

Perceptual enhancement prior to intended and involuntary saccades

Michael Puntiroli

Faculté de Psychologie et des Sciences de l'Éducation,
Université de Genève, Switzerland



Dirk Kerzel

Faculté de Psychologie et des Sciences de l'Éducation,
Université de Genève, Switzerland



Sabine Born

Faculté de Psychologie et des Sciences de l'Éducation,
Université de Genève, Switzerland
Laboratoire Psychologie de la Perception, UMR 8242,
Université Paris Descartes, France



Prior to an eye movement, attention is gradually shifted toward the point where the saccade will land. Our goal was to better understand the allocation of attention in an oculomotor capture paradigm for saccades that go straight to the eye movement target and for saccades that go to a distractor and are followed by corrective saccades to the target (i.e., involuntary saccades). We also sought to test facilitation at the future retinotopic location of target and nontarget objects, with the principal aim of verifying whether the remapping process accounts for the retinal displacement caused by involuntary saccades. Two experiments were run employing a dual-task design, primarily requiring participants to perform saccades toward a target while discriminating an asymmetric cross presented briefly before saccade onset. The results clearly show perceptual facilitation at the target location for goal-directed saccades and at the distractor location when oculomotor capture occurred. Facilitation was observed at a location relating to the remapping of a future saccade landing point, in sequences of oculomotor capture. In contrast, performance remained unaffected at the remapped location of a salient distracting object, which was not looked at. The findings are taken as evidence that presaccadic enhancement occurs prior to involuntary and voluntary saccades alike and that the remapping process also indiscriminately accounts for the retinal displacement caused by either.

Introduction

Vision science strives to determine how attention is distributed over objects in our surroundings, the relation this distribution has with upcoming eye movements, and the information that is extracted during the process. The allocation of covert attention is a competitive process jointly influenced by bottom-up and top-down factors (Cave & Wolfe, 1990; Wolfe, 1994), in which each perceived object is processed according to local salience-based features (e.g., brightness) and weighted by task relevance (H. J. Müller & Krummenacher, 2006; Zehetleitner, Proulx, & Müller, 2009). Accordingly, when salient objects are displayed along with a search target, they compete for attentional resources and have been shown to cause substantial interference (Bacon & Egeth, 1994; S. I. Becker, 2007; Fecteau & Munoz, 2006; Folk & Remington, 1998; Folk, Remington, & Johnston, 1992; Lamy, Tsai, & Egeth, 2003; Theeuwes, 1991, 1992; Yantis & Hillstrom, 1994). For example, it will be more difficult to look for a target triangle in a set of squares, when one of the squares is of an outstanding color or brightness. In studies requiring a rapid eye movement to the search target, the eyes may even be inadvertently directed toward such a salient distracting object (oculomotor capture; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). But do distractors that attract the eyes also benefit from enhanced perceptual processing prior to the execution of the involuntary saccade?

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Shifts of attention before involuntary saccades

Presaccadic shifts of attention found specifically at locations where the targets of intentional saccades were displayed (Deubel & Schneider, 1996; Schneider & Deubel, 2002) demonstrate the tight coupling between attention and saccades. Just before a voluntary eye movement, attention is narrowly focused (Zimba & Hughes, 1987), centered almost exclusively around the saccade target location (Kowler, Anderson, Doshier, & Blaser, 1995), and the corresponding perceptual facilitation effects continue to increase up until the moment the eye movement is initiated (Deubel, 2008; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). However, it is less clear where attention is directed when the eyes are captured by a salient distracting object in a purely bottom-up fashion.

Peterson, Kramer, and Irwin (2004) argued that attention briefly visits the capturing object before subsequently being directed to the target. They presented a probe (a C or mirror C) at the capture location that was either compatible or incompatible with the subsequent response to the target (likewise, a C or mirror C; presented as a color singleton). On capture trials, they found longer manual response times to the target when a compatible probe was presented at the capture location, compared with incompatible trials. The authors argued that attention visited the distractor, thus explaining the counterintuitive reverse compatibility effects. However, others (see, for example, Eimer & Schlaghecken, 2003) relate reverse compatibility effects to response processes and not to perceptual or attentional factors. Moreover, Zhao, Gersch, Schnitzer, Doshier, and Kowler (2012) explain how fixating a target offers no guarantee that it will be attended. Aspects of objects are more frequently missed when they are irrelevant to the task, proving that integrated object representations are not an inevitable consequence of an eye movement fixation (Droll, Hayhoe, Triesch, & Sullivan, 2005). In fact, particular visual routines dependent on the immediate behavioral context may allow only information required at a given moment to be extracted (Hayhoe, 2000). This could be the case in oculomotor capture, in which, despite an (involuntary) saccade being made, the perceptual representation of the object at the saccade endpoint (i.e., the salient distractor) may remain poor. Our first question thus concerned presaccadic perceptual facilitation effects at distractor locations.

Predictive remapping of targets and nontargets

A second question concerns presaccadic enhancement at other nontarget locations. Mechanisms that can cause a shift of attention to nontarget locations in preparation

of upcoming saccades have been documented in recent years. Predictive remapping relates to the change in spatial profile of the receptive fields of neurons at the time immediately preceding the saccade (Burr & Morrone, 2011; Hall & Colby, 2011; Wurtz, Joiner, & Berman, 2011). Remapping was first documented by Duhamel, Colby, and Goldberg (1992) and is thought to allow us to keep track of interesting parts of a scene while compensating for eye movements (Cavanagh, Hunt, Afraz, & Rolfs, 2010; for overview, see Mathôt & Theeuwes, 2011). Remapping, as a theoretical stance, would posit that just before we make an eye movement to an intended location, an interesting stimulus in our visual display that draws attention to it will be remapped. The neuronal activation associated with the stimulus's position on the retina would find itself at a completely irrelevant position, once the eye movement is completed, if it were not remapped. For that reason, just before the movement is initiated, the neural activation is partly shifted in the direction opposite to the upcoming movement. The direction and amplitude of the upcoming saccade is used to shift the activation (associated with attention found at the interesting stimulus) in the opposite direction from it. This allows the activation to once again coincide with the stimulus's location when the eyes land on their destination (Cavanagh et al., 2010). Moreover, Jonikaitis, Szinte, Rolfs, and Cavanagh (2013) found that a salient nontarget object can be predictively remapped, so as to keep track of it after the saccade.

A particular case for remapping of relevant objects can be seen in the remapping of eye movement targets in saccade sequences: Before a sequence of saccades is initiated, attention is not only allocated to all future saccade targets (Baldauf & Deubel, 2008; Godijn & Theeuwes, 2003), but their locations are predictively remapped, such that perceptual enhancement has been found at nontarget locations (Rolfs et al., 2011).

The two specific remapping situations mentioned above will be examined in the current study. The first experiment will examine the remapping of a nontarget object, similarly to that in Jonikaitis et al. (2013), with the difference that here the object being remapped is a distractor competing for resources with the target. It is unclear whether a rejected distractor (one that does not capture gaze) is remapped, as it may not serve a particular purpose for it to be treated differentially after the eye movement is completed. Much will depend on whether the rejected distractor location is enhanced or suppressed. The second experiment will examine remapping when a sequence of two saccades is made, much like in Rolfs et al. (2011), but rather than two intended saccades, the sequence will be made up of one involuntary saccade to the distractor, followed by one intended saccade to the target. It is unclear what happens to the perceptual enhancement effects related to predictive remapping in the context of oculomotor

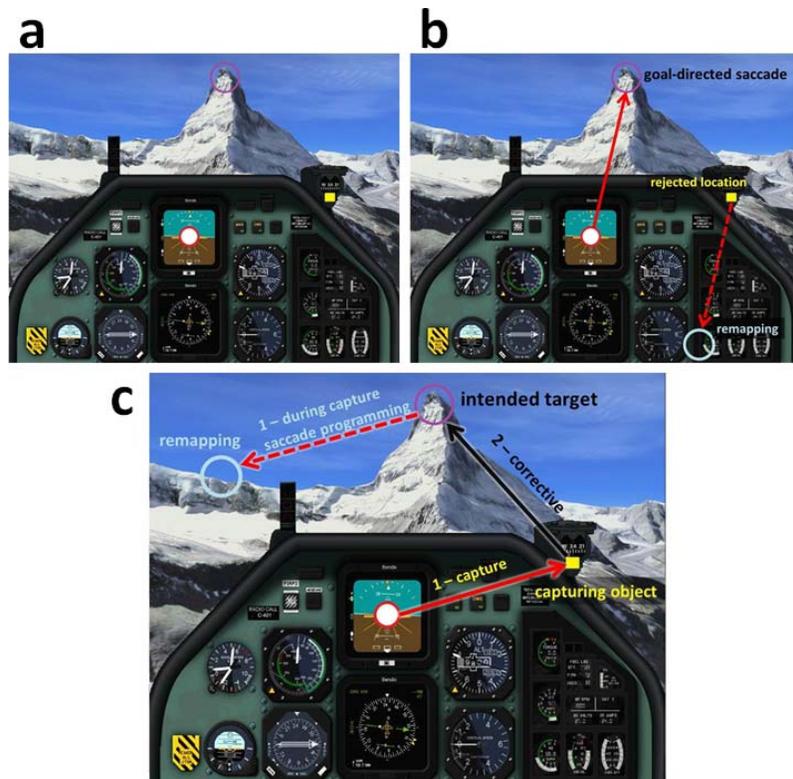


Figure 1. Predictive remapping. (a) While fixating the central indicator on the cockpit (white circle), the pilot proceeds to shift gaze to the nearest mountain summit (purple circle), to assess possible danger. Just before moving the eyes, a flash appears (yellow square) beneath the magnetic compass in the upper right corner. (b) The pilot manages to move his eyes to the summit (goal-directed saccade) and ignore temporarily less useful information (flash). Before saccade initiation, the flash is registered by a population of neurons with receptive fields at this location. To keep track of the flash, activity at this location is remapped to a novel location (white circle) corresponding to a population of neurons with receptive fields at the retinal location the flash will have after the saccade. This way, attention is maintained on points of interest across saccades. (c) The flash captures the pilot's gaze, inducing an involuntary eye movement toward it. The eyes briefly visit this location (1-capture) before being diverted to their intended location (2-corrective). If attention also briefly visits this location, the intended target (the summit) may be remapped to a novel location (white circle) relative to the first saccade so that attention is placed on the summit once the eyes land on the flash.

capture. That is, whether attention is allocated almost exclusively to the saccade target (the intended landing point) with visual attention largely ignoring the capturing location and not accounting for the retinal displacement caused by this first, involuntary, saccade. In this case, facilitation at the remapped location of the saccade target would not be found at a location relative to the initial capturing saccade. Alternatively, attentional resources would be allocated to both saccade landing points (distractor and saccade target) and in sufficient measure to allow for the remapping of the saccade target to lead to perceptual benefits. Mirpour and Bisely (2012) conducted a single-cell study using memory-guided saccades. They found that the remapping-related activation was stronger when there was a reward associated with fixating a particular stimulus (i.e., the object being remapped). This highlighted the fact that the remapping process is sensitive to the amount of activation found at the area of interest. There may well be quantitative differences in remap-

ping activation depending on the status of the object being remapped (target or not, suppressed or not). Furthermore, involuntary saccades may be associated with less attentional enhancement, thus having an impact on perceptual effects related to remapping.

Purpose of study

We explicitly tested the allocation of attention at target and nontarget locations by probing critical locations with briefly flashed stimuli requiring a discrimination choice. We compared involuntary to voluntary saccades and also compared the time course of the two. Second, we explored remapping effects expecting (a) facilitation at the remapped location of a salient object when a straight-to-target saccade is performed (seen in Jonikaitis et al., 2013; see Figure 1b), (b) the remapping mechanism to account for the retinal displacement caused by

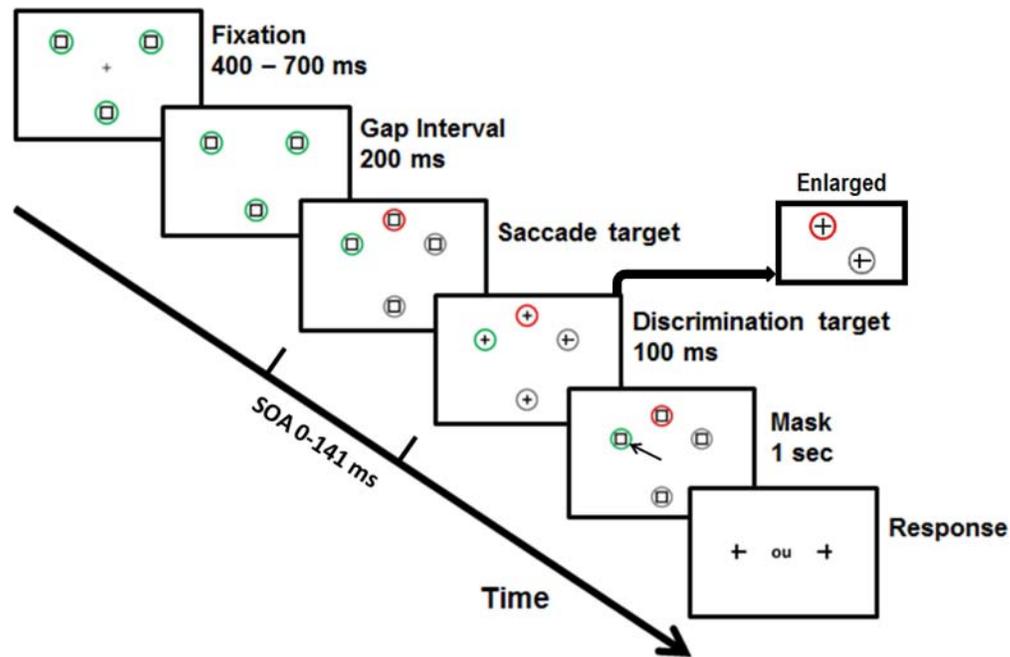


Figure 2. Sequence of events in Experiment 1. All stimuli were initially presented on screen in the assigned saccade target color (green in the example). Gaze had to remain within 1.5° of the fixation cross, which disappeared after a random delay of 400 to 700 ms. After 200 ms of its disappearance, the display color change occurred, leaving only one object of the assigned color (saccade target). On 75% of trials, a distractor (red in this example) appeared at a previously unoccupied location (in between two of the presented objects). The discrimination target was an asymmetric cross (in the example shown at the gray placeholder position to the right of the distractor, where the remapping of the distractor in retinotopic coordinates is thought to take place; see enlargement) flashed for 100 ms in one of the objects and was displayed after one of seven possible SOAs (0–141). After eye movements, participants stated whether the vertical bar of the asymmetric cross was displaced to the left or right (left in the illustration).

involuntary saccades as it does for voluntary saccades (seen in Rolfs et al., 2011; see Figure 1c), and (3) greater facilitation for the remapping of a saccade target than for a salient object, as the remapping mechanism has shown greater enhancement associated with highly attended, meaningful locations (seen in Mirpour & Bisley, 2012).

Experiment 1

Experiment 1 was designed to assess the presaccadic allocation of attention at target and nontarget locations in straight-to-target saccades and in capture saccades. Although we employed a modified version of a widely used oculomotor capture paradigm (e.g., Born, Kerzel, & Theeuwes, 2011; Theeuwes et al., 1998; Theeuwes et al., 1999), the amount of capture trials per participant (less than 5% of total trials) was not sufficient to allow adequate testing of our hypotheses for capture sequences. Still, we could explore how the presence of an onset distractor affects performance in target-directed saccades, both at the distractor location and

all other locations, including the remapped location of the distractor.

Methods

Participants

Fourteen participants, all female, aged between 19 and 26 years, took part in Experiment 1. All were psychology students from the University of Geneva. All participants received course credits for their efforts.

Apparatus

The experiment was written in Matlab 2011b (The MathWorks Inc., Natick, MA) using the Psychophysics and EyeLink Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) and run on a Dell Optiplex 755 system. The stimuli were displayed on a 21-inch CRT monitor (NEC MultiSync FE2111SB), which ran on 85 Hz and was set to 1280×1024 pixels. Viewing distance was 50 cm, allowing approximately 30 pixels per degree of visual angle. The EyeLink1000 desk-mounted eye tracker was used to record eye movements (SR Research Ltd., Mississauga, Ontario, Canada) at a

sampling rate of 1000 Hz. Participants were seated in a dimly lit room and placed their head within a fixed chin and forehead rest. Movements from only the right eye were recorded.

Stimuli

We employed a fixation cross consisting of two gray lines subtending approximately $0.3^\circ \times 0.3^\circ$. Stimuli were presented at 5° from the center of the screen. Circles were drawn with a radius of 1.5° and pen width of 0.33° (10 pixels). Crosses and masking squares were made up of bars of $1.4^\circ \times 0.17^\circ$. The stimuli in the display were gray, green, or red, 36.4, 29.9, and 16.3 cd/m^2 , respectively, displayed on a gray background of 25.8 cd/m^2 .

Design and procedure

The sequence of events in the main experimental blocks is illustrated in Figure 2. Participants had to carry out a dual task: directing a saccade toward a color singleton circle while simultaneously performing a perceptual discrimination task. Initially, the fixation cross and three colored circles were presented (green or red; counterbalanced across participants). After a variable delay of 400 to 700 ms, the fixation cross disappeared, leaving all other stimuli unaltered. This was done to facilitate low reaction times by bypassing the ocular fixation reflex (gap paradigm; Saslow, 1967). Following this gap interval lasting 200 ms, only one circle remained colored and served as the saccade target, whereas the other two circles turned gray. A distractor circle appeared on screen on 75% of the trials and was presented at a previously empty location when the color change in the other circles occurred. In the “green” group, the saccade target was green, whereas the distractor was red, and in the “red” group, these colors were inverted. Light gray crosses subsequently appeared within the circles at a variable delay (0, 24, 47, 71, 94, 118, or 141 ms). One of these crosses was asymmetric and served as the discrimination target: Its vertical bar was slightly shifted to the left or right. It was initially offset at 0.3° from the center, and a 2-down 1-up staircase rule was employed throughout the experiment, with a step size of 0.1° and a minimum offset fixed at 0.05° if the staircase ran down to 0° . This procedure ensured discrimination across all trials at approximately 71% correct for each participant. The asymmetric cross could appear in any of the stimulus locations (saccade target, distractor, or a placeholder circle). All crosses were presented for 100 ms and then masked. When the saccade had been executed within the afforded time window ($<600 \text{ ms}$) and the masking squares displayed for 1 s, the participant was required to

identify the correct perceptual target (left or right shift) flashed during the trial by tapping one of two buttons on a PC keyboard. Auditory feedback (tone) was received whenever the response was not correct. On-screen feedback was also received at the end of each trial, whenever eye movement errors were made (see below for criteria).

Participants initially carried out four single-task blocks. The initial two were saccade-only blocks in which the goal was to perform a rapid saccade to the circle that did not change color, training saccade target identification and speed of execution. These were followed by two discrimination-only blocks in which gaze was kept locked on the central fixation cross while covertly attending to the stimuli. The task objective was to detect the briefly flashed asymmetric cross present at one of the locations, with the aim of getting participants used to perceiving the discrimination target without having to make eye movements. Once the training was completed, the dual-task, combining both single tasks, was carried out. Participants were instructed to move their eyes as fast and accurately as possible to the saccade target and that correct ocular movements were the primary task.

The experiment lasted 4 hr, including the training session mentioned above, and was distributed over four sessions on separate days. Each block was made up of 105 trials, and participants ultimately carried out a differing number of blocks (ranging from 9 to 15 blocks) depending on the speed of response and ease of calibration of the eye-tracking system. All experiments were approved by the ethics committee of the Faculty of Psychology and Educational Sciences of the University of Geneva.

Eye movement data analyses and feedback

Preliminary analysis of eye movement data was carried out after each trial. Saccade onsets and offsets were detected using the default algorithm of the EyeLink1000 parser (velocity criterion of $30^\circ/\text{s}$, acceleration criterion of $8000^\circ/\text{s}^2$). Trials were followed by a written feedback message on the screen if (a) saccadic latencies were shorter than 50 ms (anticipation), (b) saccade latencies were longer than 350 ms, (c) gaze deviated by more than 1.5° from the display center at the time of saccade onset (failure to fixate), (d) no saccade was directed to the saccade target, or (e) a blink was detected. In discrimination-only trials, a fixation control was performed and an error message was shown if (a) a failure to fixate or (b) a blink was detected. After the experiment, saccade onset and offset criteria were manually checked with the help of a graphical visualization for at least some trials for each participant, and median saccade reaction times in the various conditions were computed.

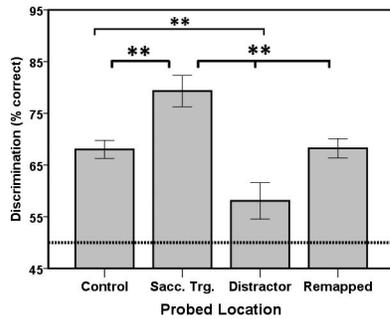


Figure 3. Discrimination performance at the three locations probed in Experiment 1. Error bars represent the standard error, with scores adjusted for between-subjects variability for within-subjects effects (Bakeman & McArthur, 1996) following the method by Cusineau (2005).

Results

Data exclusion

Data from two participants who had more than 50% of their trials excluded were omitted from analyses. One other participant was excluded for calibration failures. For the remaining participants, trials were removed if gaze deviated by more than 1.5° from the initial fixation cross (3.3%) and if the saccade landed on an object prior to masking (17.3%). Furthermore, trials in which the discrimination target was presented for longer than 120 ms due to technical issues were discarded (0.4% of trials). All other errors combined accumulated to 6.3% (e.g., anticipatory saccades before color change, 0.9%; no valid saccade detected, 0.7%; blinks, 0.5%; and the combination of all possible errors, 4.2%). Valid trials were therefore 72.7% of the total. Finally, of the valid trials, those in which the saccade was directed at a placeholder (5%) or at the distractor (1.5%) were also excluded. Our initial purpose was to examine capture saccades toward the distractor as well as target-directed saccade. However, as the percentage of capture saccades was too small to allow for analysis, we chose to analyze only those saccades directed straight to the target.

Perceptual discrimination

The primary goal of the experiment was to investigate how visual attention was distributed across objects in the display. To measure this, we obtained the percentage of correct discrimination responses at each probed location: control, saccade target, distractor, and remapped location of the distractor. The distractor in our study could appear at any of three possible locations, in between the presented stimuli. However, only trials in which the distractor was present (three-fourths) and appeared adjacent to the saccade target (two-thirds) were included in this first analysis. Trials in which the distractor appeared opposite the saccade

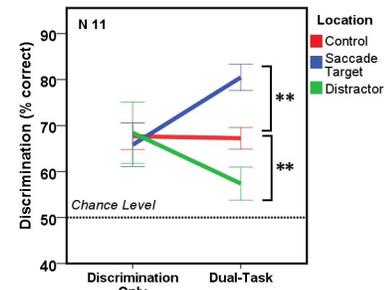


Figure 4. Discrimination performance at the three probed locations with (dual task) and without (discrimination only) eye movements in Experiment 1.

target do not have an equivalent location for the remapped distractor location. The control and remapped locations coincided with the two gray placeholder locations, the former at a neutral location whereas the latter at the distractor's remapped location. A one-way analysis of variance (ANOVA) with four levels, one per location, was carried out on the arcsine-transformed percentage correct values gathered at each location. The main effect of location was significant, $F(3, 39) = 32.966$, $p < 0.001$, partial $\eta^2 = 0.72$. We next performed paired t tests (Figure 3) that showed there was a significant difference in performance at all locations, except between the control and the remapped locations (mean difference 0.2%), $t(13) = 0.19$, $p = 0.85$. Performance at the saccade target differed significantly from that at the control (mean difference = 13.4%), $t(13) = 5.6$, $p < 0.001$; distractor (mean difference = 23.7%), $t(13) = 7.11$, $p < 0.001$; and remapped locations (mean difference = 13.1%), $t(13) = 6.1$, $p < 0.001$. This confirmed the occurrence of a presaccadic attentional shift to the saccade target, leading to substantial facilitation at this location. Surprisingly, performance at the distractor was worse than at the control location (mean difference = 10.3%), $t(13) = 4.65$, $p < 0.001$. How perceptual discrimination at the locations changed over time, leading up to the saccade, is reported in the Supplementary material (Time Course Analysis section). In short, the gradual buildup of attentional facilitation at the saccade target already found in numerous previous studies was confirmed (e.g., Deubel, 2008). No differences across time were found at any of the nontarget locations.

Whereas the target was a color singleton with respect to the initial placeholder display, the distractor was an onset singleton with a color different from the target. To test whether the observed differences were due to the oculomotor task or may have been influenced by the target and the distractor being singletons, we compared our results to performance in the discrimination-only control blocks, in which participants were required to maintain central fixation while attending to the objects. Note that from here onward, we grouped

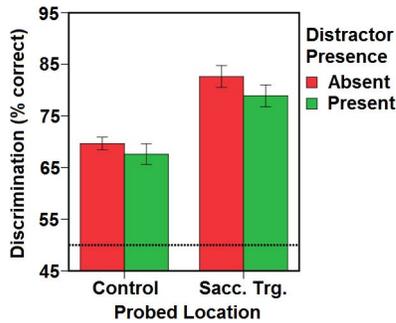


Figure 5. Discrimination performance as a function of distractor presence and probed location in Experiment 1. Sacc. Trg. = saccade target.

both gray placeholders together (control and remapped) because there were no performance differences and treat them as control. Three participants were omitted from this analysis because of a lack of trials. A 3×2 mixed ANOVA was employed, in which the first factor was the probed locations (control, saccade target, and distractor) and the second was task type (discrimination only versus dual task). This highlighted a main effect of probed location, $F(2, 40) = 6.81$, $p = 0.003$, partial $\eta^2 < 0.25$, and a significant interaction between probed location and task, $F(2, 40) = 12.55$, $p < 0.001$, partial $\eta^2 < 0.38$. The main effect of task type was not significant: $F(1, 20) = 0.63$, $p = 0.438$, partial $\eta^2 < 0.03$. Post hoc paired t tests confirmed there were no differences between locations in the discrimination-only task (differences smaller than 4%), t 's(10) < 0.82 , p 's > 0.433 , whereas we saw that all locations differed significantly from each other in the dual task (Figure 4). This confirmed that the differences that emerged in the dual task at the saccade target and distractor locations were both due to their role as target and distractor, respectively, and not due to their being color singletons or abrupt onsets.

In the preceding section, we observed that perceptual performance at the distractor location was worse than at the other locations. We argue that this effect reflects distractor suppression mechanisms. However, an alternative explanation would be that the distractors fell into an attentional inhibitory surround of the target. It has been shown that performance can be poorer at an object positioned closely to a target, compared with further away (Bahcall & Kowler, 1999), suggesting that attentional selection of one object results in inhibition of perceptual processing for neighboring objects (Mounts, 2000). When we analyzed the two-thirds of trials with the distractor closer to the target, comparing these to the one-third of trials in which the distractor was opposite the target, we saw that performance did not differ between conditions. A 3 (locations) $\times 2$ (distractor distance: near versus far) ANOVA was carried out that yielded no effect for distractor

distance, $F(1, 13) = 2.07$, $p = 0.66$, partial $\eta^2 = 0.02$, and no significant interaction, $F(2, 26) = 2.36$, $p = 0.11$, partial $\eta^2 = 0.15$, whereas the effect of location was significant, $F(2, 26) = 34.09$, $p < 0.001$, partial $\eta^2 = 0.72$. This points to an active suppression of the distractor color singleton occurring in equal measure at all locations, regardless of target proximity. Further, the facilitation at the saccade target is not affected by the distance of the distractor.

Last, we inspected whether the presence of a distractor was affecting the allocation of visual attention at the control and saccade target locations. A 2 (distractor presence) $\times 2$ (location) within-subjects ANOVA found a small but significant performance decrease of 3.6% when a distractor was present, $F(1, 13) = 8.37$, $p = 0.013$, partial $\eta^2 = 0.39$ (see Figure 5), showing that the distractor reduced attentional allocation at the control and target locations. Paradoxically, attention diverted from these locations did not benefit distractor processing, as made evident in the first analysis, where we observed worse performance at the distractor location. Further, the effect of location reported in the previous section was confirmed, $F(1, 13) = 73.42$, $p < 0.001$, partial $\eta^2 = 0.85$. There was no significant interaction, $F(1, 13) = 1.22$, $p = 0.289$, partial $\eta^2 = 0.09$.

Saccadic reaction times

To assess whether the location of the discrimination target (control, distractor, saccade target) or the color of the objects (green-red) influenced saccadic reaction times of saccades directed to the saccade target, a one-way ANOVA was carried out on distractor present trials. No significant difference on saccadic reaction times was observed for probed location, $F(2, 24) = 1.53$, $p = 0.237$, partial $\eta^2 = 0.11$. Thus, the observed differences in discrimination performance across locations cannot be explained by a speed-accuracy tradeoff. Recall that the distractor had a detrimental effect on discrimination performance overall, which was not specific to any one location (see present vs. absent analysis above; Figure 5) and not due to the distractor drawing attention to itself, as performance at this location was very low (see Figure 3). Comparing saccadic reaction times in distractor present (277 ms) versus absent (298 ms) trials showed that the presence of the distractor led to swifter saccade initiation (mean difference = 21 ms), $t(13) = 6.07$, $p < 0.001$.

Discussion

In Experiment 1, we originally set out to test for presaccadic attention shifts in capture saccades. Although the number of capture trials turned out to not be sufficient to adequately investigate the hypothesis, we could still effectively investigate the influence the

distractor's presence had on presaccadic attentional enhancement in target-directed saccades. Unsurprisingly, the saccade target received the most enhancement. The distractor location was seen to receive less enhancement than all other locations, despite its being a visual onset. Presenting the distractor at an inhibited region, in between the potential saccade targets, appears to have led to its processing being compromised. This appeared to be dependent on the movement preparation toward the possible targets, as performance at the distractor was not worse than at other locations in the discrimination-only task (i.e., in the absence of eye movements). Performance at the distractor was found to be equally low regardless of its closeness to the saccade target, therefore excluding biased competition-induced suppression (e.g., Hickey et al., 2011; Mounts, 2000) as the principle cause. With the distractor being presented in the large majority of trials (75%), it is likely that participants acquired a suppression strategy (H. J. Müller, Geyer, Zehetleitner, & Krummenacher, 2009) to effectively carry out the task. Lastly, it is clear the distractor was treated differently than the placeholders, but this did not lead to any remapping effect in terms of transfer of suppression to its remapping location. Performance at the rejected distractor's remapped location was in fact no different from that found at the control location. We can therefore conclude that although a saccade target receives location-specific enhancement in the time leading up to the saccade (which steadily builds up; also see Supplementary material), a distractor onset appearing in between potential targets is suppressed, and this suppression does not influence performance at its remapped location. In the absence of a target, when no eye movements are required, presaccadic perceptual facilitation effects at the distractor locations return to baseline.

Experiment 2

We now turn to Experiment 2, in which the main purpose was to increase target selection difficulty in order to induce involuntary saccades toward a competing salient distractor. The well-known additional-singleton paradigm (e.g., Theeuwes, De Vries, & Godijn, 2003) allowed us to achieve an adequate number of capture sequences per participant (roughly one-fourth) and to test for facilitation at the endpoint of an involuntary saccade and the time course of the enhancement. The stimulus display also allowed predictive remapping effects to be studied; facilitation was tested at the distractor's remapped location, in straight-to-target saccades (as in Jonikaitis et al., 2013), and at a future saccade destination's remapped location (as in Rolfs et al., 2011), when a capture sequence was

performed. The goals were therefore (a) to test whether a distractor location that induces a capture sequence is enhanced prior to the saccade; (b) if there is enhancement, study the time-course of the enhancement compared with goal-directed saccades; (c) to verify whether a salient distractor is remapped when the eyes go straight to the target; and (d) to determine whether there is evidence of the remapping of a saccade target prior to an involuntary eye movement when capture happens.

Methods

Participants

A total of 13 participants (nine male, four female, with one having participated also in Experiment 1) were tested in Experiment 2, with ages ranging from 19 to 32 years. They were run in a minimum of 8 nonconsecutive 1-hr sessions and a maximum of 10 sessions. Data from another eight participants were excluded midway through the study, with five participants reporting they could not see the perceptual stimulus being flashed (discrimination performance at chance level) whereas two participants attained perceptual discrimination scores below the 60% mark even in the most favorable conditions. One participant chose not to return for the continuation of the study once the course credits were obtained. All were paid or received course credits for their participation.

Apparatus

The apparatus was the same as in Experiment 1.

Stimuli

The fixation cross, perceptual stimuli (flashed discrimination crosses), and masking squares did not differ from those employed in Experiment 1. Surrounding stimuli were diamonds and circles, presented at 5° from the center of the screen. The diamonds were 3.2° diagonal, whereas the circles were 3° in diameter.

Design and procedure

Although the nature of the dual task remained identical to that in Experiment 1 (i.e., directing a saccade toward an eye movement target and discriminating a perceptual stimulus), the visual display and experimental sequence underwent a number of changes (see Figure 6). A fixation cross was initially displayed, varying randomly between 1 and 1.3 s, after which it disappeared for 200 ms, followed by the stimuli. These consisted of six objects in each trial, four identical, one

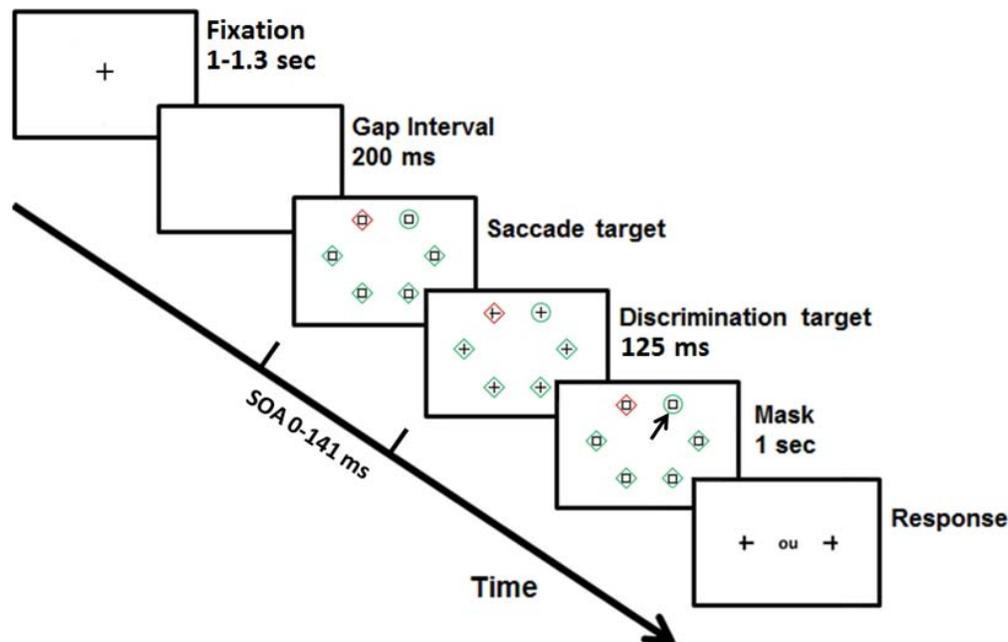


Figure 6. Sequence of events in Experiment 2. Participants were told to move their eyes to the shape singleton as soon as the objects appeared on screen. During the saccade latency period, perceptual stimuli (crosses) were displayed within the objects and masked before the eye movement (symbolized by an arrow in the mask display; arrow was not shown in the actual experiment) was initiated. One flashed cross was asymmetric (in the example depicted within the color singleton distractor) and the shift of its vertical bar required forced-choice discrimination at the end of the trial.

shape singleton acting as the saccade target, and one color singleton acting as the distractor.

Participants were instructed to fixate the cross and to move their eyes as fast as possible to the shape singleton once the objects came on screen. The saccade target shared the same color (either green or red) as the rest of the objects on screen, except for the distractor, which was of the opposite color. The distractor shared the same shape as the other nontarget stimuli. The distractor was present on 75% of trials, whereas it was substituted by a placeholder of the same appearance as all other nontarget objects in 25% of trials. The distractor was always presented adjacent to the saccade target. Shapes and colors of saccade targets and distractor varied randomly from trial to trial. The objects were presented initially containing a masking square. After one of five randomly selected stimulus onset asynchronies (SOAs) ranging from 0 to 140 ms (where 0 means simultaneous to the appearance of the objects), the perceptual stimuli briefly replaced the masks. The crosses were identical to those employed in Experiment 1 but this time displayed slightly longer (for 125 ms) before being masked once again.

Even though each object contained a flashed cross, the asymmetric target cross could appear within only one of four locations: the saccade target, the distractor, the control, and the remapped location. The latter two were defined as follows: When a straight-to-target saccade was performed, the remapped location was a

location in retinotopic coordinates corresponding to the predictive remapping of the color singleton distractor (see the right panel in Figure 7). In capture sequences, the remapped location instead corresponded to the retinotopic remapping of the saccade target (see the right panel in Figure 8). Each block was made up of 160 trials, and a minimum of 24 blocks were carried out.

Results

Data exclusion

Trials in which the discrimination target was presented for longer than 135 ms or no eye-tracking recording was obtained because of technical issues were immediately discarded (2.5% of trials). Of all remaining data, trials were removed if the saccade landed on an object prior to masking (7.3%), if gaze deviated by more than 1.5° from the initial fixation cross (3.8%), if the eyes never landed on the saccade target (4.6%), or if the saccade was initiated prior to the saccade target being presented for 50 ms (3.1%). Blinks, late saccadic responses taking longer than 600 ms to initiate, and trials in which multiple errors occurred accumulated to <3%. The percentage of valid trials left for analysis was 78.3%. Of these valid trials, we examined those in which the first saccade was directed straight to the eye movement target (48.1%) and saccades in which an

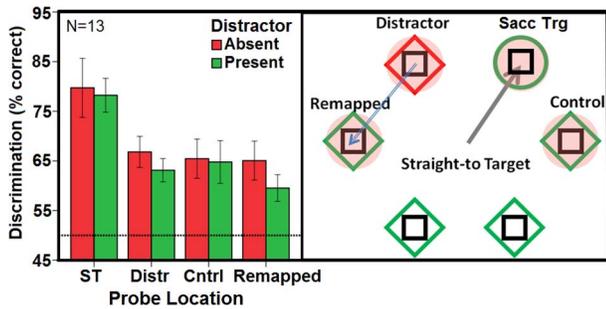


Figure 7. Discrimination performance in Experiment 2 for straight-to-target saccades. The scores from the four probed locations (saccade target, rejected distractor, predictive re-mapping of a salient object, and control) when the distractor was present or absent (replaced by a placeholder; i.e., another green diamond in the illustration). The probed locations are illustrated and highlighted on the right. The gray arrow indicates the saccade, whereas the blue arrow indicates remapping of the salient color singleton object.

oculomotor capture sequence occurred, with an initial saccade directed to the distractor followed by a corrective saccade to the intended saccade target (27.3%).

Perceptual discrimination

Straight-to-target saccades: Overall performance and distractor absent versus present trials: First, we examined the allocation of attention prior to saccade initiation, for those eye movements directed straight to the target. Note that the distractor and control locations were always on either sides of the saccade target. A 4×2 within-subjects ANOVA on the arcsine-transformed percentage correct values for the four probed locations (saccade target, rejected distractor, remapping of a salient object, and control) and the two distractor conditions (absent – present) was performed. A statistically significant main effect for probe location was observed, $F(3, 36) = 52.76$, $p < 0.001$, partial $\eta^2 = 0.81$, highlighting that attention was not allocated evenly across the displayed objects. The main effect of distractor presence was found to also be significant, $F(1, 12) = 10.71$, $p = 0.007$, partial $\eta^2 = 0.47$, confirming the slightly detrimental effect of distractor presence on performance overall already found in Experiment 1 (66.4% with vs. 69.3% without distractor). No significant interaction was found between probed location and distractor presence, $F(3, 36) = 1.42$, $p = 0.253$, partial $\eta^2 = 0.11$, emphasizing that the presence of a distractor did not have a location-specific effect on performance (not even at the distractor location itself; that is, the color singleton distractor did not benefit from perceptual facilitation when compared with the distractor absent trials, when another nonsalient placeholder was presented in its stead; see Figure 7).

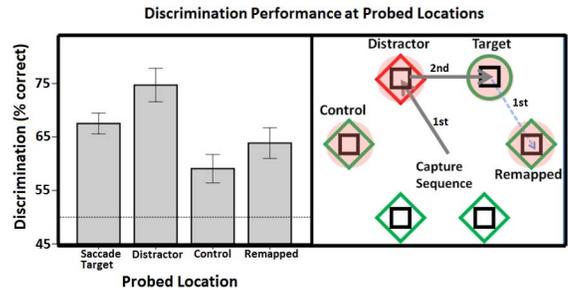


Figure 8. Perceptual discrimination scores for oculomotor capture trials, at the four probed locations, highlighted in red in the right diagram. The gray arrows indicate the saccades (first capture then corrective), whereas the dashed blue arrow indicates remapping of the saccade target triggered by the first capture saccade.

We conducted a series of post hoc tests to better assess the distribution of attention across the different locations. Performance was better at the saccade target than the distractor (mean difference = 16.2%), $t(12) = 8.3$, $p < 0.001$; the control (15.5%), $t(12) = 13.4$, $p < 0.001$; and the remapped locations (19.1%), $t(12) = 9.43$, $p < 0.001$, confirming the large perceptual benefits at the saccade target already found in Experiment 1. Performance at the remapped location was marginally worse than at the control (mean difference = 3.6%), $t(12) = 2.13$, $p = 0.055$, and distractor location (2.87%), $t(12) = 3.61$, $p = 0.004$, respectively. Given the layout of our stimuli, one may be tempted to assume that this small difference between the remapped location and the other two may indicate an attentional spread around the saccade target, as control and distractor locations were on either side of it, whereas the remapped location of the distractor was further away. However, in a supplementary analysis, we found some modulations in performance at the distractor location based on its salience (less luminant red vs. more luminant green distractors; see Supplementary Figure S2). The difference was not strong enough to drive the critical three-way interaction (distractor presence \times probe location \times distractor color), $p = 0.463$. Still, we think the observation warns against concluding that there was an even spread of attention around the saccade target and that the distractor was treated similarly to its non-singleton counterpart on the other side of the target. Our technique might not have been sensitive enough to detect the differences.

Saccadic reaction times: It took participants on average 284 ms to initiate the goal-directed saccade to the saccade target. We tested whether the location of the perceptual target or the presence of the distractor affected saccadic reaction times. To that end, a 4×2 repeated-measures ANOVA was run, with four levels for the location of the probe and two levels for distractor presence. No main effect was found for

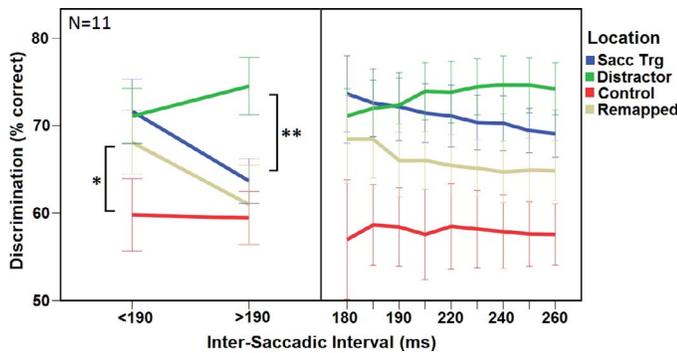


Figure 9. Performance in Experiment 2 as a function of how close in time the two saccades were, where the x-axis indicates the cutoff point, up to which trials were included. The left panel shows discrimination performance as a function of the temporal gap between the saccades being smaller or larger than 190 ms. The right panel shows discrimination performance as a function of increasing intersaccadic intervals, going from 180 to 260 ms. The shorter the intersaccadic interval, the more attention is allocated to the saccade target and, in turn, to its remapped location. Sacc Trg = saccade target.

probed location, $F(3, 36) = 0.58$, $p = 0.632$, partial $\eta^2 = 0.05$, or for distractor presence, $F(1, 12) = 2.67$, $p = 0.128$, partial $\eta^2 = 0.18$, proving the perceptual task or the distractor's presence did not affect the motor task. The interaction was also not significant, $F(3, 36) = 0.15$, $p = 0.93$, partial $\eta^2 = 0.01$.

Oculomotor capture trials: Overall performance: We define oculomotor capture trials as those in which the eyes went initially to the distractor (first saccade) and then to the eye movement target (second saccade). This sequence of saccades is therefore made up of an erroneous saccade that is then corrected successfully. The remapped location now corresponds to the remapped future saccade destination (see the right panel in Figure 8). A one-way within-subjects ANOVA was run on the arcsine-transformed percentage correct values for the four probed locations, highlighting a significant main effect of location, $F(3, 36) = 15.95$, $p < 0.001$, partial $\eta^2 = 0.57$.

Focusing on the four locations, the largest amount of visual attention was now allocated to the distractor, surpassing even the saccade target. Paired t tests highlighted a significant difference between the distractor location and all remaining locations (differences larger than 8.3%), t 's(12) > 3.95 , p 's < 0.002 . Even involuntary saccades were therefore seen to be preceded by a shift of covert attention toward their endpoint, leading to perceptual enhancement at the distractor location prior to the distractor-directed saccade being initiated. The presaccadic time course of this activation is illustrated in the supplementary section. Still, participants were also significantly better at discriminating at the saccade target than at the

control (mean difference = 8.9%), $t(12) = 5.0$, $p < 0.001$. This indicated that a portion of attentional resources was being allocated to the saccade target, the eyes' second landing point. Significantly better discrimination performance was also recorded at the location corresponding to the remapping of the saccade target than at the control location (mean difference = 4.9%), $t(12) = 2.36$, $p = 0.036$, emphasizing that a sequence of saccades in which the first is involuntary leads to the remapping of a future saccade destination, much the same way as a sequence of voluntary saccades (see Rolfs et al., 2011). Furthermore, no difference in facilitation was observed between the saccade target and its remapped location (mean difference = 4%), $t(12) = 1.71$, $p = 0.113$,

Influence of the intersaccadic interval: We sought to further examine the possibility that the distractor was temporarily mistaken for the saccade target and that the initial saccade was intended rather than erroneous. By focusing on the time spent fixating the distractor (intersaccadic interval), before initiating the corrective saccade to the saccade target, it was possible to distinguish between types of capture sequences. Those sequences in which the participant spent very little time on the distractor before moving the eyes onto the saccade target can be taken as an indication that the second saccade may have been programmed before the first saccade was completed (see w. Becker & Jürgens, 1979). We believe this preprogramming of the second saccade reflects a sequence in which the first movement is realized to be erroneous and starts to be corrected, presumably midflight or even before the first saccade has been initiated. A longer time spent fixating the distractor, on the other hand, before initiating the corrective saccade, is indicative of saccades being relatively separate one from the other, without parallel programming having taken place. Trials were divided into two groups with short and long intersaccadic intervals, respectively. We wanted a cutoff value that would allow us to observe performance in saccades that were closely programmed in time but also keep most participants in the analysis. This was set at 190 ms. A 4×2 within-subjects ANOVA was carried out for the four probed locations and two intersaccadic time durations (see Figure 9). A significant difference was found for the main effect of location probed, $F(3, 30) = 16.55$, $p < 0.001$, partial $\eta^2 = 0.62$, and for the main effect of intersaccadic duration, $F(1, 10) = 12.44$, $p = 0.005$, partial $\eta^2 = 0.55$. Importantly, there was also a significant interaction, $F(3, 30) = 5.58$, $p = 0.011$, partial $\eta^2 = 0.36$.

Parallel programming with short intersaccadic time intervals (<190 ms) led to an equal distribution of attentional resources to distractor and target locations (mean difference = 1%), $t(10) = -0.34$, $p = 0.74$, suggesting parallel programming with equal allocation

of attention to the two locations. This led in turn to strong perceptual facilitation at the remapped location of a future saccade destination over the control location (mean difference = 10.5%), $t(10) = 2.55$, $p = 0.029$. It is also noteworthy that even when the sequence of saccades was performed in very rapid succession, with the first saccade to the distractor clearly being involuntary, there was still presaccadic facilitation at the capturing distractor location. Instead, when participants fixated longer (>190 ms) between one saccade and the other, attentional deployment considerably favored the distractor over the saccade target (mean difference = 14.3%), $t(10) = 5.98$, $p < 0.001$, suggesting that the distractor was erroneously identified as the target and received most attentional resources. No difference in performance was seen between remapped and control locations when the time between the saccades was long (mean difference = 1.9%), $t(10) = 0.56$, $p = 0.584$. Thus, for short and long intersaccadic intervals, performance at the remapped location was seen to be highly related to that at the saccade target, apparently mirroring the enhancement.

Discussion

In summary, Experiment 2 provided evidence of a location-specific shift of presaccadic covert attention at the endpoint of a goal-directed saccade, in straight-to-target saccades, and at the endpoint of an involuntary saccade (capture saccades). In straight-to-target saccades, enhancement was in fact seen only at the saccade target, with little facilitation or suppression seen at any of the rejected locations. In contrast to Experiment 1, detrimental performance at the rejected distractor location was not seen. In sequences of capture saccades, performance was strongly dependent on the intersaccadic interval. When there was a lengthy delay between the capture and corrective saccades (i.e., long intersaccadic interval), most attention was allocated to the salient capturing distractor. When there was very little delay between saccades (i.e., short intersaccadic interval), attentional resources were distributed far more evenly between both saccade landing points (distractor and target); this, in turn, led to stark facilitation at the remapped location of the saccade target. No facilitation was instead observed at the remapped location of a salient (but not looked at) distractor object, in straight-to-target saccades.

General discussion

The present study provided evidence that involuntary eye movements induced by a salient object in the

environment are preceded by an obligatory and location-specific shift of attention. Enhanced perceptual performance was found at the endpoint of a saccade, prior to its execution, whether this was a goal-directed saccade toward a target (Experiment 1 and 2) or an involuntary saccade to a salient capturing object (Experiment 2). Thus, the mechanism that allows attention to focus in on a target location before a voluntary saccade is made (Deubel, 2008; Deubel & Schneider, 1996; Godijn & Theeuwes, 2003; Rolfs et al., 2011) is also called into play when an involuntary stimulus-driven saccade is made. The mechanism, often taken as evidence of the tight coupling between attention and eye movements, appears to be relatively unconcerned about task goals. Presaccadic shifts of attention, instead, seem to be a defining characteristic of all saccades (see also Born, Mottet, & Kerzel, 2014). It is likely that our visual system cannot afford visual processing delays where attention lags behind or is caught by surprise whenever something in the environment catches our gaze.

Perceptual performance at the endpoint of voluntary and involuntary saccades

Two points of diversion between involuntary and goal-directed saccades did, however, emerge. First, the enhancement observed exclusively at the saccade target location for intended saccades was distributed differently for capture sequences. We see evidence of spatial attention being allocated in parallel to two saccade destinations, similarly to what was reported by Godijn and Theeuwes (2003) and Rolfs et al. (2011). These authors, however, observed more attention being allocated to the first saccade target than to the second. In the current study, we see that when there was very little delay between the capture and corrective saccades, attention was distributed relatively evenly at both saccade destinations. This points to a more equal distribution of attentional resources when the first saccade is identified as erroneous, leading to a greater emphasis on the following saccade destination than what was seen in Godijn and Theeuwes (2003) and Rolfs et al. (2011), in which both saccades were voluntary. Second, the time-course analysis (Supplementary material, Time course analysis) suggests that activation at an involuntary saccade endpoint appears to begin closer in time to saccade initiation, compared with voluntary goal-directed saccades. We see evidence in Experiment 2 of enhancement at a salient object that captures the eyes starting in between 85 and 60 ms before the saccade, whereas their goal-driven counterparts led to facilitation over 130 ms before saccade initiation in Experiment 1 and over 100 ms in Experiment 2 (with

evidence in the literature of presaccadic enhancement as early as 250 ms; Deubel, 2008). Despite the timeline of the activation of involuntary saccades being shifted closer to saccade initiation and enhancement not reaching the peak seen in straight-to-target saccades, the occurrence of a location-specific shift of covert attention that increases in the time leading up to the saccade is beyond doubt.

Perceptual facilitation at the saccade target's remapped location

With regard to perceptual facilitation at nontarget locations, evidence for the remapping of a future saccade destination was observed prior to involuntary eye movements. When there was little delay between involuntary eye movement and its corrective counterpart, before any saccade was initiated, participants allocated attention at the landing point of the two saccades and predictively remapped the saccade target. Similarly to the remapping of a future saccade destination in a sequence of voluntary saccades (Rolfs et al., 2011), attention accounts for involuntary saccades and predictively remaps locations of interest, in anticipatory fashion. Performance at the remapped location of the saccade target, in fact, appeared to mirror the performance levels observed at the saccade target location (see Figure 9). This is in line with the views of Mirpour et al. (2012), in which the remapping process is sensitive to enhancement levels observed at the object of interest. Lastly, Duhamel et al. (1992) define remapping as a process that depends on the intention to move and that neurons anticipate the retinal consequences of intended eye movements. The current findings show how the remapping mechanism extends beyond voluntary movements; attention can be maintained on objects of interest while accounting for the retinal displacement across eye movements, whether these are intended or involuntary.

Alternative accounts: saccadic momentum and biased competition

So far, we attribute our enhancement effects at the so-called remapped location exclusively to remapping. However, could there be alternative accounts? Saccadic momentum (Smith & Henderson, 2009) refers to a tendency the saccadic system has to continue in the same direction as the last executed saccade (Anderson, Yadav, & Carpenter, 2008). Similarly, it has been shown that attention is biased toward the direction of the last attentional shift (Bennett & Pratt, 2001). Also, when an eye movement is performed in the presence of a nontarget object, facilitation can be found not only at

the attended object's pre- and postsaccadic locations but also at various locations in between (Harrison, Mattingley, & Remington, 2012), suggesting attention spreads in the direction of the upcoming eye movement (see also Mathôt & Theeuwes, 2010). However, no literature within this context is present, to the authors' knowledge, suggesting deviations of attention direction associated to momentum, which would be necessary for attention to envelop the remapped location in the current study after having visited the saccade target. Instead, much evidence points to attention selection as being relatively sharp and narrow at an attended location or locations (e.g., M. Müller, Malinowski, Gruber, & Hillyard, 2003). For the reasons stated, saccadic momentum seems inadequate to effectively explain the facilitation found at the remapped location without presupposing a diversion of attention direction unrelated to the direction of the saccade to the target. Furthermore, if the spread of presaccadic attention from the distractor to the saccade target was fuzzy enough to lead to facilitation also at the remapped location, we would expect that when most attentional resources are allocated to the distractor (when the delay between capture and corrective saccades is long), the control location would also benefit from increased facilitation. It is, after all, in the distractor's proximity and roughly in the same direction. Instead, performance at the control location remained unaffected. Biased competition-based explanations (Desimone & Duncan, 1995; Hickey et al., 2011) were also explored, proving an unsatisfactory framework to explain the current finding, as changes in distractor luminance led to differences in performance at the distractor alone and not the target (Supplementary Figure S2). In other words, the distractor did not prove to bias the competition with regard to the target. This held true also for target-distractor proximity (Experiment 1), in which no biased-competition effects were found. These proved unfruitful frameworks at explaining the cause of the shift of attention to the so-called remapped location, which instead predictive remapping elegantly accounted for.

Perceptual performance at the salient distractor's remapped location

No evidence was found for the remapping of a salient nontarget object (Experiment 1 and Experiment 2, straight-to-target saccades). In contrast to the findings by Jonikaitis et al. (2013), who gave a clear account of the remapping of an attended, but not foveated object, participants in the current study did not display facilitation (or suppression, which may have been expected in Experiment 1) at the remapped distractor location. Furthermore, the changes in

luminosity at the attended distractor object in Experiment 2, which led to changes in performance at the distractor itself, did not affect performance at its remapped location in any way (further details in Supplementary Figure S2). One possible explanation is that activation was not sufficiently high to lead to it being remapped before the saccade. After all, despite its salience, performance at the distractor location was not different from the controls in Experiment 2. Another possible explanation for this is that the distractor location in our study could be considered a rejected target location and most definitely interfered with target selection. In line with the salient-signal-suppression hypothesis (Caputo & Guerra, 1998; Kumada & Humphreys, 2002; Sawaki & Luck, 2010; Burra & Kerzel, 2013), participants may have successfully suppressed signals arising from the salient distractor when searching for the target. It was recently shown that salience-driven distraction is mitigated by a suppressive mechanism, reducing the salience of potentially distracting stimuli (Gaspar & McDonald, 2014). Such a mechanism, in trials in which the distractor did not lead to oculomotor capture, may have led to a successful suppression of the salient distractor object and, in turn, to no remapping.

Perceptual performance at the salient distractor location

Perceptual performance at the location of an onset singleton distractor was worse than at control locations in Experiment 1. This effect could not be explained by its status as a sudden-onset singleton, which may have masked the perceptual target more strongly (see discrimination-only analysis, Figure 4), nor was it due to the distractor being presented closer to the saccade target than the control locations, thus potentially falling into an inhibitory surround of the attended target. In addition, the distractor's proximity to the target did not lead to a performance bias at the saccade target location. Instead, we think the distractor was actively suppressed. At the beginning of the trial, the placeholders were potential target locations, requiring attention to be directed at these locations. Subsequent to this initial distribution of attention, the distractor and the target were revealed. The nontarget regions in between potential targets could have been inhibited, such as suggested by McSorley, Haggard, and Walker (2009). With the distractor presented at an inhibited region, its processing could have been compromised.

Moreover, occurrence of the distractor in a large majority (75%) of trials, as well as being presented in a salient nontarget color, could also have induced additional inhibition. Moher, Abrams, Egeth, Yantis, and Stuphorn (2011) found that when participants

expected a distractor, rapid suppression occurred. Furthermore, frequently displayed distractors that are defined in another dimension and physically more salient than the target provide a high incentive for suppression (H. J. Müller et al., 2009; Zehetleitner et al., 2009). Thus, participants in our study could have acquired a suppression strategy (H. J. Müller et al., 2009), limiting distractor processing to initial stages. Hence, contrary to our expectations, the distractor was not drawing resources directly to itself. Even more surprisingly, distractor presence led to faster saccadic reaction times. However, it also had a detrimental effect on discrimination performance at all other locations. This indicates that, despite its location being inhibited, the distractor still had a disruptive impact on behavior. This is in line with Tsal and Makovski's (2006) notion of a process-all mechanism, in which attention is initially distributed to all presented items regardless of their relevance.

Concluding remarks

In conclusion, the endpoint of an involuntary eye movement benefitted from a location-specific shift of covert attention, prior to the movement being initiated. The specificity and incremental nature of the enhancement bore no difference from that observed for saccades going straight to their intended target. The timeline of the enhancement, instead, might differ slightly between the saccade types, with involuntary saccades leading to presaccadic enhancement only 70 to 80 ms prior to saccade initiation. This led us to conclude that all eye movements undergo the same process of location-specific enhancement buildup. Distractors that did not induce an involuntary eye movement were not perceptually enhanced. When the same distractor that on occasion captured gaze was instead correctly rejected, no enhancement was observed. When, on the other hand, the distractor was a visual onset appearing in between possible saccade targets, it appeared to be suppressed, as performance was below baseline. Furthermore, the attention-allocating process tightly linked to eye movements appears to also be the guiding force behind the remapping mechanism. Predictive remapping of a saccade target, in fact, also brought about location-specific presaccadic enhancement, perfectly accounting for the retinal displacement caused by involuntary movements. These shifts of covert attention appeared to be entirely associated with the motor command. No evidence was instead seen for the remapping of enhancement or suppression of an attended distractor object that was not fixated. Overall, the current findings show how the remapping mechanism extends beyond voluntary

movements alone, accounting also for the retinal displacement caused by involuntary movements.

Keywords: visual attention, saccades, bottom-up, top-down, predictive remapping, oculomotor capture

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Corresponding author: Michael Puntiroli.

E-mail: michael.puntiroli@unige.ch.

Address: Université de Genève, Faculté de Psychologie et des Sciences de l'Éducation, Genève, Switzerland.

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Supplementary material

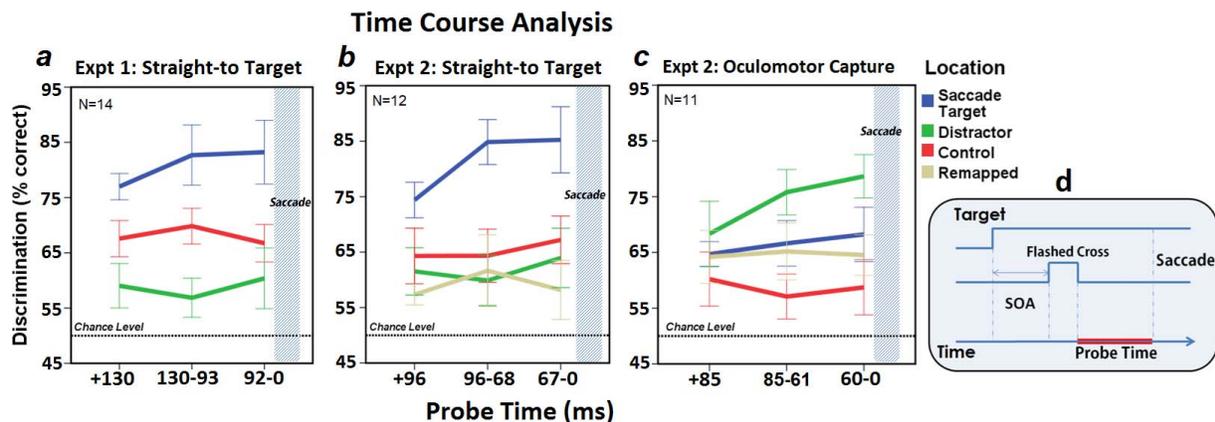
Time course analysis

In order to test whether attention allocated to the displayed objects differed over the time leading up to the saccade (similarly to Deubel, 2008; Jonikaitis et al., 2013; Rolfs et al., 2011), we split the data into three time bins. Note that the discrimination stimulus was flashed at varying SOAs in order to present the perceptual stimulus at various times before the onset of the saccade, which was unpredictable on a given trial. For each trial, we determined post hoc the time interval between offset of the perceptual stimulus (flashed crosses) and the onset of the saccade. Binning according to this interval, we could study the amount of attention allocated to the objects depending on the stage of saccade preparation. Or, in other words, we determined discrimination performance, time locked to the beginning of the imminent movement (see Supplementary Figure S1d).

We chose to split the data using fixed time bins (not percentiles). In Experiment 1 concerning straight-to-target saccades, these were 0 to 92, 93 to 130, and 130+, where 0 indicated the time of saccade initiation. We did not test for postsaccadic visual attention. The choice of these specific bins allowed a fairly equal distribution of trials, but of course with some variability across

participants (minimum: 12 trials; maximum: 613 trials per time bin and participant). A 3×3 within-subject ANOVA was carried out, testing performance differences in the discrimination task across three time bins and three locations. A significant main effect was found for probed location, $F(2, 26) = 38.9$, $p < 0.001$, partial $\eta^2 = 0.75$, but not for time bin, $F(2, 26) = 1.98$, $p = 0.158$, partial $\eta^2 = 0.13$. There was a significant interaction between location and time, $F(4, 52) = 2.93$, $p = 0.029$, partial $\eta^2 = 0.18$, highlighting how the length of the time interval between the flashed cross and the movement affected attentional deployment (displayed in Supplementary Figure S1a through c).

Post hoc analysis was carried out by means of 3 one-way ANOVAs to examine specific performance differences at each location for each of the time intervals. Temporal differences were seen to be specific to the saccade target, with a significant difference in performance depending on time of saccade initiation in relation to the perceptual stimulus, $F(2, 26) = 3.41$, $p < 0.048$, partial $\eta^2 = 0.21$. Instead, performance at the remaining locations did not change in the time leading up to the saccade, $F_s(2, 26) < 0.95$, $p_s > 0.399$, partial $\eta^2 < 0.07$. Paired t tests emphasized that discrimination performance was significantly better when the cross was flashed 93 to 130 ms before the saccade rather than +130 ms (mean difference = 8.6%), $t(13) = 2.65$, $p = 0.02$. Performance was also significantly better in those trials when the cross was flashed directly (0–92 ms) before the saccade rather than +130 ms (mean difference = 13%), $t(13) = 2.45$, $p = 0.029$. Furthermore, a substantial activation at the saccade target location was already observable in the +130 time bin, with performance here found to be significantly better than



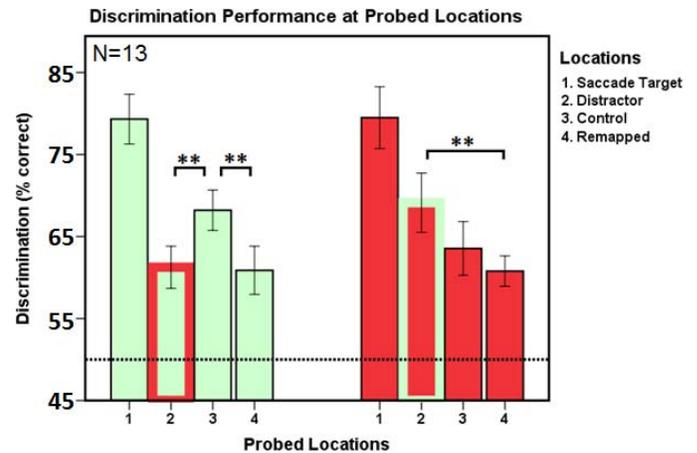
Supplementary Figure S1. Results of the three time course analyses. (a, b) Perceptual discrimination scores in Experiments 1 and 2 as a function of the time the probe was flashed prior to the saccade. Both graphs relate to goal-directed saccades going straight to the target. (c) Perceptual discrimination scores in Experiment 2 for involuntary saccades going to the distractor (then corrected by a second saccade to the target). (d) Illustration of the interval (probe time) considered for subdivision of the data into time bins. Probe time = time of perceptual target offset (flashed crosses) to time of saccade onset. Error bars represent the standard error, with scores adjusted for between-subjects variability for within-subject effects.

at the control (mean difference = 24.6%), $t(13) = 4.47$, $p = 0.001$.

In Experiment 2, data relating to the straight-to-target saccades were again split up into three time bins: 0 to 68, 69 to 96, and +96 ms. However, as a consequence of the fixed bins, one participant had to be excluded from the analysis due to a lack of short-interval trials. We ran a 4×3 within-subject ANOVA on the arcsine-transformed percentage correct values, with four locations where attention was measured and three time intervals. We found a statistically significant main effect for location, $F(3, 33) = 38.39$, $p < 0.001$, partial $\eta^2 = 0.78$, and for the main effect of time bin, $F(2, 22) = 5.13$, $p = 0.015$, partial $\eta^2 = 0.32$.

Importantly, the interaction between location and time was also significant, $F(6, 66) = 2.77$, $p = 0.018$, partial $\eta^2 = 0.20$. In order to better explore the temporal differences at the locations, four separate one-way within-subject ANOVAs were carried out, one for each location. A significant difference in performance over time was seen only at the saccade target, $F(2, 22) = 8.03$, $p = 0.002$, partial $\eta^2 = 0.42$, demonstrating an increase in performance at this location the closer in time the saccade was to the perceptual target. No significant effect across time was observed at all remaining (nontarget) locations, $F_s(2, 22) < 0.868$, $p_s < 0.434$, partial $\eta^2 < 0.07$. From the first bin chosen, +96 ms, performance at the saccade target already differed significantly from that at the control (mean difference = 11.1%), $t(11) = 3.85$, $p = 0.003$. This emphasized that the enhancement at the saccade target location occurred earlier in time, as suggested by other accounts (see Deubel, 2008).

In Experiment 2, relative to capture sequences, three cut-off points were chosen: 0 to 60, 61 to 85, and +86 ms. Two participants were excluded due to a lack of data in certain conditions. A 4×3 within-subject ANOVA was conducted for the four locations and the three time bins. A significant main effect was observed for location, $F(3, 30) = 15.21$, $p < 0.001$, partial $\eta^2 = 0.60$; the interaction was also significant, $F(6, 60) = 2.5$, $p = 0.033$, partial $\eta^2 = 0.20$. The main effect for time was not significant, $F(2, 20) = 1.8$, $p = 0.191$, partial $\eta^2 = 0.15$. A series of post hoc one-way within-subject ANOVAs was carried out. A significant difference in discrimination performance was observed at the distractor location across time, $F(2, 20) = 6.9$, $p = 0.005$, partial $\eta^2 = 0.41$, while no difference over time was reported at the remaining locations, $F(2, 20) < 0.81$, $p > 0.46$, partial $\eta^2 < 0.07$. Performance at the distractor began to differ from that at the control from 61 to 85 ms (difference = 20.7%), $t(10) = 5.59$, $p < 0.001$, while it did not reach significance in the +85 ms bin (9.0%), $t(10) = 1.88$, $p = 0.09$. A significant difference emerged between conditions when comparing performance directly at the saccade target in straight-to-target



Supplementary Figure S2. Graph illustrating discrimination performance affected by color differences across the four locations for straight-to-target saccades in Experiment 2. The distractor was always of the opposite color from the rest of the stimuli for each color condition: green condition with red distractor (left) and red condition with green distractor (right). Note that the colors were of different luminance (green > red).

saccades and at the distractor in capture saccades for the time bin farthest away from saccade execution (mean difference = 7.5%), $t(10) = 3.09$, $p = 0.011$. This highlighted that strong, location-specific enhancement probably occurs earlier for voluntary straight-to-target saccades than for capture saccades.

This highlighted how enhancement over time, leading up to the saccade, happens at the end point of an involuntary saccade as it happens for voluntary goal-directed intended saccades. The only noticeable difference between these two types of saccades may be the timing of the activation, with enhancement at a location visited by an involuntary saccade occurring closer in time to saccade initiation. In straight-to-target saccades, discrimination performance at the saccade target was already at 75% and significantly different than that at the control approximately 100 ms before the saccade, while at approximately 90 ms before the involuntary saccade performance at the capturing object was still in the high 60s and did not differ significantly from that at the control. Performance at the saccade target and remapped location instead remained relatively constant in the time leading up to the saccade. We suspect this may be due to a great number of trials in which the saccade target either was not yet identified or had indeed been identified but not sufficiently attended to before the saccade to the distractor took place. Without stark improvement over time at the saccade target, no improvement over time would be expected at its remapped location.

In Experiment 2, saccade target and remapped location were unaffected by changes in saliency at the distractor. We found performance at the saccade target

to be better than that at the distractor, control, and remapped locations whether the target was green (mean differences larger 13.1%), $t_s(12) > 5.56$, $p_s < 0.001$, or red (mean differences larger than 12.1%), $t_s(12) = 3.5$, $p_s < 0.004$. This replicated results of Experiment 1, confirming that most attentional resources are concentrated at the saccade target regardless of low-level features. Differences in color at this location in fact left performance unaffected (difference = 0.1%), $t(12) = 0.02$, $p = 0.985$. In order to tease apart differences in attention allocated to nontarget locations, we compared performance at the distractor, control, and remapped locations to expand on the probe location \times color ANOVA interaction reported in Results.

A series of paired t tests comparing performance at the nontarget locations per color highlighted that when the stimuli were green, participants were significantly better at discriminating at the control location than at the distractor (mean difference = 7.4%), $t(12) = 3.87$, $p = 0.002$, and remapped location (7.7%), $t(12) = 3.42$, $p = 0.005$. Given that the distractor and control locations are on either side of the saccade target, it seems that a

less luminous color singleton on one side receives less attention than a more luminous control object on the other side. In the red stimuli condition, performance was no longer better at the control than at the distractor, but a marginally significant difference favoring the distractor was observed (5.9%), $t(12) = 1.88$, $p = 0.084$. Discrimination capability was also significantly better at the distractor than at the remapped location (8.9%), $t(12) = 3.89$, $p = 0.002$. A more luminous green distractor was therefore seen to receive more allocated attention than its less luminous red counterpart (8.4%), $t(12) = 3.08$, $p = 0.01$. Furthermore, we did not see any evidence of the changes in distractor salience affecting performance at its remapped location (difference between the remapping of a red and green distractor = 0.1%), $t(12) = 0.07$, $p = 0.943$. The differences in performance seen at the distractor, when this was either red or green, did not translate into any difference in facilitation at its respective remapped location (see Supplementary Figure S2).