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A BIASED-COMPETITION APPROACH TO SPATIAL CUING: COMBINING EMPIRICAL STUDIES AND COMPUTATIONAL MODELLING

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Abstract

We examined the effects of cue luminance on visual orienting. Experiment 1 established that the commonly-found early facilitation and late inhibition of return (IOR) effects were independent of cue luminance with single cues in terms of effect size. However, IOR was delayed in the low luminance cue condition compared to the high luminance cue condition. In contrast, Experiment 2 revealed that, with dual cues of mixed luminance, both facilitation and IOR effects were found only with bright cues. When cues had equal luminance, however, there were cuing effects for two cued locations but only when the cues were bright. The data were accommodated in a neural network model of biased competition in which cuing effects emerge at more than one location provided input activation is sufficient to overcome competitive damping of the selection system.

Introduction

In the classical spatial cuing paradigm (Posner, 1980), participants see a briefly presented non-informative spatial cue either on the left or the right of fixation. This cue is then followed by a target stimulus either at the cued location or on the opposite side of space. Typically, when there are relatively short time intervals between the cue and target, participants are faster in detecting a target at the same location as the cue compared to when the stimuli fall on opposite sides (the ‘early facilitation effect’). A standard interpretation of this early facilitation effect is that it stems from the reflexive orienting of spatial attention towards the sudden appearance of the cue, which results in more efficient processing of targets at that location (Folk, Remington, & Johnston, 1992; Posner, 1980; Posner & Cohen, 1984; Yantis & Hillstrom, 1994; Yantis & Jonides, 1984). However, when the time interval between the cue and target is increased, the cuing effect is reversed and participants are faster to respond when target and cue are on opposite sides of space rather than at the same location (the ‘inhibition of return effect’, IOR). One account of this later reversal of the facilitation effect is that it originates from an inhibitory signal which prevents attentional re-orienting to previously attended locations (Hunt & Kingstone, 2003; Klein, 1988; Klein, 2000; Maylor & Hockey, 1985; Posner et al., 1984; Posner, Rafal, Choate, & Vaughan, 1985). Inhibition of attended locations would encourage orienting towards novel locations and prevent attention from over-committing to a particular location (Klein, 1988; Klein, 2000; Ogawa, Takeda, & Yagi, 2002; Posner et al., 1984).

In recent years there has been growing evidence that attentional orienting is implemented in the brain as a competitive process (Chelazzi, Miller, Duncan, & Desimone, 1993; Desimone & Duncan, 1995; Duncan, 2006; Duncan, Humphreys, & Ward, 1997; Heinke & Humphreys, 2003; Mavritsaki, Heinke, Allen, Deco & Humphreys, 2011; Heinke & Backhaus, 2011). According to the “biased-competition theory of attention”, incoming stimuli compete for cortical representation and the winner of this competition is selected for an action – for example, to make a saccade to the target (e.g., Chelazzi et al., 1993). There is evidence that the competition for selection can be biased by various factors including working memory (Soto, Heinke, Blanco & Humphreys, 2005), visual saliency (Itti & Koch, 1998) and task context (Duncan, 2006; Humphreys & Riddoch, 2001). When applied to the spatial cuing procedure, biased-competition theory suggests that the stimuli at different spatial locations compete for selection. With a short SOA between the cue and the target, the cue biases this spatial competition in favour of the cued location resulting in the early facilitation effect. IOR may then reflect a later–acting bias against previously selected locations (see Heinke & Humphreys, 2003; for a computer model of these two hypotheses).

Whether all cuing effects can be conceptualised in terms of competition for selection can be questioned, however. Consider a study by Wright and Richard (2003). In their first experiment spatial cuing was realized by presenting a variable number of horizontal lines (1, 2, 3 or 4 lines) at 8 possible locations arranged in a circle around a fixation cross. After 100ms a target line, either tilted to right or to the left, appeared and participants had to indicate the line’s orientation. The target could appear either just above a horizontal line (the cued condition) or at a location where no line was present (the uncued condition). Wright and Richard found that, when there was a single cue (only one horizontal line), the RT benefit for cued over uncued trials was higher than in the multiple cue conditions; however the number of lines in the multiple-cue condition did not alter the cuing effect. The drop in cuing in the multiple- relative to the single cue condition was attributed to competitive interactions between the cues. To explain the residual cuing effect that remained, Wright and Richard argued that performance was also affected by sensory enhancement (when the target appeared at the same location as the cue), which was not affected by spatial competition during selection. Evidence supportive of the argument for sensory enhancement came from their Experiment 3 which showed that the cuing effect was proportional to the luminance of the multiple cues. This result fits with the idea that bright cues should enhance sensory processing more than dim cues.

The present study

The present study set out to test Wright and Richard’s proposal for there being both sensory and attentional components of visual cuing effects, using both experimental tests of the effects of cue luminance on performance (Part 1) and computational modelling within a biased competition framework, to assess how far this approach can be taken.

The experiments manipulated cue luminance. If there is a pure sensory effect which is sensitive to cue luminance, then we should expect a larger cuing effect from a brighter cue even when a single stimulus is presented. On the other hand, given that there is minimal attentional competition when a single cue is present, then minimal effects of cue brightness may be predicted from an attentional account. These proposals were assessed in Experiment 1. Note that there is evidence for both hypotheses in the literature. Mele et al. (2008) showed that changes in cue luminance can modulate the early facilitatory effect of cuing,   In their case, though, the variation in luminance also altered the perceptual quality of the cue (subliminal vs. supraliminal). Here we will explore the effect of cue luminance when the dim cue remains supraliminal. On the other hand Lambert and Shin (2010) presented evidence that luminance plays little role in rapid orienting of attention. In their experiment the spatial cues consisted of two different letters simultaneously presented on both sides of the screen. In order to manipulate attentional orienting one of the two letters was frequently followed by the appearance of the target (a simple square) and participants were informed about this link at the start of the experiment. In addition the two letters were presented at two different levels. Lambert and Shin (2010) reported that participants were faster in detecting the target at the “cued” location (frequent letter – target link). However, this benefit was unaffected by the brightness of the cuing letter. Note that in contrast the identification of the dimmer letter was significantly impaired with lower contrast. Lambert and Shin (2010) argued that these results suggest that different brain pathways are involved in identification and in attentional orienting. However, it is possible the perceptual effect is superseded by the endogenous orienting of attention due to the identification process. The present paper aims to replicate Lambert and Shin’s (2010) using exogenous cuing.

Experiment 2 provided a further test of Wright and Richard’s (2003) suggestion by using simultaneous cues. Here we extended the spatial cuing procedure to four locations to include an uncued condition for performance with dual cues. As in Wright and Richard (2003) we included two equal luminance conditions, a dim-dim condition and a bright-bright condition. Finally we included a new bright-dim condition. According to the biased-competition account, any competition for selection between the cues should be won by the bright cue. As a consequence, there should only be facilitatory cuing at the location of the bright cue and none at the location of the dim cue (RTs to a target at the location of a dim cue should not differ from RTs to targets at uncued locations). However, if there is a perceptual-based facilitation component, the dim cue should still induce a facilitation effect relative to the no-cue baseline, albeit an effect that is smaller than the facilitation from the bright cue. Note that a study by Kean and Lambert (2003) supports the differential effect between brighter and dimmer cue proposed by both hypotheses. They showed that saccadic latencies were faster to targets presented at the location of a bright cue than at the location of a dim cue, when the cues appeared simultaneously. This measures the relative bias between the bright and dim cued locations, but it does not show whether there was facilitation at both locations, since appropriate uncued baseline conditions were not included. In the dual-cue conditions with bright-bright and dim-dim cues, attentional competition should be equal between the cues, with the consequence that cuing should decrease and it should differ little between these two conditions – although, if one of the cues eventually wins the competition then some facilitatory effect may arise[1]. Relative to the bright cue in the bright-dim condition, this facilitatory effect should be smaller and, relative to the dim cue, the facilitatory effect should be larger (since the dim cue should always lose the competition for selection in the bright-dim condition).

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[1] This argument is based on the commonly-made assumption that the luminance contrast between stimuli is reverse proportional to speed of the convergence of the competition. In the equal luminance condition the contrast is solely induced by noise and therefore fairly small. Hence we assume that within the timeline of the early SOAs, competition is not fully resolved in favour of one of the cues.

In addition to examining the effects of cue luminance on early facilitatory cuing, we also evaluated the effects on IOR. Posner and Cohen (1984) argued that IOR is caused by the perceptual processing of the cue. Their suggestion was based on findings under double cue conditions. When double cues were presented, the early cuing effect decreased (consistent with an attentional component to performance). However, there was no evidence for a linked decrease in IOR, as would be the case if IOR stemmed from attentional orienting to the cue (indexed by the early facilitation effect). This assumption has gained further support from the work of Tassinari and colleagues (Tassinari, Agliotti, Chelazzi, Peru & Berlucchi, 1994; Tassinari & Berlucchi, 1993). They found that, even if there is no early facilitation effect, IOR can still be found under some circumstances (see also Danziger, Kingstone, & Snyder, 1998; Enns & Richards, 1997). Additional support comes from the study by Mele et al. (2008). They presented supraliminal and subliminal cues (see above) and found IOR in both cases, though the effect was reduced with the low luminance cues. Evidence for the perceptual account has led to the development of the two component model of IOR (e.g. Klein 2000). According to this model, the biphasic outcome of many cuing experiments (early facilitation followed by later inhibition, for cued relative to uncued locations) results from a combination of facilitation and inhibition. Facilitation and inhibition are assumed to operate independently and both are started by the onset of the cue. At early SOAs the facilitatory process “masks” the inhibitory process leading to detection times being speeded when the cue and target fall at the same location. However at longer SOAs attention is redirected to a different location leaving only inhibitory effects caused by the initial perceptual processing of the cue.

Other evidence however questions the perceptual account of IOR. Maylor (1985) also used a double cue condition and found that, like the early facilitation effect, IOR was reduced compared to a single cue condition Maylor argued that the IOR and early facilitation effects are linked and that IOR is a direct consequence of attending the cued location. Further support for the involvement of attention in IOR arose from the finding that IOR was influenced by secondary tasks (e.g. pursuit eye tracking of a predictable or unpredictably moving dot on the screen). Finally, Klein, Christie and Morris (2005) examined the spatial distribution of IOR in a multiple-cue procedure and found that multiple cues induced an inhibitory gradient centred in the direction of the net vector of the multiple cues. The magnitude of the inhibitory gradient was independent of the number of cues. Again, these findings go against the proposal that there is solely a perceptual cause of IOR (where inhibition should be found at each location where a cue appeared).

This paper tested the perceptual and attentional accounts of IOR. Table 1 lists all predicted outcomes for IOR for the different accounts crossed with the potential outcomes for early SOAs (facilitation). In the following we focus on the most important predictions. For Experiment 1 (single cue conditions), the perceptual account of predicts that IOR should depend on cue luminance, and should be larger for brighter cues. However, if the attentional hypothesis is correct, then the level of IOR should be independent of the cue luminance when only a single cue occurs. For Experiment 2 (dual cues), the perceptual hypothesis predicts (again) that IOR should depend on the level of cue luminance. The attentional hypothesis makes different predictions. In the bright-dim condition, the biased competition hypothesis suggests that attention is directed to the brighter cue. IOR should only be found at bright cued location and no IOR should occur at the location of the dim cue (relative to the no cue baselines). Note that a failure to find IOR at the location of the dim cue may co-occur with evidence for early facilitation at this location, if IOR is attention-dependent and the early facilitation effect reflects a change in perceptual coding following the cue. When the cues have equal luminance, there should be a reduced attentional bias, though one of the cued locations may still be selected. It follows that there should be a reduced IOR effect, even with bright cues, Furthermore, since the competition should be balanced for bright-bright and dim-dim cues, then there should be no increase in facilitation for the bright-bright over the dim-dim cue conditions (contra to the predictions of the perceptual account).

Based on the empirical results from Experiments 1 and 2, we developed a formal biased competition account of selection and attentional cuing in Part 2, to provide a proof of principle analysis of whether a biased competition approach could account for the data.

Comment [S1]: I found this table is difficult to understand

Condition	potential early facilitation effects	Prediction of attentional IOR hypothesis	Prediction of perceptual IOR hypothesis
Exp .1	No luminance effect	No luminance effect	Luminance effect
	Luminance effect	Luminance effect	
Exp.2: same lum. cues	No luminance effect	No luminance effect	Luminance effect
	Luminance effect	Luminance effect	
Exp.2: diff. lum. cues – dimly cued loc.	no facilitation	No IOR	IOR
	facilitation	IOR	

Comment [S2]:

Table 1. The table summarizes the predictions for the IOR-effects (two right columns) for the two experiments. The predictions can depend on the hypothetical causes of IOR (attentional vs. perceptual) and the nature of the early facilitation effect. Note that for the bright cue in the different luminance cue condition in Exp. 2 we expect an IOR-effect in all situations.

Experiment 1: Single cues

The design of this experiment followed closely Posner’s (1980) design. In addition we introduced two levels of cue luminance to examine the influence of this factor on both the early facilitation effect and on inhibition of return. The manipulation of cue brightness here provides a test of whether is a perceptual influence on the level of facilitation and on IOR.

Method

Participants

Twenty-three volunteers, ten females and nine male, 18 to 31 years of age, from the University of Birmingham participated in the experiment. They were either paid or received course credit for their participation in an approximately 25 minute session. All participants reported normal or correct-to-normal vision. All except one were right handed.

Apparatus

Stimulus presentation and data collection were performed using E-Prime 1.1. Stimuli were presented on a 17-inch SAMSUNG monitor controlled by a personal computer and responses were recorded with a standard keyboard.

Stimuli

The stimulus display (see Figure 1) consisted of a fixation cross (0.7˚ × 0.7˚), presented on the centre of the screen, and two outline boxes, aligned horizontally to the left and right of the fixation cross. The distance between the fixation cross and the centre of each box was 8.1˚. Each box extended 4.9˚ in width and 3.6˚ in height. The target was a hash sign (#) with 1.0˚ in width and 1.6˚ in height displayed in the centre of one of the two boxes. All stimuli were presented in white (68.37 cd/m^2) on a black background (4.31 cd/m^2). The thickening of the frame of one box for 150ms served as cue whereby the width of the thickening manipulated the cue luminance. The large luminance increase was a change from 0.05˚ to 0.2˚ frame size and a change from 0.05 to 0.1˚ implemented the small luminance increase cue.

(Figure 1 about here)

Procedure

The experiment was conducted in a quiet room, dimly illuminated with a halogen lamp. Participants were given both written and oral instructions for the task. Sitting at distance of approximately 57 cm from the computer screen participants were instructed to maintain fixation throughout and not to make any eye movements. Eye movements were not monitored, as previous studies showed that participants generally successfully maintain fixation (Castel, Pratt, & Drummond, 2005; Muller & Findlay, 1987; Pratt & Abrams, 1995). Participants were asked to respond to the onset of the target as quickly and as accurately as possible by pressing the space bar on the keyboard in front of them. RT and response were record by the computer. To discourage anticipatory responses, on 11.11% of trials no target appeared. Participants were told to withhold responses on these catch trials. Participants were also told that cues are uninformative about the target's location.

The trial sequence is shown in Figure 1. Each trial began a central fixation cross and two empty peripheral boxes. After 1000ms, one of the boxes thickened for 150ms either to a frame size of 0.2° or to 0.1° (see Gabay & Henik, 2010 for a similar manipulation of cue presentation). After intervals of 50, 250, 500 or 800 ms (the SOAs), the target (#) appeared in the centre of a box. The target remained visible until the participants responded or 3000 ms had elapsed. Detection time was measured from the target onset to response. All factors (cue luminance, cue location, SOA, target location) were randomized and occurred with equal probability.

Comment [S3]: They only manipulated size to present the cues, but not specialise this to luminance (even though they used the term "brightness"). Therefore, I am not sure whether this example is enough.

After the experimenter had ensured that the participants had understood the instructions, the participants completed about 10 practice trials until they were able to perform the task correctly. The responses for these trials were not recorded or analysed. The experiment was divided into three blocks of 180 trials each and participants were encouraged to take a short break after each block.

Design

The experiment consisted of a 2 (luminance: bright/dim) × 2 (cue: cued/uncued) × 4 (SOA: 50/250/500/800 ms) repeated measures design. There was a total of 540 trials, 60 of which were catch trials. The remaining 480 trials were randomised with respect to trial type, with each condition being equally probable. Each of the experimental conditions contained 30 trials.

Data analysis

Trials with responses prior to the onset of the target and with reaction times (RTs) less than 100 ms or greater than 1000 ms were considered as errors and excluded from the analysis. Individual participants were also excluded if either they made an excessive proportion of errors (greater than 10%) or an excessive proportion of false alarms (greater than 15% on catch trials) Following this, trials with RTs above or below three standard deviations (SDs) from a mean of a particular condition were also removed. This procedure was repeated until there was no more trial to be removed (Van Selst & Jolicoeur, 1994).The remaining data were analysed with 2x2x4 within-participants ANOVA and Greenhouse Geisser correction was applied where necessary.

Results

No participants were excluded. The mean error rate was 3.42%. The mean RTs are showed in Figure 2a[2]. A 2 × 2 × 4 within-participants ANOVA was conducted with cue luminance (bright or dim), target location (cued or uncued) and SOA (50 ms, 250 ms, 500 ms or 800 ms) as factors. The main effect of cue luminance was significant ($F(1, 22) = 14.07$, $p < 0.01$). RTs were 5.61 ms faster following bright relative to dim cues. The main effect of SOA was also significant ($F(1.51, 33.16) = 23.52$, $p < 0.001$). No other main effect was reliable. The interaction between cue luminance and SOA was significant ($F(3, 66) = 3.75$, $p < 0.05$) so was the interaction between target location and SOA ($F(3, 66) = 26.12$, $p < 0.001$). The three way interaction between cue luminance, target location and SOA was also significant ($F(3, 66) = 3.35$, $p < 0.05$).

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[2] In this figure and all other figures the error bars were determined by a method proposed by Cousineau (2005). This method adjusts the standard confidence interval for the fact that we used a within-participants design.

The significant main effect of SOA results from the U-shaped relationship between RTs and SOA (see Fig. 2a) and this is a well-documented effect for experiments of this type (e.g. Kean & Lambert, 2003; Niemi & Naatanen, 1981; Posner, 1980). The pattern is usually interpreted as the result of an alertness effect caused by the onset of the cue. At first alertness increases (and RTs decrease) with increasing SOA, as participants have more opportunity to prepare for the appearance of the target. However, at longer SOAs, alertness declines and RTs increase.

(Figure 2 about here)

To exclude this alertness effect from further analyses, we subtracted the RTs in the uncued condition from the RTs in cued condition. This difference characterizes the spatial cuing effect in term of benefits and costs (Fig. 2b) - positive differences indicating facilitation effects (benefits) and negative differences IOR effects (costs).

The RT Benefits/Costs were entered into a 2 (cue luminance: bright/dim) × 4 (SOA: 50/250/500/800 ms) ANOVA. It revealed a significant main effect of SOA ($F(3, 66) = 26.12$, $p < 0.001$) and a significant interaction of cue luminance × SOA ($F(3, 66) = 3.35$, $p < 0.05$). No other effects were reliable. Due to the interaction between cue luminance and SOA, performance was analysed with four planned t-tests comparing the bright luminance condition with the dim luminance condition at each SOA. This analysis revealed a significant effect of cue luminance at SOA 500 ms (t (22) = -2.53, $p < 0.05$) but none at the other SOAs. Further t-tests confirmed that following bright cues, facilitation was obtained at SOA 50 ms ($t(22) = 6.48$, $p < 0.001$) and IOR was obtained at the two long SOAs (500ms: t (22) = -3.13, $p < 0.01$; 800ms: t (22) = -3.27, $p < 0.01$). Following dim cues, facilitation was obtained at SOA 50 ms (t (22) = 3.66, $p < 0.01$) and IOR was obtained at SOA 800ms (t (22) = -3.01, $p < 0.01$) but not at SOA 500 ms ($p = 0.20$). Overall, these results suggest that, at an SOA of 800 ms, both luminance levels generated an IOR-effect of similar size. However and importantly, for a 500ms SOA only the high cue luminance caused IOR. Alongside this, there was a significant difference in the size of cuing effects between the two cue luminance conditions at SOA 500 ms. Hence, the results can be interpreted as IOR being delayed but increased to the same size at a later stage in the low compared to the high luminance cue condition.

Discussion

The experiment examined that influence of cue luminance on spatial cuing. Overall there was evidence for an alertness effect typical for this type of detection task with catch trials (e.g. Kean & Lambert, 2003; Niemi & Naatanen, 1981; Posner, 1980). After removing this alertness effect by calculating the RT Benefits/Costs, the results showed the classical early facilitation effect and a late IOR effect. Interestingly, there was no effect of cue luminance at early or (very) late SOAs. However, the results indicated a late onset of IOR in the dim cue condition compared to the bright cue condition.

The effects of cue luminance on IOR can be interpreted in various ways. One possibility, consistent with the perceptual hypothesis, assumes that the magnitude of IOR will reflect the strength of perceptual processing. If perceptual processing is weak (e.g., with a dim cue) then IOR will be weak and delayed, as we observed. The results could also be accounted for in terms of an attentional orienting, however, if the strength of orienting is greater to a bright than a dim cue. One result against this, however, is that the early facilitation effects did not differ across the different levels of cue brightness, suggesting that orienting to the cue was matched across the brightness conditions. This lack of an effect of cue brightness on the early facilitation effect is also not consistent with the suggestion by Wright and Richard (2003) that facilitation is also influenced by sensory enhancement from the cue. However, as Wright and Richard (2003) suggested, it is possible that the perceptual effect is superseded by the selection of a single winner and only becomes apparent when competition between cues prevents attention from being attracted to either of them. This possibility will be tested in the following experiment where two simultaneous cues are presented.

Experiment 2a: Single cues 4-location

Since the number of potential location (competitors) increases in 4-location than 2-location experiment, dim cue might not sufficient to produce any cueing effects. This experiment aims to replicate the findings in experiment 1 in a 4-location setting. The same cues as in Experiment 1 were used. Two SOA 100 ms and 800 ms were sampled, where both cueing effects were unaffected by cue luminance.

Methods

Participants

Fifteen volunteers, thirteen females and two males, 18 to 22 years of age, from the University of Birmingham, took part. Participants were paid £3 or received course credits for a session of approximately 25 minutes. All participants reported normal or correct-to-normal vision. All except two are right handed.

Apparatus

This was the same as for experiment 1.

Stimuli

The stimulus displays were similar to those in experiment 1, except that there were four boxes on the display (Figure 3). The stimulus display consisted of a fixation cross subtending 0.7˚ × 0.7˚, presented on the centre of the screen, and four outline boxes, aligned to the four corners of the fixation cross. The distance between the fixation and the centre of each box was 7.4˚. Each box subtended 4.9˚ in width and 3.6˚ in height. The target was a hash sign (#) with 1.0˚ in width and 1.6˚ in height displayed in the centre of one of the four boxes.

(Figure 3 about here)

Procedure

The procedure followed very similar to experiment 1, with the following exceptions: the cue presented among those 4 locations instead of 2 locations.

Design

The experiment consisted of a 2 (cue luminance: bright/dim) × 2 (target location: cued/uncued) × 2 (SOA: 100/800 ms) repeated measures design. There were 576 trials, 64 of them catch trials. Whining each luminance and SOA condition, there were 32 cued trials and 96 uncued trials.

Results

The same error and outlier removal procedure was carried out as Experiment 1. One participant who had a high error of 12.70% was excluded. The mean error rate per participant for remaining individuals was 2.40%.

The means of the remaining RTs for each condition are presented in Figure 4a. A 2 × 2 × 2 within-subjects analysis of variance (ANOVA) was conducted with luminance (bright or dim), target location (cued/uncued) and SOA (100 ms or 800 ms) as factors. The main effect of cue luminance was significant (F (1, 13) = 8.69, $p < 0.05$). RTs were 9.87 ms faster in the bright cue condition than in the dim cue condition. No other factor exhibited a significant main effect ($p > 0.05$). In addition, the interaction between target location and SOA was significant (F (1, 13) = 15.85, $p < 0.01$). A 16.11 ms facilitation effect was obtained at SOA 100 ms (t (13) = 4.25, $p < 0.01$), which turned into a 16.33 ms inhibition effect at SOA 800 ms (t (13) = -2.75, $p < 0.05$). No other interaction reached significance ($p > 0.05$).

Discussion

This experiment indicated that both bright and dim cue luminance conditions showed similar early facilitation and late inhibition effects, replicating the findings of Experiment 1 but now using a four-location display.

(Figure 4 about here)

Experiment 2b: Dual cues

Experiment 2b extended Experiment 1 and 2a by introducing simultaneous cuing. There were three luminance conditions: a bright cue paired with a dim cue (bright-dim condition), two bright cues (bright-bright condition) and two dim cues (dim-dim condition). Also two more locations were included. With the four locations it was possible to measure the cuing effect relative to RTs to targets appearing at uncued locations in each condition. As explained in the Introduction these conditions test the influence of perceptual enhancement on the early facilitation effect and IOR.

Method

Participants

Twenty-nine volunteers, twenty-three females and six males, 18 to 28 years of age, from the University of Birmingham participated in the experiment. They received course credits for their participation in an approximately 50 minute session. All participants reported normal or correct-to-normal vision. All except three were right handed.

Apparatus

This was the same as for Experiment 1.

Stimuli

The stimulus display (see Figure 5) consisted of a fixation cross extending 0.7˚ × 0.7˚, presented on the centre of the screen, and four outline boxes, aligned with the four corners of the fixation cross. The luminance of the stimuli was the same as for Experiment 1. The distance between the fixation and the centre of each box was 7.4˚. Each box subtended 4.9˚ in width and 3.6˚ in height. The target was a hash sign (#) with 1.0˚ in width and 1.6˚ in height displayed in the centre of one of the four boxes. As in Experiment 1 the two cue luminances were implemented by thickening the frames of the boxes. The large luminance increase was a change from 0.05˚ to 0.2˚ frame size and a change from 0.05 to 0.1˚

implemented the small luminance increase cue. Two cues were always presented at diagonally opposite locations (Figure 5).

(Figure 5 about here)

Procedure

The procedure was the same as Experiment 1, with the following exceptions: two cues were presented simultaneously rather than one single cue. The cues could either have the same (bright-bright, dim-dim) or different luminance values (bright-dim). Four SOAs were used: 50ms, 250ms, 500ms, 800ms.

Design

The equal luminance condition consisted of a 2 (cue luminance: bright/dim) × 2 (target position: cued/uncued) × 4 (SOA: 50/250/500/800 ms) repeated measures design. The bright-dim condition consisted of a 3 (target position: bright/dim/uncued) × 4 (SOA: 50/250/500/800 ms) repeated measures design. The experiment consisted of a total of 952 trials, half in the bright-dim and half in the equal luminance condition. 56 trials were catch trials. In the remaining trials, cues and targets appeared equally likely at each location (in equal luminance condition levels of each factor were equal but in bright-dim condition the uncued trials were as twice as the cued trials).

Data analysis

The results were analysed in the same as in Experiment 1.

Results

Two participants were excluded, one of which had a high response error rate of 16.07% on catch trials and the other did not follow the instruction and had head movements during the experiment. The mean error rate for the remaining participants was 2.91%.

Bright-dim condition:

Figure 7 shows the mean RTs at each condition for simultaneous bright-dim cues. An ANOVA was conducted with target position (brightly cued, dimly cued or uncued) and SOA (50 ms, 250 ms, 500 ms or 800 ms) as within-subject factors. The main effect of SOA was significant (F (3, 78) = 37.24, $p < 0.001$). The target position × SOA interaction was also significant (F (6, 156) = 11.18, $p < 0.001$). No other effect was significant. As in Experiment 1, the results exhibited a U-shape relationship between RTs and SOA indicating an alertness effect typical for detection tasks with catch trials. In order to eliminate the alertness effect and to extract the spatial cuing effect, the benefits and costs was calculated by subtracting RTs in the uncued conditions from those in the cued conditions.

(Figure 6 about here)

The resulting benefit-costs were analysed with a 2 (luminance: bright/dim) × 4 (SOA: 50/250/500/800 ms) ANOVA (see Figure 6a for the results). The analysis revealed a significant main effect of SOA (F (3, 78) = 8.88, $p < 0.001$) and a significant luminance × SOA interaction (F (3, 78) = 12.86, $p < 0.001$). No other effect was significant. Given the interaction between luminance and SOA, four planned t-tests compared the bright conditions with the dim conditions at each SOA. The results showed that the RTs to cued targets appearing at the location of the bright cue were significantly different compared with those appearing at the location of the dim cue at SOAs 50 ms (t (26) = 3.96, $p < 0.001$), 500 ms (t (26) = -4.45, $p < 0.001$) and 800 ms (t (26) = -3.61, $p < 0.01$). Further one sample t-tests confirmed that there was neither facilitation nor IOR at the location of the dim cue ($p = 0.43$; 0.38; 0.13; 0.16 respectively at each SOA). The bright condition showed a significant facilitation at SOA 50 ms (t (26) = 4.69, $p < 0.001$); IOR at SOA 500 ms (t (26) = -2.64, $p < 0.05$) and IOR at SOA 800 ms (t (26) = -4.06, $p < 0.001$) ($p = 0.66$ at SOA 250 ms).

Equal luminance condition:

Figure 7a shows the mean RTs for each condition for the two equal luminance cues (bright-bright and dim-dim). An ANOVA was conducted with luminance (bright or dim), target location (cue or uncued) and SOA (50 ms, 250 ms, 500 ms or 800 ms) as within-subject factors. The main effect of cue luminance was significant (F (1, 26) = 53.89, $p <$ 0.001), indicating overall that RTs were faster to targets appearing after bright cues (348.49 ms) compared to dim cues (359.05 ms). The main effect of SOA was significant (F (2.2, 57.1) = 44.33, $p < 0.001$). The interactions between target location and SOA (F (3, 78) = 5.81, $p <$ 0.01), and between cue luminance and SOA (F (3, 78) = 7.34, $p < 0.001$) were significant. The cue luminance × target location × SOA interaction was nearly significant (F (3, 78) = 2.30, $p = 0.083$).

(Figure 7 about here)

In order to remove general effects of alertness, the benefits and costs of cuing were calculated (see Figure 7b). These results were analysed with a 2 (cue luminance: bright/dim) × 4 (SOA: 50/250/500/800 ms) ANOVA. The ANOVA revealed a significant main effect of SOA (F (3, 78) = 5.81, $p < 0.01$) and a nearly significant cue luminance × SOA interaction (F (3, 78) = 2.30, $p = 0.083$). 4 paired sample t-tests were compared to contrast effects between bright and dim cues at each SOA and cuing effects were nearly significant at SOA 50 ms and 500 ms (0.066; 0.76; 0.075; 0.42 respectively). Interestingly, the bright condition showed significant effects at SOA 50 ms (t (26) = 3.28, $p < 0.01$) and 500 ms (t (26) = -2.74, $p < 0.05$), but not at SOA 250 ms and 800 ms (0.50; 0.26 respectively). The dim condition did not show any significant effect at any SOA (p = 0.18; 0.32; 0.63; 0.95 respectively).

Comparison between bright-dim cue and equal luminance cues

To explore the relationship between the bright-dim cuing condition and the equal luminance cuing condition, we analyzed the cuing effect in these conditions with a three-way ANOVA. The factors were cue luminance (dim vs. bright), SOA and cue type (same luminance, different luminance). The analysis showed a significant main effect of SOA (F (2.5, 64.4) = 12.91, $p < 0.001$) as was the interaction between cue luminance and SOA (F (3,

78) = 8.55, $p < 0.001$). There was neither significant cue type main effect nor any interaction with cue type. Given the interaction between cue luminance and SOA, four paired sample *t*-tests were compared to the bright with the dim conditions at each SOA. Cuing effects from bright cues differed from those with the dim cues at SOA 50 ms (t (26) = 3.70, $p < 0.01$) and 500 ms (t (26) = -4.38, $p < 0.001$) ($p = 0.97$ at SOA 250 ms and $p = 0.68$ at 800 ms). In a one sample t-test, the bright cue showed significant effects at SOA 50 ms (t (26) = 4.89, $p < 0.001$), SOA 500 ms (t (26) = -4.15, $p < 0.001$) and SOA 800 ms (t (26) = -2.93, $p < 0.01$). The dim cue did not show any significant effects in one-sample t-tests.

Note that this analysis is statistically more powerful than the analysis of the equal luminance. Hence the significant effect of the bright cue is more reliable and suggests that the lack of significance (or borderline significance) in the equal luminance condition due to the lack of power.

Comparison with Experiment 1

A further analysis compared the cuing effects of the bright cue in the bright-dim condition with the cuing effects of the bright single cue condition in Experiment 1. Only SOA was significant (F (3, 144) = 43.13, $p < 0.001$). Hence, cuing effects did not differ for the bright cue in the bright-dim condition relative to those for the single bright cue (Experiment 1). A similar analysis also compared the cuing effects of the bright cue in the bright-bright condition with the cuing effects of the bright single condition in Experiment 1. SOA was significant (*F* (3, 144) = 27.48, $p < 0.001$) and the experiment × SOA interaction was also significant (*F* (3, 144) = 2.96, $p < 0.05$). However, the paired sample t-tests at each SOA did not reveal significant effects. Nevertheless, an inspection of the two cueing effects (Fig. 2b vs. 7b) shows that facilitation and inhibition in the dual cue condition are slightly less pronounced than in the single cue condition.

An analysis compared the dim cue bright-dim condition with the dim single cue condition in Experiment 1. SOA was significant (*F* (2.5, 120.8) = 6.90, $p < 0.001$) and the experiment × SOA interaction was also significant (*F* (3, 144) = 3.94, $p < 0.05$). An analysis also compared the dim cue dim-dim condition with the dim single condition in Experiment 1. SOA was significant (*F* (3, 144) = 5.56, $p < 0.01$) and the experiment × SOA interaction was also significant (*F* (3, 144) = 2.77, $p < 0.05$). Note that these results were expected as Experiment 1 shows a cuing effect for the dim cue whereas Experiment 2b shows not cuing effect.

Discussion

The results showed that the bright-bright condition led to a similar cuing effect (early facilitation and late IOR) as the single cue condition with cues of the same luminance (in Experiment 1). However and surprisingly, the dim-dim condition did not show any cuing effect, contradicting results with single cues of the same luminance where there were cuing effects (Experiment 1). The bright-dim condition also did not show a cuing effect for targets presented at the location of the dim luminance cue, whereas there was a cuing effect for the detection of targets appearing at the location of the bright cue.

The results are difficult to reconcile with Wright and Richard's (2003) suggestion that the facilitation effect is based on a combination of a perceptual and attentional component, as no effects at dimly cued locations were found, in neither the bright-dim condition nor the dim-dim condition - despite the fact that the dim single cue produced a cuing effect in Experiment 1) (see also the pilot study of Experiment 2). This is particularly striking at the short SOA, where our experimental procedure is perhaps closest to that of Wright and Richard's (2003) procedure. The results in the bright-dim condition favour the biased-competition hypothesis without any apparent contribution from sensory enhancement. According to the biased competition hypothesis the two cues compete for selection, with the bright cue winning. Consequently, the bright luminance cue leads to an early facilitation whereas the dim luminance cue does not affect target detection, and hence should not differ from the no-cue condition (as we observed). Similarly the IOR-effect the results favour an attentional explanation over a perceptual account as the IOR-effect only occurs in conditions where facilitation was also found (with bright cues). Moreover the fact that the bright-bright condition showed an IOR-effect is not consistent with Wright and Richard's (2003) suggestion that facilitation in this condition is only due to perceptual process enhancement. Instead our results favour the findings by Maylor (1985) where equal luminance cues attract still some attention.

However, it is less clear how to interpret some of the other results - notably performance in the equal luminance cue conditions at the short SOAs. Why does the bright-bright condition lead to a cuing effect and not the dim-dim condition? Note that there were facilitation effects at both luminance levels in the single cue condition. In Part 2 of the paper we present a computational implementation of the biased competition account, to examine whether this is capable of explaining this puzzling data pattern.

Comment [DH4]: I am deleting this paragraph because it pre-empts the simulation results thereby contributing to the reviewers' opinion that the modelling does not add to the understanding of the effect.

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Part 2: A computational model of biased selection

To assess whether the results could be accounted for in terms of biased competition, a computational model based on the biased competition theory of attention is present this part of the paper. We based the present instantiation of the biased competition theory on a model proposed by Wilson and Cowan (1972). The core assumption of this approach is that spiking-rates of simulated neurons are sufficient to capture neural information processing (see chapters in Heinke, & Mavritsaki, 2009; for further discussions on different abstraction levels in computational modelling). We sought to assess if there was a qualitative match between the empirical data and effects of cue luminance and SOA in a model reflecting biased competition for selection. Also note that with this modelling effort we aim to explain our data with concepts that have been already used to explain a broad range of evidence on visual attention (see Deco & Zihl, 2001; Heinke & Humphreys, 2003; Mavritsaki et al., 2011; Heinke & Backhaus, 2011; for examples). In other words the current model has already been supported by many other experimental evidences and does not represent a model specifically implemented for the current data. Therefore the current model is part of an attempt to develop a unifying theory of visual attention.

The model focused on the following results:

1) In Experiment 1 (single cues at two locations) the early facilitation effect was independent of cue luminance. However the onset of the IOR was delayed in the dim cue condition compared to the bright cue condition.

2) In Experiment 2 only bright cues, either in the equal luminance condition or the different luminance condition, produced both facilitation and inhibition effects.

3) The effects with bright, single cues (Experiment 1) were similar to bright double cues (Experiment 2).

(Figure 8 about here)

(Figure 9 about here)

The Model

Figures 8 and 9 illustrate the structure of the model (see the Appendix for the mathematical details). Central to the model is the Wilson & Cowan (W&C)-circuit (Fig. 10; Wilson & Cowan, 1972). The structure of the W&C-circuit consists of a layer of neurons. The behaviour of the neurons is described through non-linear dynamical equations derived from a mean-field approximation of neural populations (see Amitt & Tsodyks, 1991; for details). To adapt the model to the spatial cuing experiment here, the neurons were assumed to represent the spatial locations in the experimental set-up. The connections within the W&C-layer include a global inhibitory feedback loop and an excitatory feedback loop at the level of individual neurons (see Fig. 8). Crucially, this global inhibition represents an implementation of the biased competition theory (see Deco & Zihl, 2001; Heinke & Humphreys, 2003; Mavritsaki et al., 2011; Heinke & Backhaus, 2011; for examples) and should not be confused with the inhibitory signal realising the IOR-effect.

In this paragraph we will give an overview of the model and in the following paragraph we discuss how the model relates to the experimental data found in Experiment 1 and 2. The model is constructed from two modules (see Fig. 9), the selection network and the IOR network. The selection network is based on a single W&C-layer receiving input directly from the cue and target stimuli. The network simulates how spatial selection is modulated by cuing. The magnitude of output activation is considered to inversely correlate with RTs for target detection - the higher the output activation the shorter the RTs. The output of the selection network feeds into the IOR network. The IOR network is made up of two W&C-layers. The first layer operates as memory layer to store selected locations. The second layer generates an inhibitory signal for attended locations and a facilitation signal for unattended locations. The output of the second layer feeds back to the input of the selection network in an inhibitory way. In order to realize the commonly-found delay of the IOR-onset, the feedback signal from the IOR network is delayed. Also it is important to note that the division of the IOR module into a memory layer and an inhibition layer is of merely technical importance in this paper and exploring this two-layer IOR network experimentally goes beyond the scope of this paper.

The selection network represents an implementation of the biased-competition theory for the spatial cuing experiments presented in this paper. The competition process in this network mimics the spatial selection process. It presumes that the higher the output activation of an individual neuron is, the more likely it is that the corresponding location will win the competition for selection. Consequently, the efficiency of detecting the target increases with increasing output activation which, in turn, is related to participants' reaction times. The competition process can be biased through the two inputs, the cuing signals and the inhibitory signal generated in the IOR network. In other words, the inhibitory signal is crucially dependent on the first layer "attending" to (selecting) the cue. Hence, the architecture of the model follows Maylor's (1985) proposal and corroborated by our data that IOR is linked to attending to a cued location. Hence, the model cannot simulate experimental findings where IOR occurs independently of any early facilitation effects. In the General Discussion we will return to this point and discuss possible ways of generalizing the model.

Finally, it is important to note that the model only focuses on the spatial selection process and does not implement the process of discriminating targets from distractors or response generation (see Heinke & Humphreys, 2003; Heinke & Backhaus, 2011 for computational models where target discrimination is considered). This is justifiable as the spatial cuing characteristics represent a crucial manipulation in the current experiments whereas target detection and response generation can be assumed not to be directly affected by the different cuing conditions. Another crucial manipulation in the experiments is the variation of SOA. This is modelled through the simulated time. The thinking behind this approach is that the time course of output activation relates to the time course of the efficiency of target detection (reaction times) and the presentation of the target allows the experimenter to take a snapshot as the efficiency of responding (the output activation) varies.

Method

The parameters and the mathematical details of the model can be found in the Appendix. Depending on the number of locations simulated the model consisted of two or four neurons in each layer (cf. Experiments 1 and 2 here). Most parameters were the same across all simulations. However, some small changes were necessary to ensure successful behaviour with the different numbers of locations (see the Appendix). The duration of the input signals mimicked the presentation time of the cuing signals in the experiments. Bright and dim cues were simulated by varying the magnitude of the input into the initial W&C layer. As discussed earlier, the output activation of the selection layer is related to reaction times: The higher the output activation, the faster the reaction time. Also as discussed earlier, the simulated time relates to SOA.

(Figure 10 about here)

Simulation results and discussion for Experiment 1

Figure 10 shows the simulated time course of “selection” (output of the selection network) for Experiment 1. The top graph depicts the outcome for the bright single cue with gray lines and gray markers and the result with the dim single cue in black lines and black markers. For the sake of clarity the bottom graph depicts the results as a cuing effect. Here the black line represents the outcome for the bright cue and the gray line shows the simulation result for the bright cue. The simulation results show that very early on following the cue, the bright and dim cues produced different activations. However, this difference disappears and the conditions do not vary subsequently until the inhibitory signal from the IOR-network reaches the selection network and, subsequently, activity decreases (between 200ms and 250ms in the present simulations). On the other hand there is no activation at the uncued location (activation remains at floor). Within the model, the facilitation for cued over uncued locations occurs because, at short SOAs, the target benefits from the activation states established by the cue. This is an example of the selection account of facilitatory cuing (see the Introduction). This simulation result mimics the experimental finding that there is at most only a small effect of cue luminance on the early facilitation effect. However, the simulations also indicate that at very short SOAs it may have been possible to find an effect of cue luminance. In empirical studies, this may be difficult to detect due to the influence of other factors such as forward masking.

For longer SOAs, the simulations again mimic the experimental findings. The reduction of activation at cued locations and the subsequent increase of activation at the uncued location corresponds to the onset of IOR. This is also reflected by a negative cuing effect. As with the facilitatory effects of cuing, the simulations show no luminance effect on the size of IOR - again matching the current experimental findings. However, interestingly, the onset of IOR was delayed in the dim cue simulations compared to the bright cue simulations. This results from the fact that the output activation of the selection network is slightly delayed when the cue is dim. This delay is picked up by the IOR-network and, in turn, produces a delayed IOR-onset. In other words, the model explains the delayed IOR-onset as an indirect consequence of a cue luminance effect on the selection stage.

Even though critical outcomes are mimicked by the model the overall temporal behaviour of the model is fairly "binary" whereas the human participants show a more smooth transition from facilitation to inhibition. However, it is possible that the processes not taken into account in the model, such as target discrimination and response selection, lead to a smoothing of the transition.

(Figure 11 about here)

Simulation results and discussion for Experiment 2

Simulations of the data from Experiment 2 used four locations rather than two (cf. Experiment 1). Figure 11 confirms that the simulations with a single cue with four potential target locations still showed no luminance effect. Figures 12 and 13 document the simulation results with double cues.

(Figure 12 about here)

Figure 15 shows that the model mimics the experimental results for the bright-dim condition. Here inhibition in the W&C-layer suppresses neurons with smaller input activation values, generating ‘winner take all’ behaviour in the bright-dim condition. Due to weak activation following a dim cue, neither early facilitation nor later IOR effects emerge. Interestingly, Figure 16 demonstrates that the model can also simulate the results of the equal luminance cuing conditions. In order to understand this, it is important to know that, in this situation, the final states of the neurons in the W&C-layer depend on two factors (see the Appendix): the size of the input activation and the strength of global inhibition. If the input activation is sufficiently large compared to the global inhibition, the global inhibition cannot prevent activation from occurring at more than one location. As a consequence, there is cuing at more than one location in the bright-bright condition. In contrast, if the input activation is small in comparison to global inhibition, and two inputs are active, the global inhibition prevents both neurons from generating output activation. The consequence is that there is no cuing effect from two dim cues. This provides an existence proof that the effects of equal cue luminance can be simulated using a ‘pure’ biased competition approach.

(Figure 13 about here)

General Discussion

This paper aimed to advance our understanding of the mechanisms underlying attentional orienting as assessed in the classical spatial cuing procedure (Posner, 1980). Most current accounts assume that attentional orienting is implemented in the brain as a competitive process, as outlined by the biased competition theory of attention (Chelazzi, Miller, Duncan, & Desimone, 1993; Desimone & Duncan, 1995; Duncan, 2006; Duncan, Humphreys, & Ward, 1997; Heinke & Humphreys, 2003). Within the framework of this theory, spatial cues exert a location-specific bias into the competitive processes in the brain. When there is a short SOA between a cue and a target, this bias facilitates the selection at the cued location – the early facilitation effect. However, at long SOAs IOR is observed at cued locations (Posner & Cohen, 1984). To explain this, an additional inhibitory signal is typically assumed to occur, biasing the competition away from cued locations. This inhibitory bias will enable unattended locations to be selected. On one account, this inhibitory signal is automatically generated after perceptual processing of the cue (based on findings that IOR can occur without the early facilitation effect; Tassinari et al., 1994; Tassinari & Berlucchi, 1993; Danziger et al., 1998 ; Enns & Richards, 1997; Mele et al., 2008). A second hypothesis suggests that the IOR is a consequence of attending to cued locations (e.g. Maylor, 1985), and the bias only sets-in once the orienting response has taken place.

Experiment 1 here assessed whether cue luminance influences the spatial bias, responsible for the facilitation effect at short SOAs. There was no evidence for a cue luminance effect on the early facilitation effect. This is consistent with attention being drawn equally efficiently to bright and dim cues (see also Lambert & Shin, 2010 for supporting evidence). For IOR, there was evidence of a delay in inhibition with a dim cue, although the magnitude of the IOR cost did not vary when SOA was longer (800 ms). Given that the early facilitation effect was equally large for bright and dim cues, the lack of a cue brightness effect on the magnitude of IOR could be accommodated by an attentional orienting account – attention is drawn to each cue type equally effectively, and this in turn leads to equally ‘deep’ IOR effects. On the other hand, the perceptual account would suppose that any weaker perceptual processing of the dim cue would lead to IOR that is reduced in magnitude. This was not observed. However, we did find that IOR was relatively delayed for dim cues. We return to discuss the data on delaying the IOR effects when we discuss the computational model of biased competition.

Experiment 2 explored the nature of the spatial bias and the IOR-effect under double cue conditions. To include an appropriate baseline for this cuing condition, the experimental set-up was extended from two locations to four. This allowed facilitation and IOR to be measured against performance when the target appeared at uncued locations. A pilot study showed that the single cue data from Experiment 1 could be replicated when targets and cues could appear at four locations. However, under dual cue conditions, cue luminance modulated performance. When a bright cue was paired with a dim cue (bright-dim condition), RTs were facilitated if targets fell at the location of the bright cue (at short SOAs), but there were no differences in RTs to targets at the location of dim cues and those to targets at uncued locations. When the cues were both bright (the bright-bright condition) targets falling at these locations were again facilitated, and this was followed by IOR for the cued locations. In contrast, there was no evidence for any cuing effect (neither facilitation nor inhibition) when two dim cues were presented. Performance in the bright-dim condition fits an account explaining IOR in terms of attentional orienting, since IOR only occurred for locations where the ‘winning’ attentional cue was presented (the location of the bright cue)(see Maylor, 1985). However, the data from the double cue conditions fits less easily with this account unless there is allocation of attention to more than one location with bright cued. Effects with two dim cues, though, are less easy to explain.

To account for these results a computational model was developed based on the biased competition hypothesis of attention (for similar models see Deco & Zihl, 2001; Heinke & Humphreys, 2003; Mavritsaki et al., 2011; Heinke & Backhaus, 2011). The model postulates that spatial selection is implemented by competition between location-coded neurons in a “selection network”, with this competition being implemented by inhibitory connections between neurons representing these locations. This inhibition should not be confused with the inhibition implementing the IOR-effect. The model assumes that spatial cues bias spatial competition for selection immediately from the onset of the cues. With single cues and a short cue-target SOA there is facilitated processing because the initial activation from the cue pushes the network into a state that benefits processing when the subsequent target appears at the cued location. This is equally effective for bright and dim cues, so there are minimal effects of single cue luminance on the early facilitation effect. Importantly this also simulates the results from the bright-dim condition where bright cues win the competition (generating an early facilitation effect) and suppress the selection of the location occupied by the dim cue (so no facilitation effect occurs). Interestingly, performance under equal luminance cue conditions depends on the setting of input activation in relation to global inhibition. When input activation is sufficiently strong (e.g., with bright cues), the tendency for global inhibition to generate a winner-take-all effect can be overridden and there is activation of both locations occupied by bright cues. However, in the dim-dim condition the inhibition between the two locations is enough to suppress the activation from both cues, with the result that no cuing effect is elicited. This implementation of the biased-competition model suggests that the current findings can result from the relationship between spatial inhibition and cue luminance. This explanation also suggests a resolution of an apparent contradiction between the current results and those of Maylor (1985). Maylor (1985) reported that her double cue condition resulted in less facilitation than the single cue condition. In contrast here there appeared to be either full cuing effects (2 bright cues) or no effect (2 dim cues). It is possible that, in prior results showing intermediate effects, the brightness of the cues might have generated some activation over above the levels of global inhibition, though not sufficient to generate the maximum effects found with bright cues. Finally, also note there is an alternative way of reconciling the results from Experiment 2a and 2b.[3] It is possible participants adapt to a certain level of cue luminance, especially in situations where dim and bright cues appear inter-mixed. In this case (Experiment 2b) the threshold for dim cue may be increased, preventing them from a generating a cuing effect. However, we would argue that this explanation is less parsimonious than our model as the model explains Experiment 2a and 2b with the same parameter setting. Nevertheless we concede that this explanation cannot be ruled out from our results and future experiments need to test this hypothesis.

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[3] We would like to thank Herman Mueller for this suggestion.

It is not entirely clear how to reconcile our findings with Wright & Richard's (2003) study. Experiment 1 does not contradict their findings as they demonstrated a luminance effect for multiple-cue conditions. However in Experiment 2 we used multiple cues and we still not found a luminance-based facilitation effect. There are at least two possible explanations. Their design used four cues with eight possible locations. This may have increased the competition effects and resulted in a stronger contribution of cue luminance to facilitation. Alternatively, our computational model suggests that the level of cue luminance relative to the competition plays a crucial role. In their design they used lower luminance levels together with four cues. Again this may have led to no winners attracting attention and subsequently unmasked a luminance effect. Future research would need to explore these possibilities in more detail.

Our second line of enquiry focused on IOR. In the IOR-literature there are at least two hypotheses about the source of IOR. At present there is a consensus that IOR is directly initiated by perceptual processes related to the cue (Tassinari et al., 1994; Tassinari & Berlucchi, 1993; Danziger et al., 1998; Enns & Richards, 1997; Mele et al., 2008) and not the consequence of attending a cued location (e.g. Maylor, 1985). However, the present results are more consistent with the attentional account of IOR than with the perceptual hypothesis. This conclusion is based on the fact that facilitation and IOR in Experiment 2 were strongly connected. This interpretation also informed the structure of the computational model. In the computational model the IOR-effect is generated through an IOR-network that biases competitive selection away from cued locations. The input into the IOR-network is provided by the selection network. Hence the IOR-network generates only IOR to locations that have been attended to by the selection network. Interestingly, this structure also allowed us to simulate the delayed onset of IOR found in Experiment 1. The simulations also showed that, even with single cues, there could be a cue luminance effect on the early facilitation effect at very short SOAs – though this dependency is difficult to detect experimentally as, at short SOAs, masking would hide this effect. The delayed IOR effects can be thought of as resulting from "echoes" of this luminance effect, since this delayed onset in the selection network is passed onto the IOR-network which in turn generates a delayed IOR-signal for selection network.

The question remains on how our results can be reconciled with the perceptual account of IOR. On this view, the perceptual IOR effect runs parallel to attentional effects from the cue. This attentional effect initially "masks" the inhibition and the inhibition is only revealed at later SOAs (the two component model, e.g. Klein 2000). This assumption could be implemented by restructuring our computational model. In this new model the IOR-network would run in parallel to the selection network and it would receive the sensory input directly. The output of the IOR-network could inhibit the output of the selection layer. Now in order to simulate our experimental findings, the IOR-network would have to duplicate the behaviour of the selection layer, e.g. no inhibition in the dim-dim condition. Because of this duplication this alternative structure was rejected, as it is less parsimonious than the model presented here and also the focus here was on simulating the current experimental findings. However, it is not inevitable that operations in the brain are restricted to a parsimonious structure. For instance, years of brain evolution could have resulted in duplications of functionalities (see Heinke & Mavritsaki, 2009; for more discussions). Moreover and importantly, the redundant-network approach could implement most elements of the standard view on IOR. Hence, it is possible to simulate early onset of IOR (Tassinari et al. 1994; Tassinari & Berlucchi, 1993) by giving the IOR-network slightly different properties to the selection layer. Moreover, the model may be applied to simulate evidence that the onset of IOR is not hard-wired. For instance, some studies (Cheal & Chastain, 2002; Lupianez et al., 1997; Lupianez & Milliken, 1999; Lupianez et al., 2001) have found that the time course of cuing effects depends on task difficulty, with the onset of IOR occurring earlier in simple detection than in more complex discrimination and identification tasks. Future work will need to look at ways of integrating these factors into the IOR-network.

A final point to note is that the current evidence for maximum cuing in the double cuing condition with bright cues fits with the argument that attention can be allocated to more than one location (e.g. Awh & Pashler, 2000; Kramer & Hahn, 1995). According to the computational account put forward here, whether there is divided attention to multiple locations for focused attention at one location is determined by the strength of the stimulus and the level of global inhibition. It will be interesting to explore whether this general explanatory framework can accommodate the different patterns of data on divided and focused attention.

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Figure Captions

Figure 1. Trial sequence used in Experiment 1. After fixation, one of the peripheral cues was presented with large luminance increase or small luminance increase cue for 150 ms. After a variable length of SOA, the target was presented randomly at either the left or right the location. Note that in the actual experiment, the black and white portions of this figure were reversed.

Figure 2. Results of Experiment 1. (a) Mean reaction times (b) cuing effects.

Figure 3. Trial sequence used in experiment 2a. After the fixation, one of 4 boxes presented with large or small cue for 150 ms. After variant SOAs, the target presented randomly at either of the 4 location. Note that in the actual experiment, the black and white portions of this figure were reversed.

Figure 4. Trial sequence used in Experiment 2. After fixation, two of the boxes were brightened with either a bright or dim cue for 150 ms. After various SOAs, the target was

presented randomly at any of the 4 locations. Note that in the actual experiment, the black and white portions of this figure were reversed.

Figure 5. Results of Experiment 2a.

Figure 6. Results of Experiment 2b for the bright-dim conditions. (a) reaction times (b) cuing effects

Figure 7 Results of Experiment 2b for the equal luminance cuing conditions. (a) reaction times (b) cuing effects

Figure 8 The Wilson&Cowan (W&C)-circuit (Wilson & Cowan, 1972). The W&C-circuit is central to the computational model presented here. It consists of a layer of neurons. The connections within the W&C-layer are designed to produce global inhibitory feedback and excitatory feedback at each individual neuron.

Figure 9. Architecture of the computational model.

Figure 10. Simulations of Experiment 1. The simulated time corresponds to SOA in the experiments. Since the output activation does not change after 400 ms, only shorter SOAs are shown. Figure (a) shows the output activation of the selection network. The output activation is related inversely to RTs. Figure (b) shows the difference between the activation at the cued location and at the uncued location, i.e. the cuing effect.

Figure 14. Simulation result for Experiment 2a – with single cues either bright or dim. Since the output activation does not change after 300 ms, only shorter SOAs are shown. Figure (b) shows the difference between the activation at the cued location and at the uncued location, i.e. the cuing effect.

Figure 15. Simulation result for Experiment 2b – bright-dim condition. (a) Since the output activation does not change after 300 ms, only shorter SOAs are shown. Figure (b) shows the difference between the activation at the cued location and at the uncued location, i.e. the cuing effect.

Figure 16. Simulation result for Experiment 2b – bright-bright condition and dim-dim condition. Since the output activation does not change after 300 ms, only shorter SOAs are shown.

Figure 1

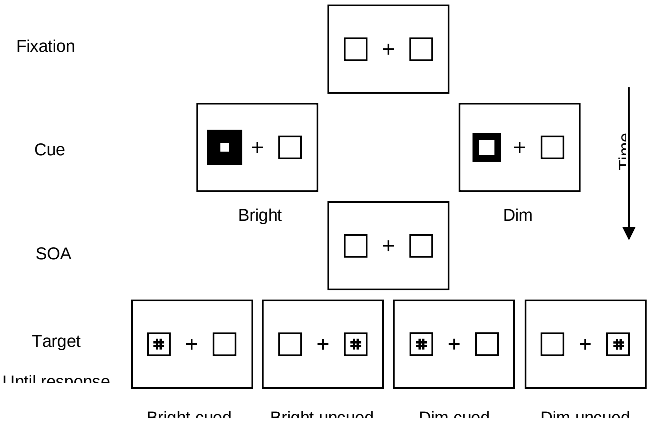

Fixation
Cue
Bright
Dim
Time
SOA
Target
Until response
Bright cued
Bright uncued
Dim cued
Dim uncued

Figure 2 a)

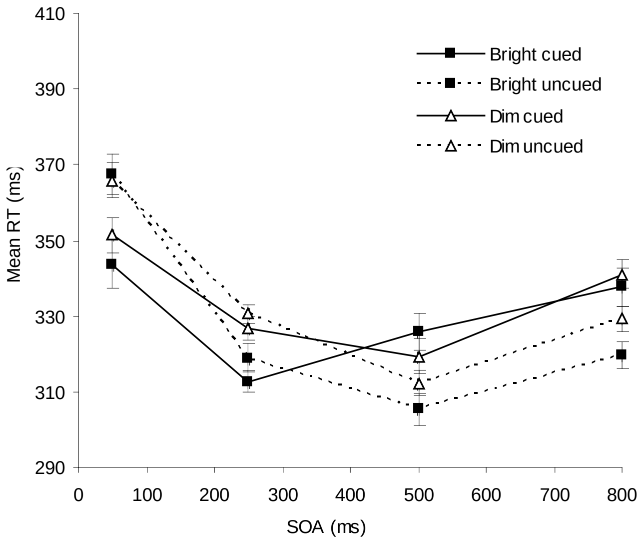


Figure 2 b)

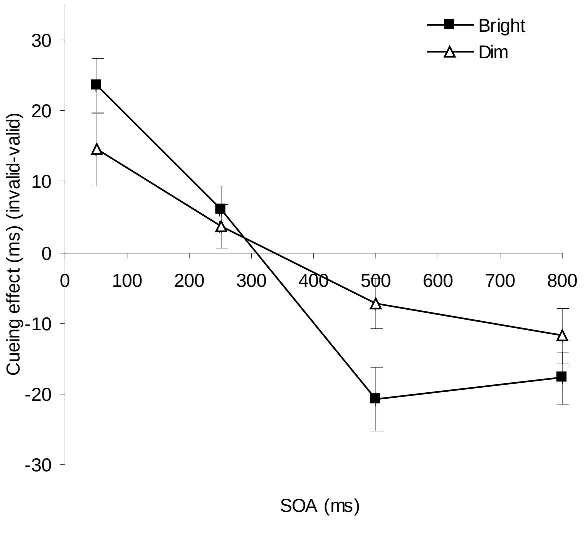


Figure 3

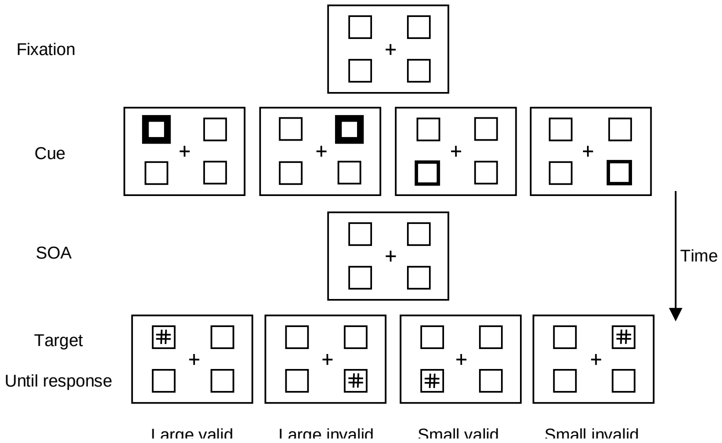
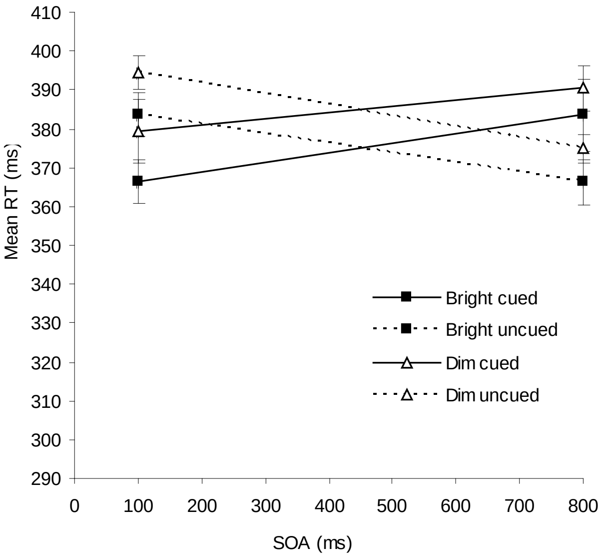

Fixation
Cue
SOA
Time
Target
Until response
Large valid
Large invalid
Small valid
Small invalid

Figure 4



Mean RT (ms)
410
400
390
380
370
360
350
340
330
320
310
300
290
0
100
200
300
400
500
600
700
800
SOA (ms)
Bright cued
Bright uncued
Dim cued
Dim uncued

Figure 5

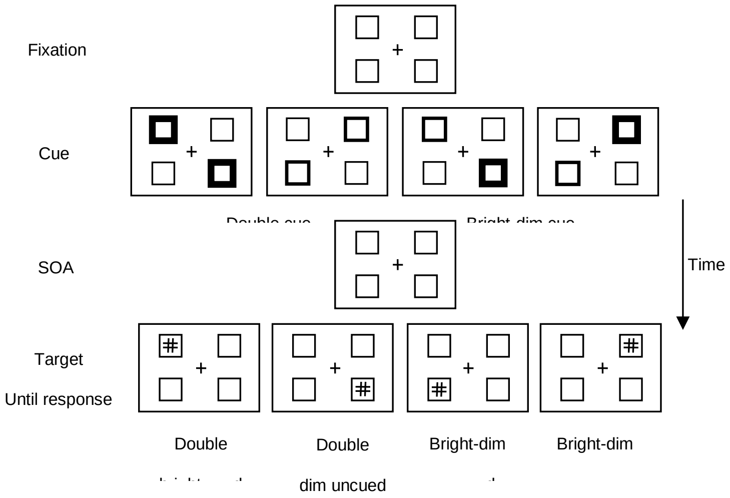

Fixation
Cue
SOA
Target
Until response
Time
Double
Double
dim uncued
Bright-dim
Bright-dim

Figure 6 a)

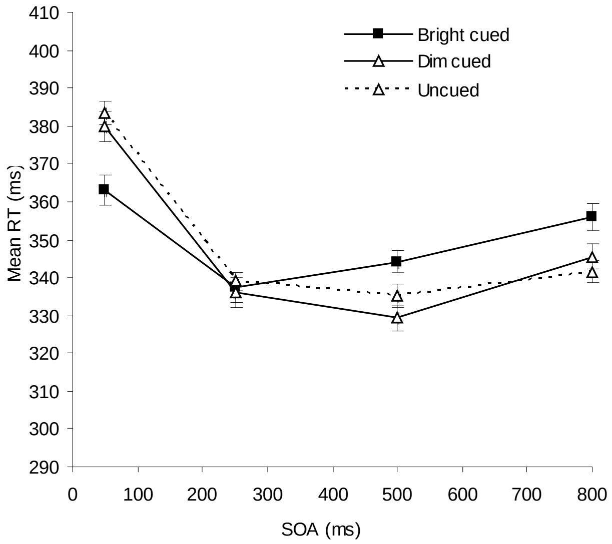


Figure 6 b)

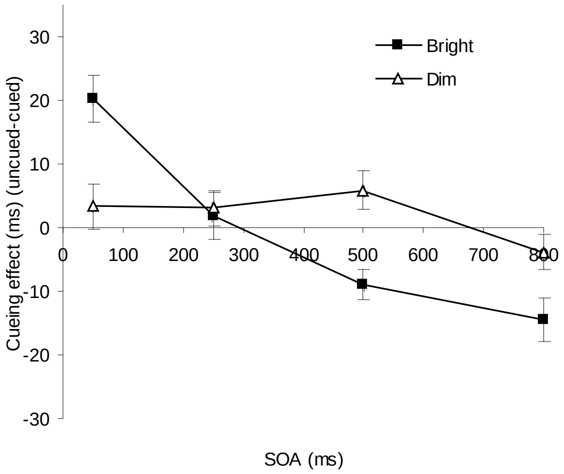


Figure 7 a)

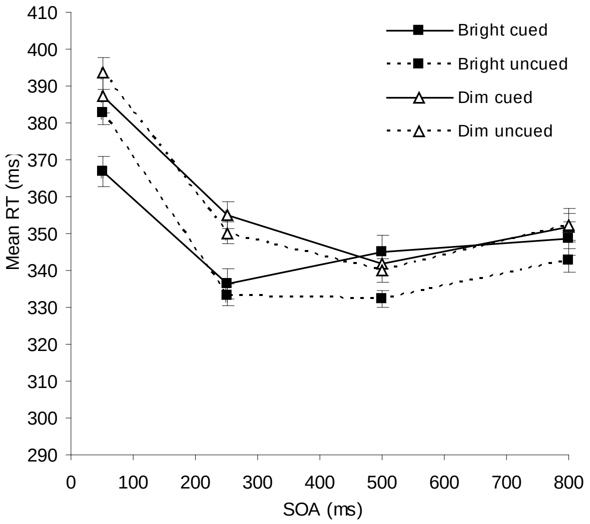


Figure 7 b)

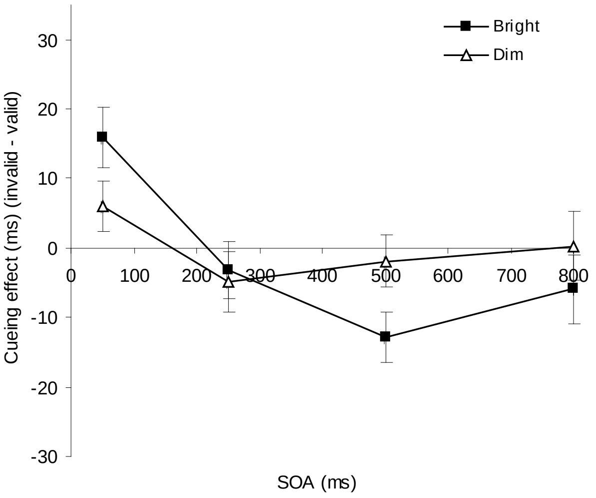


Figure 8

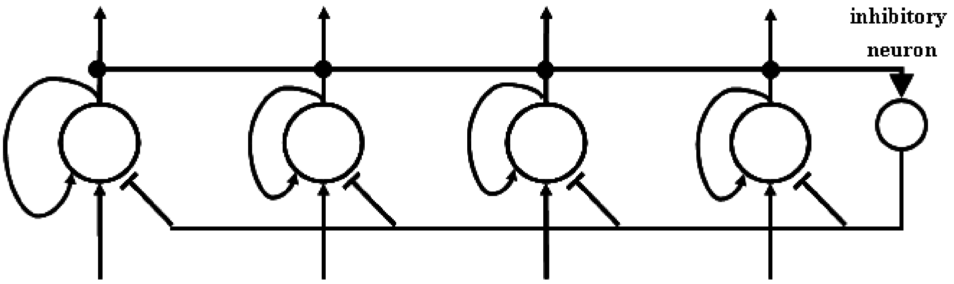


Figure 9

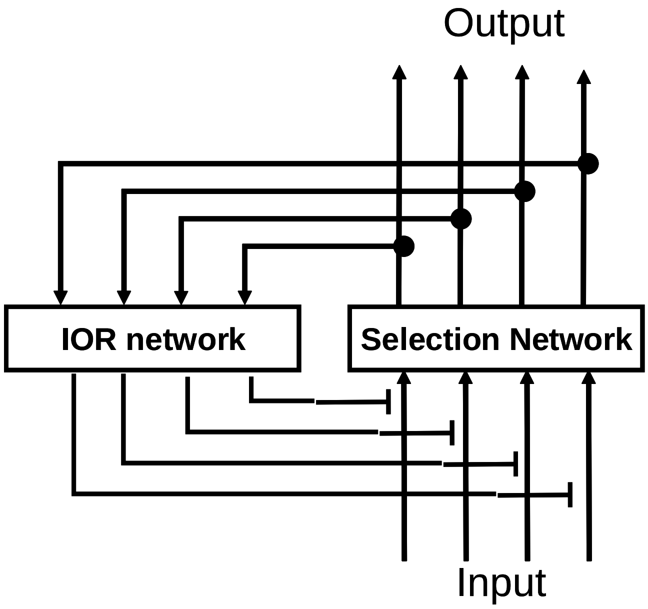
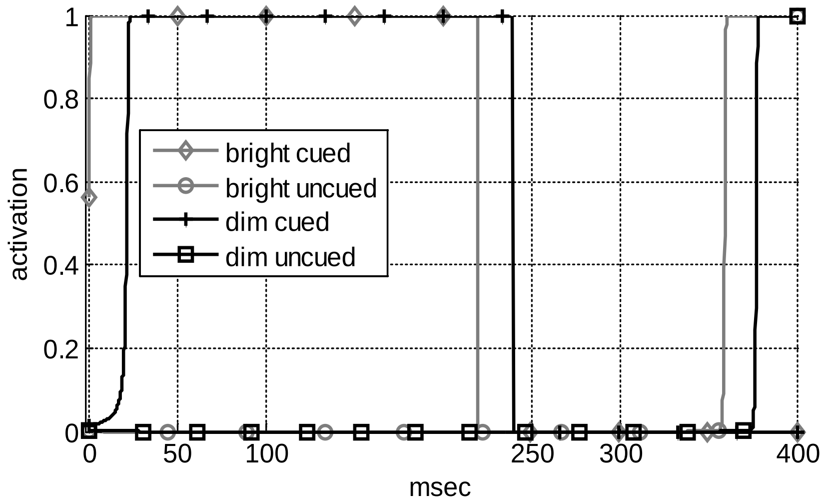


Figure 10 a)



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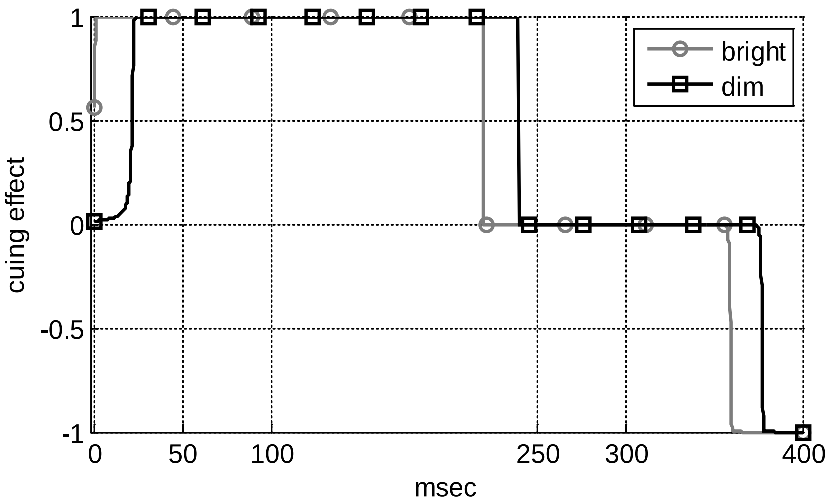

Figure 11 a)

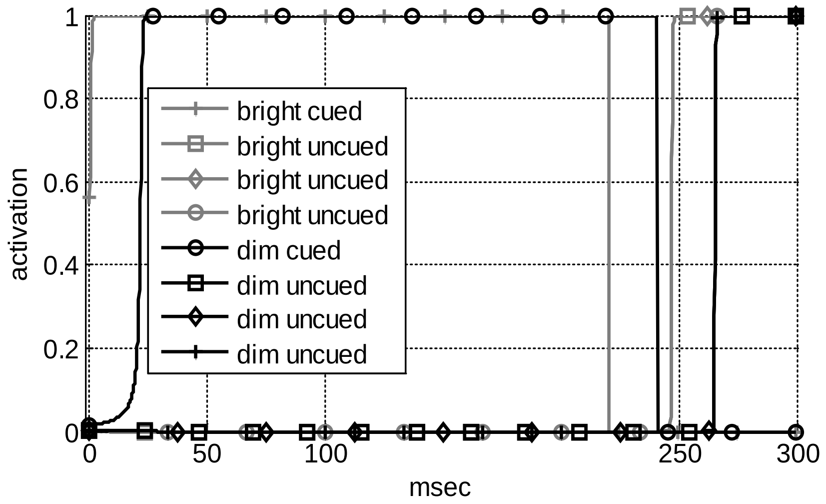

Figure 11 b)

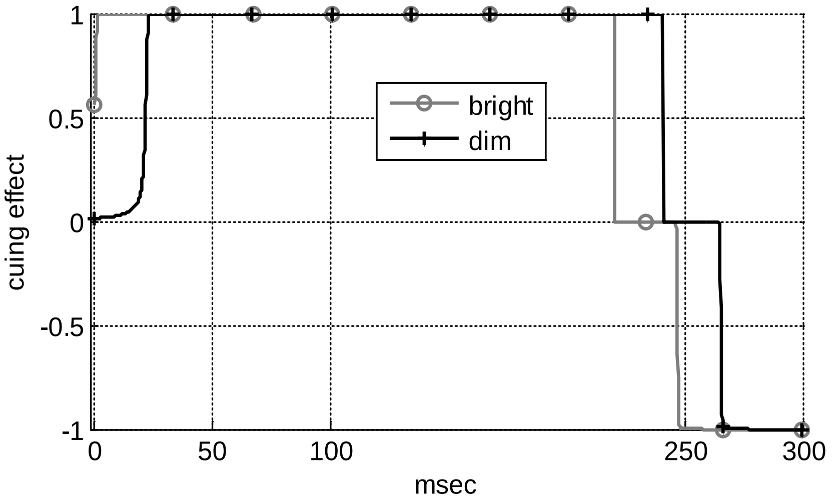

Figure 12 a)

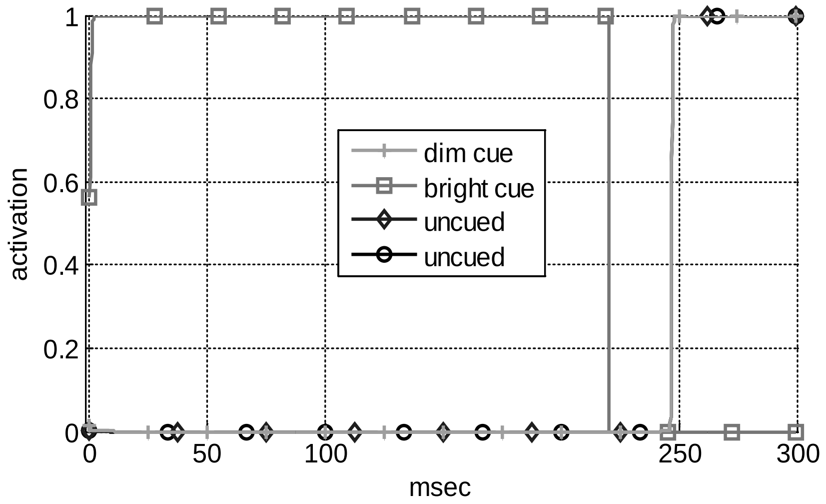

Figure 12 b)

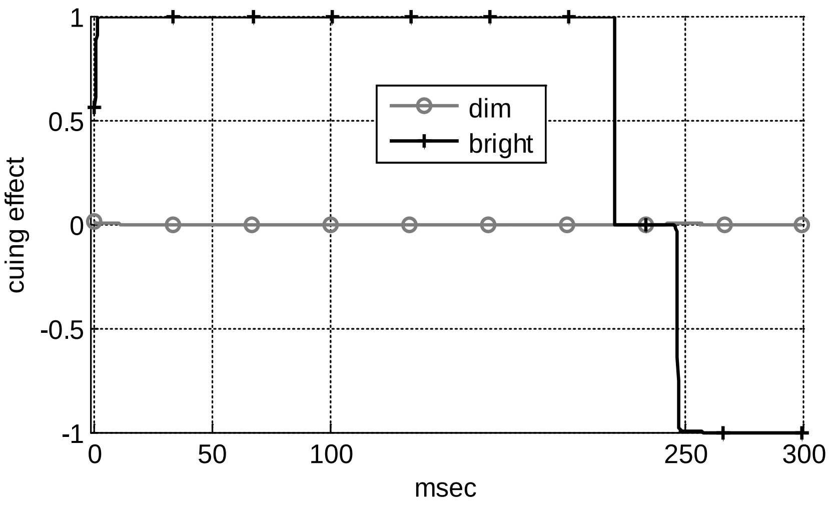

Figure 13 a)

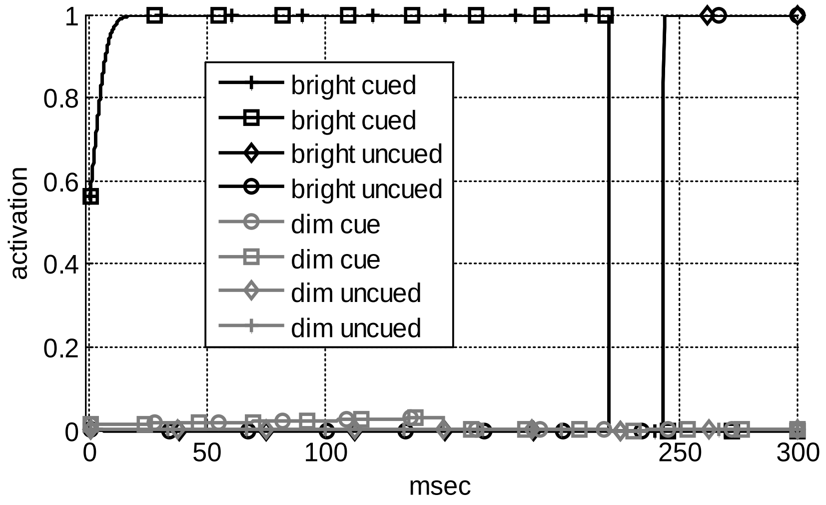

Figure 13 b)