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Sabine Born and Dirk Kerzel

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Time-Course of Feature-Based Top-Down Control in Saccadic Distractor Effects

Sabine Born and Dirk Kerzel
Université de Genève, Switzerland

Saccadic reaction time (SRT) is more strongly slowed by target-similar than dissimilar distractors (similarity effect). The time course of this similarity effect was investigated by varying target contrast and analyzing SRT distributions. With foveal distractors, the similarity effect increased with increasing SRT, suggesting that top-down enhancement of target features increased over time. This allowed for successful saccades to the peripheral target, but also entailed larger distraction by target-similar stimuli. Similarity effects with peripheral distractors did not increase with SRT, which we attribute to location-based inhibition containing the growing enhancement of target features. Strong inhibition was likely with peripheral distractors because they always appeared at the same task-irrelevant location. Prior inhibition with foveal distractors was weaker because this would have partially released fixation and entailed anticipations.

Keywords: saccade, latency, distractor, top-down, time course

A well-known phenomenon in saccadic reaction times (SRTs) is that the saccadic response to a target stimulus is delayed when a distractor is presented simultaneously and at a certain distance from the target (e.g., Benson, 2008; Bompas & Sumner, 2009; Lévy-Schoen, 1969; Ludwig, Gilchrist, & McSorley, 2005; Walker, Kentridge, & Findlay, 1995; White, Gegenfurtner, & Kerzel, 2005). The effect is strongest when the distractor is presented in the fovea (Walker, Deubel, Schneider, & Findlay, 1997). It is explained by competitive processes between target- and distractor-related signals in a retinotopically organized saccade motor map. Target and distractor signals may either directly inhibit each other in such a way that it takes longer for one of the two signals to reach a critical threshold for saccade initiation (e.g., Godijn & Theeuwes, 2002; Munoz & Fecteau, 2002; Trappenberg, Dorris, Munoz, & Klein, 2001). Alternatively, the distractor signal may strengthen fixation-related activity, which in turn leads to longer SRTs as fixation activity needs to be overcome in order to execute a saccadic eye movement (Findlay & Walker, 1999).

Recently, we have shown that the effect of foveal distractors can be modulated in a top-down manner (Born & Kerzel, 2009). Participants had to perform a search task: they had to select a predefined target (e.g., a green Gaussian blob) from two possible peripheral stimuli (one gray, one green Gaussian) presented in opposite hemifields. When presenting a foveal distractor along

with the peripheral stimuli, the distractor effect was stronger when the foveal distractor was similar to the target (same color) than when it was dissimilar. It is important that these similarity effects were much weaker or absent when target features were made irrelevant to the task. We suggested that the search task imposed a top-down setting for the target's defining feature. The top-down setting also modulated the impact of the foveal distractors: Distraction by foveal stimuli sharing the target feature was enhanced and distraction by dissimilar foveal stimuli was reduced. Along these lines, larger effects of target-similar distractors in various other paradigms (e.g., Becker, Ansorge, & Horstmann, 2009; Ludwig & Gilchrist, 2002; Mulckhuysse, van Zoest, & Theeuwes, 2008) suggest that there may be global feature-based enhancement or inhibition in the oculomotor system: signals of all stimuli that possess task-relevant features are enhanced (irrespective of whether it is a target or a distractor signal), while signals of stimuli with task-irrelevant features are inhibited. Global feature-based modulations of neural behavior have been reported in cortical visual areas in studies using functional magnetic resonance imaging (fMRI) techniques (e.g., Saenz, Buracas, & Boynton, 2002), electrophysiological measures such as event-related potentials (see Vierck & Miller, 2008 for a review) and steady-state visual evoked potentials (e.g., Andersen, Müller, & Hillyard, 2009), as well as single-cell recordings in monkeys (see Maunsell & Treue, 2006 for a review). These modulations may be passed on to the oculomotor system via an extensive network of descending cortical projections (Fecteau & Munoz, 2006). In fact, strong support for feature-based modulations of the response in oculomotor neurons comes from single-cell recordings in the frontal eye field (Bichot & Schall, 1999). When monkeys performed a conjunction search task, the neural response was strongest to a target presented in the response field of the neuron, followed by intermediate responses to a distractor that shared one feature with the target (either same color or same shape). The weakest responses were found for a distractor

Sabine Born and Dirk Kerzel, Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, Switzerland.

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Correspondence concerning this article should be addressed to Sabine Born, Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, 40 Boulevard du Pont d'Arve, 1205 Genève, Switzerland. E-mail: sabine.born@unige.ch

that did not share any feature with the target (different color and different shape).

Further studies have shown that feature-based top-down control of saccades evolves over time (Ludwig & Gilchrist, 2003; Mulckhuysen et al., 2008; van Zoest & Donk, 2008; van Zoest, Donk, & Theeuwes, 2004). Accordingly, saccades with very short SRTs are much less influenced by top-down mechanisms than saccades with long SRTs. For instance, van Zoest and Donk (2008; van Zoest et al., 2004) asked subjects to saccade to a singleton target of a predefined feature that was embedded in a field of homogenous background stimuli. Along with the target, a second singleton (the distractor) was presented that could be more salient or less salient than the target. SRTs were ordered from fastest to slowest and for each SRT bin, the proportion of initial saccades directed to the target or the distractor was determined. Very fast saccades were often directed to the stimulus that was most salient, irrespective of whether this stimulus was the target or the distractor. However, the proportion of erroneous saccades to the distractor decreased with increasing SRT. In other words, the influence of saliency decreased over time and saccadic choice depended more and more on stimulus features. Thus, feature-based top-down influences on the oculomotor system may progressively increase over time. Note, however, that van Zoest and Donk (2008; van Zoest et al., 2004) only examined the influence of distractors dissimilar to the target. Therefore, it is not clear whether target features were enhanced or whether dissimilar features were inhibited. In particular, whether interference for similar distractors increases over time because of global feature-based enhancement of target features remains an open question.

Moreover, it has been established that saccades which land on the correct target show deviations of the saccade trajectory in the presence of distractors. With short SRTs, saccade trajectories deviate toward a distractor, whereas with long SRTs, saccade trajectories deviate increasingly away from the distractor (McSorley, Haggard, & Walker, 2006, 2009; Mulckhuysen, Van der Stigchel, & Theeuwes, 2009; Theeuwes & Godijn, 2004). These trajectory deviations away from a distractor are supposed to reflect location-based inhibition of the distractor (see Van der Stigchel, 2010 for a recent review). The observation that trajectories first deviate toward and later increasingly away from a distractor may be taken as evidence that distractor inhibition evolves over time. It is interesting that some studies suggest that feature-based mechanisms interact with distractor inhibition (Ludwig & Gilchrist, 2003; Mulckhuysen et al., 2009). At short SRTs, saccades deviate more strongly away from dissimilar distractors; at long SRTs, saccades deviate more strongly away from similar distractors. Mulckhuysen et al. (2009) assume that similar distractors may initially produce an enhanced distractor signal. Therefore, inhibition of similar distractors may not have advanced as much as for dissimilar distractors at short SRTs. To explain the larger deviations for similar distractors at long SRTs, they further suggest that similar distractors elicit stronger inhibition than dissimilar distractors. Although location-based inhibition was mostly invoked to account for saccade trajectory deviations, we assume that it may also affect other saccade parameters. In particular it may modulate the distractor effect found in SRTs. Under the assumption that the distractor inhibits the target directly (e.g., Godijn & Theeuwes, 2002; Munoz & Fecteau, 2002; Trappenberg et al., 2001), inhibition of the distractor should release the target from inhibition. That is, the slowing caused by

the distractor should decrease because the distractor loses its inhibitory effect on the target. As distractor inhibition grows over time, the distractor effect is expected to be weaker for slow than for fast saccades. In the alternative framework by Findlay and Walker (Findlay & Walker, 1999; Walker et al., 1997), similar modulations of the distractor effects are expected. Findlay and Walker suggested that distractors may slow saccades because the fixate system is activated. If the distractor is inhibited, activation of the fixate system should be reduced. Regardless of the exact model of oculomotor control, location-based inhibition of the distractor is expected to attenuate the slowing caused by the distractor.

In sum, previous research suggests that distractor interference may be shaped by two different mechanisms predicting opposite time courses for the effects of target-similar distractors. On the one hand global enhancement of target features is supposed to lead to increasing distractor interference. Note, however, that increasing interference from similar distractors over time, though plausible, has never been demonstrated. On the other hand, distractor interference may decrease over time due to increasing inhibition of the distractor location. These inhibitory processes may even be stronger for target-similar than dissimilar distractors.

The aim of the current study was twofold: First, we tried to isolate effects of global feature-based top-down control on saccadic eye movements to examine their time course. In particular, we hypothesize that distractor interference by similar distractors increases. Second, we investigated how location-based information interacts with feature-based control. The question is whether the same time-course for feature-based processing is obtained when the location carrying the relevant feature is inhibited. Although previous studies have already suggested interactions between feature- and location-based processes (Mulckhuysen et al., 2009), they never manipulated the balance between the two mechanisms. In contrast, we explore feature-based enhancement with strong and weak location-based inhibition. If the two mechanisms are independent, the time-course of feature-based enhancement is not expected to change. If, however, there is cross-talk between the two mechanisms, strong location-based inhibition may alter the time-course of feature-based control. To further bridge the gap between previous studies, effects of global feature-based modulations and location-based distractor inhibition were examined in the same saccade parameter: saccadic reaction time. Previous studies investigated feature-based modulations in error rates (i.e., percentage of saccades directed to the distractor) or SRTs and location-based inhibition in saccadic curvature (see above).

Essentially, we compared two fixed distractor locations: Experiment 1 examined the effect of foveal distractors to maximize the effects of global feature-based top-down control. With foveal distractors, location-based inhibition is expected to be small. The reason is that observers need to maintain fixation at the location of the foveal distractor until they have identified the target. Inhibition of the fixation region prior to target selection would result in increased oculomotor readiness (Findlay & Walker, 1999) with the likely consequence of anticipatory saccades or saccades going into the wrong direction. Therefore, we expect similarity effects with foveal distractors to reflect feature-based mechanisms with only little contamination from location-based inhibition. In Experiment 2 we used a peripheral distractor that appeared at a fixed location above the fixation line, but was never looked at by the participants.

This setting should create optimal conditions for modulations by location-based inhibition as the peripheral location of the distractor can be inhibited because it is never response-relevant.

Experiment 1

In Experiment 1 we examined how feature-based top-down control shapes the effects of foveally presented distractors over time. To create optimal conditions for feature-based top-down settings, we used a search task (see Born & Kerzel, 2009): On most trials, two peripheral stimuli (one gray, one green) were presented in opposite visual hemifields and observers had to saccade to a stimulus of a predefined target feature that was specified at the beginning of the experimental session. Sometimes, an additional foveal distractor was presented that was likewise either gray or green, that is, either target-similar or dissimilar. To investigate the effect over time, we varied target contrast. Target contrast has previously been shown to be very efficient in manipulating SRTs (Born & Kerzel, 2008; Ludwig, Gilchrist, & McSorley, 2004; White, Kerzel, & Gegenfurtner, 2006). We expect feature-based top-down control to prevail, because location-based inhibition of the fixation region prior to target selection would result in error saccades and hence should be weak.

Methods

Participants

Ten psychology students at the University of Geneva completed Experiment 1. All reported normal or corrected to normal vision and were naïve as to the purpose of the experiment. They ranged from 19 to 30 years of age.

Stimuli

The central fixation stimulus consisted of a horizontal black line of 3×1 pixels ($0.10^\circ \times 0.03^\circ$) on a gray background (CIE 1976 LUV coordinates: $l = 66$, $u' = 0.18$, $v' = 0.45$). Targets and distractors were Gaussian blobs with a standard deviation of 0.42° . They were either gray or green. The gray luminance-defined distractors were presented at 50% Weber contrast (with respect to the background), the green distractors were presented at 50% the color contrast our monitor was able to produce (peak values of the Gaussians in CIE 1976 LUV coordinates: $l = 33$, $u' = 0.18$, $v' = 0.45$ for the luminance, $l = 66$, $u' = 0.15$, $v' = 0.50$ for the color distractor). Targets were presented at three different contrast levels: high, medium, and low. We intended to equate SRTs for luminance and color targets in these three conditions. We previously found that a gray target presented at 50% Weber contrast produced faster SRTs than a green target at the 50% color contrast of our monitor (Born & Kerzel, 2009). For the gray luminance targets, we therefore chose contrasts of 50% ($l = 33$, $u' = 0.18$, $v' = 0.45$), 30% ($l = 46$, $u' = 0.18$, $v' = 0.45$) and 10% ($l = 59$, $u' = 0.18$, $v' = 0.45$) as high, medium and low contrast, respectively. The corresponding green targets were presented at 100% ($l = 66$, $u' = 0.12$, $v' = 0.56$), 70% ($l = 66$, $u' = 0.14$, $v' = 0.53$) and 50% ($l = 66$, $u' = 0.15$, $v' = 0.50$) color contrast. Note, however, that these values were chosen somewhat arbitrarily and were not tested in advance to produce similar SRTs.

Equipment

Stimuli were generated using a ViSaGe Visual Stimulus Generator (Cambridge Research Systems Ltd., Rochester, U.K.) and displayed on a Gamma-corrected 21" CRT monitor (Mitsubishi Diamond Pro 2070SB) running at 100 Hz. The screen's resolution was set to 1024×768 pixels and the viewing distance to 67 cm. Eye movements were recorded using a CRS High Speed Video Eyetracker (Cambridge Research Systems Ltd., Rochester, U.K.) at a sample rate of 250 Hz. The participant's head was stabilized by a chin and a forehead rest. Viewing conditions were binocular.

Design and Procedure

After a random fixation period of 500 – 1200 ms, the central fixation line disappeared and a target Gaussian was presented at 5° of eccentricity either to the left or right on the horizontal meridian. Targets could either be defined by luminance or color. The participants' task was to execute a saccade to the target as fast as possible. The target's defining feature (luminance/color) was blocked over trials. Moreover, targets were presented at high, medium or low contrast. The target could appear alone (no distractor control trials; 25%). However, on most trials (75%), a peripheral distractor of the other feature was presented on the opposite side (always at 50% luminance or color contrast). Thus, participants had to perform a search task: They had to select the target out of two possible peripheral stimuli (peripheral only condition). On 2/3 of these trials, an additional foveal distractor was presented along with the two peripheral stimuli. The foveal distractor was either similar (same defining feature) or dissimilar (opposite defining feature) from the target. The sequence of events is illustrated in Figure 1. Except for the target feature (which was blocked), all conditions (target direction: left/right, target contrast: high/medium/low and distractor condition: no distractor/peripheral only/foveal similar/foveal dissimilar) were varied orthogonally, randomly interleaved and presented with equal likelihood. Trials were separated by an intertrial interval of ~ 1 s. After invalid trials (for criteria see the next paragraph), an error message was presented that informed the participant about the type of error (anticipation, blink . . .) and stayed on for two seconds. The experiment was run in two 50-min sessions. The first session consisted of six blocks of 120 trials with a luminance target, the second session of six blocks with a color target or vice versa. Half the participants started with the luminance, half with the color target. The experimental procedure was approved by the ethics committee of the Faculty of Psychology and Educational Sciences of the University of Geneva.

Analyses

Gaze coordinates were recorded during the entire duration of a trial. Saccade onsets were detected using a velocity criterion of $30^\circ/s$ The first saccade with an amplitude $>1^\circ$ found in a prespecified time window (250 ms before and 600 ms after target onset) was considered as the saccadic response in a given trial. Trials were excluded, however, if no saccade was found within the time window, if the saccade was executed into the wrong direction, if the first saccade was anticipatory (i.e., if it occurred before stimulus onset or with an SRT <80 ms), if gaze deviated by more than 1.5° from the display center at the

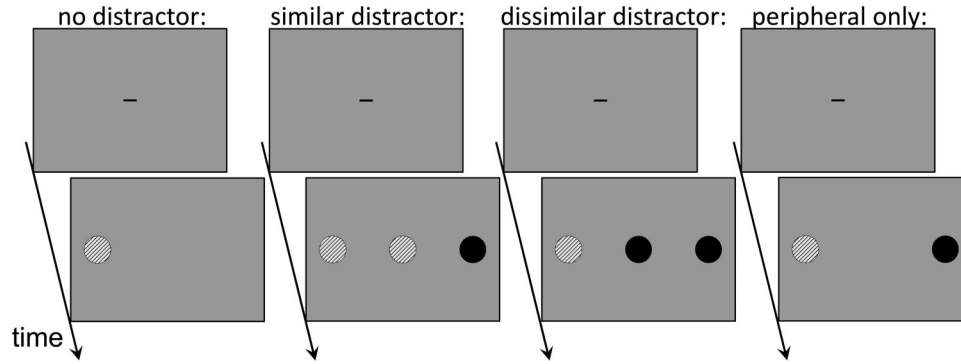


Figure 1. Sequence of events and conditions in Experiment 1. At the beginning of each trial, observers had to fixate the central fixation line. Upon appearance of the stimulus display, a saccade to the predefined peripheral target stimulus (here: the hatched circle; in the figure always presented to the left, in the actual experiment presented randomly to the left or right) had to be made. The target display was then followed by a blank screen during the intertrial interval. Targets and distractors were gray or green Gaussians symbolized by black and hatched circles (not drawn to scale). The target remained the same in a block of trials and four different conditions were presented randomly in a block: In no distractor trials, only the target was presented. In all other conditions, a second peripheral stimulus was presented in the opposite hemifield. Peripheral distractors were necessarily different from the target to provide a unique target. In the peripheral only condition, the target and a peripheral distractor were shown. In two other conditions, an additional foveal distractor was presented. Because the foveal distractor was at a nontarget location, it could be similar to the target (here: hatched) without causing confusion or dissimilar (here: black).

time of saccade onset (i.e., violation from the fixation instruction), if the saccadic landing position (horizontal gaze coordinate of the first sample with a velocity $<30^\circ$) deviated more than 1.5° from the center of the target or the eye tracker lost track between the beginning of the time window and the end of the saccade (e.g., as the result of a blink). Median SRTs in the various distractor and no distractor control conditions were computed for each participant.

Results

In total, 7.3% of all trials were classified as invalid and therefore discarded from analysis. The mean SRTs across individual median SRTs are illustrated in Figure 2. We first analyzed baseline SRTs in the no distractor control conditions (see dotted lines in Figure 2).

A 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium, low) repeated-measures analysis of variance (ANOVA) revealed a significant main effect of target contrast, $F(2, 18) = 38.31$, $p < .001$, confirming that our contrast manipulation was successful in varying SRTs (182 ms, 190 ms, and 203 ms for high, medium and low contrast, respectively). Further, there was a significant main effect of target feature, $F(1, 9) = 18.07$, $p = .002$, indicating that latencies were generally shorter for luminance (180 ms) than for color targets (204 ms). The interaction between target contrast and target feature did not reach significance, $F(2, 18) = 0.77$, $p = .479$.

We examined the impact of the foveal distractors in two different ways. First, we calculated similarity effects, that is, the differ-

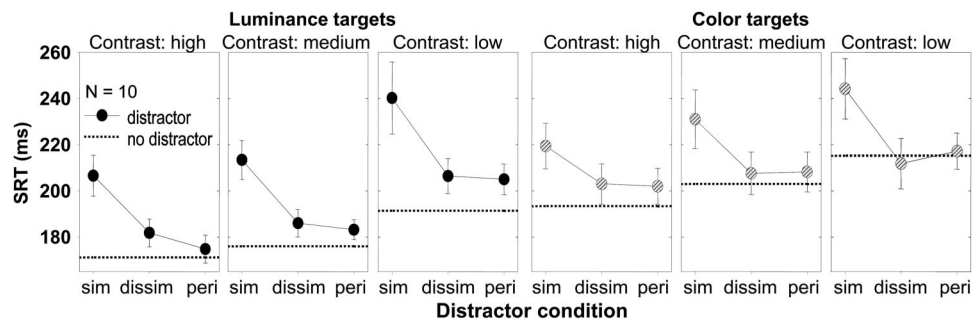


Figure 2. Saccadic reaction times (SRTs) as a function of target feature, target contrast, and distractor condition in Experiment 1. Dotted lines in the graphs mark the no distractor control conditions. Error bars show the 95% confidence interval of the difference between the respective distractor condition and the no distractor baseline (that is, if error bars do not cross the dotted lines, the respective condition shows SRTs significantly different from the no distractor condition, $p < .05$). Sim: similar condition, dissim: dissimilar condition, peri: peripheral only condition.

ence in SRT between similar and dissimilar distractor conditions. This comparison has the advantage of including equivalent conditions in which there were always three stimuli (one foveal and two peripheral). Second, we calculated the difference between the similar and dissimilar conditions and the peripheral only condition. Because there was no foveal distractor in this condition, one may consider the peripheral only condition as “neutral” to determine whether the additional foveal distractor caused facilitation or distraction. However, it is known that “neutral” conditions are often not what they pretend to be, mostly because the task demands in the “neutral” condition are different (de Gonzaga Gawryszewski, Riggio, Rizzolatti, & Umiltà, 1987; Jonides & Mack, 1984). Here, the peripheral only condition has one stimulus less than the similar and dissimilar conditions which may make the task easier. It is therefore not entirely clear whether increases or decreases in SRT relative to this condition result from facilitation or inhibition and the findings should be interpreted with caution.

Figure 2 suggests that similarity effects increased across contrast conditions. We tested this by subjecting the difference values (SRT in the similar condition – SRT in the dissimilar condition) to a 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium, low) repeated-measures ANOVA. A significant main effect of target contrast emerged, $F(2, 18) = 7.23, p = .005$, confirming stronger similarity effects with decreasing target contrast (21, 25, and 33 ms for high, medium and low contrast, respectively). Neither the main effect of target feature, $F(1, 9) = 0.76, p = .406$, nor the interaction between target feature and target contrast were significant, $F(2, 18) = 1.06, p = .366$.

To examine the impact of similar and dissimilar foveal distractors with respect to the peripheral only condition, we then ran 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium, low) repeated-measures ANOVAs on these difference values (SRT similar – SRT peripheral only; SRT dissimilar – SRT peripheral only). In particular, examining the effects of similar distractors is indicative of global feature-based top-down control. For similar distractors, both the main effects of target contrast, $F(2, 18) = 3.38, p < .057$, as well as target feature, $F(1, 9) = 4.56, p = .062$, approached significance. These effects indicate that overall, the interference from similar distractors increased slightly with

decreasing target contrast (25, 27, and 31 ms for high, medium and low contrast, respectively) and that overall, more interference from similar distractors was found in the luminance than color target condition (32 vs. 22 ms, respectively). The interaction between target feature and target contrast did not reach significance, $F(2, 18) = 1.71, p = .209$. For dissimilar distractors, both main effects reached significance: $F(2, 18) = 5.40, p = .015$, for target contrast and $F(1, 9) = 11.74, p = .008$, for target feature. As for similar distractors, the effect of target feature suggests more interference in the luminance than in the color target condition (4 vs. –2 ms, respectively). In contrast to similar distractors, the interference from dissimilar distractors got weaker with decreasing target contrast (4, 1, and –2 ms for high, medium and low contrast, respectively). The interaction between target feature and target contrast did not reach significance, $F(2, 18) = 0.51, p = .609$.

To consolidate that our results were due to increasing SRTs, and not decreasing target contrast, we ran the same analyses, but divided responses into fast and slow by median split. Separately for every participant, every target feature, target contrast, and distractor condition, we ranked SRTs from fastest to slowest and divided them into two equally sized bins (i.e., 50% fastest vs. 50% slowest responses). Figure 3 illustrates the results. Subjecting similarity effects to a 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium, low) \times 2 (SRT bin: fast vs. slow) repeated-measures ANOVA revealed a significant main effect of target contrast, $F(2, 18) = 10.69, p = .001$, confirming that similarity effects increased with decreasing target contrast (22, 27, and 32 ms for high, medium and low contrast, respectively). It is important that there was also a significant main effect of SRT bin, $F(1, 9) = 11.78, p = .007$, indicating that similarity effects were larger for slow (31 ms) than for fast responses (23 ms). The interaction between target contrast and SRT bin likewise reached significance, $F(2, 18) = 9.39, p = .002$, indicating that the effect of SRT bin on the similarity effect was strongest for low contrast targets and decreased with increasing contrast. No further effect reached significance.

When analyzing the difference values between the similar distractor condition and the peripheral only condition in a 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium,

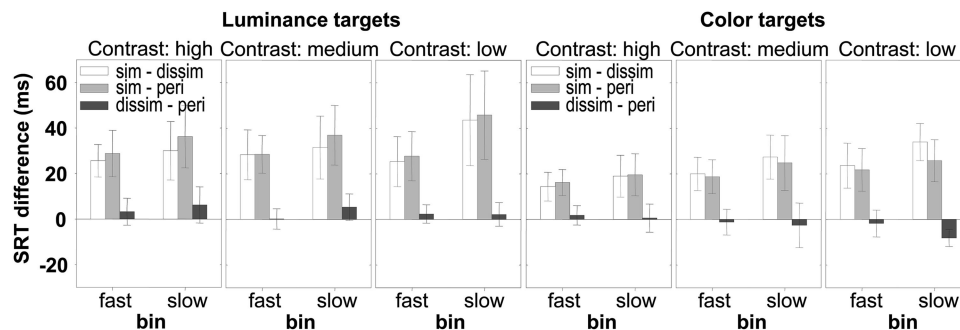


Figure 3. Saccadic reaction time (SRT) differences as a function of target feature, target contrast and SRT bin in Experiment 1. Sim–dissim: SRT in similar condition–SRT in dissimilar condition (similarity effect); sim–peri: SRT in similar condition–SRT in peripheral only condition; dissim–peri: SRT in dissimilar condition–SRT in peripheral only condition. Error bars represent the 95% confidence interval of the respective difference value (that is, if error bars do not cross the zero line, the respective SRT difference is significantly different from zero, $p < .05$).

low) \times 2 (SRT bin: fast vs. slow) repeated-measures ANOVA, we found a significant main effect of target feature, $F(1, 9) = 8.43$, $p = .018$, pointing to more interference from similar distractors in the luminance than color target condition (34 vs. 21 ms, respectively). The main effect of target contrast was only marginally significant, $F(2, 18) = 2.76$, $p = .090$, indicating a slightly increasing effect of similar distractors with decreasing target contrast (25, 27, and 30 ms for high, medium, and low contrast, respectively). It is important, however, that the main effect of SRT bin was significant, $F(1, 9) = 10.78$, $p = .009$, confirming that the impact of similar distractors increased with increasing SRT (24 ms for fast, 32 ms for slow responses). There was also a significant two-way interaction of target feature and SRT bin, $F(1, 9) = 5.59$, $p = .042$, showing that the increase across latency bins was larger in the luminance than in the color target condition. No further effect reached significance. Repeating the same analysis for dissimilar distractors, only the main effects of target feature, $F(1, 9) = 5.00$, $p = .052$, and target contrast, $F(2, 18) = 3.54$, $p = .051$, approached significance. These effects point to overall slightly more distractor interference in the luminance than color target condition (3 vs. -2 ms, respectively) and to a slightly decreasing distractor effect with increasing target contrast (3, 0, and -1 ms for high, medium, and low contrast, respectively). No further effect reached significance.

Discussion

Experiment 1 produced strong similarity effects: SRTs when a similar distractor was presented at fixation were substantially longer than when a dissimilar distractor was presented (see also Born & Kerzel, 2009). Moreover, similarity effects increased with decreasing target contrast. We interpret this result as a growing influence of global feature-based top-down control over time. In order to correctly execute the saccade, signals of all stimuli with target features are enhanced, while task-irrelevant features are inhibited. The temporal interpretation is supported by the additional analysis including SRT bins: within each contrast condition, the similarity effect was stronger for the 50% slowest responses than for the 50% fastest responses. Further, interference from similar distractors compared to the peripheral only condition increased over time: The effect of SRT bin showed that slower responses showed more distractor interference by a target-similar distractor (relative to peripheral only condition) than faster responses, suggesting that the target's features were globally enhanced. In contrast, interference from dissimilar distractors with respect to the peripheral only condition decreased slightly with decreasing target contrast, but there was no effect of SRT bins. Thus, evidence for inhibition of dissimilar features over time seems less robust. Note also, that our manipulation of foveal distractors was successful in the sense that location-based inhibition did not seem to play a prominent role. If progressive location-based inhibition of the distractor location was prevailing, then distractor effects should have decreased over time for both types of distractors (dissimilar and similar), but the results showed only a slight decrease for dissimilar distractors and the opposite effect for similar distractors.

Experiment 2

Experiment 1 showed that in a search task, distractor effects of foveal distractors were dominated by progressive enhancement of the target feature which caused larger distraction by target-similar stimuli over time. Location-based distractor inhibition, if present, could not override this effect. We conjecture that the lack of location-based inhibition is accounted for by our experimental design: foveal distractors do not permit inhibition of the distractor location until the saccade target has been found. Prior inhibition of the fixation region would have resulted in increased oculomotor readiness with the likely consequence of anticipatory saccades or saccades going into the wrong direction. An analysis of the error trials in Experiment 1 revealed that there were indeed very few of these errors (only 0.4% of trials could be classified as anticipations and 0.7% of trials were executed into the wrong direction). As a result, it is likely that very little prior inhibition at fixation was at play. In Experiment 2, we examined how inhibition of the distractor location may interact with feature-based top-down control over time. To this end, we examined the effect of a peripheral distractor presented at a fixed location above the fixation line.

Methods

Participants

Ten new psychology students at the University of Geneva completed Experiment 2. None of them had participated in Experiment 1. All reported normal or corrected to normal vision and were naïve as to the purpose of the experiment. They ranged from 18 to 24 years of age.

Design and Procedure

In Experiment 2, instead of a foveal distractor, we now presented a second peripheral distractor that was always placed at an eccentricity of approximately 3° of visual angle above the fixation line. Like the foveal distractor in Experiment 1, this additional peripheral distractor was either similar or dissimilar to the target. Participants were instructed that they should ignore this distractor and to fully concentrate on the stimuli on the horizontal meridian. The sequence of events is illustrated in Figure 4. As before, targets were presented at high, medium, or low contrast. In all other respects (design, stimulus parameters, equipment, and analyses), Experiment 2 was identical to Experiment 1.

Results

In total, 10.7% of all trials were classified as invalid and therefore discarded from analysis. The results of Experiment 2 are illustrated in Figure 5. Again, baseline SRTs in the no distractor control conditions increased with decreasing target contrast (187, 193, and 210 ms for high, medium and low contrast, respectively), $F(2, 18) = 65.95$, $p < .001$, and SRTs were shorter for luminance (185 ms) than for color targets (209 ms), $F(1, 9) = 23.75$, $p = .001$. The interaction between target contrast and target feature did not reach significance, $F(2, 18) = 1.67$, $p = .217$.

In contrast to Experiment 1, Figure 5 suggests that similarity effects did not increase across contrast conditions. A 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium,

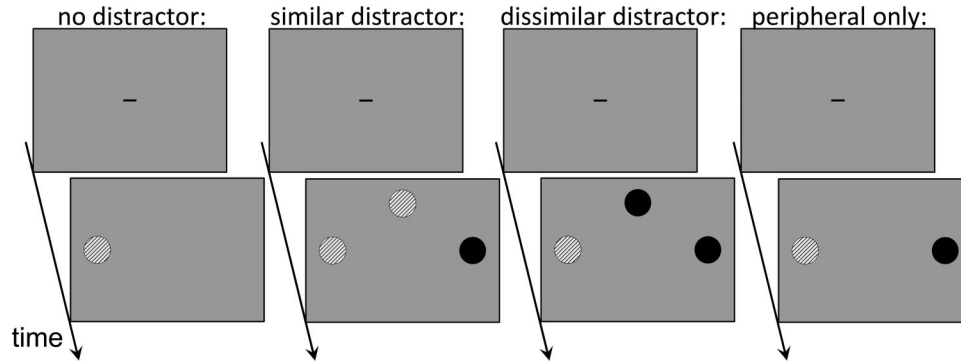


Figure 4. Sequence of events and conditions in Experiment 2. The task was the same as in Experiment 1 (saccade to the hatched target). However, instead of a foveal distractor, an irrelevant peripheral distractor 3° above the fixation line could be presented that was either similar or dissimilar to the target. Conventions as in Figure 1.

low) repeated-measures ANOVA on the similarity effects confirmed that there was no significant main effect of target contrast, $F(2, 18) = 0.09, p = .916$. Likewise, neither the main effect of target feature, $F(1, 9) = 3.07, p = .114$, nor the interaction between target feature and target contrast were significant, $F(2, 18) = 1.27, p = .305$. Overall, the similarity effect was 18 ms.

Subtracting SRTs in the peripheral only condition from the SRTs in the similar and dissimilar distractor conditions and analyzing these difference values in 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium, low) repeated-measures ANOVAs revealed the following results: For similar distractors, only the main effect of target feature reached significance, $F(1, 9) = 27.76, p = .001$, indicating again stronger interference from similar distractors in the luminance target condition (17 ms) than in the color target condition (5 ms). The main effect of target contrast (20, 20, and 11 ms for high, medium, and low contrast, respectively), $F(2, 18) = 1.31, p = .295$, as well as the interaction between target feature and target contrast, $F(2, 18) = 2.56, p = .105$, did not reach significance. The same was true for dissimilar distractors: there was a significant main effect of target feature, $F(1, 9) = 56.81, p < .001$. Figure 5 indicates that this main effect was due to dissimilar distractors in the color target condition producing shorter SRTs than in the peripheral only condition (-15 ms), whereas small interference effects were found in the luminance condition (1ms). No significant main effect of target contrast

was found (-6 ms, -6 ms, and -9 ms for high, medium, and low contrast, respectively), $F(2, 18) = 1.40, p = .273$, and the interaction between target feature and target contrast did not reach significance, $F(2, 18) = 1.10, p = .356$.

Including SRT bin as a factor in the analyses revealed the following results that are illustrated in Figure 6. The 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium, low) \times 2 (SRT bin: fast vs. slow) repeated-measures ANOVA on the similarity effects only revealed that the interaction between target contrast and SRT bin approached significance, $F(2, 18) = 3.12, p = .068$. Figure 6 suggests that similarity effects slightly increased for slower compared to faster responses in the high contrast conditions, but slightly decreased for slower responses in the low contrast conditions. No further effect reached significance.

When analyzing the difference values between the similar distractor condition and the peripheral only condition in a 2 (target feature: luminance vs. color) \times 3 (target contrast: high, medium, low) \times 3 (SRT bins: fast vs. slow) repeated measures ANOVA, we found a significant main effect of target feature, $F(1, 9) = 24.12, p = .001$, indicating overall more interference in the luminance than color target condition (17 vs. 5 ms, respectively). There was also a marginally significant main effect of target contrast, $F(2, 18) = 3.45, p = .054$, revealing overall slightly decreasing interference from similar distractor with decreasing target contrast (13, 13, and 8 ms for high, medium, and low contrast, respectively). No

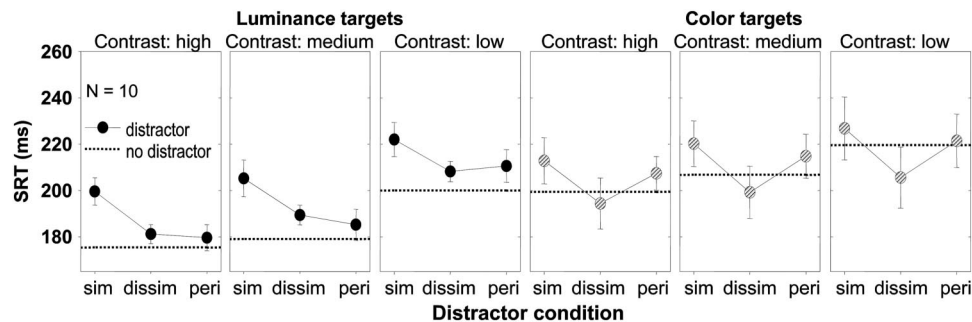


Figure 5. Saccadic reaction times (SRTs) as a function of target feature, target contrast, and distractor condition in Experiment 2. Conventions as in Figure 2.

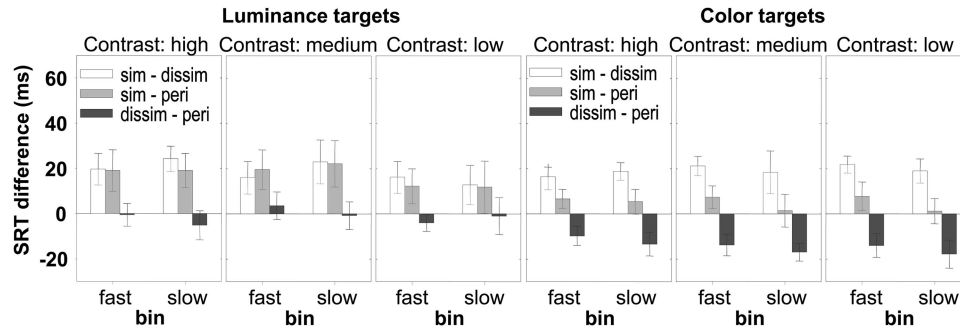


Figure 6. SRT differences as a function of target feature, target contrast, and SRT bin in Experiment 2. Conventions as in Figure 3.

further effect reached significance. For dissimilar distractors, we also found a significant main effect of target feature, $F(1, 9) = 45.81$, $p < .001$, revealing less interference, or rather more facilitation in the color than luminance target condition (-14 vs. -1 ms, respectively). There was also a marginally significant main effect of SRT bin, $F(1, 9) = 3.73$, $p = .086$, pointing to slightly more facilitation from dissimilar distractors for slow than fast responses (-9 vs. -6 ms, respectively). Further, the interaction between target feature and target contrast was marginally significant, $F(2, 18) = 3.14$, $p = .067$. Figure 6 suggests that for luminance targets, dissimilar distractors were most disruptive at the medium contrast level, whereas for color targets, facilitation increased with decreasing target contrast.

Discussion

As in Experiment 1, we also found similarity effects in Experiment 2. However, the similarity effects did not increase with decreasing target contrast or slower responses. Experiment 1 showed that the influence of foveal distractors is progressively modulated by global feature-based mechanisms. In particular, interference from target-similar distractors increased over time. The present experiment shows that distractor presentation at a response-irrelevant location that allows for location-based distractor inhibition results in a different time course. We presume that distractor inhibition interacted with the build-up of feature-based processes. More precisely, location-based inhibition may have opposed the enhancement of similar distractors, keeping the magnitude of the similarity effects constant over time. Note, that some weak trends toward decreasing distractor interference with low target contrast or slower responses could be observed with dissimilar as well as similar distractors. Dissimilar distractors in the color target condition even showed facilitation effects, that is, SRTs were shorter with the additional distractor than in the peripheral only condition and sometimes even shorter than in the no distractor control trials (see Figure 5). Similar facilitation effects have already been reported for foveal and peripheral distractors when presenting the distractor prior to the target (Ross & Ross, 1980; Walker et al., 1995; Wijnen & Ridderinkhof, 2007) or when presenting a foveal distractor at much higher contrast than the target (Born & Kerzel, 2008). We only found facilitation for the dissimilar (luminance-defined) distractors in the color target condition. At the moment, we can only speculate about why this was

the case. For instance, it may play a role that luminance stimuli are processed faster than color stimuli (see Bompas & Sumner, 2008 for a review of related findings). Thus, the luminance distractors may have elicited facilitation effects because their corresponding signals arrived earlier in the oculomotor system than the color signal from the target (see also Born & Kerzel, 2011). Further, one may speculate whether facilitation effects may only be elicited by stimuli that do not possess features relevant for target selection.

General Discussion

Feature-Based Top-Down Control Over Time

In the present study, we examined the influence of feature-based top-down modulations of saccadic distractor effects over time. Previous research suggested that feature-based top-down modulations in the oculomotor system may increase with increasing SRTs (van Zoest & Donk, 2008; van Zoest et al., 2004). However, up to now, no evidence has been reported for increasing interference from target-similar distractors over time to support global feature-based enhancement of task-relevant features. Our results confirm strong feature-based top-down modulations of saccadic distractor effects. In our search task, the distractor effects for target-similar foveal (Experiment 1) and irrelevant peripheral (Experiment 2) distractors were larger than for dissimilar distractors. It was important that the similarity effect for foveal distractors increased with decreasing contrast and increasing SRTs. Moreover, analyses of the difference between similar and dissimilar distractors and the peripheral only condition indicated that the stronger similarity effects over time were not only due to a decreasing influence of the dissimilar distractors. Analyses across contrast levels as well as SRT bins suggested that the distractor effect for similar foveal distractors increased with increasing SRT. We conclude that ongoing feature-based target selection processes modulate neuronal activity in the oculomotor system: the signals of all stimuli possessing task-relevant target features are progressively enhanced to insure correct saccades to the target. At the same time, this mechanism also strengthens interference from similar distractors.

Interactions Between Feature-Based and Location-Based Top-Down Control Over Time

Whereas the similarity effects increased over time for foveal distractors in Experiment 1, they did not change over time for peripheral distractors with fixed location. In Experiment 2, distractor effects for similar and dissimilar distractors showed small tendencies to decrease. The decrease was equivalent for the two distractor types, keeping similarity effects constant. We suggest that location-based inhibition of the distractor signal interacted with feature-based modulations. Progressive enhancement of similar distractors was overlaid by increasing location-based distractor inhibition. According to studies examining saccade trajectory deviations, location-based inhibition of similar distractors may even be stronger than for dissimilar distractors with the result that similarity effects decrease and even reverse over time (Ludwig & Gilchrist, 2003; Mulckhuysen et al., 2009). One may have expected then, that similarity effects also decrease over time in Experiment 2. However, when comparing results from different saccade measures (e.g., trajectory deviations vs. SRTs), one has to consider that the different measures may reflect slightly different underlying neurophysiological or model parameters. For instance, saccade trajectory deviations are thought to reflect the state of activation at the distractor location at the time of saccade onset, that is, at a precise moment in time (e.g., McSorley et al., 2009; Van der Stigchel, 2010). In contrast, distractor effects in SRTs are more likely to reflect the sum of all distractor-related influences on the target signal during the entire period between target onset (or sometimes even prior to target onset) and saccade initiation. Assuming for instance a rise-to-threshold model in which a saccade toward the target is initiated when the target signal has reached a critical threshold (e.g., Carpenter & Williams, 1995), all influences that speed up or prolong the rise-to-threshold affect when the saccade is initiated. Accordingly, the effect of similar distractors in our Experiment 2 may have been shaped by two antagonistic processes: feature-based enhancement and location-based inhibition. For dissimilar distractors, however, both processes pointed into the same direction: feature-based inhibition was coupled with location-based inhibition. Assuming that location-based inhibition was stronger for similar than dissimilar distractors (Mulckhuysen et al., 2009), the net changes over time or contrast might have been the same for similar and dissimilar distractors. In consequence, the finding that similarity effects did not decrease over time in Experiment 2 does not speak against but supports the hypothesis that location-based inhibition is stronger for similar distractors.

Note, that although they did not change with time, we did observe similarity effects in Experiment 2 even for the fastest SRTs. This suggests that feature-based mechanisms seemed to have prevailed early in time and were later modulated by location-based inhibition, masking or even overriding the progressive feature-based control observed in Experiment 1. Our idea that location-based inhibition grows after target onset may seem at odds with neurophysiological (e.g., Basso & Wurtz, 1998; Dorris & Munoz, 1998) as well as behavioral findings (McSorley et al., 2009; Rolfs & Vitu, 2007; Van der Stigchel & Theeuwes, 2006) which suggest that prior knowledge of target or distractor location influences activity in the saccade map already before stimulus onset. Along these lines, one may presume that the location of our peripheral distractor is inhibited in advance. Any incoming dis-

tractor signal is then added to a lower baseline level of activity. While such mechanisms may have been at play in Experiment 2, we believe that it is not the only inhibitory influence on the distractor signal. Work on saccade trajectory deviations has demonstrated that inhibition at the distractor location (i.e., deviations away from the distractor) is stronger when the distractor is actually present compared to a condition in which the distractor is not present, but was expected to appear (Van der Stigchel & Theeuwes, 2006). This suggests that there is an additional inhibitory mechanism that affects the incoming distractor signal. Assuming that the strength of this “reactive” inhibition changes with feature-based information (stronger inhibition of target-similar distractors; Mulckhuysen et al., 2009), it is likely that it operates either in the same or even a later time window than global feature-based enhancement and inhibition.

Beyond Oculomotor Research

Our results may not only relate to observations from oculomotor research. Spatial cuing studies suggest that a cue may only capture attention when its features match the observer’s current attentional control setting (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). In other words, spatial cues may only affect manual reaction times when they are similar to the target. Some studies looked at the time course of the spatial cuing effect by varying the SOA between cue and target, albeit only for nonmatching (i.e., dissimilar) cues (Folk & Remington, 1998; Theeuwes, Atchley, & Kramer, 2000). Ansoorge and Heumann (2003; Experiment 3) examined the time course of similar cues that never matched the location of the subsequent target. They found decreasing interference of the cue over time. This is in line with the results of our Experiment 2; as the cue was never presented at the target location in their experiment, it could be progressively inhibited by a location-based mechanism. Gibson and Amelio (2000) examined whether inhibition of return (IOR, i.e., the slowing of a manual or saccadic response after a long cue-target interval) is likewise contingent on top-down control settings. They found IOR in manual RTs when an onset target was preceded by an onset cue, but no IOR for a color cue; neither cue produced IOR with a color target. One may speculate whether IOR may be related to the location-specific inhibition processes that we address in the current study.

Further, interactions between feature-based and location-based top-down control have been reported in preview search tasks measuring manual RTs. In preview search, participants typically have to perform a conjunction search: the target is defined by a combination of two features. For instance, participants have to indicate the presence of a blue *H* among green *H*s and blue *A*s (Watson & Humphreys, 1997). When one set of distractors (the green *H*s) was presented (“previewed”) 1000 ms before the remaining stimuli were added to the display (including the target, if present), search was as efficient as if the green *H*s were not present at all. The authors explained this preview benefit by assuming that the previewed items can be inhibited through a location-specific mechanism that they called visual marking. In a subsequent study (Watson & Humphreys, 2005), they also showed that the onset of irrelevant distractor disks after preview display onset (the green *H*s) but prior to the onset of the target display (the addition of the blue *A* distractors with the blue *H* target, if present) can disrupt the

location-based inhibition of the previewed items, but only when the distractor disks share the target color (blue). They concluded that the onset of irrelevant distractors that match an anticipatory set for a specific target feature can disrupt the location-specific visual marking. However, onsets that did not match the target feature set did not disrupt preview search. Along these lines, in our Experiment 2, only the onset of the similar distractor may have disrupted the inhibition of the distractor location. Consequently, similar distractors produced interference, whereas dissimilar distractors did not. Note, however, that the facilitation effects found for luminance distractors in the color target condition in our Experiment 2 suggest that dissimilar distractors were not simply ignored, but could be used to speed up the saccadic response.

Conclusions

In sum, we found evidence for the presence and interactions of various top-down control mechanisms that mediated distractor effects over time. For foveal distractors, feature-based target-distractor similarity effects prevailed and increased over time. The distractor effect for target-similar distractors increased with increasing SRTs, while the effect of target-dissimilar distractors stayed relatively constant or decreased slightly. For peripheral distractors, we likewise found effects of target-distractor similarity. However, they did not increase over time but were overlaid by another top-down control mechanism. We argue that this mechanism is location-specific and corresponds to distractor inhibition previously described in studies measuring saccade trajectory deviations. To conclude, top-down control of saccadic eye movements is a highly heterogeneous phenomenon. Different mechanisms may be flexibly engaged to optimize performance according to task demands.

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