

Spatial and feature-based effects of exogenous cueing on visual motion processing

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Abstract

In two experiments, we investigated the effects of exogenous cueing on visual motion processing. The first experiment shows that the typical pattern of reaction time (RT) effects, namely early facilitation and later inhibition of return (IOR), can be obtained using a color change as exogenous cue and a direction change as target. In the second experiment, we manipulated the validity of the cue independently with respect to location and feature using transparent motion stimuli. Facilitation of RTs with short cue-target interstimulus-intervals (ISIs) was only evident for targets with both the valid location and the valid feature. Furthermore, at longer cue-target intervals, RTs were prolonged for targets at the cued location, irrespective of the cued feature. These results demonstrate spatial and feature-based components of early facilitation and purely spatial IOR.

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1. Introduction

Visual attention is the mechanism that allows us to choose behaviorally relevant information from the immense amount of input that impinges on our eyes. The flexible allocation of attention to spatial locations (e.g., Posner, 1980), different sensory features (like one particular color or motion direction)¹ (e.g., Sáenz et al., 2003), and objects (e.g., Blaser, Pylyshyn, & Holcombe, 2000) is the central ability of our visual system to dynamically react to changing aspects of our environment and to varying behavioral goals.

In vision, cueing studies have provided insight in the dynamics of location-based, feature-based, and object-based attentional shifts. In general, such studies can be distin-

guished based on the nature of the cue: symbolic cues (arrows, etc.) are used for endogenous (or voluntary) orienting while peripheral cues (flashing stimuli, etc.) activate exogenous (or automatic) orienting processes (Posner & Cohen, 1984). In the case of exogenous cueing, subjects generally react faster and more accurately after valid cues, but only for short intervals between the cue and target. If the cue-target interstimulus interval (ISI) exceeds around 300ms, reaction times will be slower (Posner & Cohen, 1984), and responses less accurate (Handy, Jha, & Mangun, 1999) for targets at the cued location than for targets at the uncued location. This latter effect of a peripheral cue has been termed *Inhibition of Return* (IOR) (see Klein, 2000 for a recent review). It has been suggested that IOR plays an important role in visual foraging behavior in that IOR prevents attention from permanently focussing onto or revisiting the most salient stimulus (Klein, 1988; Itti & Koch, 2000).

The effects of exogenous cueing have not only been investigated in the spatial domain, but also with respect to feature-based and object-based attentional processes. Tipper, Driver, and Weaver (1991, 1994) were first to show

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¹ 'Feature' refers to a particular property within a stimulus dimension, e.g., upwards motion is a feature within the stimulus dimension of motion, and red is a feature within the stimulus dimension of color (cf. Sáenz, Buračas, & Boynton, 2003).

object-based IOR. To dissociate location-based and object-based IOR, they cued a moving object and found that, at long cue-target ISIs, responses were not inhibited for the initially cued location but inhibition moved with the cued object to its new location. Furthermore, with stationary stimuli, object-based and location-based inhibitory effects have been shown to combine in an additive fashion (Leek, Reppa, & Tipper, 2003). However, other groups have failed to find independent location-based and object-based mechanisms of IOR (Christ, McCrae, & Abrams, 2002; McAuliffe, Pratt, & O'Donnell, 2001).

To investigate feature-based effects of IOR, typically a nonspatial stimulus attribute, such as color (Kwak & Egeth, 1992; Law, Pratt, & Abrams, 1995) or shape (Riggio, Patteri, & Umiltà, 2004), is repeated (valid condition) vs. non-repeated (invalid condition) for cue and target. The results obtained in these studies are mixed, in that some groups found feature-based inhibitory effects (Law et al., 1995; Riggio et al., 2004), whereas others did not (Kwak & Egeth, 1992). However, in most of the studies, spatial and nonspatial attributes of the stimuli have not been manipulated independently (e.g., cues and targets were always presented at fixation (Kwak & Egeth, 1992; Law et al., 1995)), thereby confounding spatial and feature-based effects of IOR. In addition, repetition of stimulus features might lead to adaptation (at least when presented at the same location) (e.g., Clifford, 2002; Muller, Metha, Krauskopf, & Lennie, 1999) or repetition blindness (Fox & de Fockert, 2001; Kanwisher, 1987; Taylor & Klein, 1998).

Here, we investigate spatial and feature-based effects of exogenous cueing on visual motion processing using an experimental design that allows the independent manipulation of spatial and nonspatial stimulus attributes. In the first experiment, we show that spatial IOR can be obtained using a cue-target combination of stimulus attributes that are processed in two different visual pathways (Felleman & Van Essen, 1991; Ungerleider & Mishkin, 1982), namely a color change (ventral pathway) serving as the cue and a change in motion direction (dorsal pathway) serving as the target. In the second experiment, we independently vary the validity of the cue with respect to location and feature in order to disentangle spatial and feature-based effects of exogenous cueing. With short cue-target ISIs, we find facilitation of RTs only when the cue is valid with respect to both location and feature. Additionally, in conditions with longer cue-target ISIs, we obtain IOR for the cued location, irrespective of the previously cued feature. These results demonstrate location- and feature-based components of exogenous shifts of attention.

2. Methods

2.1. Experiment 1

Ten naive subjects (age 20–28, 6 female, 4 male) with normal or corrected-to-normal vision participated in the experiment. All subjects gave informed written consent and were paid for taking part in an one hour session in which they completed 5 blocks of 100 trials each. One subject was

excluded from the data analysis since his performance was more than three standard deviations below the sample mean.

The experiment was conducted in a dimly illuminated and quiet room. Stimuli were presented on a VGA monitor (Quatographic, Color Station Professional) operated at a refresh rate of 85 Hz and a spatial resolution of 40 pixels/deg. Stimulus presentation and recording of responses was controlled by custom-made software running on an Apple Power Mac G4. Subjects placed their head on a chin-rest or a bite-bar positioned 57 cm from the monitor. During the trials, eye-movements were monitored using an infrared eyetracking system (ISCAN ETL-200). In case eye position deviated more than 1.5 deg from a central fixation point the experiment was paused by the experimenter and subjects were re-instructed to maintain fixation.

The stimulus was composed of two circular apertures (radius 1.8 deg) of moving dots (dot density: 8 pixels/deg²) centered 5 deg to the left and the right of the fixation point. Dots were gray (12 cd/m²) on a black background, subtending 0.05 deg of visual angle in width. The dots in each aperture coherently moved at a speed of 7 deg/s, in one of 4 possible directions (45, 135, 225, and 315 deg deviation from vertical). In each trial, the directions of the two dot patterns differed by at least 90 deg. During the course of the trial, some dots changed their color to red. For each participant separately, flicker fusion photometry was conducted to achieve sub-

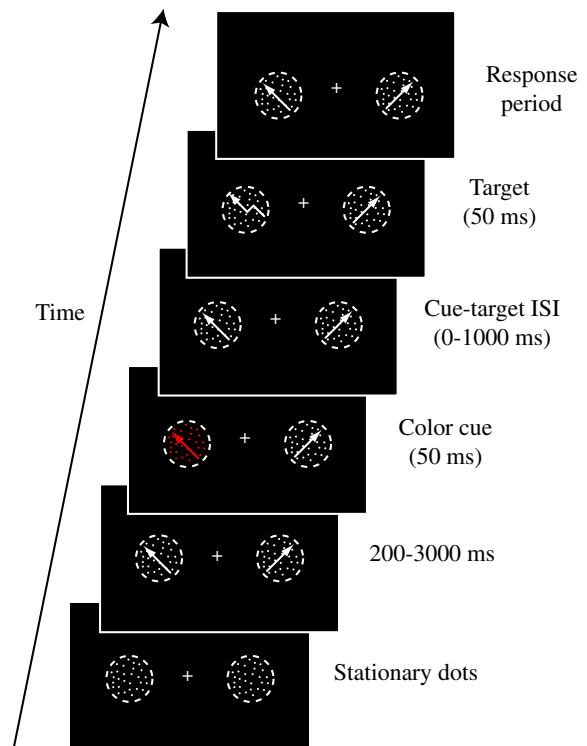


Fig. 1. Schematic trial structure for Experiment 1. Two random dot patterns were presented to the left and right of fixation. After trial start, the dots in the apertures moved coherently in directions differing by at least 90 deg for 200–3000 ms. Randomly during this time period a cue consisting of a color change to red (50 ms duration) appeared in one of the apertures. This cue was followed by a target defined as a brief change in the direction of motion (except for a ‘catch trial’ condition, in which no target was presented, see below). The subjects’ task was to respond as quickly as possible to the direction change (or to withhold the response in case of a ‘catch trial’). The example illustrates a valid trial since the target direction change occurs in the previously cued motion pattern. Note that the dashed outlines of the apertures as well as the arrows symbolizing the movement of the dots were not present in the actual experiment. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

jective isoluminance for the gray and red colors. While the intensity of the gray was held constant for all subjects, the intensity of the red gun was adjusted by each subject until minimal flicker was perceived at a flicker rate of 16 Hz. The adjusted intensity of the red gun was averaged across 25 trials and the result was used in Experiment 1.

Fig. 1A shows a schematic layout of the trial structure. At the beginning of each trial, stationary dots were presented in the apertures. When subjects initiated the trial by pressing the space bar on a computer keyboard, the dots in the two apertures started moving.

Seventy-five percent of the trials were ‘cued trials,’ 25% were ‘catch trials’ (Fig. 2). For the ‘cued trials,’ three different conditions were presented with equal probabilities, namely valid, invalid, and neutral trials. Hence, across trials cues were completely unpredictable with respect to the upcoming target location. In the valid and invalid trials, 200–3000 ms after trial start, the dots in one of the apertures changed their color to red. The color change lasted for 50 ms and served as the exogenous cue. A variable time interval (0–1000 ms) after cue-offset (cue-target ISI), the dots in either the same (valid condition) or the opposite (invalid condition) aperture underwent a direction change of 23 deg and returned to their original direction after another 50 ms. In the neutral trials, the color change occurred in both stimuli such that no particular location was cued. For all ‘cued trials’ the subjects’ task was to detect the direction change and respond with a keypress (‘H’) as quickly as possible. Reaction times below 100 ms were considered anticipatory responses, reaction times above 1000 ms were counted as misses. The ‘catch trials’ were identical to the ‘cued trials’ except that no direction change (i.e., target) followed the cue, i.e., the dots continued to move in their original direction until trial end (signal absent trials). Thus, no response was required. ‘Catch trials’ were randomly interleaved with the ‘cued trials’ and served the purpose of preventing subjects from forming temporal expectancies and making anticipatory responses. After each trial, subjects received auditory feedback.

For each condition, RTs for correct ‘cued trials’ were sorted according to the cue-target ISI into 5 bins of 200 ms width (0–200, 200–400, 400–600, 600–800, and 800–1000 ms). For the statistical analysis of reaction times, a two-way ANOVA with the within-subject factors cueing (valid, invalid, neutral) and ISI (5 levels) was used. When appropriate, significance levels were corrected for violations of the sphericity assumption using the Greenhouse–Geisser method; however, original degrees of freedoms are reported.

2.2. Experiment 2

In Experiment 2, the same circular apertures and trial sequence as in Experiment 1 were used (Fig. 3). Here, each stimulus consisted of two superimposed populations of dots moving in opposite directions, resulting in a percept of transparent motion. The two dot populations always moved in the same opposite directions in the two apertures (45/225 deg or 135/315 deg deviation from vertical). Stimulus parameters were identical to those used in Experiment 1 except for dot density. In Experiment 2, each individual surface contained only half the dots (4 pixels/deg²) in order to keep the overall dot-density constant across experiments. To compensate for the reduced dot density in each single surface the duration of the cue color change was doubled to 100 ms.

Using two transparent motion stimuli allowed the presentation of two different features (i.e., motion directions) superimposed at a single spatial location, and to repeat the same feature (i.e., same motion direction) at two different spatial locations. Since the color-cue and the direction-target always occurred in only a single motion direction in a single dot pattern, we were able to independently manipulate the cue-validity with respect to location and feature (Fig. 4). Again, the cue was entirely unpredictable regarding the location and the direction of motion of the subsequent target.

For example, in the ‘valid location, valid direction’ condition the target occurred in the same location and in the same motion direction as the preceding cue. Analogously, the ‘invalid location, valid direction’ condition consisted of a target direction change occurring in the dot pattern opposite from the cued dot pattern, but in the population of dots moving in the same motion direction as the population of dots that served as the cue. The combinations of cue validity with respect to location (valid/invalid location) and motion direction (valid/invalid feature) yielded four different trial types. Additionally, a ‘neutral condition’ was presented in which the cue appeared simultaneously in one surface of each stimulus, such that no particular location or direction was cued. As in Experiment 1, the ratio of ‘cued trials’ and ‘catch trials’ was 3:1, cued surface, location and the directions of motion were randomized across trials.

Twelve naive subjects (age: 20–31, 5 female, 7 male) participated in two 1 h sessions conducted at different days. One subject was excluded from the data analysis because performance was below 50% in the catch trial condition (44% correct). As in the first experiment, trials were sorted into bins of 200 ms width according to the cue-target ISI. For the statistical

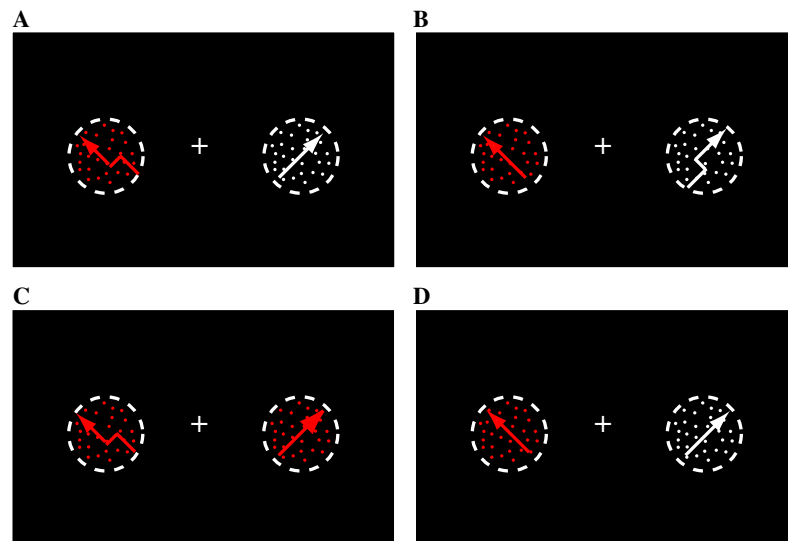


Fig. 2. Conditions for Experiment 1. For purpose of illustration the cue is drawn in the same frame as the target, which was not the case in the actual experiment (see Fig. 1). (A) Valid condition: cue and target in the same aperture. (B) Invalid condition: cue and target in different apertures. (C) Neutral condition: the cue appears in both apertures. (D) Catch trial: no target. The ratio of catch trials was 25%, conditions (A–C) were presented with equal probabilities. The location of the cue and the two directions of motion were randomly varied across trials.

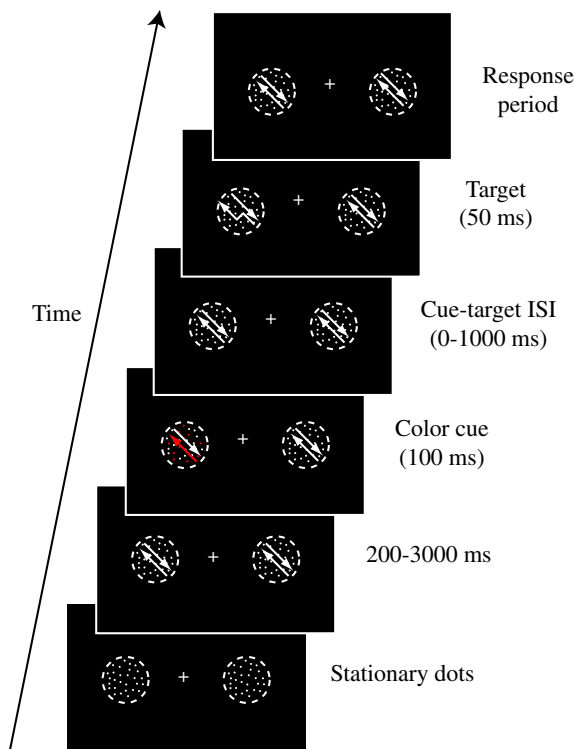


Fig. 3. Schematic trial sequence for Experiment 2. Two superimposed surfaces moving in opposite directions were presented to the left and right of fixation. After 200–3000 ms a color change in one surface served as the exogenous cue. Since the cue appeared only in a single direction of motion at a particular location we can independently manipulate the validity of the cue with respect to location and feature. The subjects' task was to respond as quickly as possible to the change in direction that could follow within 1000 ms after cue offset. In neutral trials, the cue was presented in one direction of each aperture, such that no particular location or feature was cued. In 'catch trials' no target followed the cue. The example illustrates a trial in the condition 'valid location, valid direction' since the target occurs in the cued aperture and in the cued direction of motion.

analysis of RT data, a three-way ANOVA with the within-subject factors location (valid, invalid), direction (valid, invalid), and ISI (5 levels) was used. When appropriate, significance levels were corrected using the Greenhouse–Geisser correction; however, original degrees of freedom are reported. RTs in the neutral condition were compared against RTs in the other cued trials in post-hoc comparisons.

3. Results

3.1. Experiment 1

In the first experiment, we investigated whether an exogenous color-cue affects processing of subsequent motion targets. Across subjects, performance for cued trials was 94.8%, for catch trials 96.5%.

Mean reaction times for Experiment 1 are shown in Fig. 5. The ANOVA for RTs revealed a significant main effect of ISI ($F(4, 32) = 8.35, p < 0.01$), indicating that RTs vary as a function of cue-target ISI. More importantly, the effects of exogenous cueing depend on the level of cue-target ISI, as reflected in the significant interaction between these factors ($F(8, 64) = 2.56, p < 0.05$). In trials with short

cue-target ISIs (0–200 ms), subjects were faster in both the valid and neutral condition than in the invalid condition (462/470 ms vs. 496 ms, respectively; $p < 0.05$, Newman–Keuls). In contrast, for longer cue-target ISIs (200–400 and 400–600 ms), this pattern first disappears and then reverses. This crossover effect is significant for ISIs between 400 and 600 ms with responses to targets after valid and neutral cues being on average 13 ms slower than responses to targets at uncued locations (436/433 ms vs. 422 ms, respectively; $p < 0.05$, Newman–Keuls). For longer cue-target ISIs, there was no significant difference between the conditions.

3.2. Experiment 2

In Experiment 2, we investigated location- and feature-based effects of exogenous cueing, using transparent motion stimuli. In this experiment, performance for cued trials (76.9%) and catch trials (82.1%) were lower compared to Experiment 1 ($t(18) = 4.9, p < 0.001$ for cued trials, and $t(18) = 2.4, p < 0.05$ for catch trials), and mean RTs across all conditions were slower (444 ms vs. 507 ms; $t(18) = 2.2, p < 0.05$) in Experiment 2 than Experiment 1. These differences probably reflect an increased target detection difficulty due to the presence of a second, overlapping dot surface.

Mean RTs for Experiment 2 are shown in Fig. 6. Along with the increased RTs compared to Experiment 1 goes an increase of the crossover latency in which facilitation changes to inhibition (600–800 ms bin). This agrees with the proposal that the onset of IOR might vary with the difficulty of the task (Lupiáñez, Milan, Tornay, Madrid, & Tudela, 1997; Lupiáñez, Milliken, Solano, Weaver, & Tipper, 2001). The reasoning is as follows: the more difficult the task, the more attention will be devoted to the target processing, and hence to the processing of the cue (Folk, Remington, & Johnston, 1992); the more intensely attention will be allocated to the cue, the longer attention will dwell on it (Klein, 2000), and the longer facilitation will last after the exogenous cue.

An overall three-way ANOVA (location \times direction \times ISI) on RTs revealed a main effect of ISI ($F(4, 40) = 5.96, p < 0.05$), indicating that RTs vary as a function of cue-target ISI. A main effect of location ($F(1, 10) = 5.25, p < 0.05$) indicates that, on average, responses to targets at the cued location were faster than responses to targets at the uncued location (491 ms vs. 507 ms). This effect is, on average, larger for targets with the cued feature as revealed by the interaction between location and direction ($F(1, 10) = 5.69, p < 0.05$). In addition, we obtain a significant interaction between location and ISI ($F(4, 40) = 7.32, p < 0.001$), showing that the effect of spatial cueing changes, on average, with ISI. Most importantly, the three-way interaction is also significant (location \times direction \times ISI, $F(4, 40) = 3.03, p = 0.05$). Post hoc comparisons revealed significant differences between the cueing conditions for the ISI bins 0–200, 200–400, and 600–800 ms. For the first and second ISI bin,

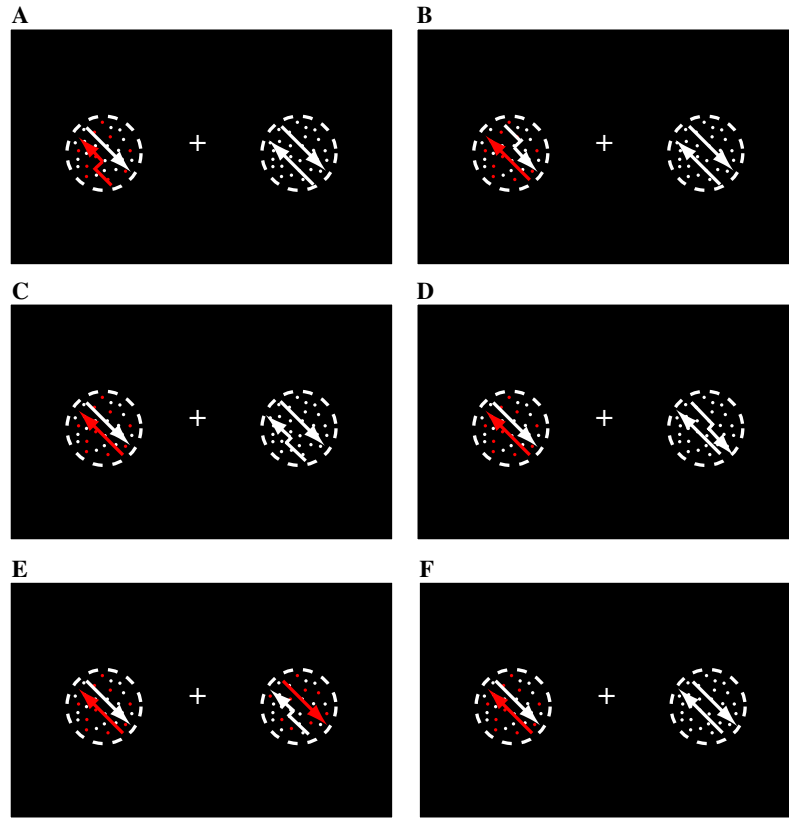


Fig. 4. Conditions in Experiment 2. (A) Valid location, valid direction. (B) Valid location, invalid direction. (C) Invalid location, valid direction. (D) Invalid location, invalid direction. (E) Neutral condition. (F) Catch trial. The ratio of catch trials was 25%. Conditions (A–E) were presented with equal probability. Note that, in the actual experiment, the cue and the target were not presented at the same time.

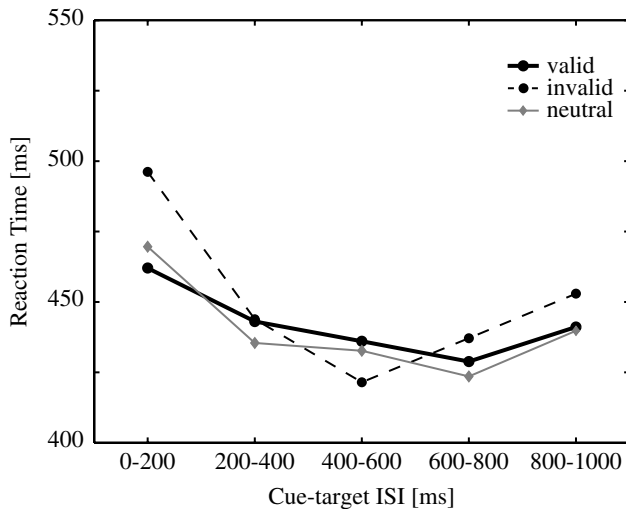


Fig. 5. Mean reaction times for Experiment 1. In conditions with short cue-target ISIs RTs are faster after both valid and neutral cues compared to invalid cues (466 ms vs. 496 ms; 0–200 ms ISI). However, for longer cue-target ISIs, this pattern reverses, and targets in the uncued dot pattern are responded to faster compared to both cued and neutral targets (435 ms vs. 422 ms; 400–600 ms ISI).

a separate two-way ANOVA with factors location and direction revealed a main effect of location ($F(1,10) = 10.77$, $p < 0.01$ (0–200 ms ISI); $F(1,10) = 6.42$, $p < 0.05$

(200–400 ms ISI)), indicating that, on average, responses to targets in the cued location were faster than responses to targets in the uncued location. Moreover, we obtain a significant interaction between location \times feature ($F(1,10) = 8.82$, $p < 0.05$ (0–200 ms ISI), $F(1,10) = 11.28$, $p < 0.01$ (200–400 ms ISI)). Post hoc comparisons show that RTs are fastest to targets appearing at the cued location and in the cued feature ('valid location, valid direction'), while there is no significant difference between the other cueing conditions (496 ms vs. 565 ms for 0–200 ms, 483 ms vs. 522 ms for 200–400 ms; $p < 0.05$, Newman–Keuls). Additionally, there is a significant benefit for targets at the cued location and with the cued feature compared to the neutral condition for the ISI bin 0–200 ms (496 ms vs. 538 ms; $p < 0.05$, Newman–Keuls). This difference vanishes in the subsequent ISI bin. A cross-over of RTs is evident in the 600–800 ms bin. Here, RTs to targets at the cued location are slower than RTs to targets at the uncued location (483 ms vs. 456 ms, $F(1,10) = 5.52$, $p < 0.05$, main effect of location). Importantly, this effect does not depend on the cued feature ($F(1,10) = 0.16$, $p = 0.6$, interaction between feature and location). There is also no significant difference between RTs to targets at the cued location and RTs in the neutral condition for both the third (400–600 ms) and fourth ISI (600–800 ms) periods.

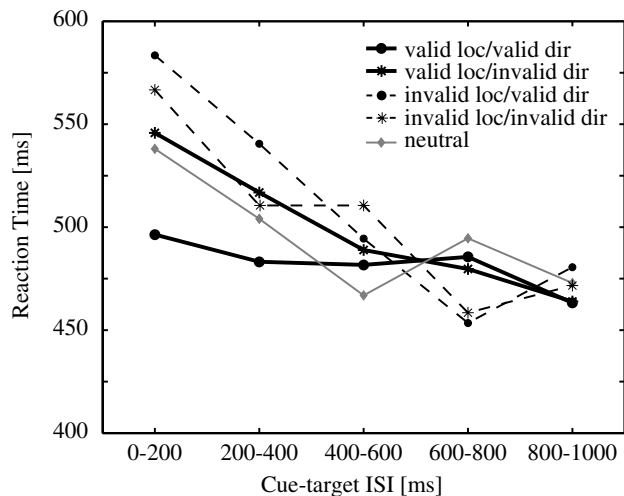


Fig. 6. Mean reaction times for experiment 2. At cue-target ISIs between 0–200 ms and 200–400 ms RTs are fastest if the target occurs in the previously cued location and direction (496 ms vs. 565 ms for 0–200 ms; 483 ms vs. 522 ms for 200–400 ms) compared to the other cueing conditions. While for the earliest targets, a benefit of the ‘valid location, valid direction’ compared to the neutral condition (538 ms) is present, this difference disappears between 200 and 400 ms. At longer cue-target intervals (600–800 ms), RTs are slower for targets appearing in the cued location compared to the uncued location (483 ms vs. 456 ms). There is no difference between RTs in the neutral condition and RTs to validly cued targets in neither the third or fourth ISI period.

4. Discussion

In two experiments, we show spatial and feature-based effects of exogenous cueing on the processing of visual motion using an experimental design that does not confound cueing of location and cueing of feature. We find that, with short cue-target ISIs, detection of a change in direction of motion at the cued location is facilitated as evidenced by faster RTs to validly cued targets (Experiment 1). When further dissociating spatial and feature-based effects of the cue (Experiment 2), it becomes evident that this facilitation is feature-specific, such that targets occurring in the cued aperture (location) and in the cued direction of motion (feature) yield the fastest responses. In contrast, when the cue-target ISI is in the range of 400–600 ms (Experiment 1) or 600–800 ms (Experiment 2), RTs to targets at the cued location are prolonged. This late inhibitory effect on RTs seems to be purely spatial.

By using a cue-target combination consisting of two different stimulus attributes processed in different visual pathways, namely a color change serving as a cue and a direction change constituting the target, we can infer that simple sensory interactions are not likely to cause the sequence of facilitatory and inhibitory effects of the cue. Furthermore, since we are not repeating the same feature for the cue and the target, we can exclude repetition blindness as an explanation for the effects in our experiments (Fox & de Fockert, 2001). Rather, we interpret the findings as attention being initially reflexively drawn to the cued

feature at the cued location, and later being oriented away from such tagged locations.

4.1. Mechanisms and neuronal substrates

Although the effects of exogenous cueing have been studied extensively using behavioral techniques, the underlying physiological processes remain unclear. So far, few studies have investigated the brain areas and mechanisms involved in automatic orienting as well as the physiological consequences of exogenous cueing on sensory processing.

4.1.1. Initial attraction of attention

In line with numerous previous studies, we find an initial facilitation of RTs to cued compared to uncued targets for short cue-target ISIs in both experiments. In Experiment 1, this initial difference does not seem to be due to a speed-up of RTs relative to the neutral condition (although the data show a trend in this direction), but seems caused primarily by prolonged responses to targets at the uncued location. In contrast, in the second experiment, RTs in the ‘valid location, valid feature’ condition are considerably faster than the neutral and all other cueing conditions. This difference between the two experiments is surprising, and we can only speculate about the causes: Maybe processing of the neutral cue led to fast responses in the first experiment since task difficulty was low and attention was attracted in a split-focus fashion (e.g., Awh & Pashler, 2000; McMains & Somers, 2004) to both apertures with little or no cost after the neutral cue. Further experiments testing different neutral cues are needed to examine the facilitatory component after exogenous cueing relative to a neutral condition.

A number of recent studies employed transparent motion stimuli to investigate the effects of exogenous cueing on motion processing. They found that, after a salient change in one of two spatially superimposed, rotating surfaces performance in a subsequent discrimination task was strongly reduced for the uncued surface (e.g., Mitchell, Stoner, Fallah, & Reynolds, 2003; Reynolds, Alborzian, & Stoner, 2003; Valdés-Sosa, Cobo, & Pinilla, 2000). This benefit in performance for discrimination in the cued surface lasted for a couple of hundreds of milliseconds. Thus, the facilitatory effect on performance has a similar time-course than the RT effect we observed in Experiment 2. The fact that the three studies cited above did not vary spatial location but presented the cue and target at fixation might have disguised a potential subsequent location-based inhibition that would have affected both features similarly.

As has been proposed in computational models of bottom-up attentional processes (Itti & Koch, 2000; Itti & Koch, 2001), location-based facilitation of RTs with short cue-target ISIs could be interpreted as arising from a peak in activity in a feature-unspecific, retinotopically organized global ‘saliency map,’ reflexively drawing attention to the most salient (i.e., cued) location. This ‘saliency map’ is thought to receive input from multiple feature-specific

maps that each encode spatial contrast in one specific feature dimension, like orientation, color, or motion. Directing attention to the location corresponding to the peak activity in such a feature-unspecific saliency map would yield a purely spatial-based attentional advantage. Evidence for representation of saliency, not stimulus features per se, has been found for neurons in the pulvinar (Robinson & Petersen, 1992), parietal cortex (Gottlieb, Kusunoki, & Goldberg, 1998), in the frontal eye fields (FEF) (Thompson & Schall, 2000; Thompson, 2001), and in the superior colliculus (SC) (Kustov & Robinson, 1996). However, to account for a feature-based component in the initial orienting of attention as found in Experiment 2 one would need to assume an additional, feature-specific mechanism, e.g., incorporation of feature information in the global saliency map or interactions with distributed feature-specific computations of saliency (e.g., Desimone & Duncan, 1995; Hamker, 2004).

4.1.2. Inhibition of return

IOR has been proposed to be a crucial mechanism of attentional orienting in that it prevents attention from permanently focusing on the most salient stimulus (Itti & Koch, 2001; Klein, 1988). According to this notion, attention is able to shift to different stimuli with decreasing saliency in the visual scene by transient inhibition of neurons in the ‘saliency map’ encoding the attended stimulus (Itti & Koch, 2000, 2001).

Experiments 1 and 2 both demonstrated IOR for longer cue-target ISIs when targets appeared at the cued location. Consistently across the experiments, this disadvantage for the previously cued location seems to be primarily caused by a benefit for the uncued location, since RTs to targets in the uncued location are considerably faster than RTs to targets after both spatially valid and neutral cues. Thus, instead of being a true inhibition of the attended stimulus, the effect might rather be interpreted as a facilitation of previously unattended locations. On the other hand, our neutral cue, consisting of a salient change in both apertures, might have led to similar inhibitory processes than the valid cue. To disentangle these opposing interpretations further experiments using a different neutral cue, e.g., a change at fixation, need to be conducted.

The finding that IOR seems to operate in a purely spatial manner has immediate functional plausibility.² When searching for an item with defining characteristics (e.g., a certain color) in a cluttered visual scene spatial IOR biases the system toward processing of new locations if the item has not been found at the previously attended location. This mechanism seems crucial for efficient attentional employment. In contrast, it would seem an inappropriate strategy if the attended feature, which defines the target item, would be inhibited across the entire visual field by a global feature-based IOR.

Single-unit recordings in the lateral intraparietal (LIP) area in awake behaving monkeys have revealed a potential neural correlate of a transient spatial-based inhibition (Bisley & Goldberg, 2003). In this study, typical effects of exogenous cueing on behavior (lower contrast thresholds with short ISIs, higher contrast thresholds with long ISIs for targets at the cued location) correlate with the ensemble activity in LIP. Shortly after a transient cue-related activity, the LIP population response is increased for neurons with receptive fields (RF) responding to the cued region compared to neurons whose RFs are located at the opposite target location. After a period of 80–90 ms without any significant difference between the two population responses, the firing rate of the neurons coding the cued region decreases below the firing rate of those coding the opposite target location.

Along the lines of the motor theory of IOR (Rafal, Calabresi, Brennan, & Sciolto, 1989; Sapir, Soroker, & Berger, 1999), single unit studies in the superior colliculus (SC), a critical node in the visual orienting pathway, propose a collicular contribution to IOR (Dorris, Klein, Everling, & Munoz, 2002; Fecteau, Bell, & Munoz, 2004). For short cue-target intervals, Fecteau et al. (2004) showed that the initial facilitation of saccadic RTs is accompanied by an enhanced neural response to the target in the SC. Similarly, prolonged RTs correlate with a suppression of the target-related responses in the SC (Dorris et al., 2002; Fecteau et al., 2004) and reduced target-related responses at the cued location have been found in the event-related scalp potential (ERP) recorded in humans. At long cue-target intervals, P1 amplitudes are reduced when targets appear at the cued location, suggesting that exogenous cueing can influence sensory processing in the extrastriate cortex (Hopfinger & Mangun, 1998; McDonald, Ward, & Kiehl, 1999). Using event-related fMRI IOR has been linked to areas commonly activated during oculomotor/motor planning (frontal and supplementary eye fields) (Lepsien & Pollmann, 2002; Mayer, Seidenberg, Dorflinger, & Rao, 2004) as well as attentional orienting (posterior parietal, superior and middle temporal, anterior cingulate and thalamic areas) (Mayer et al., 2004).

4.2. Perceptual effects vs. shifts of criterion

Traditionally, the effects of stimulus-driven or bottom-up capture of attention have been interpreted as reflecting perceptual effects. Recently, an alternative explanation has been advanced, namely a simple change in criterion for targets at attended vs. unattended locations (Eckstein, Thomas, Palmer, & Shimozaki, 2000; Verghese, 2001). In case of the Posner cueing paradigm, Eckstein, Shimozaki, and Abbey (2002) propose an ideal-observer model that weights the information at cued and uncued locations as a function of the cue validity. They find close agreement of psychophysical data with the model and no evidence for a change in the quality of the visual signal, which suggests a

² We thank one anonymous reviewer for pointing out this issue.

change in criterion rather than a perceptual benefit of attention. While RT data cannot distinguish between shifts of sensitivity vs. criterion, one should note that simple weighting of information according to the cue-validity cannot account for effects after uninformative precues as used in this study. Using a signal-detection measure of perceptual sensitivity in a design with unpredictable cues, Handy et al. (1999) showed that the typical pattern of RTs, namely early facilitation and later IOR, is also found for sensitivity measures like d' and A' . Similarly, an irrelevant singleton in a search array seems to attract attention such that target detectability seems reduced (Theeuwes, Kramer, & Kingstone, 2004). Finally, Carrasco, Ling, and Read (2004) recently demonstrated that uninformative exogenous cues alter the perceived contrast of the cued items, at least with a short cue-target ISI. Unfortunately, our design does not allow us to determine the signal detection measures d' and β in order to directly test for changes in sensitivity vs. decision criterion. While it is straightforward to calculate hit rates for the various cue-target ISIs for the different signal present conditions, it is impossible (except for the neutral cueing condition) to categorize false alarms with respect to the various valid or invalid cueing conditions. Moreover, there is no obvious way to sort the false alarms into the cue-target ISI bins. Clearly, further experiments will be needed to dissociate changes in sensitivity from changes in criterion over time in an exogenous cueing task.

5. Summary

In summary, we show spatial and feature-based influences of exogenous cueing on motion processing. By using a cue-target combination that avoids simple sensory interactions we infer that exogenous automatic attentional processes can best account for the results. With short cue-target ISIs, we find a benefit for targets at the valid location and with the valid feature, probably reflecting attentional orienting to the cued item. In contrast, with long cue-target ISIs, responses to targets are slower when they occur at the cued location irrespective of the cued feature. This finding underlines the notion that IOR might facilitate orienting to novel spatial locations.

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References

Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance*, 26(2), 834–846.

Bisley, J., & Goldberg, M. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, 299(5603), 81–86.

Blaser, E., Pylyshyn, Z., & Holcombe, A. (2000). Tracking an object through feature space. *Nature*, 408, 196–199.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, 7(3), 308–313.

Christ, S., McCrae, C., & Abrams, R. (2002). Inhibition of return in static and dynamic displays. *Psychonomic Bulletin & Review*, 9(1), 80–85.

Clifford, C. (2002). Perceptual adaptation: Motion parallels orientation. *Trends in Cognitive Sciences*, 6(3), 136–143.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.

Dorris, M., Klein, R., Everling, S., & Munoz, D. (2002). Contribution of the primate superior colliculus to inhibition of return. *Journal of Cognitive Neuroscience*, 14(8), 1256–1263.

Eckstein, M., Shimozaki, S., & Abbey, C. (2002). The footprints of visual attention in the posner cueing paradigm revealed by classification images. *Journal of Vision*, 2(1), 25–45.

Eckstein, M. P., Thomas, J. P., Palmer, J., & Shimozaki, S. S. (2000). A signal detection model predicts the effects of set size on visual search accuracy for feature, conjunction, triple conjunction, and disjunction displays. *Perception & Psychophysics*, 62(3), 425–451.

Fecteau, J., Bell, A., & Munoz, D. (2004). Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *Journal of Neurophysiology*, 92(3), 1728–1737.

Felleman, D., & Van Essen, D. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1, 1–47.

Folk, C., Remington, R., & Johnston, J. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 18(4), 1030–1044.

Fox, E., & de Fockert, J. (2001). Inhibitory effects of repeating color and shape: Inhibition of return or repetition blindness? *Journal of Experimental Psychology: Human Perception and Performance*, 27(4), 798–812.

Gottlieb, J., Kusunoki, M., & Goldberg, M. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, 391(6666), 481–484.

Hamker, F. H. (2004). A dynamic model of how feature cues guide spatial attention. *Vision Research*, 44, 501–521.

Handy, T., Jha, A., & Mangun, G. (1999). Promoting novelty in vision: Inhibition of return modulates perceptual-level processing. *Psychological Science*, 10(2), 157–161.

Hopfinger, J., & Mangun, G. (1998). Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science*, 9(6), 441–447.

Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40(10–12), 1489–1506.

Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Review Neuroscience*, 2(3), 194–203.

Kanwisher, N. (1987). Repetition blindness: Type recognition without token individuation. *Cognition*, 27(2), 117–143.

Klein, R. (1988). Inhibitory tagging system facilitates visual search. *Nature*, 334(6181), 430–431.

Klein, R. (2000). Inhibition of return. *Trends in Cognitive Sciences*, 4, 138–147.

Kustov, A., & Robinson, D. (1996). Shared neural control of attentional shifts and eye movements. *Nature*, 384(6604), 74–77.

Kwak, H.-W., & Egeth, H. (1992). Consequences of allocating attention to locations and to other attributes. *Perception & Psychophysics*, 51, 455–464.

Law, M., Pratt, J., & Abrams, R. (1995). Color-based inhibition of return. *Perception & Psychophysics*, 57, 402–408.

Leek, E., Reppa, L., & Tipper, S. (2003). Inhibition of return for objects and locations in static displays. *Perception & Psychophysics*, 65(3), 388–395.

Lepsien, J., & Pollmann, S. (2002). Covert reorienting and inhibition of return: An event-related fMRI study. *Journal of Cognitive Neuroscience*, 14(2), 127–144.

Lupiáñez, J., Milan, E., Tornay, F., Madrid, E., & Tudela, P. (1997). Does IOR occur in discrimination tasks. Yes, it does, but later. *Perception & Psychophysics*, 59(8), 1241–1254.

- Lupiañez, J., Milliken, B., Solano, C., Weaver, B., & Tipper, S. (2001). On the strategic modulation of the time course of facilitation and inhibition of return. *Quarterly Journal of Experimental Psychology*, *54*(3), 753–773.
- Mayer, A., Seidenberg, M., Dorfinger, J., & Rao, S. (2004). An event-related fMRI study of exogenous orienting: Supporting evidence for the cortical basis of inhibition of return? *Journal of Cognitive Neuroscience*, *16*(7), 1262–1271.
- McAuliffe, J., Pratt, J., & O'Donnell, C. (2001). Examining location-based and object-based components of inhibition of return in static displays. *Perception & Psychophysics*, *63*(6), 1072–1082.
- McDonald, J., Ward, L., & Kiehl, K. (1999). An event-related brain potential study of inhibition of return. *Perception & Psychophysics*, *61*(7), 1411–1423.
- McMains, S., & Somers, D. (2004). Multiple spotlights of attentional selection in human visual cortex. *Neuron*, *42*(4), 677–686.
- Mitchell, J., Stoner, G., Fallah, M., & Reynolds, J. (2003). Attentional selection of superimposed surfaces cannot be explained by modulation of the gain of color channels. *Vision Research*, *43*(12), 1323–1328.
- Muller, J., Metha, A., Krauskopf, J., & Lennie, P. (1999). Rapid adaptation in visual cortex to the structure of images. *Science*, *285*(5432), 1405–1408.
- Posner, M. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Posner, M., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–555). Hillsdale, NJ: Erlbaum.
- Rafal, R., Calabresi, P., Brennan, C., & Sciolto, T. (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(4), 673–685.
- Reynolds, J., Alborzian, S., & Stoner, G. (2003). Exogenously cued attention triggers competitive selection of surfaces. *Vision Research*, *43*(1), 59–66.
- Riggio, L., Patteri, I., & Umiltà, C. (2004). Location and shape in inhibition of return. *Psychological Research*, *68*, 41–54.
- Robinson, D., & Petersen, S. (1992). The pulvinar and visual salience. *Trends in Neurosciences*, *15*(4), 127–132.
- Sàenz, M., Buračas, G., & Boynton, G. (2003). Global feature-based attention for motion and color. *Vision Research*, *43*(6), 629–637.
- Sapir, A., Soroker, N., & Berger, A. (1999). Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nature Neuroscience*, *2*(12), 1053–1054.
- Taylor, T., & Klein, R. (1998). Inhibition of return to color: A replication and nonextension of Law, Pratt, & Adams (1995). *Perception & Psychophysics*, *60*, 1452–1456.
- Theeuwes, J., Kramer, A., & Kingstone, A. (2004). Attentional capture modulates perceptual sensitivity. *Psychonomic Bulletin & Review*, *11*(3), 551–554.
- Thompson, K., & Schall, J. (2000). Antecedents and correlates of visual detection and awareness in macaque prefrontal cortex. *Vision Research*, *40*(10–12), 1523–1538.
- Thompson, K. G. (2001). From attention to action in frontal cortex. In J. Braun, C. Koch, & J. Davies (Eds.), *Visual attention and cortical circuits* (pp. 137–157). MA: MIT Press.
- Tipper, S., Driver, J., & Weaver, B. (1991). Object-centred inhibition of return of visual attention. *Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *43*(2), 289–298.
- Tipper, S., Weaver, B., Jerreat, L., & Burak, A. (1994). Object-based and environment-based inhibition of return of visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(3), 478–499.
- Ungerleider, L., & Mishkin, M. (1982). Two cortical visual systems. In D. Ingle, M. Goodale, & R. Mansfield (Eds.), *Analysis of visual behavior* (pp. 49–86). MA: MIT Press.
- Valdés-Sosa, M., Cobo, A., & Pinilla, T. (2000). Attention to object files defined by transparent motion. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(2), 488–505.
- Vergheze, P. (2001). Visual search and attention: a signal detection theory approach. *Neuron*, *31*(4), 523–535.