A monocular, unconscious form of visual attention

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Sudden changes in our visual field capture our attention so that we are faster and more accurate in our responses to that region of space. The underlying mechanisms by which these behavioral improvements occur are unknown. Here we investigate the level of the visual system at which attentional capture first occurs by presenting cues to one eye and then a target to either the same or the opposite eye. We show that monocular cues initially only shorten response time if the target is presented in the same eye as the cue suggesting that the initial capture of attention occurs at monocular levels of the visual system. We use dual-cues that cannot be distinguished by binocular parts of the visual system but are detectable at monocular levels to show that performance enhancements occur entirely unconsciously and are not due to local sensory interactions. Furthermore, we show that the spatial and temporal properties of the new monocular cueing effect differ from standard binocular cueing. Our results inspire a monocular competition model where visual stimuli compete to generate a salience map at monocular levels of representation.

Introduction

We direct our attention to those objects in the visual scene that are relevant for our behavior. The attention shifts that depend on our behavioral goals are called endogenous. There is also a second, goal-independent form of so-called exogenous attention shifts. We cannot help but notice objects that suddenly and unexpectedly appear in the visual scene. Our attention is immediately captured by such a salient event (Egeth & Yantis, 1997; Jonides, 1981; Posner, 1978; Posner & Cohen, 1984; Posner, Snyder, & Davidson, 1980), as reaction times (RTs) to a stimulus that appears at the same location as the cue are shorter and perceptual accuracy improves (Posner, 1978; Posner et al., 1980; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989). There is much evidence that part of the behavioral improvements that follow a sudden-onset cue can be explained by sensory activations caused by the cue interacting with a subsequently presented target. For example behavioral improvements following sudden-onset cues are still present when the cues are non-informative about the target location (Müller & Rabbitt, 1989), when participants

are actively instructed to ignore the cue (Remington, Johnston, & Yantis, 1992) and when multiple cues are presented at the same time (Solomon, 2004; Wright & Richard, 2003). Crucially however transient cues also worsen performance at uncued locations compared to neutral locations (Posner, 1978; Posner et al., 1980). This finding indicates that transient cues lead to an allocation of processing resources to the location of the cue, and that sensory interactions cannot fully account for the effects of the cue on processing of subsequent targets.

The neuronal mechanisms underlying the exogenous capture of attention are not fully understood. Electrophysiological studies in monkeys have shown that neural responses in the parietal cortex are stronger following a sudden-onset stimulus than a stimulus that is brought into the neuron's receptive field by an eye movement (Gottlieb, Kusonoki, & Goldberg, 1998). Furthermore, parietal neurons appear to track the locus of attention during the sudden onset of a stimulus (Bisley & Goldberg, 2003). Combining these findings with evidence from functional imaging studies it has been suggested that a network of areas in the parietal and frontal cortex is responsible for attentional capture (Corbetta & Shulman, 2002). The pulvinar may participate in this network as well, as other

studies have found evidence linking activity in the pulvinar to shifts of attention and calculations of saliency (Petersen, Robinson, & Morris, 1987; Posner, 1980; Rafal & Posner, 1987; Robinson & Petersen, 1992; Shipp, 2004).

Recent studies also obtained evidence for effects of exogenous cueing at the earlier processing level of the superior colliculus where neural responses are boosted for a brief period after presentation of an exogenous cue (Fecteau, Bell, & Munoz, 2004; Fecteau & Munoz, 2006). Thus, earlier processing levels could contribute to exogenous cueing effects, just as has been observed for endogenous attention shifts that are associated with changes in the activity of neurons in the superior colliculus (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004), area V1 (Roelfsema, 2006), and even in the lateral geniculate nucleus (McAlonan, Cavanaugh, & Wurtz, 2008). One fMRI study demonstrated that exogenous cueing increased neuronal activity in early visual areas but observed only a marginal effect in area V1, at the lowest level of the visual cortical processing hierarchy (Liu, Pestilli, & Carrasco, 2005). The issue of the processing level at which exogenous cueing effects first emerge therefore remains unresolved.

If attentional capture by a salient event influences neuronal activity in early processing levels, then it is of importance to know if the saliency calculations are carried out in early visual areas and then inherited by higher areas (Li, 2002) or whether the saliency effects in early visual areas reflect attentional feedback from higher areas (Corbetta & Shulman, 2002; Liu et al., 2005). To investigate this issue we designed experiments to test whether sudden-onset cues produce attentional effects at monocular levels of the visual system, where information from the two eyes has not yet been combined. Almost all neurons in higher areas are driven by both eyes (Zeki, 1978), and scenarios where higher areas feed back to enhance processing related to one eye only are therefore unlikely. Evidence for cueing effects at monocular levels would indicate that exogenous attention influences processing at early processing levels and that higher brain areas inherit some of these effects from the early visual areas. The idea of attentional effects at monocular processing levels was recently addressed by Zhaoping (2008), who investigated whether monocular singletons, which are stimuli that differ in their eye-of-origin from the surrounding stimuli, attract attention. The study demonstrated that visual search is facilitated if the target of the search is presented to one eye while the distracters are presented to the other eye. Similarly, the boundary between two textures was found to be more salient if it coincided with a change in ocularity, so that the elements of one of the textures were presented to one eye while the elements of the other texture were presented to the opposite eye. If the ocular border was at a different location than the texture boundary, however, the RT was slowed and participants made more errors. These results suggest that ocularity can act as a cue during search and texture segregation, attracting attention towards the spatial location of ocular contrast in a similar manner as attention is attracted to luminance or color contrast. Monocular processing in the pop-out task appears to occur outside conscious awareness (Zhaoping, 2008), in accordance with an earlier study demonstrating that observers are not able to discriminate the eye-of-origin of a visual stimulus nor are able to detect ocular differences between stimuli (Wolfe & Franzel, 1988). Thus, the monocular attention effects described by Zhaoping imply a remarkable dissociation between attention and awareness.

Many properties of monocular attention remain unknown. Is the monocular effect restricted to pop-out tasks where ocularity biases selection just like orientation or color, or can monocular attention also contribute to exogenous cueing? If so, what are the temporal properties of monocular attention? Is monocular attention associated with costs and benefits in processing? Can monocular sudden onset cues bias selection in the absence of awareness, just as in a pop-out task? To address these questions, we here adapted an exogenous cueing paradigm (Müller & Rabbitt, 1989; Posner & Cohen, 1984) where a sudden-onset cue precedes a visual target. We used a mirror-stereoscope to determine whether an attentional cue presented to one eye is able to influence the RT of participants to targets presented in the opposite eye and to compare these effects to targets present in the same eye. We indeed observed a monocular effect in this modified Posner task, because a monocular cue caused most facilitation for targets presented to the same eye. By varying the time between the onset of the cue and the onset of the target (the cue-target onset asynchrony) we studied the time-course of the monocular attentional effects. In addition we developed a dual-cue technique to reveal processing differences between perceptually identical stimuli that are only distinct at the monocular processing levels. Finally, we will provide a description of the spatial profile of cue-target interactions within and between the two monocular representations.

General methods

Participants

A total of 89 participants took part in our experiments. All reported normal or corrected-to-normal visual acuity. The participants were healthy volunteers, naive about the purpose of the experiment. They were paid €10 for their participation in a single 1-hour session (Experiment 1) or
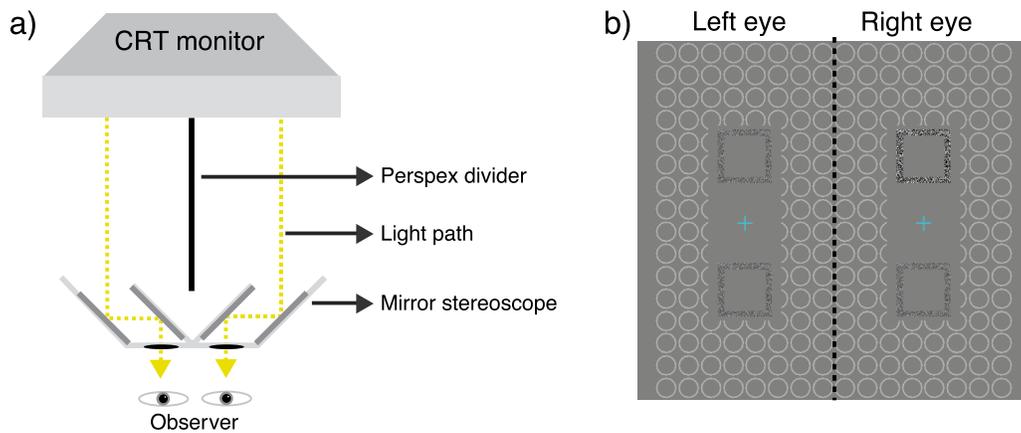
Figure 1. Screenshot and experimental setup. a) Experimental setup. Stimuli were presented dichoptically using a mirror stereoscope. b) Screen-capture showing the attentional cue used in Experiment 1. The contrast of the frames has been enhanced in this image for improved visibility. The light-gray circles were present to aid fusion and participants perceived only two frames, one above and one below the fixation point. The dashed line indicates the location of the Perspex divider.

€20 for participation in two separate one hour sessions (Experiments 2, 3 and 4).

Set-up of the stereoscope

Before the experiment the participants' eye dominance was measured using the hole-in-the-card test. A mirror stereoscope (Sokkia, Japan) was used to separate images from different halves of the monitor screen so they fell exclusively into each eye (Figure 1a). To ensure complete separation of the images a black, opaque sheet of perspex was placed at the center of the monitor. The complete eye-to-screen distance including the path through the mirrors was 65 cm. Before beginning the experimental trials a calibration routine was run to ensure proper fusion of the images. Firstly, a set of Nonius lines was displayed to the inferior and superior visual field of each eye and the participants were allowed to adjust the horizontal displacement of these lines to achieve alignment. Secondly the noise-patterned frames used in the experiment were displayed (Figure 1b) and participants were allowed to move these within a limited range from the fusion point to achieve stable fusion. Once fusion was achieved a patterned image and the fixation cross were displayed on the screen, and these remained present for the entire duration of the experiment, aiding the participants in maintaining stable fusion. Participants were instructed that if, at any time, fusion failed they were to pause and attempt to regain stable fusion before recommencing the experiment. Two participants were rejected before completing the experimental sessions as they were unable to regain fusion after a failure. The remaining participants reported stable fusion with very occasional failures in fusion which could easily be regained.

Stimulus and task

The stimuli consisted of four 'frames' (Figure 1b) presented on a gray background with a luminance of 11.2 cd.m^{-2}. The frames consisted of one pixel noise at 33% contrast and they were 3.8° wide in all experiments, except in Experiment 3 where we varied frame size. We also presented a background pattern consisting of light-gray circles to aid, and stabilize, fusion of the images (Figure 1b). Each trial began with a fixation cross color-change from red (during the inter-trial interval) to cyan. After a variable period (500 ms $\pm$ 118 ms) the cue was shown. The cue consisted of an increase in contrast of one (Experiments 1, 3 and 4), two or four (Experiments 2 and 4) of the noise-patterned frames to 100% contrast. The cue duration was 50 ms in Experiments 1 and 3, in Experiments 2 and 4 the cue remained at high contrast until the participant responded. The cue was followed after a variable cue-target onset asynchrony (CTOA) by the target, this was an oriented Gabor patch of 100% contrast (2.2 degrees in diameter, tilt ± 60 degrees from vertical, wavelength: 1.8 cycles/degree, space constant: 0.35 degrees, phase: 0 degrees cosine, i.e. with a central white stripe). The participants' task was to indicate the orientation of the Gabor target as quickly as possible using the arrow keys on the PC keyboard. After the participant's response the inter-trial interval began again (588 ms).

Experiment 1—A monocular cueing effect

In this experiment we adapted a Posner-cueing paradigm (Posner & Cohen, 1984) so the cue, which was an

increase in contrast of one of four frames, and the target, which was an oriented Gabor stimulus, could be presented to different eyes. We reasoned that if the attentional capture associated with a sudden-onset cue happens, even partially, at monocular levels of the visual system then the Posner cueing effect would be stronger when both cue and target are presented to the same eye compared to different eyes. We therefore tested whether the level of attentional capture, as evidenced by a speeding of RT at validly cued compared to invalidly cued locations, was different when the cue and target appeared in the same eye or in different eyes.

Methods

Twenty-five naïve participants (18 female, age range 18–25) took part in this study. We used a $3 \times 2 \times 2$ factorial design with cue-target onset asynchrony (CTOA: 50, 150 or 400 ms), cue validity (valid and invalid) and the eye to which the target was presented (same or different to the cue) as factors (see Figure 2a). The target appeared to the participants in a cued location on 50% of trials (Valid trials) and for the remaining trials at an uncued location (Invalid trials), the cue therefore had no predictive value. Unbeknownst to the participants we also varied the eye to which the target was presented. In 50% of trials the target was presented to the same eye as the cue whereas in the other 50% of trials the target was presented to the other eye. The participants completed 600 trials of the main experiment, and the trial order was pseudo-randomly chosen so that each condition was repeated 50 times at each CTOA. Visual feedback was given if the participants made an incorrect response or their RT was longer than 1 s, such trials were repeated at the end of the experiment. Slow-responding participants with mean RTs across all conditions of over 600 ms were removed from the analysis (2 participants failed to meet this criterion, leaving 23 participants in total). The removal of slow-responding participants affected neither the statistics nor the conclusions drawn from the data.

Results

The RTs in this experiment can be seen in Figures 2b and 2c shows the magnitude of the cueing effect as the difference in RT between validly and invalidly cued trials. As expected, participants responded significantly faster to validly cued targets compared to invalidly cued ones at all tested cue-target onset asynchronies (CTOAs) (three-way repeated measures ANOVA: main effect of cue-validity, $F_{1,44} = 63.4$, $p < 0.001$). Surprisingly, we also observed a significant interaction between cue-validity, CTOA and eye of presentation ($F_{2,44} = 4.59$, $p = 0.016$). This interaction was driven by an interaction between cue validity and eye of presentation at the 50 ms CTOA ($F_{1,22} =$

6.71, $p = 0.017$). At this CTOA, RTs were significantly faster at validly cued locations compared to invalid locations when the target was presented to the same eye as the cue (paired *t*-test; $t_{(22)} = 5.36$, $p < 0.001$, Bonferroni corrected), but not if a valid cue was followed by a target in the other eye ($t_{(22)} = 1.26$, $p = 0.22$). The eye-specific cueing effect was relatively large as participants were around 20 ms faster when the cue appeared in the same eye as the target compared to when they appeared in opposite eyes (Figure 2c). At longer CTOAs this effect disappeared, as evidenced by the lack of interaction between cue-validity and eye of presentation (CTOA = 150 ms and CTOA = 400 ms, $F < 1$). There were no significant differences in error rate between conditions (Kruskal–Wallis test, $p > 0.05$, see Figure 3).

Conclusions

Our results show that there is a monocular component underlying part of the exogenous cueing effect. If a brief cue is presented to one eye, RTs to a target that is presented to the same eye immediately after the cue are shortened and this benefit does not transfer to the other eye. At delays larger than 150 ms, however, we find good transfer of the cueing effect, as the RTs were similar regardless of whether the cue and target were presented to the same, or different eyes. After this short delay, the binocular stages of the visual system are responsible for the behavioral benefits. The magnitude of this binocular cueing effect is around 33 ms (at the 150 ms CTOA), which is comparable to the cueing effects observed in previous studies presenting cue and target to both eyes (Posner, 1978).

These results support a previous study (Zhaoping, 2008) showing that monocular, unconsciously presented ocular singletons can influence performance in a pop-out task. The present results show that monocular effects also occur in the Posner cueing task, which permits an investigation of the time-course. We find that monocular levels of the visual system are responsible for the early behavioral enhancements following a transient cue. At a delay of 50 ms after cue onset participants were only significantly faster at responding to validly cued targets presented in the same eye as the cue. This is a surprising result, given that the [Val, Diff] condition appears to the participant as a validly cued target, exactly like the [Valid, Same] condition. In Appendix A we show that the participants cannot discriminate between these two conditions (Control Experiments 1 and 2) and are unable to report the eye of origin of the cue even if the cue is presented for long durations and this is the only task of the participants (Control Experiment 4). And yet, there is approximately a 20 ms RT difference between the conditions where the stimuli appear in the same and different eyes. A possible interpretation of this result is that the earliest attentional effects following a sudden onset cue are due to a
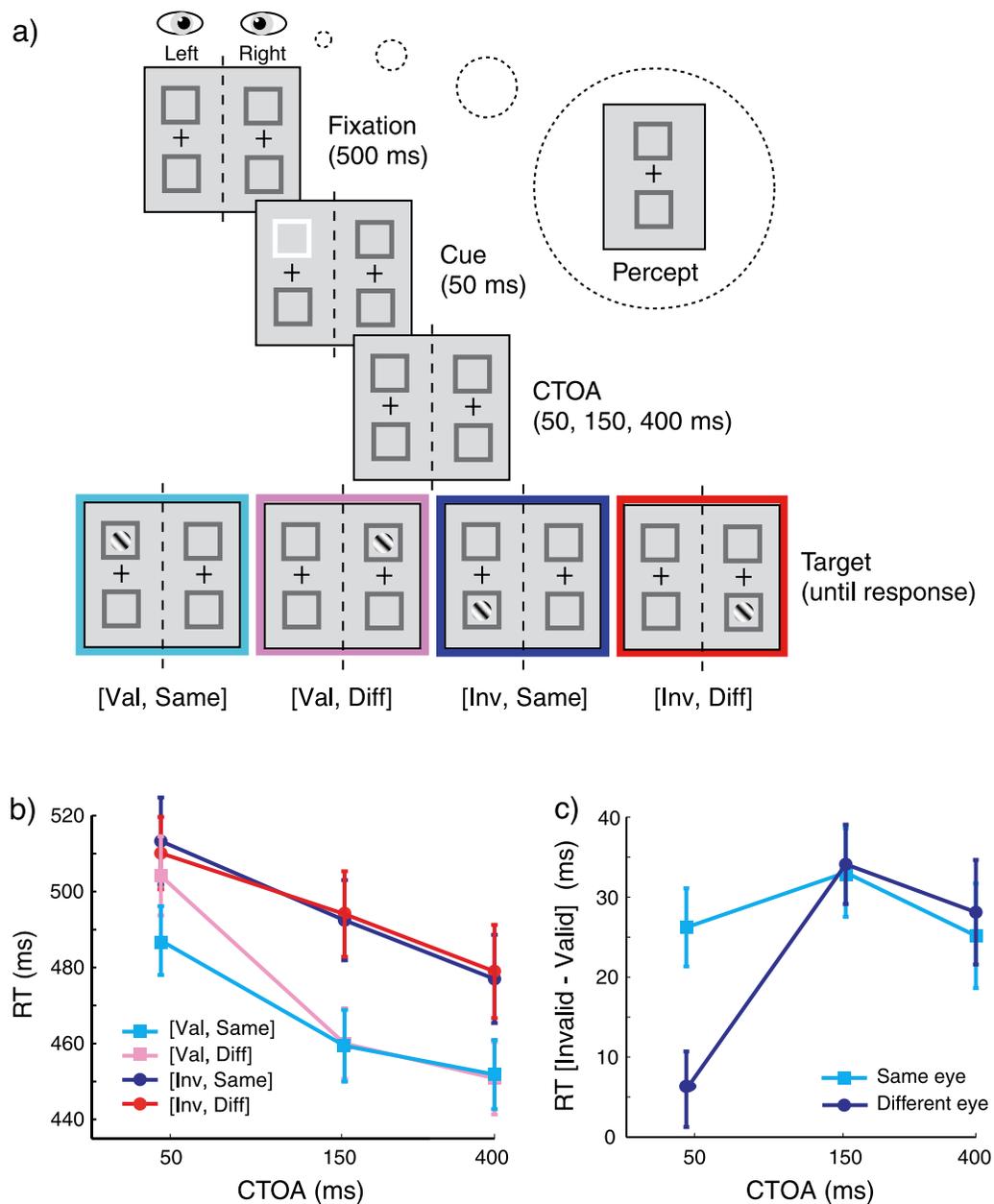
Figure 2. Experiment 1—Stimulus sequence and results. a) The design of Experiment 1. Participants fused the left and right eye images together as depicted in the 'Percept' bubble. The cue was an increase in contrast of one of the frames from 33% to 100%. The target was a tilted Gabor-patch (2.2 diameter, ±60° tilt). The participants' task was to indicate the direction of tilt as quickly as possible. The relative position of the cue and target determined the condition as indicated by the four colored panels, these colors correspond to the colors of the lines in the RT plot in b. The name of the condition is indicated below. b) The mean RTs of 23 participants to validly (square symbols) and invalidly cued (circle symbols) targets that could either appear in the same eye (blue/cyan lines) or the opposite eye (red/pink lines) as the cue. Error bars are ± one *SEM* across participants. The main-effect of binocular validity can be seen at later CTOAs as the difference between the light and dark colors. The monocular cueing effect is evident at the 50 ms CTOA as the difference between the pink and cyan line. c) The RT difference between validly and invalidly cued targets for conditions in which cue and target were presented to the same eye (cyan line) and different eyes (blue line). Positive numbers indicate a speeding of RTs to validly cued targets relatively to invalidly cued targets.

monocular form of visual attention. Stimuli could compete with each other in monocular space in an analogous manner to how stimuli compete in binocular space to form saliency maps (Fecteau & Munoz, 2006; Itti & Koch, 2000; Li, 2002) and transient cues could increase the saliency of the location of the cue at a monocular level of representation. This competitive interaction can be envisaged as the neural response to the cue suppressing other
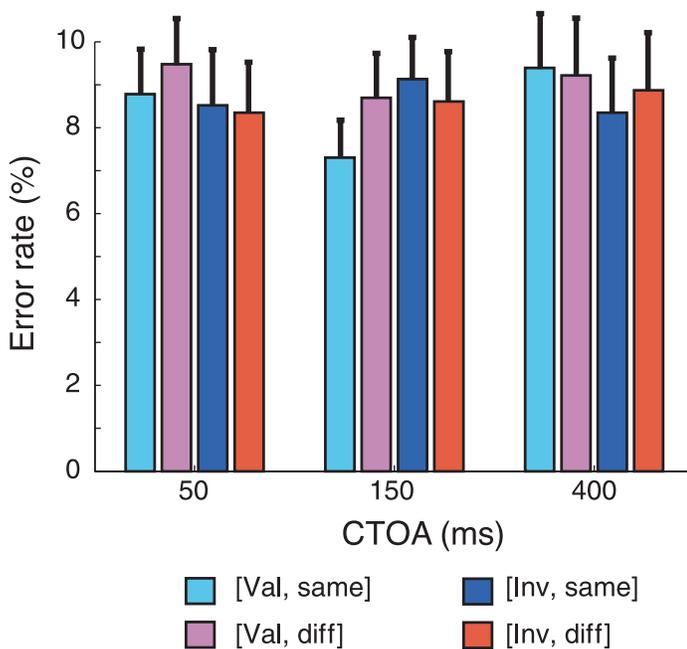
Figure 3. Error-rates from Experiment 1. The average error-rate from each condition of Experiment 1. Error-bars show *SEM* across participants. There were no significant differences in error-rates between the conditions.

possible target locations at a monocular level of representation so that the response to targets presented to the same monocular location as the cue is relatively enhanced, leading to comparatively faster RTs at monocularly cued locations compared to uncued locations.

However, other interpretations of this result are possible. Firstly the results of Experiment 1 are consistent with the idea that the earliest attentional effects following a sudden-onset cue are due to sensory interactions between the cue and the target at monocular levels of the visual system. This explanation would predict that any condition where target and cue are presented at the same location monocularly produces fast RTs and also that the magnitude of the cueing effect depends on the distance between cue and target. We will test these predictions in Experiments 2 and 3. Secondly it is possible that cues presented in one eye lead to a suppression of targets presented to the opposite eye. Such an effect would be reminiscent of the suppression that occurs during binocular rivalry (Blake & Logothetis, 2002; Wilke, Logothetis, & Leopold, 2003). We note, however, that there was no rivalry in the stimuli we presented, binocular fusion was very stable and participants never reported rivalry when asked after the experiment. Nevertheless, our results are perhaps due to a form of competition between the eyes that also contributes to binocular rivalry. A related interocular phenomenon is flash suppression, where a suddenly appearing stimulus in one eye suppresses the perception of an image presented to the other eye (Wilke et al., 2003; Wolfe, 1984). Such a competition between eyes can take one of two forms. It is

possible that a cue presented to one eye suppresses the entire representation of the other eye, irrespective of the relative positions of target and cue. We note, however, such a global eye-suppression would predict that the [Inv, Diff] condition would produce slower RTs than the [Inv, Same] condition as targets in the [Inv, Diff] were presented in the eye opposite to the cue. This is not what we observed, as the [Inv Same] and [Inv, Diff] condition produced very similar RTs. Experiment 2 will further test if a cue in one eye tends to suppress the entire representation of the other eye.

Another form of competition between the eyes that could contribute to the monocular cueing effect is interocular suppression between monocular representations of the same retinotopic position (Baker & Meese, 2007; Macknik & Martinez-Conde, 2004; Meese & Hess, 2004, 2005; Sengpiel, Blakemore, & Harrad, 1995). The cue would suppress target locations in the eye opposite to the cue, but only at the same retinotopic position. Such a spatially specific suppression effect could explain why the RTs in the [Val, Diff] condition were significantly slower than RTs in the [Val, Same] condition, while the RTs to the [Inval, Same] and [Inval, Diff] conditions were similar. We will formally test this idea in Experiment 4.

Experiment 2—Isolating the monocular cueing effect

In Experiment 1 we observed a monocular cueing effect in addition to the classical binocular cueing effects (Posner & Cohen, 1984). We found that these effects had different times courses allowing us to disentangle the binocular and monocular processes in time. We designed Experiment 2 to determine whether we could completely isolate the monocular effects described in Experiment 1 from classic binocular cueing effects. To achieve this aim we used dual cues; cues which were presented simultaneously at two locations (Figure 4a). The cues were always arranged so that, after binocular fusion, both possible target locations appeared to be cued to the observer. In this way we removed any binocular attentional effects from the experiment while leaving the underlying monocular differences intact. Therefore any RT differences between cued and uncued locations in this experiment cannot be attributed to attentional capture at binocular levels of processing. This experiment also allows us to test whether unconscious cues capture attention. When viewed binocularly the differences between the cued and uncued locations were entirely unconscious (see Appendix, Control Experiment 3).

To test for the possibility, described above, that a monocular cue gives rise to a global suppression of the non-cued eye, we created two different cue distributions:
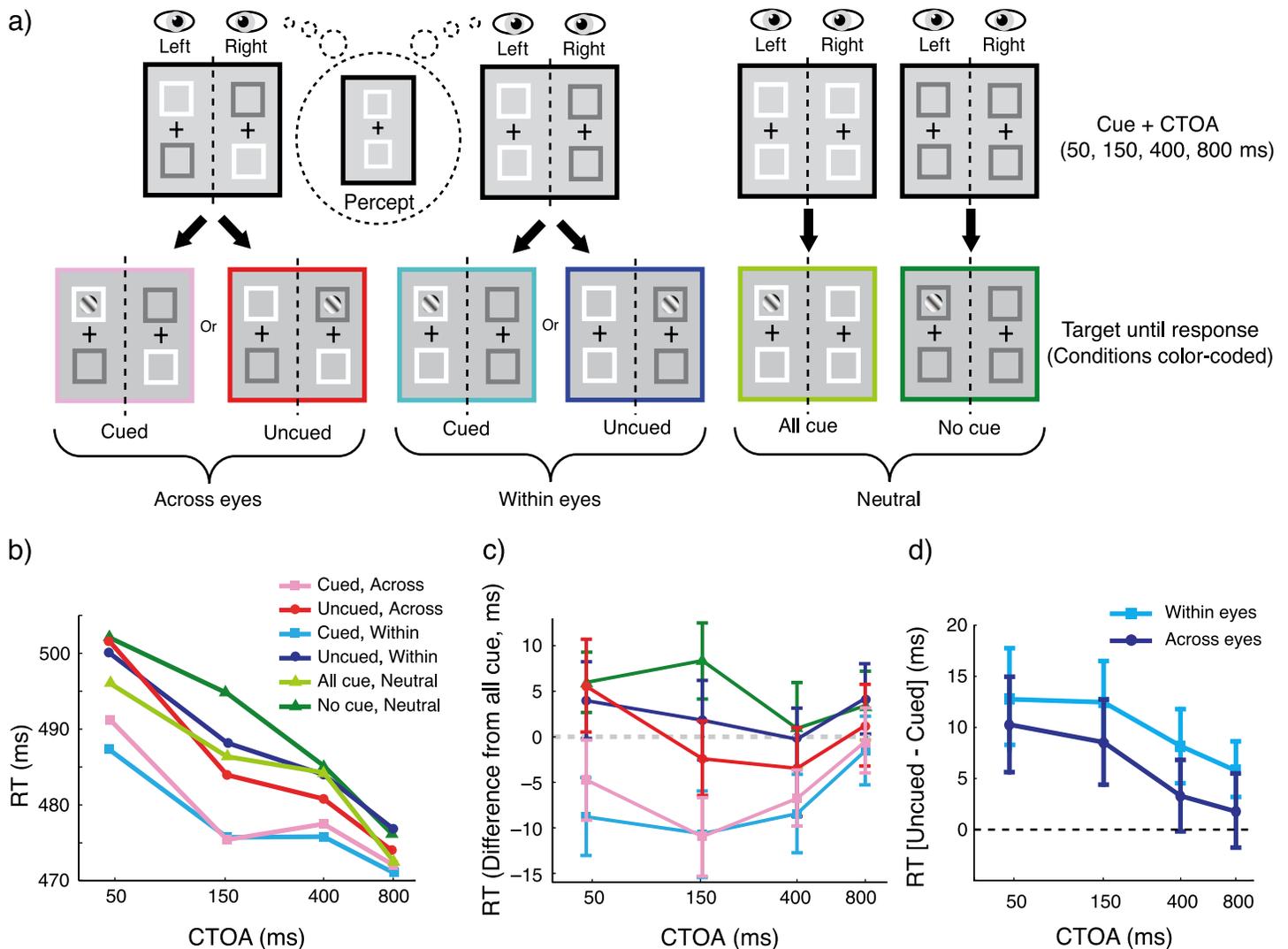
Figure 4. Experiment 2: Monocular cueing outside awareness. a) Stimulus sequence in Experiment 2. In all trials with cues, the perception of the participants was identical, as pictured in the percept bubble (although the cue appeared slightly higher in contrast in the all-cue condition). The colors represent the conditions. b) Results from the 25 participants showing the effect of CTOA for the different conditions. c) Results after normalization by subtracting the mean RT of the all-cue condition at each CTOA. Responses to targets presented at cued locations (square symbols) were significantly faster than to those at uncued locations (circle symbols) at the first three CTOAs. Uncued locations did not differ significantly from the all-cue control (the gray-dashed baseline). d) The size of the monocular effect for the two different cue distributions (Within and Across the eyes) shown as the difference in RT between cued and uncued positions.

"within-eye" in which both cues were presented to the same eye and "across-eyes" in which one cue was presented to each eye (Figure 4a). If the results of Experiment 1 were due to a general dominance of the cued eye, then the RT difference between cued and uncued locations should be greater for the 'within-eye' condition where both cues appear in the same eye than in the across-eyes condition where the cues are balanced across the eyes. Participants were unable to distinguish between these two conditions in a control experiment (Appendix, Control Experiment 3).

This experiment will also test whether the effects we observed in Experiment 1 were due to local sensory interactions between the cue and the target. To test this hypothesis we included an 'all-cue' neutral condition in which all possible target locations were cued in both eyes. In this condition local interactions between cue and target were present at all the monocular locations, but there was no competitive advantage for any of the cue locations over the others. If the monocular cueing effect is produced by local interactions then participants' RT in the all-cue condition would be identical to those at cued locations and faster than those at uncued locations in the dual cue conditions. If however the effects we observed were due to competition between the stimuli (be it monocular attention or local or global interocular suppression) then we would expect RT differences between the all-cue and the dual-cue conditions.

Methods

The experiment consisted of two dual-cue conditions: within eyes and across-eyes, and two neutral conditions the all-cue and the no-cue condition (Figure 4a). In the 'within eyes' condition both cues were presented to the same eye whereas in the 'across eyes' condition one cue was presented to each eye. The dual-cue conditions looked identical to the participants; both frames appeared to increase in contrast and, when asked after the experiment, they confirmed that they were completely unaware of the underlying monocular differences (see also Appendix, Control Experiment 3). In both these conditions the target was presented 50% of the time at a cued location and 50% of the time at an uncued location, again these conditions appeared identical to the observer. The all-cue condition appeared very similar to the dual-cue conditions, the cues actually appeared at slightly higher contrast than in the dual cue conditions due to binocular fusion, but this was never commented upon by participants, even when explicitly asked after the experiment. The no-cue condition appeared perceptually quite distinct as it was the only condition in which both possible target positions appeared uncued to the observer. We used four different CTOAs in this experiment, 50, 150, 400 and 800 ms. For the no-cue condition the target appeared at the CTOA that would have been used had there been a cue present, i.e. the "CTOA" was timed from the beginning of the trial. Furthermore we changed the cue duration from Experiment 1, instead of 50 ms the cue now remained at a high contrast until the participant responded, this was done to investigate the effect of cue duration and to prevent effects caused by the contrast offset of the cue (Theeuwes, 1991).

In summary this experiment was a $4 \times 2 \times 2 + 4 \times 2$ factorial design with the factors being CTOA, Cue (Cued/Uncued) and Cue Distribution (within/across) plus the two neutral conditions at each CTOA. Trials were presented in a pseudorandom order so that each condition was shown 25 times for each CTOA (counting correct trials only) and two complete sessions were completed per participant giving 50 correct trials per condition. There were 28 participants who took part in this experiment (21 female, age range 19–27), three were excluded for having a mean RT of longer than 600 ms. Aside from the differences noted above the same basic methods were employed as in Experiment 1.

Results

Figure 4b shows how the cues influenced RT. We observed a significant effect of whether the target appeared at a cued or uncued location, despite these conditions appearing identical to the observers ($4 \times 2 \times 2$ ANOVA: $F_{1,72} = 17.5$, main effect of cue, $p < 0.001$). Participants were initially 10–15 ms faster in their response to a target at a monocularly cued location than

to one at a neutrally cued location, and this effect was independent of whether the two cues appeared in the same eye or in different eyes (main effect of eye, $F_{1,72} < 1$). The longer duration of the cue caused the RT advantage to last for at least 400 ms (2×2 ANOVA at each CTOA (50, 150, 400, 800): $F_{1,24} = 7.6, 13.9, 4.3, 2.9, p = 0.011, 0.001, 0.049$ and 0.099 respectively), unlike in Experiment 1 where a brief duration cue caused only a short-lived effect (Figure 2c).

To investigate whether the monocular cues gave rise to costs or benefits, we subtracted the RT in the neutral all-cue condition from the other conditions in Figure 4c. A reduced-design 4×2 ANOVA with factors CTOA and condition (all-cue vs. cued) revealed a main-effect of condition ($F_{1,100} = 9.33, p = 0.005$) indicating that the monocular valid cues yielded shorter RTs than the all-cue condition. Furthermore, the RT in the all-cue condition was not significantly different from the RT in the uncued conditions ($F_{1,100} < 1$) (red and blue lines vs. baseline in Figure 4c). All conditions produced faster RTs than the no-cue condition ($F_{1,550} = 18.34, p < 0.001$). These effects were not caused by a trade-off between accuracy and speed because there were no significant differences in error-rate between the conditions (Kruskal–Wallis test, $p > 0.5$, Figure 5). Figure 4d provides a direct comparison of the magnitude of the monocular cueing effects by a subtraction of the valid RTs from the invalid RTs in the within-eye and between-eye conditions. We observed that the cueing effect in the within-eye condition tended to be slightly (about 3 ms) larger than in the across-eyes
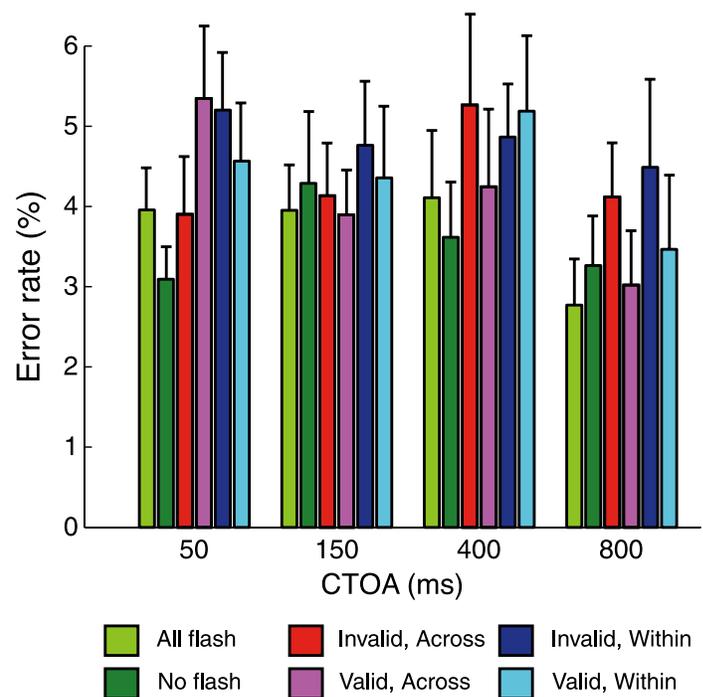
Figure 5. Error-rates for Experiment 2. Average error-rates from the different conditions of Experiment 2. No significant differences were found. Error-bars show *SEM*.

condition across all CTOAs tested (Figure 4d), but this effect was not significant (interaction between cue and eye, $F_{1,72} = 1.9$, $p = 0.18$).

Discussion

This experiment demonstrates that the monocular cueing effect persists in the complete absence of conscious, binocular cues. The critical dual-cue conditions appeared identical to the participants and yet participants' RTs were approximately 10–15 ms faster at monocularly cued locations than at uncued locations. It is therefore unlikely that the monocular cueing effect is due to feedback from binocular to monocular levels of processing. The control experiments described in Appendix A show that participants are not able to discriminate between cued and uncued monocular locations and this experiment therefore also demonstrates that unconscious cueing effects can lead to substantial differences in RTs.

All conditions produced faster RTs than the no-cue condition. This could be interpreted to mean that the RT differences we observe are due to purely facilitatory effects. However, the no-cue results should be interpreted with great caution. The no-cue condition appeared perceptually quite different to the other conditions. In all the other conditions both possible target locations were cued, indeed the other conditions all appeared identical to the observers. This raises the possibility that the slower RTs in the no-cue condition were due to high-level effects such as a lack of arousal, or the absence of a warning effect because the appearance of the cue in the other conditions predicted the timing of the target. Therefore the no-cue condition is not well-matched to the other conditions and should not be used as a neutral baseline by which to judge costs and benefits. The all-cue control is a better matched control as it appeared identical to the observers and also provided a warning signal about the timing of the target.

The results of this experiment rule out some of the possible explanations for the monocular cueing effects raised in the discussion of Experiment 1, above. We considered the possibility that the cueing effects reflect a global competition between the two eyes, where a cue in one eye slows down the processing of subsequent targets presented anywhere to the other eye. We tested this hypothesis by comparing the "Within-Eye" and "Across-Eyes" cue distributions and found no significant differences between these conditions. This indicates that most of the monocular cueing effect is not due to global competition between the eyes. We note, however, that there was a small trend for the RT effect in the within-eye condition to be approximately 3 ms faster than in the across-eye condition that failed to reach significance. It is possible that testing more participants might have revealed a very weak global competition between the

eyes that only accounts for a small fraction of the monocular cueing effect.

Experiment 2 also tested whether the monocular cueing effect observed in Experiment 1 was due to local interactions between monocular representations of the cue and the target. This hypothesis would predict that RT benefits occur for any monocularly cued position. The neutral all-cue condition in which every monocular location was cued (Figure 4a) addresses this alternative explanation, because local interactions were also present in this condition and RTs should therefore have been faster than at uncued locations. In contrast, RTs in the all-cue condition were similar to the RTs at uncued locations and significantly longer than the RTs at cued locations, implying that the monocular cueing effects were not caused by local interactions between the cue and the target. However, one should remain cautious in interpreting the RTs from the all-cue condition as more cues were presented than in the dual-cue conditions. Therefore we decided to further test the hypothesis that the monocular cueing effect might be due to local interactions between the sensory representations of the cue and the target. In Experiment 3 this was achieved by investigating the dependence of the cueing effect on the distance between target and cue.

Experiment 3—The effect of the distance between cue and target

In this experiment we investigated the effect of distance between the cue and the target on the monocular and binocular cueing effect. To this aim we repeated Experiment 1 but parametrically varied the size of the frames. The results of Experiment 2 suggest that the monocular cueing effect is not due to local sensory interactions between the cue and target. If this is true then the monocular cueing effect should not depend strongly on the distance between the cue and the target.

Methods

We repeated Experiment 1 using cues (frames) of 3.8, 5.5 and 8.9 degrees so that the distance between target and the nearest boundary of the edge of the frame was 0.8, 1.6 or 3.3 degrees, respectively. The duration of the cue was 50 ms. Twelve participants took part in this experiment (all female, age range 18–27, they were all included because their mean RTs were under 600 ms). The frame-size was blocked so that participants performed an entire run (600 trials) of one frame-size per block of trials, while the order in which the blocks were completed was varied across participants. The Gabor target was identical to that

presented in Experiment 1 and was placed at 6.6 degrees eccentricity in the center of the frame. Outlying RTs were removed by removing any RT that was more than 3 standard deviations from each participant's mean RT across all conditions.

Results

The results of Experiment 3 are shown in Figure 6a. We investigated the effect of frame-size using a four-way ANOVA with the factors being (binocular) cue-validity,
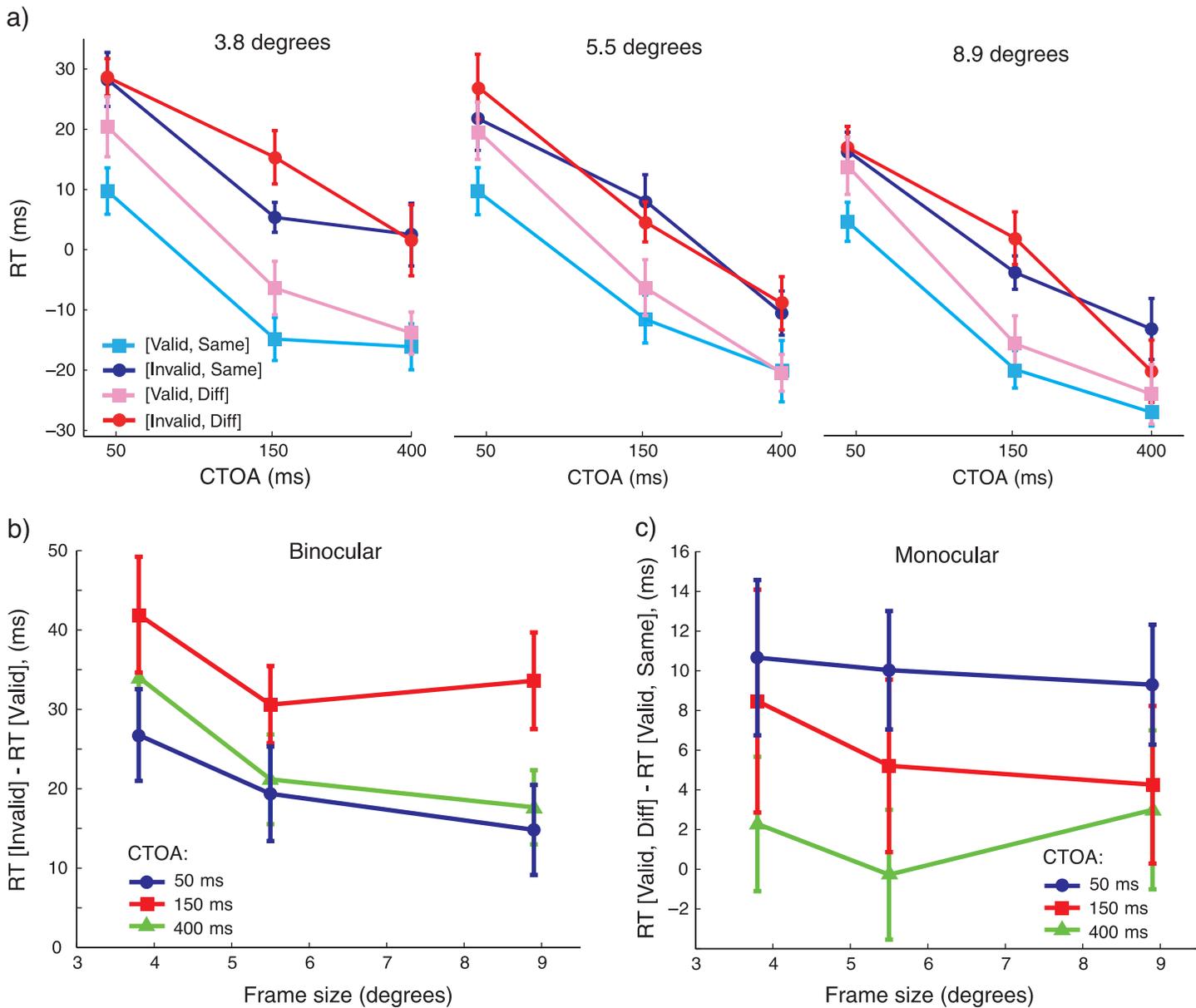

Figure 6. Experiment 3: Varying cue-size. a) Mean RTs from the 12 participants of Experiment 3 separated into the three different frame-sizes used for the cue. These sizes are indicated above each plot. Each participant's RTs were normalized by subtracting that participant's mean RT across all conditions before averaging across participants. Otherwise the format is identical to Figure 2b. Note the difference in RT between the [Val, Same] and [Val, Diff] conditions at the 50 ms CTOA persists at all three cue sizes. b) The main effect of (binocular) validity at three different CTOAs as a function of cue-size. The y-axis shows the difference in RT between validly and invalidly cued targets averaged across the same and different eye conditions. The strongest effects are seen at 150 ms CTOA (red line) while the effects are weaker at 50 ms and 400 ms CTOA. There is a clear reduction in the magnitude of the attentional effect with increasing frame-size. c) The difference in RT between validly cued targets presented in the same eye as the cue compared to validly cued targets presented in the opposite eye as a function of frame size. Note that the strongest effects are seen at the 50 ms CTOA (blue line, cue duration was 50 ms) and that they do not depend strongly on cue-size. Error bars depict *SEM* across participants.

eye of presentation, CTOA and frame-size. As expected there was a main-effect of cue-validity ($F_{1,180} = 79.21$, $p < 0.001$) because RTs to targets at a valid location were on average 13 ms shorter than RTs at invalidly cued locations. There was also a main effect of eye ($F_{1,180} = 15.15$, $p = <0.01$), as responses to target in the same eye as the cue were 4 ms faster than responses to targets in the opposite eye. Importantly we replicated the results of Experiment 1 by showing that there was a significant interaction between the cue-validity and the eye of presentation ($F_{1,180} = 6.75$, $p = 0.025$), which indicates that valid cues result in a larger RT benefit for targets presented to the same eye than for targets presented to the other eye.

There was an interaction between cue validity and CTOA ($F_{2,180} = 4.76$, $p = 0.02$) because the binocular cueing effect was stronger at the 150 ms CTOA than at the other intervals (Figure 6). There was also an interaction between Eye and CTOA ($F_{2,180} = 4.82$, $p = 0.02$) because the monocular cueing effect was strongest at 50 ms and declined at longer CTOAs (Figure 6).

It can be seen that the RT benefit of a valid, binocularly viewed cue decreased with increasing frame-size (Figure 6b) as evidenced by a significant interaction between frame size and cue validity ($F_{2,180} = 4.59$, $p = 0.02$). In contrast we found no evidence for an effect of frame-size on the monocular cueing effect because there was no significant interaction between cue-validity, eye of presentation and frame-size ($F_{2,180} < 1$). To investigate this further we carried out a series of contrasts for each-frame size at the 50 ms CTOA and observed a significant difference between the [Val, Same] and [Val, Diff] conditions at all three frame-sizes ($t_{(11)} = 2.72$, 3.36 and 3.07 respectively, all $p < 0.05$). As can be seen in Figure 6c the monocular cueing effect at 50 ms CTOA produces a consistent 10–12 ms RT advantage for the [Val, Same] over the [Val, Diff] condition regardless of the distance between cue and target. There were no significant differences between error-rates at each of the different frame-sizes (Kruskal–Wallis test, all $p > 0.3$), which indicates that the present effects are not caused by a speed-accuracy tradeoff.

Conclusions

The results of Experiment 3 give insight into the spatial properties of the monocular cueing effect, as well as the more standard binocular cueing effect. We found that the monocular effect was relatively insensitive to the distance between cue and target, as at 50 ms CTOA we observed a near constant 10 ms advantage for monocularly cued locations compared to uncued locations. In contrast, the magnitude of the standard binocular cueing effect (i.e. the difference between valid and invalid cues) became smaller as cue-target distance was increased, a result reminiscent of zoom-lens theories of attentional capture (Eriksen & St James, 1986). In addition, by using the transient cue, we replicated the findings of Experiment 1 revealing

different time-courses of monocular and binocular cueing effects. The monocular cueing effect was very rapid, having its strongest effects at the 50 ms CTOA. The binocular cueing effect was slower to develop, reaching its peak at the 150 ms CTOA. We conclude that the spatial as well as the temporal properties of the two forms of cueing are distinct.

Furthermore, this experiment rules out that local sensory interactions between the cue and the target are responsible for the monocular effect. Such a local sensory interaction should become weaker when the distance between the cue and the target is increased. However, we found that the monocular effect was relatively insensitive to changes in cue-target distance. In contrast, the magnitude of the binocular cueing effect decreased for larger distances between cue and target. Previous studies demonstrated that some of the behavioral benefits that follow a binocularly viewed cue depend on local sensory interactions (Wright & Richard, 2003) and our binocular cueing effects are consistent with this idea. These results, combined with the results of Experiment 2, show that the monocular cueing effect is not driven by local sensory interactions between the cue and target. After ruling out local sensory interactions we must conclude that the monocular cueing effect is due to more global forms of competition between the stimuli.

Experiment 4—Measuring the components of monocular cueing

So far, our results have demonstrated a monocular form of cueing. The model in Figure 7a presents the most general form of the various cue-target interactions that could occur in our experiments. In the above sections we have alluded to the various types of specific models that might also describe the interactions between cues and targets. Specifically, the sensory facilitation model, the local and global forms of interocular competition and the monocular competition model are special cases of this general model. According to the sensory facilitation model, for example, the energy of the cue facilitates detection of targets at the same location, which would correspond to a positive weight w_4. The global eye suppression model, on the other hand, holds that a cue in one eye inhibits target processing in the other eye and it therefore predicts negative weights w_1 and w_2, while the retinotopically specific interocular suppression effect predicts a negative weight w_1 only. Finally, the monocular competition model proposed above holds that a cue inhibits target processing at all other monocular representations implying that the weights w_1, w_2 and w_3 are all negative. Clearly, mixtures of these models are also possible, and the precise value of all the weights of the model is an empirical question.
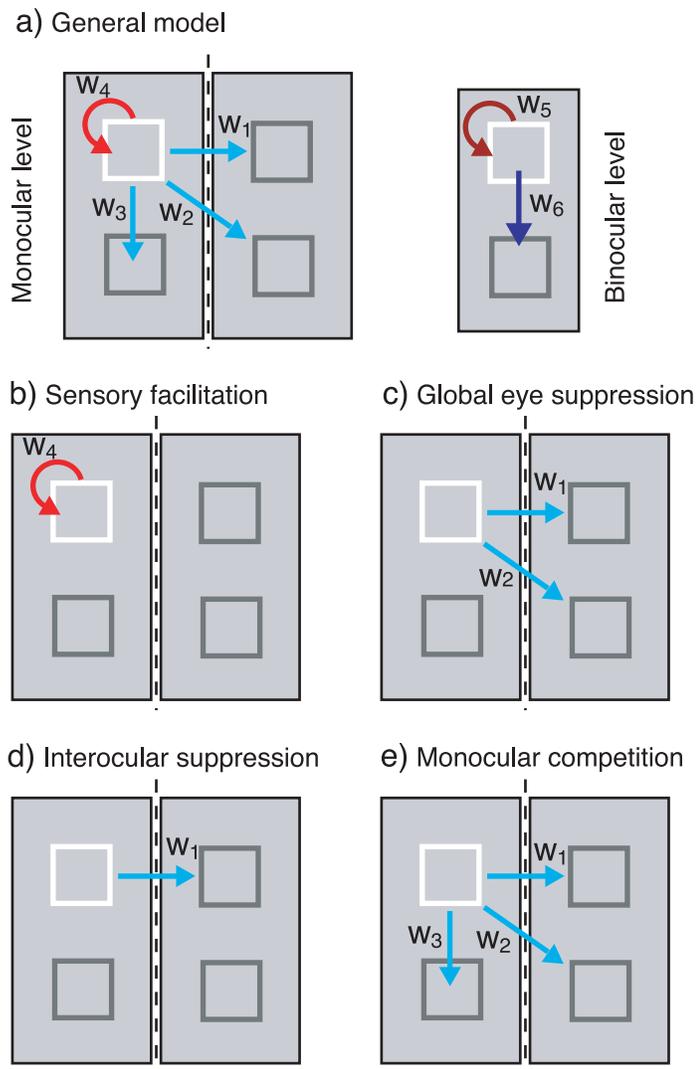
Figure 7. Modeling the underlying causes of the monocular cueing effect. a) Here we show a symbolic representation of the stimuli used in Experiment 1. The upper panel shows the stimuli at the monocular level (the left and right eye images are shown separated by a dashed line) and the lower panel shows how the stimuli would appear to the participants after binocular fusion. The arrows show the possible facilitative (red arrows) and suppressive (blue arrows) interactions that might occur after a cue (the white frame). These include retinotopically specific interocular suppression (w_1), non-specific interocular suppression (w_2), intra-ocular suppression (w_3), monocular sensory facilitation (w_4), binocular facilitation (w_5) and binocular suppression (w_6). b) A special case of the general model in which weights w_1, w_2 and w_3 are set to zero attributes the monocular cueing effect to sensory facilitation produced by the cue (i.e. $w_4 > 0$). c) Global eye suppression. By requiring w_1 and w_2 to be equal and setting w_3 and w_4 to zero we model a global suppression of all stimuli in the eye opposite to the cue. d) By setting weights w_2, w_3 and w_4 to zero we model retinotopically specific interocular suppression (i.e. $w_1 > 0$). e) By setting w_4 to 0 and requiring w_1, w_2 and w_3 to be equal we model monocular competition where the cue suppresses all other monocular target representations in the same and opposite eye.

The previous experiments provide some constraints on the values of the individual interactions. The results of Experiments 2 and 3 suggest that the RT advantages we have observed at monocularly cued locations are not due to local sensory interactions between the cue and the target only. The same eye advantage that we observed in Experiment 1 suggests an inhibitory interaction between the cue in one eye and the target in the other eye (w_1 in Figure 7). Is this effect the only inhibitory interaction as predicted by retinotopically specific interocular suppression or are there additional inhibitory interactions with other locations in the same and the other eye (w_2 and w_3)?

Experiment 4 aims to distinguish between these possibilities by directly measuring the interactions between monocular representations. In addition to the conditions of Experiment 1, we now also included a cueing condition in which both eyes were cued at the same retinotopic location, while the targets were always presented to one eye only (Figure 8a—right-hand panels, the 'Both' conditions). If we assume that the cueing effects add linearly, then this experiment will permit the direct measurement of the intra- and interocular interactions. For example, the interaction w_3 between the monocular representations of a cue and a target at a different location in the same eye can be measured by comparing the [Inv, Both] and [Inv, Diff] conditions (Figure 8c). The RT in the [Inv, Diff] condition will reflect the effect w_2 of a cue in one eye on a target at another location in the other eye. The effect w_2 is also present in the [Inv, Both] condition, but now accompanied by an additional putative source of suppression w_3 by another location in the same eye. The difference in the RT between these two conditions therefore provides a measure for the interaction between spatially separate monocular representations of the same eye (i.e. $w_3 = [w_2 + w_3] - w_2$). Similarly, the effect of a cue on the other target location in the opposite eye w_2 can be measured as the difference in RT between the [Inv, Both] and [Inv, Same] condition, because the former condition invokes two sources of inhibition, w_2 and w_3, and the latter only one, w_3 (the difference in RT provides an estimate of $w_2 = [w_2 + w_3] - w_3$). Note that the retinotopically specific interocular suppression model predicts that the RT in the [Inv, Same] and [Inv, Diff] conditions are the same as the RT in the [Inv, Both] condition (because $w_2 = w_3 = 0$), while the monocular competition model predicts that the RT in the [Inv, Both] condition is longest.

Methods

We tested 24 naïve participants in Experiment 4, three were excluded for having a mean RT of longer than 600 ms leaving 21 participants for the analysis (18 female, age range 18–28). Experiment 4 was essentially a replication of Experiment 1 except for the following details: the cue remained at a high contrast until the participant responded
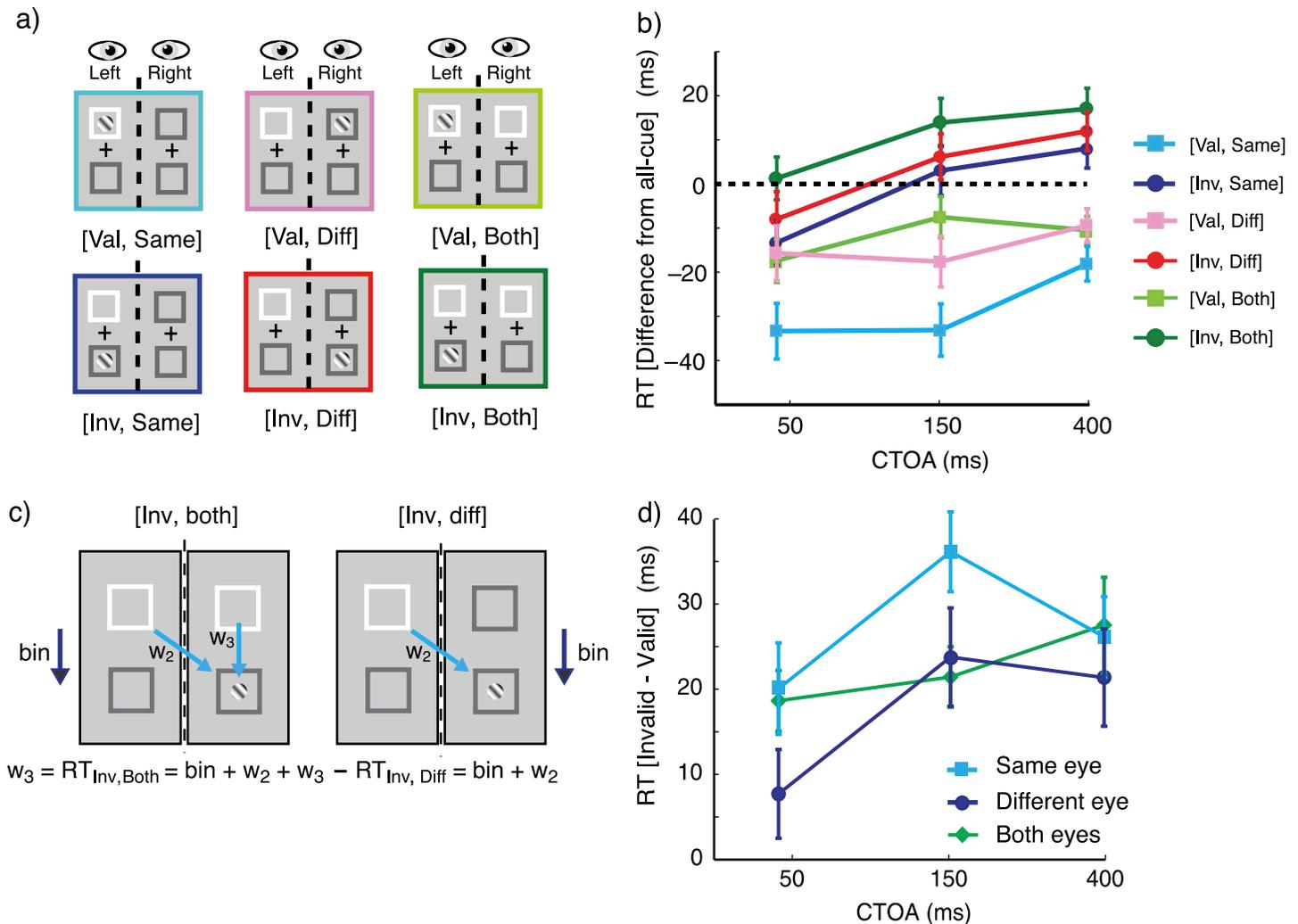
Figure 8. The stimuli and results of Experiment 4. a) The conditions of Experiment 4. This experiment contained the conditions of Experiment 1 where one monocular location was cued, and in addition conditions in which both eyes were cued (the light- and dark-green conditions). We also presented the all-cue condition from Experiment 2 (not pictured). b) The mean RTs from the 24 participants of Experiment 4. The RT from the 'all-cue' neutral condition was subtracted to act as a baseline. The critical [Both] conditions are shown in green, the format is otherwise the same as Figure 2b. c) An example of how the RTs from this experiment can be used to calculate the weights described in Figure 7. In the [Inv, Both] condition the RT to the target will be increased by the interactions w_2, w_3 and bin (the binocular effect), however in the [Inv, Diff] condition only w_2 and bin can affect the RT. The weight w_3 can therefore be calculated by subtracting the RT in the [Inv, Diff] condition from those in the [Inv, Both] condition. Similar subtractions allow calculation of the other weights (see text for details). d) The binocular validity effect is quantified for the three cue distributions (same eye, different eye and both eyes) as the difference in RT to targets presented at invalidly and validly cued locations.

and we added the [Val, Both] and [Inv, Both] conditions (Figure 8a) to the experiment. We also added the 'All-Cue' condition from Experiment 2 to act as a baseline. All these conditions were presented in a pseudo-random order. All other stimulus details and timings were the same as in Experiment 1.

Results

The basic pattern of results was very similar to those seen in Experiment 1 (Figure 8b). We first investigated the significance of the differences in RT using a $3 \times 3 \times 2$ ANOVA with factors CTOA, cue-validity and eye of presentation (same, different eye and both eyes). There was a main effect of cue-validity ($F_{1,80} = 115.21$, $p < 0.001$), because the RT at validly cued locations was, on average, 22 ms shorter than the RT at invalidly cued locations. In addition, there was a main effect of eye-of-presentation ($F_{1,80} = 22.38$, $p < 0.001$) because RT in the same eye condition was 7 ms shorter than in the different eye condition, which in turn was 6 ms shorter than the RTs in the both eyes condition. Apparently presenting a cue to both eyes simultaneously and at the same

retinotopic location produced a general slowing of RT compared to when the cue was presented to one eye only. For example, at a CTOA of 50 ms, the extra cue at the valid location in the other eye in the [Val, Both] condition added an extra 15 ms to the participants' RTs when compared to the [Val, Same] condition.

In addition, there was a significant interaction between the cue validity and eye of presentation ($F_{2,80} = 3.89$, $p = 0.029$), this effect was mainly driven by the stronger cueing effect for the Same and Both conditions compared to the Diff condition at the 50 ms CTOA. At this CTOA participants were approximately 20 ms faster at validly cued locations in the Same and Both conditions, whereas in the Diff condition participants were only around 8 ms faster (Figure 8d).

Most critical in this experiment are the [Inv, Both], [Inv, Same] and [Inv, Diff] conditions because they distinguish between the retinotopically specific interocular suppression and the monocular competition models. Importantly, we found that the [Inv, Both] condition produced significantly slower RTs than the other invalid conditions (compare the red, blue and green curves in Figure 8b). Indeed, a separate 3×2 ANOVA with factors CTOA and condition ([Inv, Both] vs. other invalid conditions) revealed a main effect of condition: $F_{1,63} = 20.36$, $p < 0.001$). There were no significant differences between error-rates in the different conditions (Kruskal–Wallis test, $p > 0.5$).

Under the assumption of a linear summation of cueing effects, we can now directly estimate the interactions between monocular representations depicted in Figure 7. We can estimate the effect w_3 of a monocular cue on a target at a different location in the same eye by a subtraction of the RT in the [Inv, Diff] condition from that in the [Inv, Both] condition ($w_3 = [w_2 + w_3] - [w_2]$), and the inhibitory weight w_3 is approximately 10 ms according to this calculation. Similarly, we can estimate the effect w_2 of a cue on a target at different location in the other eye by subtracting the RT in the [Inv, Same] from the [Inv, Both] condition ($w_2 = [w_2 + w_3] - [w_3]$) and this subtraction yields an estimate of the inhibitory weight w_2 of 13 ms. Finally, a subtraction of the RT in the [Val, Same] from that in the [Val, Both] conditions permits an estimation of the interaction w_1 between the representations of the same location in the two eyes ($w_1 = [w_1 + w_4] - [w_4]$), and this subtraction yields a suppressive effect of 17 ms.

Discussion

The main goal of this experiment was to discriminate between two of the possible explanations for the monocular cueing effect: interocular suppression and monocular competition (Figures 7d and 7e). Crucially we added a second cue at the same retinal location but in the eye opposite to the first cue. This allowed us to test whether the extra cue produces additional inhibition at invalidly

cued locations (w_2, w_3) as would be predicted by the monocular competition, but not the interocular suppression model. In line with the predictions of monocular competition we observed that the second cue caused extra inhibition, despite the fact that the single and dual-cue conditions looked very similar to the participants (when both eyes received a cue then its contrast may appear somewhat higher due to binocular summation, although the effect was never noticed by the participants when asked after the experiment). Our results support the monocular competition model that holds that a monocular cue inhibits the monocular representations of all locations in the opposite eye as well as the representations of different locations in the same eye (i.e. we found that w_1, w_2, and w_3 all increased the RT). Is this model also consistent with the results of the other experiments? To address this question, the next section provides a more formal test, comparing how well the different models for the monocular cueing effect account for the overall pattern of RTs across experiments.

Models of the monocular cueing effect

In this section we wish to compare how well the models that have been introduced above account for the pattern of RTs obtained across experiments. In the analysis we focus on the cueing effects observed at the standard frame size and the CTOA of 50 ms common to Experiments 1, 2 and 4. We did not include data from Experiment 3 in this analysis as it contained different frame sizes. As well as modeling the single and dual-cue conditions we also investigated whether our model could account for behavior in the neutral conditions (the all-cue and no-cue conditions). It is notoriously difficult to match the level of arousal, warning signals and sensory interactions in neutral conditions to those of non-neutral conditions (Wright, Richard, & McDonald, 1995). We therefore implemented two versions of our model, one including data from these neutral conditions (the all-cue condition of Experiments 2 and 4 and the no cue condition of Experiment 2) and one without these conditions so that we could compared the quality of the fit.

Methods

We modeled the RTs of the individual participants that participated in Experiments 1, 2 and 4. The parameters of the model are the weights w_1, w_2, w_3 and w_4 for the monocular cueing effects and w_5 and w_6 for the binocular effects (Figure 7). Due to the design of our experiments, we will not be able to distinguish between the binocular representation of a cue that facilitates a target at the same

location (w_5) and a binocular cue that suppresses a target at the binocular representation of another location (w_6). In our modeling we therefore only considered the difference in RT between validly cued and invalidly cued binocular representations bin, with bin = $w_5 - w_6$.

We fitted a general linear model to the average RTs of the individual participants in the various conditions under the assumption that the RT of a participant i on condition j can be modeled as follows:

$$RT_{i,j} = \beta_i + w_1 X_{j1} + w_2 X_{j2} + w_3 X_{j3} + w_4 X_{j4} + bin\, X_{j5} + \varepsilon_{i,j}. \quad (1)$$

Where β_i is a participant specific regression coefficient which equals the base RT in the absence of cueing effects, $\varepsilon_{i,j}$ is an error term and X_{j1}–X_{j5} take the value 1 if a contribution of the respective weight (w_1–w_4 and bin) to the RT is expected in condition j and 0 otherwise. For example in Experiment 2 there were no binocular interactions and therefore X_{j5} was 0 for all conditions j. Using multiple linear regression we estimated β_i, w_1–w_4 and bin.

Results

We first examined the model excluding the neutral conditions. The full model fitted the RT data extremely well ($R^2 = 0.92$, $p < 0.0001$) accounting for over 90% of the variation in participants' RT (Figure 9). Around 60% of the variance could be explained by the participants' base RT (β_i), a further 31% was explained by the suppressive and facilitative weights (w_1–w_4 and bin). When we included the data from the neutral conditions the fit of the model was no longer significant ($p > 0.05$) and the amount of variance explained by the different weights dropped to 23%. For these reasons we shall focus on the results from the model excluding the neutral conditions, and describe the possible reasons for the poor fit of the neutral conditions below. The weights that best fit the data were as follows: $w_1 = -17$ ms, $w_2 = -11$ ms, $w_3 = -11$ ms, $w_4 = 3$ ms and bin = -7 ms. The weights w_1–w_3 were significantly different from zero ($t_{244} = -4.3$, -2.8 and -2.7 respectively, all p's < 0.01) indicating that a monocular cue significantly suppresses all other monocular representations. The weight w_4 was not significantly different from zero ($t_{244} = 0.9$, $p = 0.4$) indicating no evidence for sensory facilitation. The binocular weight, bin, was slightly but significantly larger than zero ($t_{244} = -2.2$, $p = 0.03$) indicating a weak binocular cueing effect at the 50 ms CTOA. While the full model produced an accurate fit, this does not rule out the possibility that simpler models might have been able to account for the data. We therefore tested a number of reduced versions of the model of Figure 7 and compared these to the full model. The following sections describe the reduced models and the best fits of these models are shown in Figure 9.

Sensory facilitation. The pure sensory facilitation model holds that a cue facilitates a target when presented at the same monocular location and in the model we therefore set the weights w_1, w_2 and w_3 to zero while allowing w_4 and bin, the binocular cueing effect, to vary. The best fit of the model is shown in the second column of Figure 9. It can be seen that the sensory facilitation model produced a significantly ($F_{3,243} = 8.3$, $p < 0.001$) worse fit than the full model, even if we compensate for the reduced number of parameters. Specifically, the sensory facilitation model predicts that RT in the [Val, Same] condition of Experiment 4 is the same as in the [Val, Both] condition. Moreover, it predicts that the RT in the [Inv, Same] condition is the same as in the [Inv, Both] condition. The model therefore fails to capture the slowing of RT produced by the binocular cue.

Global eye suppression. This model suggests that a cue in one eye suppresses the processing of targets anywhere in the other eye. In the model we therefore set w_3 and w_4 to zero, and vary $w_1 = w_2$ and bin. The fit can be seen in the third column of Figure 9 and was significantly worse than the full model ($F_{3,243} = 8.15$, $p < 0.001$). One difference between data and model that is partially responsible for the poor fit occurred in Experiment 2 where the model predicted that a target at a non-cued monocular location should be associated with a longer RT in the within eye condition than in the across eye condition, while we observed similar RTs for these conditions.

Retinotopically specific interocular suppression. This model assumes that the interaction between corresponding locations in the two eyes w_1 is the only cause of the monocular cueing effect. We therefore set w_2, w_3 and w_4 to zero while allowing w_1 and bin to vary. The fit (fourth column of Figure 9) was significantly worse than the full model ($F_{3,243} = 2.86$, $p = 0.04$). One of the discrepancies between the data and the model occurs in Experiment 4 as the model predicts that the RT in the [Inv, Both] condition is similar to the RT in the [Inv, Same] and [Inv, Diff] conditions, while the RT of the observers was longer in this condition.

Monocular competition. The monocular competition model suggests that a cue at one monocular location inhibits target processing in the other eye as well as at other locations in the same eye, resulting in a relative advantage of targets presented to the cued monocular location of the same eye. To fit this model, we require w_1, w_2 and w_3 to be equal in magnitude, set w_4 to zero and allow bin to also vary. The fit of the model can be seen in the fifth column of Figure 9 and was not significantly worse than the fit of the full model ($F < 1$, $p = 0.67$).

Discussion

We were able to accurately model the RT of different groups of participants from three different experiments

using one simple model. This model allowed us to estimate the facilitative and suppressive interactions that occur following the cue. Noticeably weights w_1, w_2 and w_3 were all significant and negative suggesting that the cue suppresses all other target locations whereas w_4 was not significantly different from zero suggesting no significant contribution of sensory facilitation. The binocular contribution (bin) was also small and accounted for only a 7 ms difference between valid and invalid target locations at the 50 ms CTOA. The simpler designs varied in their ability to explain the RTs. The sensory facilitation, eye suppression and interocular suppression models

produced significantly worse fits than the full model. Only the monocular competition model produced a fit with a quality that was comparable to that of the full model. The main difference between this model and the other models was that the monocular competition model can account for the slower RT in the [Inv, Both] condition of Experiment 4. The results of this experiment, and in particular the excellent match between the predicted RTs produced by the monocular competition model and the actual RTs suggest that monocular competition (along with standard binocular cueing) underlies the RT differences observed in these experiments.
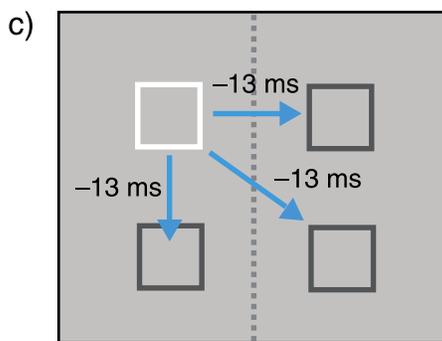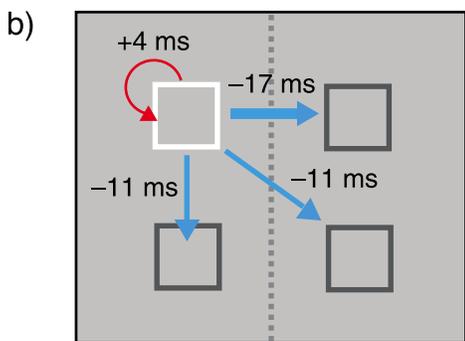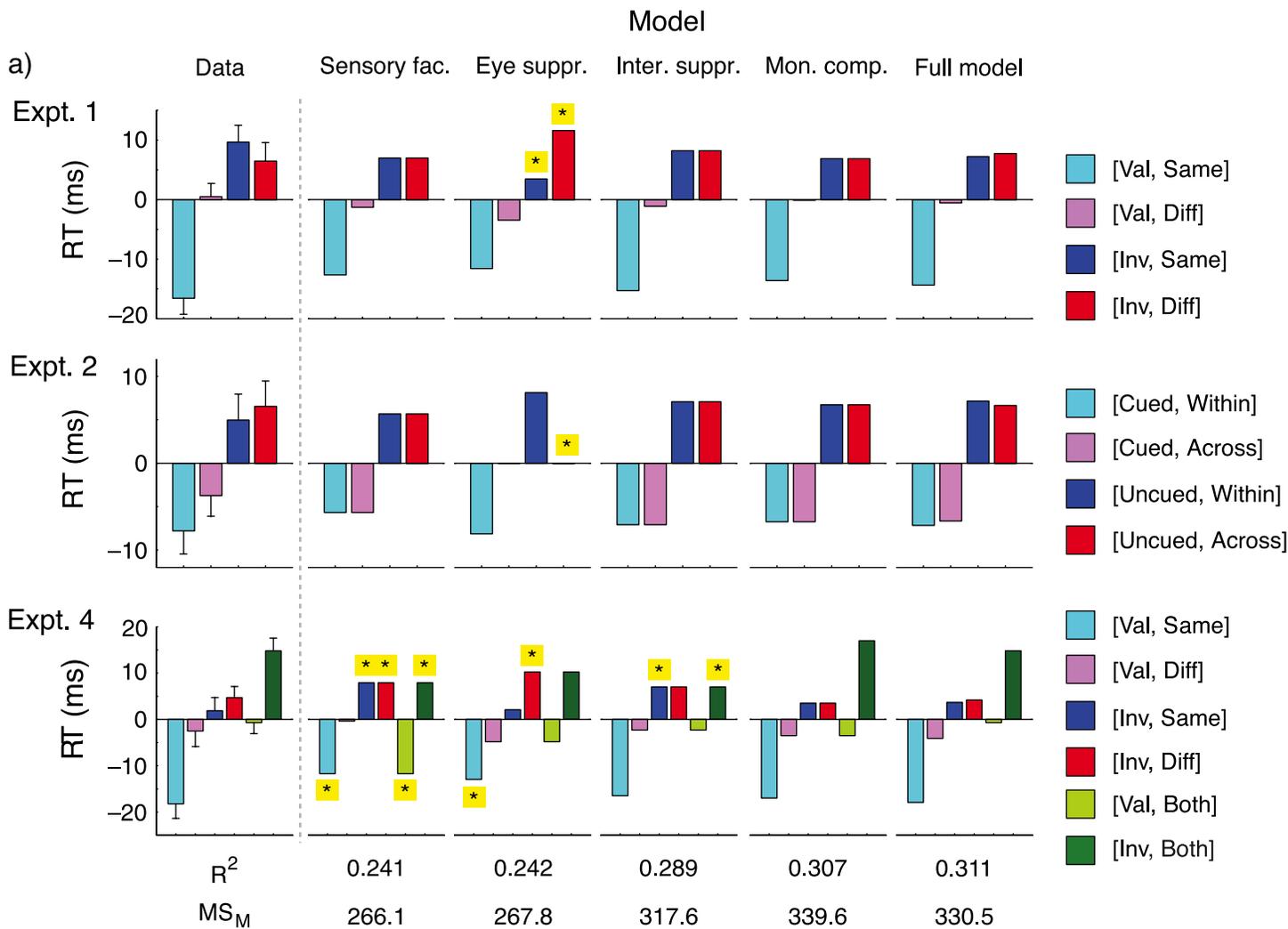
We note, however, that the model was not able to account for the RTs of the two neutral conditions. Inclusion of the neutral conditions decreased the quality of the fit so that it was not significant. An inspection of the RTs in the neutral conditions gives some insight in why these conditions were not well fit by our model. According to our model, responses in the no-cue condition should have enjoyed the least amount of suppression and therefore should have produced fast RTs, whereas the data show that the RTs in this condition were slower than in all other conditions (see Figures 4b and 4c). We have outlined in the discussion of Experiment 2 why the no-cue condition is a poor neutral control. This condition was not perceptually matched to the other conditions and did not provide a warning signal about the impending target that was present in all other conditions. In contrast, the response time in the all-cue condition should suffer from the greatest amount of suppression as all positions were cued, and it should therefore have produced the slowest RT. However, the RT in the all-cue condition was similar to that of the uncued conditions (see Figures 4b and 4c). We therefore have to consider the possibility that some of the interactions are non-linear. For example, the amount of suppression might saturate for high levels of inhibition. Saturation of inhibition could account for the differences between response times that were measured and predicted

Figure 9. Modeling of the data. a) The first column shows the mean RT data from Experiments 1, 2 and 4 at the 50 ms CTOA after subtraction of each participant's mean RT. The error-bars are the *SEM* across participants. We modeled these data using the full-model shown in Figure 7a as well as the reduced models of Figures 7b–7e with multiple linear regression (see text for details). This procedure allowed us to estimate the weights indicated in Figure 7 and predict RTs for each condition. These predicted RTs are shown in the remaining columns. In general the fit of the full model (the rightmost column) to the data was extremely good. The reduced models did not account well for the pattern of RTs, with the exception of the monocular competition model. This monocular competition model stands out because it is the only reduced model that explains the slower RTs in the [Both] conditions of Experiment 4 (green bars). The yellow asterisks mark conditions in which the models produced a particularly bad fit to the data ($|RT_{data} - RT_{model}| > 5$ ms). The fit of the models is quantified below the graphs by R^2 which shows how much variance in RT (after subtraction of each participant's mean RT across conditions) can be explained by each model, the full-model could account for around 31% of the variance in RT. Also shown in MS_M which is the mean squared error (in ms^2) of the model. This value is the reduction in squared-error accounted for by the model divided by the number of regressors in the model i.e. higher values indicate a better model. Note that the monocular competition model produces the best compromise between a small number of regressors and a small error. b) The regression weights as calculated using the full-model in the same format as Figure 7. c) The regression weights calculated using the monocular competition model.

by the model in the all-cue condition, because this was the only condition that produced three sources of inhibition, w_1, w_2 and w_3.

Discussion and conclusions

In this study we have observed a new monocular exogenous cueing effect that takes place at the earliest stages of visual processing where the information from the two eyes has yet to be combined into a binocular percept. To our knowledge, the present study is the first to show a contribution of monocular processing levels to the Posner cueing effect. By utilizing the Posner cueing paradigm, our approach provides detailed temporal information about monocular attentional capture. We found that monocular cueing is very rapid, in Experiment 1 it was evident as early as 50 ms CTOA. Our results demonstrate that the monocular cueing effect precedes the standard binocular cueing effect that requires more time to develop and reaches its peak strength at 150 ms CTOA. The monocular cueing effect also appeared to follow the timing of the cue more closely, when the cue was brief the monocular effect lasted only 50 ms and when the cue remained at a high contrast the effect was maintained for 400 ms. This stands in contrast to the standard binocular cueing effect, the duration of which was independent of the cue duration. The two effects also had a different spatial profile. The binocular effect decreased as the distance between the cue and the target was increased whereas the monocular cueing effect depended only weakly on the distance. A careful evaluation of the pattern of RTs indicated that the monocular cue inhibits the processing of targets presented at different locations in the same eye, as well as targets presented to the opposite eye. Our results therefore demonstrate that attentional capture can occur at the early monocular stages of the visual system and they thereby suggest that saliency computations begin very early in visual processing so that these effects can be inherited by higher areas (see also Li, 2002 for a similar view).

The anatomical locus of the monocular cueing effect

It is useful to consider the brain regions that could contribute to monocular cueing. Neurons that respond to only one of the eyes are found in the retina, lateral geniculate nucleus of the thalamus (LGN), V1 (Hubel & Wiesel, 1968) and the superficial layers of the superior colliculus. There are also a very small number of monocular cells in extra-striate visual areas (Hubel & Wiesel, 1968; Leopold & Logothetis, 1996; Zeki, 1978), however beyond these stages information about the eye-

of-origin of the stimulus is lost. The main effects of a monocular cue revealed by our experiments were inhibition of monocular locations in the other eye combined with inhibition at different locations in the same eye. Suppression between the neuronal representations of locations in the same eye can occur as early as the retina. Retinal ganglion cells are inhibited by information outside their receptive field, and these suppressive effects could account for the inhibitory interactions between a cue and a subsequent target presented to the same eye (w_3 in Figure 7) (Alitto & Usrey, 2008). These inhibitory interactions between monocular representations of the same eye are also found in the LGN (Alitto & Usrey, 2008; Webb, Tinsley, Vincent, & Derrington, 2005), which is at the same time the first stage where inhibitory interactions between different eyes can take place (w_1 and w_2). Inhibitory interactions between LGN neurons are partially mediated through the thalamic reticular nucleus that provides inhibition to the LGN relay cells (Crick, 1984; Singer, 1977). A recent study demonstrated that this inhibition plays a role in an endogenous cueing task (McAlonan et al., 2008). This study reported that an endogenous cue that directs attention to a particular spatial location increases the response of LGN neurons with a receptive field at that location while suppressing the activity of the reticular neurons with a receptive field at the same location (McAlonan et al., 2008). These results, taken together, indicate that the inhibitory interactions between monocular representations that underlie the cueing effects of the present study could well be mediated by the interactions between the LGN and the thalamic reticular nucleus. Future studies will, however, also have to consider the primary visual cortex as a potential site for monocular attentional effects (Li, 2002), because the monocular neurons of area V1 dedicated to the two eyes engage in various forms of inhibitory and excitatory interactions (Kato, Bishop, & Orban, 1981; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005) and area V1 contributes to endogenous and exogenous shifts of visual attention (Knierim & Van Essen, 1992; Roelfsema, 2006; Roelfsema, Tolboom, & Khayat, 2007).

Is monocular exogenous capture automatic?

There has been considerable debate in the literature as to whether exogenous cues automatically capture attention. Initial descriptions of exogenous capture (Jonides, 1981) suggested that it was an entirely automatic process that could not be suppressed. However, later studies found that top-down factors can suppress automatic capture if a participant's attention is engaged at a specific location (Remington et al., 1992; Theeuwes, 1991; Yantis & Jonides, 1990) and studies using pop-out stimuli have found that they do not automatically capture attention when the participant is not searching for a unique feature (Bacon & Egeth, 1994), but this remains a topic of debate

(Theeuwes, 2004). Our experiment is relevant for this debate by providing clear evidence for an entirely unconscious component of attentional capture at the earliest processing levels. It is likely that this form of attentional capture is entirely automatic and evades top-down control.

Our results combined with these previous findings suggest that there are at least three factors which speed RT following sudden-onset cues. 1) Pure sensory interactions between the cue and the target which will always speed RT regardless of top-down goals (Müller & Rabbitt, 1989; Remington et al., 1992; Solomon, 2004; Wright & Richard, 2003). 2) Rapid unconscious competition between stimuli that produces an automatic advantage at the location of the cue (our study, Zhaoping, 2008). 3) A slower conscious component that may be susceptible to task requirements (Bacon & Egeth, 1994). Many studies, (Klein, 2000), have also shown a yet later component which produces slowing of RT at the location of the cue known as inhibition of return (IOR). In our study we could not measure IOR as we used an orientation discrimination paradigm with non-spatially overlapping and visually distinct cues and targets. These conditions result in more long-lasting attentional enhancements but do not produce IOR. It will therefore be of great interest for future studies to determine whether IOR can also be influenced by monocular and unconscious cueing (Ivanoff & Klein, 2003).

Relation between attention and awareness

The differences between the monocular cues used in our experiment escape awareness but cause robust processing benefits and our results therefore support the dissociation between attention and awareness (see also Zhaoping, 2008). Previous studies have suggested that unconscious cues can capture attention, however these studies relied on cues presented near threshold where stimuli are sometimes detected and sometimes not (Ivanoff & Klein, 2003; McCormick & Klein, 1990) or used cues that were masked to limit their visibility (Ivanoff & Klein, 2003). These studies had to use dual-task designs to determine whether the participant perceived the cue or not, on every trial. Our study, and that of Zhaoping (2008), circumvents these issues by using robustly unconscious stimuli (see Appendix A); in our Experiment 2, for example, participants did not see differences between any of the experimental conditions (barring the increased contrast of the cue in the all-cue condition). We could therefore use a single-task paradigm in which the participants could never tell which positions were cued. The fact that we still found RT differences between monocularly cued and uncued locations shows that attentional capture can occur in the complete absence of awareness of the cue. These results support the ideas of Koch and Tsuchiya (2007) and Lamme (2003) who have argued that attention should not be equated with awareness. Our results demonstrate that stimulus-driven attention starts with an entirely uncon-

scious, rapid, monocular component that is responsible for the early (~50 ms) cueing effects. Only later (150 ms and longer) does binocular attentional processing significantly affect participants' responses and we therefore argue that attentional capture can be split into unconscious and conscious components.

Appendix A

No conscious access to monocular information

In these control experiments we tested whether participants had conscious access to monocular information about the eye-of-origin of the cue or whether cues and targets were presented to the same or different eyes. Ten new participants, naïve to the aims of the experiment, took part. The same apparatus, CRT monitor and conditions were used as in the main experiments. We used the same noise-patterned frames and Gabor targets as in the main experiments.

Control Experiment 1

In this experiment we tested whether participants were able to discriminate between a cue and target presented to the same eye and a cue and target presented to different eyes. The set up of the stimuli was identical to Experiment 1, i.e. we tested whether participants could discriminate between the [Val, Same] and [Val, Diff] conditions of Experiment 1. The participants fixated the central cross and then, after 500 ms a cue (the same cue as in Experiment 1) was presented for 50 ms. After a variable CTOA a target (the Gabor patch) was presented. The Gabor remained on the screen for 200 ms. After this period the participants were cued to make a non-speeded response whether the cue and target were presented to the same or different eyes by pressing one of two buttons on the keyboard with their right hand. We used a 2 × 2 factorial design, the two factors were whether the cue and target were presented to the same or different eyes, and the CTOA, which was either 50 or 400 ms. The trials were presented in a pseudorandom order and each trial-type was presented 50 times. Participants were informed about the underlying ocular differences between the stimuli and that in half the trials the cue and target would be presented to different eyes. They were shown examples of the stimuli without looking through the stereoscope and were allowed to practice the task beforehand. Participants were encouraged try and detect very small differences between the stimuli and were told that there may be "unconscious parts of their brain which can guide their responses therefore, even if you feel like you are guessing, you should not

always press the same button but vary your responses". The participants were given error feedback on incorrect trials to try and maximize performance. Despite these instructions one participant was removed for pressing the "Same Eye" response on every trial.

Results and discussion

Performance of the individual subjects ranged from 42.5% correct to 55.5% correct (chance level was 50% correct). None of the participants showed any significant ability to detect whether the cue and target were presented to the same eye or not with a mean performance at the 50 and 400 ms CTOA of 49.7% and 48.3%, respectively (χ^2 test, all $p > 0.05$, Bonferroni correction applied, though the p-values of all participants were larger than 0.05 before correction). The mean performance across participants (averaging across CTOAs) was 49% correct, the median score was 48.5%. This was not significantly different from chance ($p > 0.5$, Wilcoxon signed rank test). The results indicate that the difference between a cue and target presented to the same eye and a cue and target presented to different eyes is undetectable.

Control Experiment 2

In this experiment we again tested whether participants could discriminate between cues and targets presented to the same or different eyes but using a temporal forced-choice technique. On each trial there were two presentations of the cue and the target (the same cue and target as in Experiment 1 using the CTOA of 50 ms) separated by a pause of 200 ms. Within the trial we varied whether the cue/target pairs were presented to the same or different eyes so that each possible combination was tested 50 times (same/same, same/diff, diff/same, diff/diff). The cue and target were always presented so that they would appear at the same location when viewed binocularly. The participant's task was to determine whether the two presentations were identical or different and error feedback was given. For example if, in both the first and second presentations, the cue and target were presented to the lower position of the left and right eye respectively, then this would be a diff/diff trial and the participant should respond 'identical'. If however, in the first presentation both cue and target were presented to the right eye and in the second both cue and target were presented to the left eye, then this would be a same/same trial but the participant should respond 'different'. They were informed that the only difference that could exist between the two presentations was whether the cue/target pairs were presented to the same or different eyes and that on 50% of trials the two presentations would be different. They were again instructed to vary their responses.

Results and discussion

Performance of individual participants ranged from 48% correct to 59.5% correct. Two out of 10 participants showed some ability to detect the difference between identical and different presentations (Participant 3 = 59% correct, χ^2 test, $p = 0.01$. Participant 4 = 59.5% correct, χ^2 test, $p = 0.007$) but these effects did not survive a Bonferroni correction for multiple comparisons. The mean performance across participants was 52.9% correct (median = 53.5%), this was not significantly different from chance ($p > 0.05$, Wilcoxon signed rank test). The results therefore show that the difference between the [Valid, Same] and the [Valid, Diff] conditions of Experiments 1 and 4 was unconscious.

Control Experiment 3

In this experiment we tested whether participants could discriminate between the Within and Across eye cues of Experiment 2. The participants were presented with either a Within eye or Across eye cue (pseudorandomly controlled to give 50 trials of each type). The cues remained on the screen for 400 ms. The participants then had to make a forced-choice discrimination as to whether the two cues were presented to the same or different eyes. Error feedback was given.

Results and discussion

Performance ranged from 40% to 76% correct and 2 out of 10 participants showed a significant ability to detect the difference between the Within and Across eye cues; participant 1 (66% correct, χ^2 test, $p = 0.01$, Bonferroni correction applied) and participant 7 (75%, χ^2 test, $p < 0.001$, Bonferroni correction applied). The mean performance was 54.8% correct (median = 51.5%), this was not significantly different from chance ($p > 0.1$, Wilcoxon signed rank test). The results indicate that the majority of participants could not determine between the same and different eye cues. However, two of our subjects could detect this difference. It is likely that the difference between the conditions was easier to see in this experiment than the previous controls because of differences in contrast sensitivity between the two eyes in two participants. Differences in sensitivity would cause the cues in the Across eye condition to appear at slightly different contrasts and the cues in the Within eye condition to appear at the same contrast. This was precisely what was reported by participant 7 (participant 1 simply reported that he found this experiment "easier"). All other participants reported that they felt they were guessing. These results suggest that the majority of the participants who took part in Experiment 2 would not have been aware of the difference between the Within and Across eye cue conditions.

Control Experiment 4

In this experiment we tried to maximize the possibility that the participants could determine the eye-of-origin of the stimulus. Participants viewed 2 frames at 30% contrast, one in each eye presented centrally, above and below the fixation point. The contrast of one of the two frames was increased to 100% contrast and remained at the high contrast until the response of the participant. Participants reported, using a key-press, whether the contrast increase was in the left or right eye. They were given feedback on incorrect trials to try to maximize their performance. Each participant completed 100 trials.

Results and discussion

Nine out of 10 participants showed no significant ability to detect the eye-of-origin of the contrast increase (all $p > 0.05$, χ^2 test). One participant showed a significant ability to detect the eye-of-origin (Performance was 61% correct, $p = 0.028$, χ^2 test) but this effect did not survive a Bonferroni correction for multiple comparisons. The average performance level across participants was 52.5% correct (median = 52.5%), this was not significantly different from chance ($p > 0.05$, Wilcoxon signed rank test). We therefore conclude that participants did not have conscious access to information about the eye-of-origin of the cue.

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