detector of behaviorally significant events in the visual field even in the absence of conscious perception, and would be the principal source of unconscious attentional capture (Mulckhuyse and Theeuwes, 2010). By contrast, supra-threshold, consciously perceived stimuli would also capture attention through other, most likely cortical, mechanisms.

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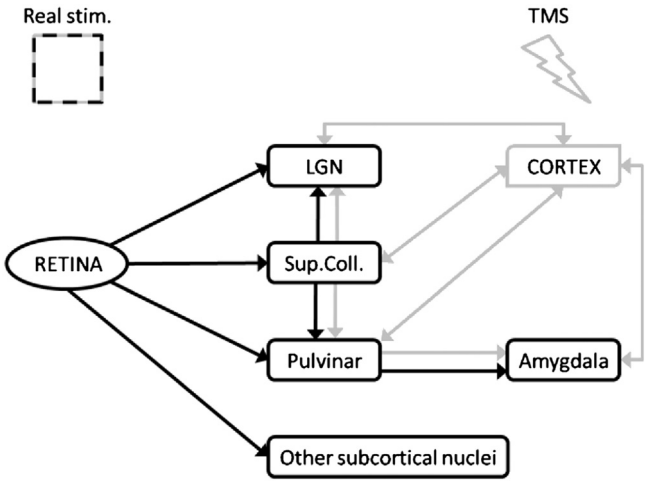

Fig. 1. Neural structures mediating attentional capture by real visual stimuli and TMS-induced phosphenes. Black arrows: driving feedforward pathways that are used by visual stimuli but cannot be accessed by TMS-induced phosphenes. Capture from phosphenes would indicate that these connections are unnecessary for capture. Gray arrows: connections that by contrast may be necessary for capture from both visual stimuli and phosphenes.

In this study, we examined whether the feedforward retinotectal pathway is necessary for any unconscious or conscious capture to occur, by probing capture in the absence of subcortical feedforward processing. We used a special type of stimuli as attention cues: transcranial magnetic stimulation (TMS) over occipital cortex (the flash in Fig. 1). The perceptual effect of TMS co-varies with its intensity: TMS at or above threshold produces a flash-like percept called a 'phosphene', often resembling a grayish ellipse a few visual degrees in size located contralateral to the stimulated cortical location. Previous studies focused primarily on determinants of phosphene perception. The results showed, for example, that phosphenes percepts (moving vs. stationary, vivid vs. vague) can be affected by interfering with the visual (Pascual-Leone and Walsh, 2001; Silvanto et al., 2005) or vestibular system (Arshad et al., 2013) before TMS. Further, pre-pulse brain excitability can predict whether or not a phosphene is seen (Dugué et al., 2011; Romei et al., 2008), with brain excitability indexed in terms of power of alpha (8–12 Hz) oscillations in visual areas (where higher alpha power indicates lower excitability; e.g., Hanslmayr et al., 2007; Toscani et al., 2010). Additionally, adapting a neuronal population to a stimulus increases the likelihood of seeing a phosphene, further suggesting that the state of the nervous system influences phosphene perception (Guzman-Lopez et al., 2011). Other cognitive states also influence phosphene perception: Visual imagery decreases phosphene thresholds (Sparing et al., 2002), while visual short-term memory content influences both the likelihood of seeing a phosphene (Cattaneo et al., 2011) and phosphene appearance (Silvanto and Cattaneo, 2010). Finally, attending to a location decreases TMS thresholds for seeing a phosphene there (Bestmann et al., 2007).

Much less is known about whether or not phosphenes themselves influence cognition. A methodological concern from brain stimulation studies is that potential effects of direct microstimulation might be confounded by capture to phosphenes (Cavanaugh et al., 2006). In the present study, we directly assessed this concern by investigating whether or not phosphenes do capture attention—albeit with an additional motivation: By using TMS over occipital cortex, we were able to bypass feedforward input into subcortical areas (Fig. 1, black connections)—and thus test whether this input is necessary for attentional capture, or whether some capture can still occur when only other pathways are available (Fig. 1, gray connections).

Materials and methods

Participants

Fourteen right-handed participants (three male, mean age 24 years), all with normal or corrected-to-normal visual acuity and naïve with respect to the purpose of the study, took part in the experiments either for monetary compensation or course credits. Two participants could not see phosphenes and were thus excluded from further analyses. Participants gave written informed consent for a TMS protocol approved by the German Psychological Association (DGPs).

Apparatus

The experiment was performed in a dimmed and sound-attenuated experimental cabin. Single bi-phasic TMS pulses were delivered using a figure-of-eight coil with an outer winding diameter of 95 mm and applied throughout to the right hemisphere with the handle pointing towards the right (PowerMAG Research, Brain Products, Germany). Stimuli were presented on a 22 inch LCD monitor with a screen refresh rate of 100 Hz, at a viewing distance of 57 cm. The background color was set to medium gray (CIE Yxy 23 cd/m^2, .32, .34) throughout the experiment.

Stimuli and procedure

The experiment consisted of three parts: (i) phosphene site localization, (ii) stimulus scaling, and (iii) the main experiment. Phosphene sites were localized by applying single TMS pulses to the right occipital lobe while participants fixated with eyes open. Stimulation intensity was increased from 50% of maximal stimulator output in 5–10% steps until a phosphene was reported or else 90% output was reached. Participants were excluded if no phosphenes had been reported after 10 consecutive stimulation trials using 90% stimulation over each of nine points spanning a 2 cm × 2 cm grid centered 2 cm dorsal and 1 cm lateral to the right of the inion. Two participants failed this criterion. In the remaining participants, the stimulation site for the experiment was chosen as that which elicited the brightest and largest phosphene that was most restricted to the contralateral visual field. Participants described the location, size, and color of the phosphene by drawing it with a vector-graphics application. In the subsequent stimulus scaling sessions, a stimulus sequence identical to one in the main session (Fig. 2) was presented, with participants having either to report whether or not they saw the cue, or to perform Landolt discrimination. A QUEST

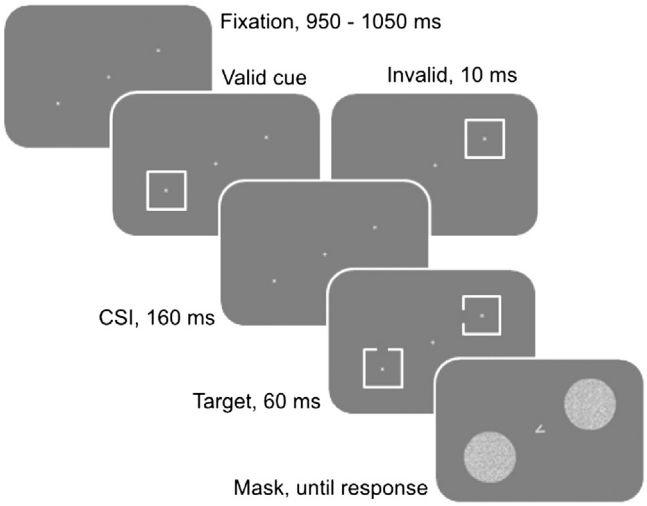

Fig. 2. Stimulus sequence per trial, along with the respective exposure durations.

staircase (Watson and Pelli, 1983) was used to adjust the real (i.e., on-screen visual stimulus) cue luminance and the TMS intensity per participant such that real and phosphene cues were reported on 75% of trials. The 75%, rather than the 50%, criterion was used because in the scaling session, participants performed a single task which permitted attention to be allocated fully to either the cue or the Landolt target. By contrast, in the main experiment, they had to distribute their attention between the cue and the Landolt stimuli. Since it is known that attentional states modulate phosphene thresholds (Bestmann et al., 2007), we aimed for a higher stimulus intensity in order to assure that, in the main experiment, our phosphene TMS was not rendered subliminal. In the following session, the gap in Landolt squares was adjusted such that responses were correct on 50% of trials. Fifty percent correct, rather than 62.5% correct (a more conventional criterion for 4AFC tasks), was used as a criterion because it afforded greater sensitivity to improvements in performance for validly cued locations and, by implication, rendered the paradigm more sensitive to attentional capture effects. This value, however, was still well above the chance level of 25%. The staircases terminated either after reaching criterion, or after 30 trials.

In the main experiment, both cue detection and Landolt discrimination were performed on every trial. Each trial started with a display consisting of a fixation cross in the center and two placeholder asterisks marking the relevant locations (Fig. 2). One placeholder was positioned at the phosphene location, and the other diametrically opposite (mean phosphene eccentricity = 6.17° of visual angle, SD = 5.43°, mean azimuth = 152° clockwise from three o'clock, SD = 103°: mean phosphene location was lower left quadrant). After a variable interval (950–1050 ms), the cue display was presented for 10 ms (one refresh cycle) and replaced by a fixation display for another 160 ms. Different types of cues were presented in different blocks (phosphene TMS, control TMS, real cues; Fig. 3). In the 'phosphene TMS' blocks, a single TMS pulse was applied over the previously localized phosphene site at phosphene-threshold (mean intensity 72% of the maximum, SD = 17%). Fig. 3, upper middle panel, shows the average percept when phosphenes were reported: on average across participants, the phosphene was a slightly yellow gray (CIE xy .34, .36), circular/oval in shape, with a longer axis length of 3.37° on average. In the 'control TMS' blocks, TMS was applied at the same intensity over a control site level with electrode position Pz but with the same laterality as the active site (i.e., the same distance to midline). Phosphenes are only rarely (if at all) elicited after TMS here and so this controls for the potential somatosensory and acoustic alerting effects accompanying the TMS pulse. In 'real-cue' blocks, visual stimuli were presented on screen as cues, consisting of an empty gray square (.32, .34). Compared to the real cues, phosphenes were reported to be filled rather than empty and to be longer than real cues (3.37° vs. 2° along the longest axis; $t = 2.75$, $p < .05$). Despite these differences, real and phosphene cues were matched in detectability (scaling session, see above), and comparing reported luminance of phosphene cues with actual luminance of real-cue stimuli (CIE Y 42 and 44 cd/m^2, respectively) revealed no significant differences ($t < 1$).

After the cues, the target display was presented, consisting of two Landolt squares, each with a gap in one of the four sides. The squares (side length = 2°, side thickness = one pixel) were bright gray (CIE Yxy 53 cd/m^2, .32, .34). The mean gap size across participants was 1.0°, SD = .29°. After 60 ms, the target display was masked by circular patches of white noise, 2.83° in diameter, and the fixation cross was simultaneously replaced by a central arrow, indicating at random which location was task-relevant. Participants reported the position of the gap (left, up, right, down) in the Landolt square on the side indicated by the arrow, responding using the arrow keys on the keyboard with their right hand. Then, participants reported whether or not they had seen a cue by pressing Y or N keys with their left hand. Participants were instructed to respond as accurately as possible. If no response was provided within 10 s, a new trial started and participants were instructed to respond faster.

The cue was either at the same or the opposite position to the task-relevant Landolt square, resulting in valid or invalid spatial cueing of the target. In 'phosphene TMS' blocks, the TMS pulse was always over the same location; cue location was thus constant, and target position therefore determined validity: on valid trials, the target was presented at the cued location. In 'control TMS' blocks, TMS location was also constant and validity was described in the same way as for phosphene TMS cues: targets appearing contralaterally to the stimulated hemisphere were considered validly cued. Encoding control TMS as valid and invalid permitted a direct comparison with phosphene TMS trials. In 'real-cue' blocks, both cue and target could appear at both locations, resulting in four possible cue-target location combinations. To make the analyses of phosphene and real cues comparable, analyses only included trials on which the real cue was presented at the phosphene location.

The main experiment thus varied (i) cue type (control TMS, phosphene, and real cue), (ii) cue validity (valid vs. invalid), and (iii) cue visibility (the cue was either seen or unseen), yielding a $3 \times 2 \times 2$ experimental design (cue type, validity, and visibility). Trials were performed in blocks of 52. Participants performed four 'control TMS' blocks, eight 'phosphene TMS' and eight 'real-cue' blocks, with order counterbalanced across participants. More trials in the 'phosphene TMS' blocks were introduced so as to assure a more reliable measure of phosphene perception, and more trials in the 'real-cue'

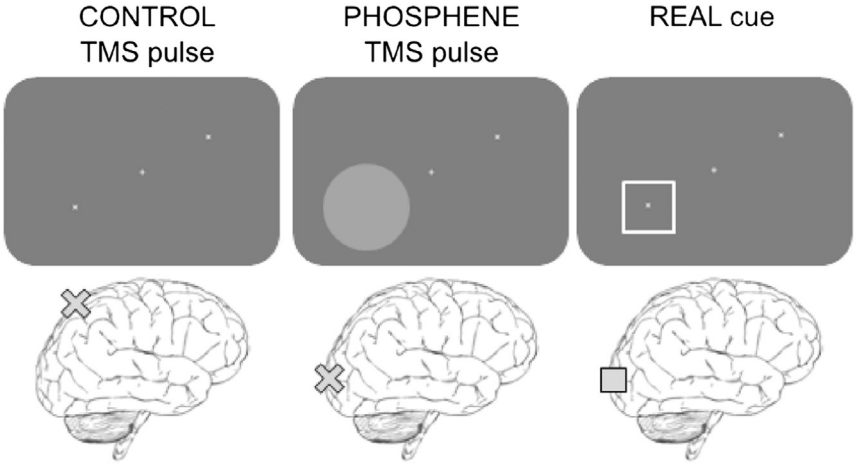

Fig. 3. Different cue types: (i) control TMS pulse over parietal cortex (left), (ii) TMS pulse over visual cortex that induced phosphene percept (center), and (iii) real cue whose cortical projection matched phosphene site (right).

blocks were introduced because real cues could appear at two possible locations.

Results

The analyses focused on testing whether or not valid cues improved discrimination. Furthermore, interactions of validity with cue type (real, phosphene, or control) and visibility (seen, unseen) were of interest. Importantly, cue visibility co-varied with cue type: a higher frequency of seen cue reports was expected in phosphene and real-cue conditions relative to control TMS. Additionally, participants differed regarding the cue visibility criterion, with some reporting cues as visible very frequently and others being more conservative. Due to co-variance between experimental variables and variance in the visibility criterion, error rates per experimental condition are inappropriate as an index of discrimination performance, and so generalized mixture models (GMMs) were used for all analyses, with participant and trial number as random factors (Baayen et al., 2008; Bates, 2005). The GMMs were run stepwise, with each step adding an experimental factor (or an interaction between factors) into the model. To assess the significance of added model terms, log-likelihood ratios (G^2) between models of lower and higher complexity as well as Akaike (AIC) and Bayesian (BIC) information criteria were computed (Tables 1 and 2). G^2 reflects the improvement in model fits associated with adding another parameter, while the AIC and BIC reflect the overall model fit penalized for model complexity.

The first analysis looked only at real-cue trials (Fig. 5, rightmost panels), where cues could appear at any of the two possible positions (A and B). The differences between the two positions were tested by a GMM of response accuracy with cue position, cue validity, and visibility as fixed factors (Table 2). This analysis revealed neither the main effect of cue position nor its interactions with validity and visibility to be significant (all $ps > .13$). Taken together, these results suggest that real cues at phosphene (A) and opposite positions (B) were processed in a similar manner, which permitted performing further analyses for real cues only at the phosphene location.

Second, cue detectability was analyzed by a GMM of cue visibility reports (seen vs. unseen) with cue type and validity as fixed factors. In one analysis, the control and phosphene TMS cues were compared, and in the other analysis, the phosphene TMS was compared with the real-cue condition. Fig. 4 depicts the probability of having seen a cue across different experimental conditions, and Table 1 shows the results of the GMM analyses. Although some cues were reported as being seen even in the control condition, cues were much more likely to be seen when either a real or a phosphene cue was presented relative to control TMS. Furthermore, valid cues were slightly more likely to be seen relative to invalid cues, independently of cue type. The GMMs analyses revealed a significant difference ($G^2 = 440.95$, $p < .001$) between control TMS and phosphene TMS cues on the one hand, and virtually no difference ($G^2 = .54$, $p = .46$) between the phosphene and real cues on the other. As indicated by low G^2, the main effect of cue validity was relatively weak, that is, cue validity did not substantially influence cue visibility.

The first two analyses showed that (i) real cues at the phosphene (A) and the opposite position (B) were processed similarly; (ii) that control and phosphene TMS resulted in different percepts; and (iii) that phosphene TMS and real cues resulted in comparably detectable percepts. In the final, third analysis, cue validity effects were tested across experimental conditions by a GMM of response accuracy with cue type (control, phosphene, real cue), validity (valid, invalid), and visibility (seen, unseen) as fixed factors. Fig. 5 shows how the probability of error responses varied across experimental conditions. As can be seen, valid cues were associated with lower error probabilities in all conditions. Furthermore, validity effects were stronger for seen than for unseen cues in both the phosphene and real-cue conditions, but not for control TMS.

The analysis including control and phosphene conditions revealed all three main effects to be significant (cue type, validity and visibility), all $G^2 > 5.60$, all ps < .05, indicating better performance for control TMS relative to phosphene TMS, valid relative to invalid cues, and seen relative to unseen cues. Furthermore, the cue type × validity interaction was significant, $G^2 = 17.86$, $p < .001$, indicating stronger validity effects for phosphene relative to control TMS. The validity × visibility interaction was also significant, $G^2 = 11.55$, $p < .001$, reflecting stronger validity effects for seen relative to unseen cues. Finally, the three-way type × validity × visibility interaction was significant, $G^2 = 5.51$, $p < .05$, indicating that seeing a cue increased validity effects for phosphenes, but not for control TMS.

The analysis involving phosphene and real-cue conditions also revealed all three main effects (cue type, validity, and visibility) to be significant, all $G^2 > 12.62$, all $ps < .001$, indicating better performance for phosphene relative to real cues, valid relative to invalid cues, and seen relative to unseen cues. Furthermore, the cue type × validity interaction was significant, $G^2 = 68.56$, $p < .001$, indicating stronger validity effects for real relative to phosphene cues. The significant validity × visibility interaction, $G^2 = 25.11$, $p < .001$, reflected stronger validity effects for seen relative to unseen cues. Finally, in contrast to the comparison between the control and phosphene conditions, the three-way interaction between cue type × validity × visibility was far from significance, $G^2 = .10$, $p = .75$, that is, the increase in validity effects for seen relative to unseen cues was comparable between phosphene and real cues.

Taken together, these analyses showed attentional capture for both phosphene TMS and real cues. Capture was approximately twice as strong for seen relative to unseen cues, irrespective of the cue type. By contrast, any capture after control TMS was weaker than capture with phosphene TMS, and it was not modified by cue visibility. These findings indicate that processes of exogenous attentional capture contributed to the cue validity effects for phosphene TMS and real cues, in contrast to control TMS.

Table 1
Results of stepwise modeling of cue visibility reports as a function of cue type (control vs. phosphenes, phosphenes vs. real cues) and cue validity (valid vs. invalid), together with degrees of freedom per model and goodness-of-fit parameters (AIC, BIC, and G^2) of the models. Lower AIC and BIC and higher G^2 values indicate better fits. The asterisks and values in parentheses next to G^2 denote the probability of the respective G^2 being different from zero. G^2 is distributed as a chi-square distribution, with degrees of freedom (df) defined as the difference between dfs for the model of higher and, respectively, lower complexity. Since GMMs were run stepwise with adding a single term at each step, the G^2 values had one degree of freedom.

Fixed effects	*df*	Control vs. phosphene cue			Phosphene vs. real cue		
		AIC	BIC	G^2	AIC	BIC	G^2
Intercept	4	10013	10040		9620	9648	
Cue type	5	9574	9608	440.95***	9621	9656	0.54 (.46)
Cue validity	6	9573	9615	2.62 (.10)	9618	9659	5.56*
Type × validity	7	9575	9623	.03 (.86)	9619	9668	.74 (.39)

Significance levels: ***.001, **.01, and *.05.

Discussion and conclusions

By presenting stimuli at detection threshold as cues in an attentional-capture paradigm, we investigated whether automatic attentional capture is determined solely by physical stimulus properties. We found stronger capture for seen than for unseen cues, despite the two types of cue being physically identical. Attentional capture has recently been demonstrated to operate not as an all-or-none process but rather more gradually, with capture strength increasing with cue contrast (Fuller et al., 2009; Zehetleitner et al., 2013). Another body of work suggests that attentional capture can be modulated through top-down factors such as task set (Ansorge et al., 2011; Folk et al., 1992; Hsieh et al., 2011). The present results demonstrate an additional determinant of capture strength

Table 2
Results of stepwise modeling of response accuracy as a function of cue type (control vs. phosphenes, phosphenes vs. real cues), cue position (A vs. B), cue validity (valid vs. invalid), and cue visibility (seen vs. unseen). Conventions as in Table 1.

Fixed effects	df	Real cue, position A vs. B			Control vs. phosphene cue			Phosphene vs. real cue		
		AIC	BIC	G^2	AIC	BIC	G^2	AIC	BIC	G^2
Intercept	4	6841	6870		10213	10241		10264	10292	
Cue type	5				10209	10244	5.60*	10254	10288	12.62***
Cue position	5	6844	6877	1.65 (.20)						
Cue validity	6	6261	6302	583.61***	10099	10141	112***	9882	9923	373.75***
Type × validity	7				10084	10132	17.86***	9815	9864	68.56***
Position × validity	7	6262	6309	2.31 (.13)						
Cue visibility	8	6079	6131	184.91***	9839	9894	246.92***	9562	9617	255.12***
Type × visibility	9				9841	9903	.02 (.89)	9564	9626	.36 (.55)
Position × visibility	9	6081	6139	.68 (.41)						
Validity × visibility	10	6071	6137	11.11***	9831	9900	11.55***	9541	9610	25.11***
Type × validity × visibility	11				9828	9904	5.51*	9543	9619	.10 (.75)
Position × validity × visibility	11	6073	6145	.13 (.72)						

Significance levels: ***.001, **.01, *05.

orthogonal to physical stimulus properties and task demands: modulation of capture by spontaneous variability in neural excitability, which can also lead to a reportable percept during threshold vision. Such spontaneous fluctuations in cortical excitability have previously been reported to influence perception (VanRullen et al., 2007; VanRullen and Koch, 2003). Accurate detection or discrimination of near-threshold stimuli, real or phosphenes, depends on the prestimulus power and phase coupling of alpha-band (10-Hz) oscillations in posterior cortical areas (van Dijk et al., 2008; Hanslmayr et al., 2007; Romei et al., 2008). These excitability changes may then drive awareness of real visual stimuli as well as of phosphenes and explain the stronger capture with seen than with unseen cues.

Furthermore, by using single TMS pulses as attention cues, we investigated the necessary neural sources of automatic attentional capture. If unconscious and conscious capture relied on different neural mechanisms, with the former being primarily mediated by feedforward processes involving the superior colliculus (i.e., retinotectal pathway) and the latter additionally involving cortical mechanisms (Lamme and Roelfsema, 2000), only seen phosphenes should capture attention. Instead, we found capture for both seen and unseen phosphene trials, suggesting that feedforward processes through the superior colliculus are not necessary for unconscious attentional capture to occur. In other words, our findings do not support the idea that the distinction between unconscious and conscious vision hinges on the involvement of feedforward retinotectal processes (e.g., Mulckhuyse et al., 2007). Converging data using other methods and stimuli suggests that this subcortical circuit does not play a key role in mediating unconscious cognitive processes (Pessoa and Adolphs, 2010). Importantly, though, while our results suggest that feedforward input to subcortex is not necessary for attentional capture, they do not imply that subcortical structures play no role in capture. A wealth of evidence points to subcortical structures being necessary for exogenous attention (Knudsen, 2011; Shipp, 2004; Wurtz et al., 2011). Our study suggests that any subcortical involvement critical for capture occurs after initial feedforward stimulus processing (Fig. 1, gray lines).

We also observed greater capture for real than for phosphene cues. This difference is likely to stem from an additional source of capture at those feedforward subcortical stages which are accessible to real cues but not to phosphene cues (Fig. 1, black lines). Alternatively, differential capture strength for phosphenes and real cues might originate from differential temporal dynamics with which the two capture attention. Since we assessed capture strength at a fixed time point (160 ms post cue onset), it is possible that capture by phosphenes was not yet at, or had already passed, its maximum. However, studies investigating the temporal dynamics of real cues showed capture to reach maximum already 100 ms post cue onset and remaining at maximum until at least 175 ms (Müller and Rabbitt, 1989). Thus, any attempt to explain the differential capture strength between phosphenes and real cues by differential temporal dynamics would have to postulate large differences—the implication being that the two capture types are also inherently different. Finally, it is unlikely that this differential capture effect is due to perceptual differences between real and phosphene cues, given that the cues were well matched for detectability (Fig. 4) and that stronger capture for real than for phosphene cues was also observed with cues that were unseen.

TMS to the occipital lobe will likely have effects that spread throughout the visual system, preventing precise localization of the neural sources that generate attentional capture to phosphenes. Occipital stimulation may interfere with striate or extrastriate cortex (Kammer et al., 2005), and with the lateral geniculate nucleus, either directly or through stimulating the underlying white matter orthodromically or antidromically (Fig. 1, gray connections). With this in mind, it is possible that neural structures other than V1 were the source of attentional capture to phosphenes in our study. However, the anatomy of the brain does not permit TMS over visual cortex to reach the feedforward driving pathways from the retina to the LGN, superior colliculus, pulvinar, or other nuclei (note the absence of feedforward connections between cortex and superior colliculi, Fries and Distel, 1983). Thus, taken together, the capture to phosphenes is unlikely to be mediated by the feedforward input from retina to subcortex. Rather than conscious and unconscious capture relying differentially on feedforward subcortical processes, our results suggest that this is actually true for capture by phosphenes and, respectively, real cues. The emerging view of the neural mechanisms underlying attentional capture is then one of multiple sources:

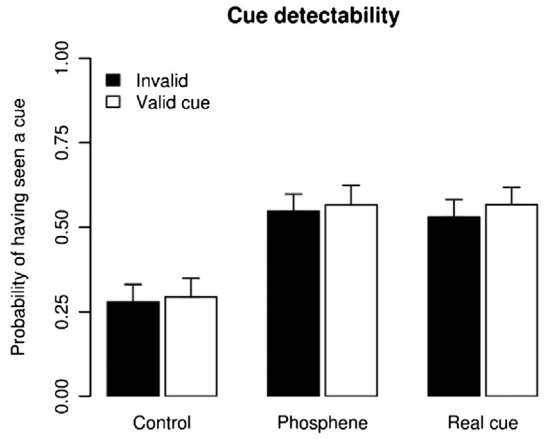

Fig. 4. Probability of having seen a cue across different cue types (control, phosphene, and real cue), separately for valid (white bars) and invalid cues (black). Error bars denote 1 SEM.

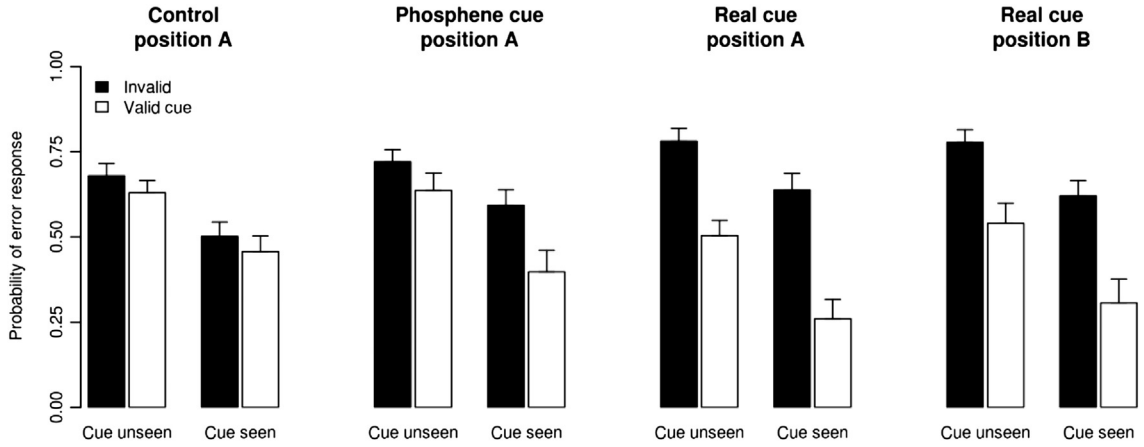

Fig. 5. Probability of error responses across different cue types and visibility (seen and unseen), separately for valid (white) and invalid cues (black). Error bars denote 1 SEM.

at least one in the initial subcortical feedforward stages and a further source beyond this, which can bring about attentional capture on its own.

In summary, feedforward input into subcortical areas is not necessary for attentional capture to occur, but capture is stronger in its presence. Two sources of attentional capture differ according to their dependence on this feedforward subcortical input, rather than their dependence on conscious awareness. Physically identical stimuli capture attention with greater strength when seen rather than unseen, suggesting that not only physical stimulus properties but also the state of the nervous system influence exogenous attention.

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