

## COGNITIVE NEUROSCIENCE

# Saccade execution suppresses discrimination at distractor locations rather than enhancing the saccade goal location

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## Abstract

As we have limited processing abilities with respect to the plethora of visual information entering our brain, spatial selection mechanisms are crucial. These mechanisms result in both enhancing processing at a location of interest and in suppressing processing at other locations; together, they enable successful further processing of locations of interest. It has been suggested that saccade planning modulates these spatial selection mechanisms; however, the precise influence of saccades on the distribution of spatial resources underlying selection remains unclear. To this end, we compared discrimination performance at different locations (six) within a work space during different saccade tasks. We used visual discrimination performance as a behavioral measure of enhancement and suppression at the different locations. A total of 14 participants performed a dual discrimination/saccade countermanding task, which allowed us to specifically isolate the consequences of saccade execution. When a saccade was executed, discrimination performance at the cued location was never better than when fixation was maintained, suggesting that saccade execution did not enhance processing at a location more than knowing the likelihood of its appearance. However, discrimination was consistently lower at distractor (uncued) locations in all cases where a saccade was executed compared with when fixation was maintained. Based on these results, we suggest that saccade execution specifically suppresses distractor locations, whereas attention shifts (with or without an accompanying saccade) are involved in enhancing perceptual processing at the goal location.

## Introduction

Our brains utilise selection mechanisms to optimally process incoming information for perception and action. The underlying neuronal processes involved in selection have been considered to be competitive in nature (Koch & Ullman, 1985; Clark, 1999; Itti & Koch, 2001; Fecteau & Munoz, 2006; Bisley & Goldberg, 2010) with enhancement of neuronal activity representing the location of interest, and suppression at other locations (Eriksen *et al.*, 1993; Desimone & Duncan, 1995; Cave & Bichot, 1999; Findlay & Walker, 1999; Reynolds & Heeger, 2009) resulting in modulations in behavioral measurements such as reaction times or discrimination performance to stimuli presented at these locations. These two mechanisms have often been shown to occur concurrently, possibly reflecting both low-level lateral inhibitory competitiveness as well as top-down and bottom-up modulation within certain brain areas (Desimone & Duncan, 1995; Munoz & Istvan, 1998; Awh *et al.*, 2003; Moore & Armstrong, 2003; Fecteau & Munoz, 2006; Sylvester *et al.*, 2008; McMains & Kastner, 2011; Suzuki & Gottlieb, 2013; Van Schouwenburg *et al.*, 2013).

It has been suggested that target selection is modulated by saccades, wherein an impending saccade to a certain location in space both enhances processing at that location and suppresses processing elsewhere (Hoffman & Subramaniam, 1995; Kowler *et al.*, 1995; Deubel & Schneider, 1996; Findlay & Walker, 1999; McPeck & Keller, 2002; Awh *et al.*, 2006; Deubel, 2008; McSorley *et al.*, 2012; Harrison *et al.*, 2013). However, the specific role of saccades in enhancement and suppression remains unclear because other processes that do not involve saccades, e.g. attention, also show both enhancement at cued locations as well as suppression elsewhere (Posner & Cohen, 1984; Kastner & Pinsk, 2004; Serences *et al.*, 2004; Pestilli & Carrasco, 2005; Sylvester *et al.*, 2008). This is additionally confounded by prevailing hypotheses that attention shifts may include saccade planning (Rizzolatti *et al.*, 1994; Deubel & Schneider, 1996; Smith & Schenk, 2012; Zhao *et al.*, 2012). Saccade countermanding, which has been extensively used to distinguish processes of saccade planning and execution (Hanes & Schall, 1995; Hanes & Carpenter, 1999; Cabel *et al.*, 2000; Logan & Irwin, 2000), is a useful paradigm to reveal the specific process of pre-saccadic perceptual facilitation with respect to attentional selection.

To clarify whether processes leading to saccade execution improve perceptual discrimination by increasing the level of distractor suppression or of enhancement of the target/cued location, we

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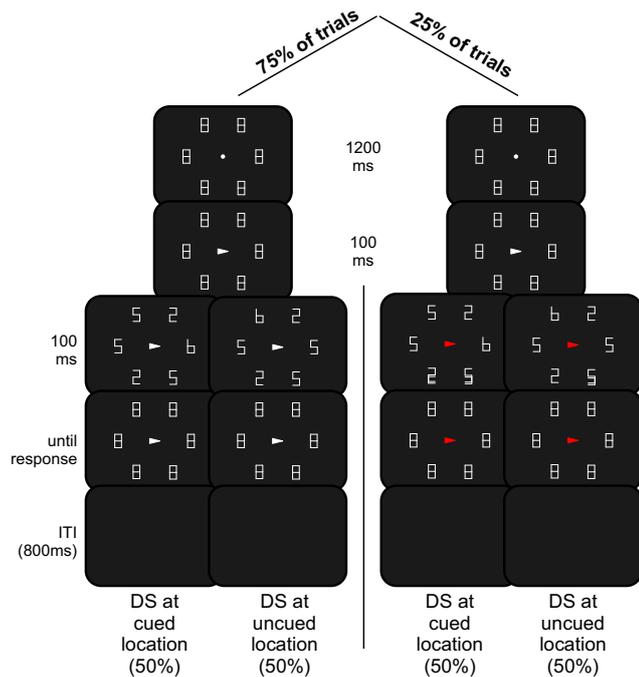


FIG. 1. Main countermanding dual-task stimuli and sequence. Each trial began with the presentation of a central fixation spot surrounded by figure eights (white) on a gray background for 1200 ms. Next, the fixation spot was replaced by a white arrow directing the participants to make a saccade as soon as possible to the corresponding figure eight. For 75% of trials (left two panels), at 100 ms after the white arrow onset, each figure eight was replaced by either one of four DSs (' $\square$ ', ' $\square$ ', ' $\square$ ', ' $\square$ ') or by one of two irrelevant symbols (' $\square$ ', ' $\square$ '). The DS appeared at the saccade goal location (indicated by the white arrow) 50% of the time (cued condition, leftward sequence) and randomly elsewhere (at one of the other five locations) the other 50% of the time (uncued condition, rightward sequence). These were replaced again by the figure eights after 100 ms. The stimuli remained on the screen until the participant's response indicated which of the four target letters appeared (regardless of where it appeared) using a game controller (four-alternative forced choice task), triggering the end of the trial. The next trial began after an intertrial interval (ITI) of 800 ms. For 25% of trials (right two panels), the arrow turned red at 0–150 ms after its onset (0 ms onset means that the arrow appeared red). In the figure, the arrow turns red at 100 ms. The remaining sequence was identical.

compared discrimination performance at cued and distractor/uncued locations in a dual discrimination/saccade countermanding task with performance during a single discrimination task without saccades. We found that discrimination performance at the cued location was similar in trials where a saccade was executed and when it was not, suggesting that saccade execution does not lead to enhancement greater than other non-saccadic processes such as knowledge or attentional allocation. In contrast, saccade execution consistently led to decreased performance at uncued locations, implying that saccades to a certain location suppress perceptual processing at all other locations.

## Materials and methods

### Participants

Fourteen participants (seven male) took part in this experiment (mean = 25.8 years of age; standard deviation = 4.34 years), one of whom was an author (A.Z.K.). Thirteen of the fourteen participants were naive as to the purpose of the experiment. All participants had normal or corrected-to-normal vision, provided written consent to

participate in the experiment, which was pre-approved by the Health Sciences Research Ethics Board at Queen's University, Kingston, Canada, and were reimbursed for their time.

### Apparatus and procedure

The participants were seated in a dimly lit room facing an LCD screen (13 × 10.5 inches, 1280 × 1024 pixels, 60 Hz refresh rate, 59.4 cm distance). Their heads were stabilised through the use of a chin rest, which was adjusted so that their eyes were centered on the LCD screen (the nose bridge was aligned to the screen center). Eye movements from the left eye were recorded using an Eyelink 1000 video-based recording system (SR Research, Mississauga, ON, Canada) at 500 Hz. The responses were executed using a Gamepad (SR Research) with four buttons (left, right, up and down) mapped to each possible choice.

The participants performed five different tasks, i.e. one main task (countermanding dual-task) and four control tasks.

The main experiment, a countermanding dual-task (Fig. 1), was a dual saccade/four-alternative forced choice discrimination task modified from previous studies (Deubel & Schneider, 2003; Khan *et al.*, 2011). During 75% of the trials (Fig. 1, left two panels), each trial began with a center white fixation spot (0.5° diameter) on a black background (luminance, 0.01 cd/m<sup>2</sup>). It was surrounded by six figure eights (white; 1.2° × 0.7°, 5.8° eccentricity). After 1200 ms, the white dot was replaced with a white arrow (0.7° × 0.5°) directed at one of the figure eights. The participants were asked to make a saccade to the figure eight specified by the arrow as quickly as possible. After another 100 ms, the figure eights all changed into different characters for a duration of 100 ms before reverting back to figure eights; one of the six figure eights transformed into one of four discrimination symbols (DSs) (' $\square$ ', ' $\square$ ', ' $\square$ ' or ' $\square$ '), whereas the other five figure eights transformed into irrelevant symbols (' $\square$ ' or ' $\square$ '). The DS appeared at the saccade goal, i.e. the location indicated by the arrow, 50% of the time (cued location), whereas for the other 50% of the trials, it appeared randomly at one of the other five locations (uncued locations). After completing the saccade, the participants were required to identify the DS, wherever it appeared, using a gamepad (four-alternative forced choice discrimination task). Their response triggered the next trial. No feedback about performance was provided.

For 25% of the time within each block of trials (Fig. 1, right two panels), the arrow turned red at a random time from 0 to 150 ms in 16.66 ms (1 frame) intervals after its appearance (for the 0 ms condition, the arrow was red when it appeared). In Fig. 1, the arrow onset is at 100 ms. This is similar to previous studies that have utilised stop probabilities from 25 to 50% as well as different delays for the stop signal onset [stop signal delay (SSD)] ranging from 0 to 450 ms. The choice of different stop probabilities and SSDs influenced the rate of successful inhibition of the saccade as well as overall saccade reaction times (SRTs) (e.g. Hanes & Schall, 1995; Cabel *et al.*, 2000; Emeric *et al.*, 2007), probably reflecting strategy changes by the participant. If the arrow turned red, the participants were asked to refrain from performing the saccade and to maintain their gaze at the fixation point but still identify the DS on that trial. Within these trials, there were also 50% cued and 50% uncued trials. All participants completed one to three training blocks until they were able to perform the saccade task as required (latencies ranging from 200 to 500 ms) and were able to perform above chance (25%) in the discrimination task during saccade trials at the cued location. They then performed six to 14 blocks of 192 trials each (1152–2688 trials) over the course of a few days to weeks (one to two blocks per session).

In the no-saccade task, the participants performed only the discrimination task with cueing (central arrow) and were asked to maintain fixation on the central stimulus during the entire trial. The trial sequence was identical to the main experiment except that the arrow never turned red. The central arrow still indicated where the discrimination letter would appear 50% of the time. The participants performed four blocks of 48 trials, interleaved throughout the blocks of the main experiment.

The participants also performed a baseline task (one block of 192 trials) during which they performed only the discrimination task without cueing. The trial sequence was identical to the main experiment except that there was no arrow indicating the likely location of the DS. Instead, the participants fixated on a small white dot during the entire trial. They were asked to discriminate the DS, which could appear with equal likelihood at any of the six locations. The majority of the participants performed this task interleaved within the final three blocks from the main experiment; three participants performed the task after completing all blocks of the main experiment.

A subset of the participants performed two additional control experiments. In the control dual-task, we investigated discrimination performance when no countermanding was necessary during the block of trials. Eight participants made a saccade on every trial (there was no red arrow presented). The experiment was identical to the main experiment, with the DS appearing at the saccade goal, i.e. the location indicated by the arrow, 50% of the time (cued location), whereas for the other 50% of the trials, it appeared randomly at one of the other five locations (uncued locations). The participants performed one block comprising 192 trials within the final blocks (five participants) or straight after the main experiment (three participants). In the ignore red arrow task, the stimuli and task sequence were identical to the countermanding dual-task except that the participants were asked to simply ignore the color change of the arrow and always execute a saccade in the arrow direction. This task was to determine whether the color change in the arrow had an influence on performance or SRTs. A subset of eight participants performed one block of 192 trials each, which was interleaved with the main experiment (five participants) or run after the main experiment (three participants).

### Data analysis

We collected a total of 34 176 trials. The saccade timing and position were automatically calculated offline using a saccade detection algorithm with a velocity criterion of 50°/s and verified visually. Trials during which the tracker lost eye position, the participants made a saccade or a blink around the time of the arrow onset until the DS offset, or during which there was incorrect fixation at the central fixation spot at the beginning of each trial were removed from the dataset (4.2% of all trials).

For the tasks with saccades, we removed all trials where the saccade onset occurred before DS offset, meaning where the saccade commenced while the DS was still visible (6.8% for main countermanding dual-task, 18.2% for control dual-task and 15.5% for control ignore red arrow task). This resulted in 22 789 of 25 728 trials (88.6%) for the main countermanding dual-task, 1229 of 1536 trials (80%) for the control dual-task and 1226 of 1536 trials (79.8%) for the ignore red arrow control task. For the no-saccade and baseline experiments, we removed trials during which the participants made a saccade, resulting in 2477 of 2688 trials (92.2%) and 2478 of 2688 trials (92.2%), respectively.

Trials in the countermanding dual-task experiment were sorted into four different behaviors of interest: (i) a successful stop trial,

during which the arrow turned red (stop signal) and no saccade occurred (amplitude  $<1.5^\circ$ ) within 500 ms of arrow onset, (ii) a successful go trial, where there was no stop signal (arrow remained white) and an appropriate saccade occurred (an SRT of  $<500$  ms, an amplitude error of  $<2^\circ$  and a directional error of  $<15^\circ$  from the center of the correct figure eight), (iii) a failed stop trial, where an appropriate saccade occurred but there was a stop signal, and (iv) a failed go trial, where a saccade did not occur even though there was no stop signal. The labels that we used here are synonymous with previous studies on countermanding, i.e. successful go = go signal trials, no-stop signal trials; successful stop = signal-inhibit trials, cancelled trials; and failed stop = signal-respond trials, non-cancelled trials (Hanes & Schall, 1995; Kornyló *et al.*, 2003; Pare *et al.*, 2003).

The discrimination performance was calculated as the percentage of trials where the DS was correctly discriminated among all trials. Where applicable, trials were grouped into two conditions: (i) cued location, where the DS appeared at the location indicated by the arrow and (ii) uncued locations, where the DS appeared elsewhere.

Repeated-measures *t*-tests and ANOVAs as well as Chi-squared tests were used for statistical analyses.

## Results

To determine how saccade execution influenced the enhancement and inhibition processes, we investigated how the discrimination performance varied depending on different saccade behaviors during the main countermanding dual-task, i.e. for successful go trials, during which the saccade was executed, successful stop trials during which the saccade was not executed and failed stop trials during which the saccade was executed erroneously, and compared these with the no-saccade task, which required only discrimination and during which no saccade was required or executed. In all tasks, whether or not they involved saccades, the DS appeared while the eyes were at central fixation. We used discrimination performance as a measure of the distribution of attentional allocation across the visual work space, which we posit is based on underlying enhancement and inhibition processes across the space.

### Main results

Figure 2 summarises the discrimination performance for the main countermanding dual-task as well as the no-saccade task. For the countermanding task, performance is shown sorted according to whether a saccade occurred (Fig. 2, left two bars, successful go trials and failed stop trials within the main countermanding task) or not (Fig. 2, right two bars, successful stop trials within the main countermanding task and the no-saccade task) separately for the cued locations (Fig. 2A) and the corresponding performance in the uncued locations (Fig. 2B). For the cued location, there was no consistent performance related to whether or not a saccade was executed. Rather, discrimination performance depended on whether the arrow turned red. Discrimination performance was equally high for the successful go trials and the no-saccade task (successful go: mean = 83.9%; no-saccade: mean = 85.5%; repeated-measures *t*-test,  $t_{13} = 1$ ,  $P > 0.05$ ). Compared with the successful go trials, discrimination performance was significantly lower for failed stop trials (where the participants performed a saccade in spite of a red arrow) at 62.8% ( $t_{13} = 4.7$ ,  $P < 0.01$ ). In addition, it was also significantly lower for successful stop trials (mean = 65%;  $t_{13} = 8.3$ ,  $P < 0.01$ ), where a saccade was correctly not executed in the presence of the red arrow.

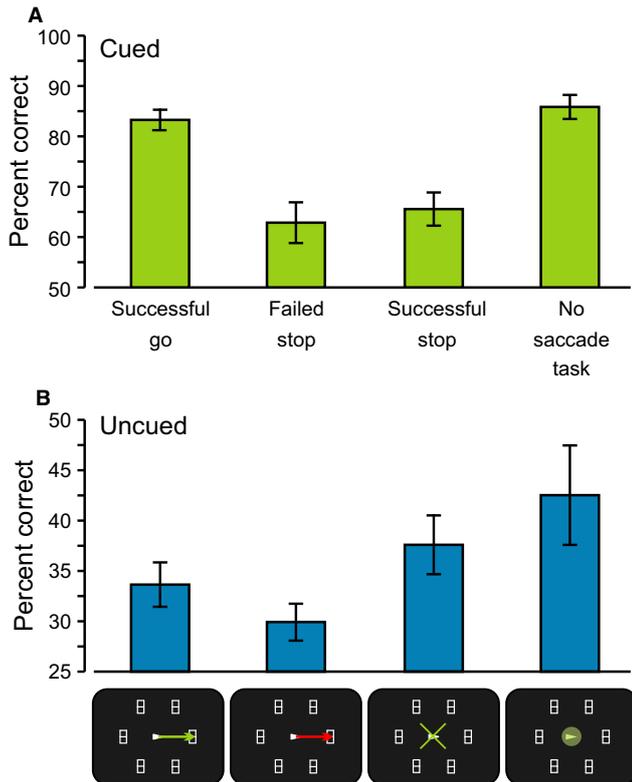


FIG. 2. Main results for countermanding dual-task and no-saccade task for different trial types. (A) Mean discrimination performance is shown for different trial types. Trial types/tasks in which saccades occurred are on the left (left two bars); these are the successful go trials, where a saccade was correctly executed according to the arrow instruction, and failed stop trials, where a saccade was executed in the direction of the arrow in spite of it being red. Trial types/tasks in which no saccade occurred are on the right; these are successful stop trials within the main countermanding dual-task, where no saccade was executed as the arrow was red, and the no-saccade task, which was a discrimination-only task and no saccade was required. Note the range in the y-axis from 50 to 100%. The bars show mean performance across all participants (error bars are SEM across participants). The icons at the bottom depict the different trial types and tasks. (B) Mean discrimination performance is shown for the uncued condition sorted in the same manner as in A. Note the range in the y-axis, which is from 25 to 50%.

For the uncued locations, performance for all trial types/tasks was significantly lower than for the cued location (Fig. 2, note y-axis range, see subsequent detailed results for statistics). More importantly, in all cases, performance for trial types where a saccade was executed elsewhere (Fig. 2, left two panels) was significantly lower than performance when there was no saccade executed (Fig. 2, right two panels; successful stop trials and no-saccade task). Specifically, compared with the successful go trials (mean = 33.6%), performance was not significantly different for failed stop trials (mean = 29.85,  $t_{13} = 1.8$ ,  $P > 0.05$ ) and both showed performance close to chance levels (25%). In contrast, for the successful stop trials, performance was significantly higher than the successful go trials (mean = 37.7%,  $t_{13} = 3.1$ ,  $P < 0.01$ ) as was the case for the no-saccade task (mean = 42.5%,  $t_{13} = 2.7$ ,  $P < 0.05$ ).

To summarise, performance at the cued location was similar whether or not a saccade was executed to the cued location. The addition of the countermanding task (red arrow) seemed to disrupt this high performance at the cued location. In contrast, performance at the uncued locations appeared to depend on whether or not a sac-

cade was executed and not on the countermanding task, with performance being lower when a saccade was executed elsewhere.

#### Baseline task, no-saccade task and successful go trials

Discrimination performance for the baseline task is shown in Fig. 3A (leftmost bar, dots represent individual performance). In this task, there was no arrow indicating the likely location of the DS, and it could appear at any one of the six positions. Because the likelihood for each location was approximately 16.6%, we presumed that the participants would spread their attention across the entire task area and no one location would be enhanced or suppressed relative to any other location. All participants performed significantly above chance level for all DS locations [mean = 54.9%, standard deviation = 12.8%,  $C^2(1) > 21$ ,  $P < 0.001$ ] and, as expected, there were no significant differences in performance across the six locations (repeated-measures ANOVA,  $P > 0.05$ ) (see Fig. S1A).

We investigated how this baseline performance changed across the task space when one location became the likely location for the DS to appear (Fig. 2, rightmost bars). The middle two bars in Fig. 3A depict the performance during the no-saccade task, which did not involve any saccades (discrimination only with eyes always fixated at center) but did have the same cueing (central arrow). The participants were asked to fixate at the central location throughout the trial and perform only the discrimination task without making a saccade. The arrow, presented on every trial, indicated the probable (50%) location of the DS. Performance was much higher at the cued location (85.5%, individual participants, range, 69–98%) than at the uncued locations (42.5%; range, 24–78%;  $t_{13} = 8.8$ ,  $P = 10^{-6}$ ,  $N = 2477$ ). In addition, compared with the baseline condition, performance was significantly better at the cued location ( $t_{13} = 8.9$ ,  $P = 10^{-6}$ ) and significantly worse at the uncued locations ( $t_{13} = 3.1$ ,  $P < 0.009$ ). There were no significant differences across DS locations (repeated-measures ANOVA,  $P > 0.05$ ) (Fig. S1B). To summarize, increasing the likelihood that the DS will appear at a certain location (as indicated by the arrow) changed the distribution of attentional resources, where performance at the cued location was improved and performance at all other locations was decreased relative to the baseline condition.

Next, we investigated whether saccade execution changed this pattern of discrimination performance. We calculated discrimination performance during the main countermanding dual-task for successful go trials, when the participants performed a saccade as directed by the white arrow and discriminated the DS at the same time (Fig. 2, leftmost bars,  $N = 15\,193$ ). Discrimination performance during successful go trials (Fig. 3A, rightmost two bars) was high at the cued location (mean = 83.9%, standard deviation = 6.9%) and close to chance at the uncued locations (mean = 33.6%, standard deviation = 8.8%), with performance being significantly different between the two ( $t_{13} = 19.2$ ,  $P < 0.01$ ). There was remarkably consistent performance (dark gray lines showing individual performances) across participants. Performance at the cued location was significantly better than baseline ( $t_{13} = 10$ ,  $P < 0.01$ ), whereas performance at the uncued locations was significantly worse than baseline ( $t_{13} = 57$ ,  $P < 0.01$ ). As mentioned previously, there was also no difference in performance between successful go trials and the no-saccade task at the cued location ( $P > 0.05$ ), whereas performance at the uncued locations was significantly worse ( $t_{13} = 2.3$ ,  $P > 0.05$ ). This is confirmed in the scatterplots comparing individual performances during the no-saccade task and the successful go trials in the main countermanding dual-task for the cued (green) and uncued (blue) locations (Fig. 3B).

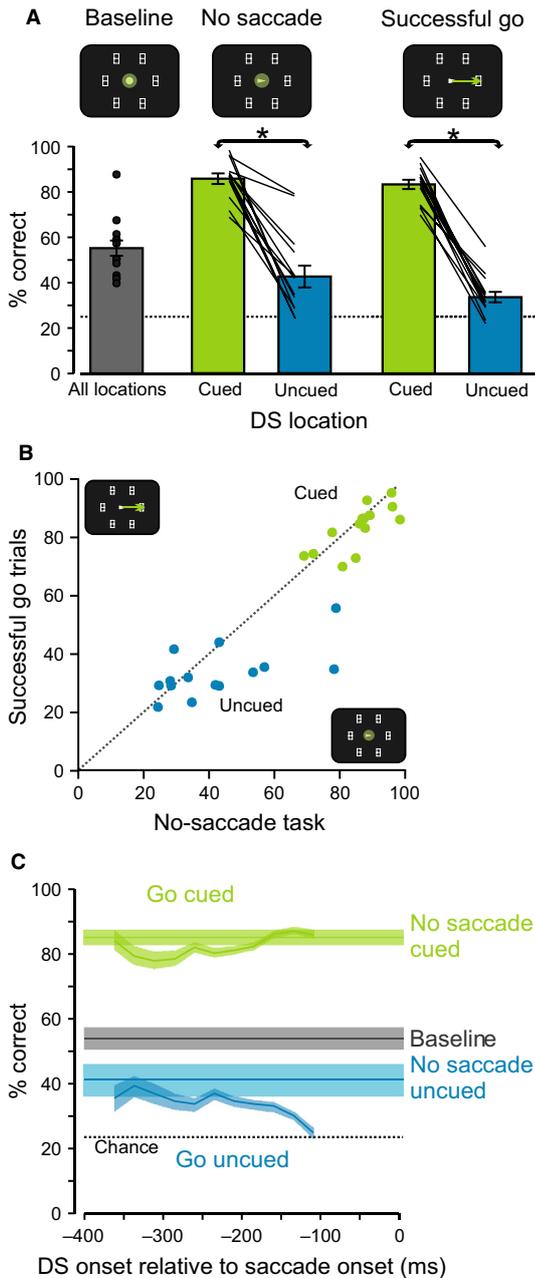


FIG. 3. Baseline, no-saccade and countermanding dual-task experiment results. (A) The leftmost gray bar depicts discrimination performance for each individual participant (black dots) as well as across all subjects (mean with SEM across participants) for the baseline task, during which the participants fixated on the central dot throughout the task, and the DS could randomly appear at any one of the six locations. Chance performance (25%) is shown by the dotted horizontal line. The middle two bars depict the performance for the no-saccade experiment, where the participants discriminated the DS, which appeared at the location indicated by the arrow 50% of the time, while remaining fixated on the central dot during the entire trial. Mean discrimination performance is for the cued (green bar, DS appeared at location indicated by the arrow, 50% of the time) and uncued (blue bar, DS appeared randomly elsewhere, 10% of the time at each location) locations along with SEM error bars across participants. The rightmost two bars depict performance during successful go trials during the main countermanding dual-task experiment. The DS appeared either at the location indicated by the arrow (also the saccade goal, cued location, green) or elsewhere (uncued location, blue). The bars show mean performance across all participants (error bars are SEM across participants). The dark gray lines are performances for individual participants. \*Significant difference at  $P < 0.05$ . (B) Scatterplot of discrimination performance for cued (green dots) and uncued (blue dots) for the successful go trials vs. the no-saccade task. The diagonal dotted line is the line of unity. Each dot represents performance for each individual subject. (C) Discrimination performance in the cued (green line plus SEM shaded area) and uncued (blue line plus SEM shaded area) locations as a function of the time between the DS onset and the saccade onset, binned into 25 ms intervals. Only bins in which there were trials from at least 12 of the 14 of the participants are shown. For comparison, performance from the no-saccade and baseline experiments is also shown.

should have a maximum effect just before saccade execution. Therefore, if the DS appeared at an uncued location just before the saccade was executed elsewhere, as is the case for saccades with short SRTs, there should be lower discrimination performance than when the DS appeared long before the saccade was executed (i.e. saccades with long SRTs).

To investigate this, we calculated discrimination performance as a function of DS onset relative to saccade onset (Fig. 3C) (25 ms bins across all participants from  $-100$  to  $-375$  ms). For comparison purposes, discrimination performance for the no-saccade cued and baseline conditions is also shown. When the DS onset was close to saccade onset (between  $-100$  and  $-175$  ms, shortest three 25 ms bins), discrimination performance for the cued location was not significantly different from the no-saccade performance (mean = 87%,  $P > 0.05$ ); however, performance in the uncued condition was significantly worse than the no-saccade task (mean = 31.3%,  $t_{13} = 2.6$ ,  $P < 0.05$ ). However, when the DS appeared long before saccade onset (between  $-300$  and  $-375$  ms, longest three 25 ms bins), performance was significantly worse for the cued location compared with the no-saccade task (mean = 76.8%,  $t_{13} = 2.36$ ,  $P < 0.05$ ) but not significantly different at the uncued locations (mean = 38.4%,  $P > 0.05$ ). In addition, when the DS onset was close to saccade onset compared with long before saccade onset, performance was significantly improved at the cued location ( $t_{13} = 2.4$ ,  $P < 0.05$ ) and significantly decreased at the uncued locations ( $t_{13} = 2.3$ ,  $P < 0.05$ ) when the DS onset was close to saccade onset compared with long before saccade onset. We also performed linear regression analyses separately for both the cued and uncued locations with time (in 25 ms bins) as a factor. For the cued location, performance did not increase significantly as a function of time closer to saccade onset ( $R^2 = 0.013$ ,  $P > 0.05$ ); however, for the uncued locations, it decreased significantly ( $R^2 = 0.04$ , performance =  $-0.035 \times \text{time} + 23.5$ ,  $P < 0.05$ ).

The results suggested that discrimination performance at the saccade goal (cued) location was never better than performance during the no-saccade task, even though it (possibly) improved as the DS appeared closer in time to the execution of the saccade. The results

These results support the notion that executing a saccade to a certain location does not enhance discrimination more than when a saccade is not executed; for both conditions, discrimination was similar, presumably based on knowledge of the likelihood of the DS appearing at that location. However, for the uncued locations, saccade execution resulted in lower performance compared with the no-saccade task, suggesting that suppression occurred at uncued locations during processes leading to saccade execution.

If saccade execution is related to inhibitory processing at uncued locations, there should be a temporal relationship between these processes and the time of saccade onset. Specifically, we expected that inhibitory processes should be greatest just before saccade execution rather than long before saccade execution. This is based on the idea of a build-up of pre-saccadic activity in saccade-related areas to a threshold that leads to saccade execution (Hanes & Schall, 1996; Pare *et al.*, 2003; Jantz *et al.*, 2013). Thus, if saccade execution results in a decrease of attentional resources at uncued locations, this

also showed that the DS was correctly discriminated much less at an uncued location the closer the DS appeared relative to the time of saccade execution, suggesting greater inhibition at distractor locations closer to saccade execution.

We also confirmed that there was no decrease in SRTs for the participants over blocks of trials due to learning, which may confound the findings above. We calculated the slopes between SRTs and chronological experimental blocks for each participant. The slopes were not significantly different from 0 for 10 of the 14 participants ( $P > 0.05$ ). Of the remaining four participants, three showed significantly increasing slopes, i.e. their SRTs increased over the blocks rather than decreased and only one participant showed a significantly decreasing slope ( $P < 0.05$ ) at the rate of 4.3 ms per experimental block, i.e. an average of 43 ms shorter SRTs over the course of the 10 blocks. Thus, we conclude that there was no consistent change in SRTs that could account for the results shown in Fig. 3C.

Next, we investigated whether discrimination performance varied for different distractor (uncued) locations. To do so, we calculated the absolute distance of the DS relative to the cued location for each trial, separated into whether the DS was in the same or in the opposite hemi-field (horizontal). Previous studies have shown a hemi-field effect on detection (Rizzolatti *et al.*, 1987; Deubel & Schneider, 1996). Figure 4 illustrates discrimination performance at the different locations [0°, cued location (green bar); 60°, uncued location one position away (dark blue, same hemi-field; light blue, opposite hemi-field); 120°, uncued location two positions away; 180°, uncued location three positions away or opposite to the cued location]. Collapsed across hemi-field, we found significantly lower discrimination performance when the uncued DS was in the same hemi-field (29.6%) as the saccade goal (cued location) compared with when the DS was in the opposite hemi-field from the saccade goal or cued location (36.2%,  $t_{13} = 3.5$ ,  $P < 0.01$ ). Within each hemi-field, we found no differences in performance for the different uncued locations (same hemi-field,  $P > 0.05$ ; opposite hemi-field,  $P > 0.05$ ). This suggests that there was an overall greater inhibition of uncued locations in the same hemi-field compared with the opposite hemi-field.

### Successful stop trials

Next, we quantified performance during successful stop trials, during which the participants did not execute a saccade but remained fixated on the central red arrow, according to the task instructions (Fig. 2, middle right bars). In this case, the participants were presumably planning a saccade but did not execute it. For these trials (Fig. 5A,  $N = 3703$ ), mean performance was significantly better for the cued location (65.1%, individual participants, range, 39–88%) than for the uncued locations (37.6%; range, 25–63%,  $t_{13} = 7.4$ ,  $P < 0.01$ ). Compared with baseline, performance was significantly better for the cued location ( $t_{13} = 2.38$ ,  $P < 0.05$ ) and significantly worse for the uncued locations ( $t_{13} = 5.4$ ,  $P < 0.01$ ).

For the cued location, successful stop trial performance was significantly worse than both the successful go trials ( $t_{13} = 8.3$ ,  $P < 0.05$ ) (Fig. 5B), as well as the no-saccade task ( $t_{13} = 6.6$ ,  $P < 0.05$ ). This reveals that some aspect of correct stop trials interfered with discriminating the DS at the cued location to a certain degree. However, performance was still better than baseline performance, suggesting that there was nevertheless some increased attention at the cued location. For the uncued locations, performance was better than during successful go trials ( $t_{13} = 3.1$ ,  $P < 0.01$ ) (Fig. 5B) but was not different from the no-saccade task ( $P > 0.05$ ), implying that discrimination performance at uncued locations was

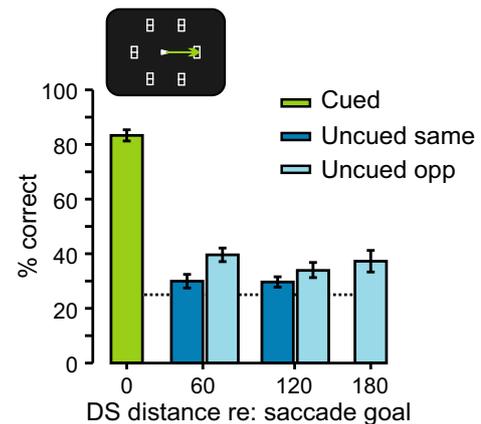


FIG. 4. Discrimination performance for successful go trials as a function of distance from saccade goal location. Discrimination performance is shown as a function of the distance (in degrees) of the DS relative to the saccade goal location, separated by hemi-field (horizontal). 0° distance is the cued condition (green error bar), 60° is one position (figure eight) away (either direction), 120° is two positions away and 180° is three positions away or opposite to the saccade goal location. The darker blue bars are discrimination performances when the DS appeared in positions that were located in the same hemi-field, whereas the lighter blue bars are performances when the DS appeared in positions that were located in the opposite hemi-field.

similar to the tasks where no-saccade was executed, consistent with our prediction.

Previous studies have shown that the ability to successfully inhibit a saccade depends on the SSD, i.e. the later that the stop signal appears after the go signal, the less successful participants are at inhibiting the saccade (Hanes & Schall, 1995; Hanes & Carpenter, 1999; Cabel *et al.*, 2000; Stuphorn & Schall, 2006; Stevenson *et al.*, 2009). This is because of competition between two processes that have been implicated in countermanding, i.e. the stop and go processes. Generally, the stop process rises to a threshold level faster than the go process (Logan *et al.*, 1984; Verbruggen & Logan, 2008), thus leading to a high probability of inhibiting the saccade at short SSDs. With increasing SSDs, the go process is more likely to reach the threshold before the stop process, thus increasing the likelihood of a saccade (Hanes & Schall, 1995; Hanes & Carpenter, 1999; Ozyurt *et al.*, 2003). This was supported in the current task; the percentage of successful stop trials decreased as a function of SSD (0 ms, 24.7%; 150 ms, 9.7%), with some participants never managing to stop for the longer SSDs. In other words, the longer SSDs resulted in higher percentages of executed saccades.

This implies that, even for successful stop trials, the longer the SSD, the higher the activation level of the go process, even if it did not reach threshold before the stop process. In other words, the longer the SSD, the closer the saccade is to being executed. We therefore hypothesized that, if the likelihood to execute a saccade is higher with longer SSDs, and the increase in the signal that leads to saccade execution is related to the suppression of distractor locations, then discrimination performance should decrease at the uncued locations for longer SSDs. Figure 5C shows discrimination performance for the cued (green) and uncued (blue) locations as a function of the SSD. As mentioned above, some participants made no successful stops for longer SSDs; therefore, we only analysed (and show) SSDs in which there were trials for every participant. Discrimination performance was not significantly different for the cued location between the shortest (0 ms) and longest (83 ms) SSD ( $P > 0.05$ ) but was significantly lower for the uncued locations

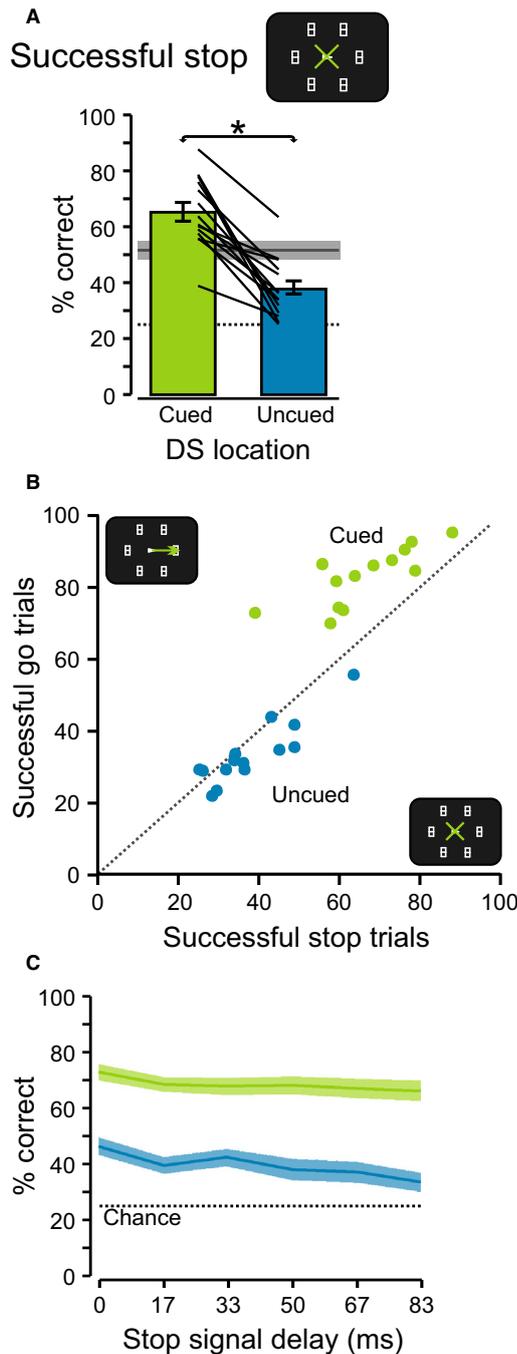


FIG. 5. Performance during successful stop trials. (A) Mean discrimination performance for all participants as a function of DS location for successful stop trials. The DS appeared at either the location indicated by the arrow (cued, green) or elsewhere (uncued, blue). The dark gray lines are performances for individual participants. The y-axis shows discrimination performance as percent correct. The horizontal dotted line denotes chance level and the horizontal solid gray line and shaded area denote baseline performance. \*Significant difference at  $P < 0.05$ . (B) Scatterplot of discrimination performance for cued (green dots) and uncued (blue dots) for the successful go trials vs. the successful stop trials (within the main countermanding dual-task experiment). The diagonal dotted line is the line of unity. (C) Discrimination performance for successful stop trials is shown for the cued (green) and uncued (blue) conditions as a function of the SSD.

( $t_{13} = 3$ ,  $P < 0.05$ ). This result is consistent with our hypothesis of decreased discrimination performance closer to saccade execution for distractor/uncued locations. Additionally, it also demonstrates

that there was no change in discrimination performance in the cued location. Both results are consistent with the findings from the successful go trials.

#### Failed stop trials

Next, we investigated discrimination performance during failed stop trials, i.e. trials during which the arrow turned red (stop signal) but the participant was unable to stop the saccade (Fig. 2, middle left bars,  $N = 2010$ ). These are trials in which a saccade was executed, and therefore we should observe the same performance in the uncued locations as for successful go trials. As shown in Fig. 6A, there was a significant difference between the two DS locations (cued, 62.8%; uncued, 29.8%;  $t_{13} = 8.1$ ,  $P < 0.05$ ). We compared mean SRTs for failed stop trials and successful go trials. Based on the hypothesis of independent go and stop processes, an emergent prediction is that SRTs for failed stop trials should be shorter than those for successful go trials (Verbruggen & Logan, 2009). Consistent with this, mean SRTs were significantly shorter for the failed stop trials (mean = 284 ms) than for the successful go trials (mean = 305 ms,  $t_{13} = 4.6$ ,  $P < 0.05$ ) (Fig. 6B). As we showed above that performance for successful go trials depended on the DS onset relative to saccade, hence SRTs, in order to compare discrimination performance for the failed stop trials with that of successful go trials, we selected successful go trials with SRTs that were within the minimum–maximum range of SRTs within the failed stop trials for each participant. For the cued condition, performance for the failed stop trials was significantly lower than that for successful go trials ( $t_{13} = 4.3$ ,  $P < 0.01$ ) (Fig. 6C); however, for the uncued locations, performance for the failed stop trials was not different from successful go trials ( $P > 0.05$ , Fig. 6C).

Performance for the cued location was also significantly lower than for the no-saccade task ( $t_{13} = 4.2$ ,  $P < 0.01$ ), but not different from performance during successful stop trials ( $P > 0.05$ ). For the uncued locations, performance was significantly lower than both the successful stop trials ( $t_{13} = 3$ ,  $P < 0.05$ ) as well as for the no-saccade task ( $t_{13} = 3.2$ ,  $P < 0.01$ ).

In summary, discrimination performance at the cued location in the failed stop trials was similar to the successful stop trials, suggesting similar interference due to the presence of the stop signal, regardless of whether or not a saccade was executed. However, for the uncued locations, performance was similar to that during successful go trials where, in both cases, a saccade was executed, and it was dissimilar to the successful stop and no-saccade conditions where a saccade was not executed.

#### Control dual-task

To determine whether discrimination performance was different because the countermanding dual-task required the inhibition of a saccade on some trials, we compared performance from successful go trials with that from the control dual-task (no red arrow present so that the participants made a saccade on every trial). This control dual-task was performed by a subset of the participants; therefore, we performed statistical analyses only within this participant group. The SRTs were shorter during the control dual-task than the countermanding task (261 vs. 301 ms,  $t_7 = 3.3$ ,  $P < 0.05$ ). As previously, to be able to compare the performance for the control dual-task and the countermanding task, we selected successful go trials with SRTs that were within the minimum–maximum range of SRTs in the control dual-task for each participant. We then compared discrimination performance within these subsets of trials; there was

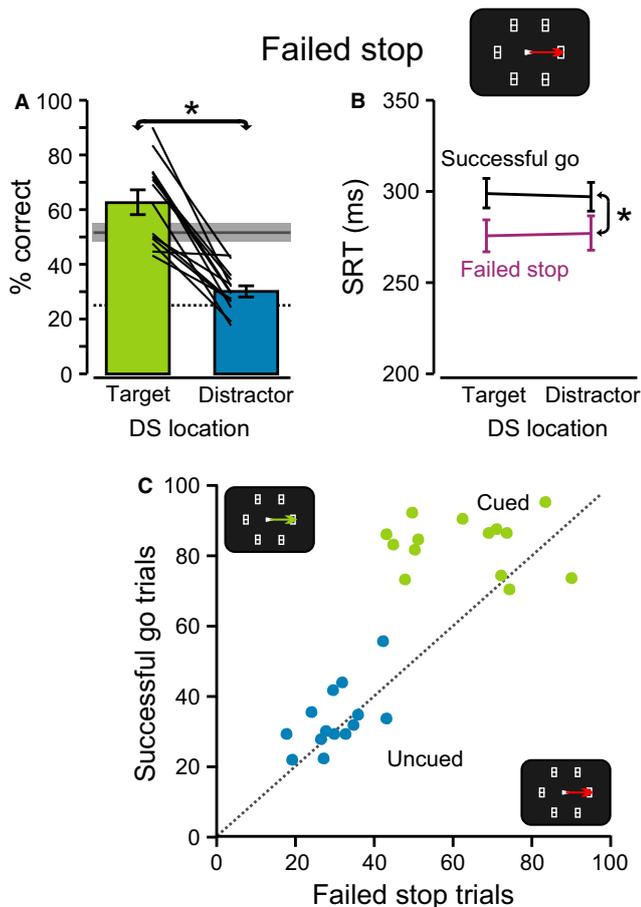


FIG. 6. Failed stop trials. (A) Mean discrimination performance for all participants as a function of DS location for failed stop trials. The bars show mean performance across all participants (error bars are SEM across participants). The dark gray lines are performances for individual participants. The y-axis shows discrimination performance as percent correct. The horizontal dotted line denotes chance level and the horizontal solid gray line and shaded area denote baseline performance. \*Significant difference at  $P < 0.05$ . (B) SRTs (in ms) are shown for failed stop trials (purple line) and successful go trials (black line) as a function of condition (congruent or not). \*Significant difference at  $P < 0.05$ . (C) Scatterplot of discrimination performance for cued (green dots) and uncued (blue dots) for the successful go trials vs. the failed stop trials (within the main countermanding dual-task experiment) with the same minimum–maximum range of SRTs. The diagonal dotted line is the line of unity.

no significant difference between the two tasks at either the cued location (control dual-task, 83.7%; successful go, 82.1%,  $P > 0.05$ ) or the uncued location (control dual-task, 33.5%; successful go, 29.7%,  $P > 0.05$ ). Moreover, performance was also similar between the two locations when plotted as a time-series as in Fig. 3C (see Fig. S2).

#### Ignore red arrow control task

Performance in the cued location for both the successful stop trials as well as the failed stop trials was lower than either the successful go trials or the no-saccade trials (Fig. 2). We investigated whether this was due to the transient change in the color of the arrow. A subset (eight) of the participants performed an ignore red arrow control block where they were asked to always make saccades to the location indicated by the arrow and to simply ignore the transient color change of the arrow. We grouped trials into whether or not

the arrow turned red (stop trials) and compared performance for the cued and the uncued locations between the two. Performance at the cued location was significantly worse during stop trials (72.9%) than during go trials (87.1%) even when the participants made a saccade during every trial ( $t_7 = 3.3$ ,  $P < 0.05$ ). In contrast, at the uncued locations, there was no difference in performance between the two (stop, 34.7%; go, 36.1%,  $P > 0.05$ ). Additionally, there were no differences in SRTs between the two groups (stop, 267 ms; go, 274 ms,  $P > 0.05$ ).

To summarize, the decrease in performance during the cued location for both successful and failed stop trials appeared to be (at least partially) due to the transient change in the color of the arrow interfering with discrimination performance at the cued location. However, there were no differences at the uncued location, as would be expected if discrimination performance was related primarily to saccade execution processes.

#### Discussion

The goal of the current study was to investigate how saccades executed to a certain location influenced visual discrimination across the work space. We used discrimination performance as a behavioral measure of the distribution of spatial resources underlying selection and compared discrimination performance at likely and unlikely locations with or without saccades. We utilized a countermanding task to uncouple the processes of saccade execution from saccade planning. We found that discrimination performance at the likely location of the DS (where it appeared 50% of the time) was equally high whether or not a saccade was executed to that location. Specifically, when the participants were asked to maintain fixation, they were able to correctly discriminate the symbol at the likely location the majority of the time (voluntary covert attention) and much better than when all six locations were equally as likely (baseline condition). Executing a saccade to this location did not additionally enhance processing to this location, even when the DS appeared shortly before saccade execution. These findings are consistent with previous studies that have also shown equivalent discrimination performance at the cued location with or without saccades, although there may be differences in the time-courses of the two (Castet *et al.*, 2006; Deubel, 2008; Filali-Sadouk *et al.*, 2010; Rolfs & Carrasco, 2012; Born *et al.*, 2013). Importantly, we show that, although performance slightly improves the closer the DS is presented in time to saccade onset, it does not improve above that during the no-saccade task (covert attention). Indeed, Deubel (2008) showed a similar pattern, i.e. that discrimination improved at the cued location as a function of DS onset relative to saccade onset but, importantly, was never better than the discrimination-only task.

Discrimination performance decreased when there was a transient change at fixation, even if a saccade was executed to the DS location, e.g. during failed stop trials. The decrease in performance might reflect a decrease in attentional resources at the saccade goal location. This finding questions the prevailing but sometimes disputed notion that saccades automatically and absolutely direct attention to the saccade goal (Rizzolatti *et al.*, 1987; Hoffman & Subramaniam, 1995; Kowler *et al.*, 1995; Deubel & Schneider, 1996; Gersch *et al.*, 2004; Moore & Fallah, 2004; Rolfs & Carrasco, 2012; Harrison *et al.*, 2013), because attentional allocation was decreased at the upcoming saccade goal even though a saccade was executed to this location.

When the DS appeared at uncued (distractor) locations, performance overall (with and without saccades) was much lower than the baseline condition, implying a withdrawal of resources from these

locations. However, we observed that discrimination at these locations was always even lower when a saccade was executed compared with when it was not. Discrimination performance decreased, sometimes close to chance in all cases when the saccade was executed, i.e. in both failed stop trials and successful go trials, and was higher in all cases when a saccade was not executed, i.e. in successful stop trials and in the no-saccade task. Moreover, the transient change at fixation appeared to have no effect on this pattern, i.e. there was no change in discrimination performance when the arrow turned red (e.g. failed stop trials) and when it did not (e.g. successful go trials). These results imply that it was mainly the execution of the saccade plan that resulted in an additional inhibition of all non-saccade goal locations. We found a dynamic relationship between saccade execution and slight discrimination enhancement at the cued location as well as strong discrimination suppression elsewhere (uncued locations); the closer that the DS was presented to the time of saccade execution, the better the discrimination was at the cued location to a small degree (deployment of the attentional shift enhancing the cued location) and the worse the discrimination was at the uncued location to a larger degree (deployment of the focusing process that inhibits the distractor locations). This is consistent with previous findings (Deubel, 2008; Rolfs *et al.*, 2011; Born *et al.*, 2014). However, discrimination performance at the saccade goal was never better than the no-saccade task, although it was worse if the DS was presented well before saccade execution.

In contrast, discrimination at distractor/uncued locations was equivalent to the no-saccade task well before the saccade but became worse the closer the time to saccade execution. This was also reflected in the successful stop trials, where discrimination became worse at uncued locations the longer the SSD, whereas it did not improve, but in fact also got worse at the cued location with longer SSD, which presumably may reflect the influence of a signal that is close to the threshold of executing a saccade (Hanes & Schall, 1996; Pare *et al.*, 2003; Jantz *et al.*, 2013).

Taken together, our findings support the notion that signals related to saccade execution influence uncued distractor locations rather than the cued location. We propose that saccade execution is associated with reducing interference from distractors. A recent study has shown that crowding is reduced when an upcoming saccade is directed to that location (Harrison *et al.*, 2013), whereas it is very difficult to distinguish closely located targets using covert attention without saccades (Bahcall & Kowler, 1999; Intriligator & Cavanagh, 2001; Harrison *et al.*, 2013). Along these lines, we recently demonstrated that a patient with unilateral posterior parietal damage was able to discriminate a target among flankers when planning a saccade to the target but not when attempting to shift attention covertly (Blangero *et al.*, 2010). The preserved pre-saccadic perceptual facilitation in this patient might rely on preserved suppression processes despite impaired enhancement processes following focal posterior parietal damage. One prediction from this proposal is that, in tasks where there are targets surrounded by flankers, covert attention shifts to the target should result in lower performance compared with when a saccade is involved. In contrast, without flankers, performance should be similar during covert and saccade trials.

It has been posited that selection of a location occurs on a theoretical priority map that integrates both bottom-up and top-down inputs (Fecteau & Munoz, 2006; Serences & Yantis, 2006; Bisley & Goldberg, 2010). Competitive interactions between different locations result in one location being enhanced, whereas all other locations are suppressed in a winner-take-all process (Itti & Koch, 2001). A number of areas have been proposed to represent a priority map, including the superior colliculus, frontal eye fields or parietal cortex, all of which

have been implicated and are involved in saccade planning (Keller & McPeck, 2002; Thompson & Bichot, 2005; Goldberg *et al.*, 2006). Within these maps, there is evidence for enhancement of neuronal activity of attended locations (Koch & Ullman, 1985; Deco *et al.*, 2002; Bisley & Goldberg, 2003; Armstrong *et al.*, 2009) as well as the suppression of activity at distractor locations (Dorris *et al.*, 2007; Falkner *et al.*, 2010) based on a combination of local inhibitory connections, as have been shown in areas such as the frontal eye fields or superior colliculus (Meredith & Ramoa, 1998; Munoz & Istvan, 1998; Munoz & Fecteau, 2002; Isa & Hall, 2009; Phongphanphane *et al.*, 2014), and bottom up as well as top-down inputs from other areas (Itti & Koch, 2001; Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Van Schouwenburg *et al.*, 2013).

The findings with this study can be thought of as reflecting these competitive processes, where increased activity at one location, due to knowledge of the likelihood of the DS appearing there, leads to decreased activity at all other locations, perhaps through local inhibitory connections, which is probably a dynamic process. However, the additional decrease in discrimination performance at distractor locations resulting from saccade execution but not from the covert attentional shift necessitates the involvement of additional inhibitory mechanisms. These could result from efference copy signals related to the eye movement but not to attentional mechanisms. Supporting this idea, neurophysiological recordings from the frontal eye fields support the existence of two different populations of neurons, one related to saccade execution and another related to attentional shifts (Juan *et al.*, 2004; Thompson *et al.*, 2005; Brown *et al.*, 2008; Ray *et al.*, 2009; Wardak *et al.*, 2011). Alternatively, different cell dynamics, such as high-frequency activity related to saccades and low-frequency activity related to attention shifts within the same population of neurons, e.g. the superior colliculus, could also have differential inhibitory effects on distractor-related activity. This inhibitory activity may in turn be transmitted to areas involved in visual processing or attention, as has been shown by neurophysiological findings in area V4 reporting dynamic effects of saccade planning on non-target locations (Han *et al.*, 2009; Steinmetz & Moore, 2010) as well as in the lateral intraparietal cortex showing suppression of activity at non-saccade goal locations (Falkner *et al.*, 2010). Finally, we found a hemi-field modulation of distractor suppression consistent with the proposed theories of interhemispheric inhibition, particularly within the field of neglect (Szczepanski *et al.*, 2010; Smigajewicz *et al.*, 2014).

What is the functional significance of suppression of distractor locations with saccades? It has been previously suggested that suppression of non-saccade locations is useful for improved performance at the saccade goal as well as improved saccade accuracy to that location (Kowler, 2008). As mentioned in the Introduction, both enhancement of the location of interest as well as suppression of the distractor locations can independently lead to better processing at the target/cued location. Moreover, improved saccade landing accuracy also enables better and faster processing at the target/cued location. Thus, the mechanisms of saccade-related distractor suppression may serve to improve processing of the selected location, but at the expense of processing elsewhere.

## Conclusions

Selection mechanisms of enhancement and suppression can be driven by both saccades as well as knowledge (voluntary covert attention). We propose that saccade execution specifically suppresses distractor/uncued locations, whereas covert attention is sufficient for enhancing locations of interest.

## Supporting Information

Additional supporting information can be found in the online version of this article:

Fig. S1. Performance as a function of DS location for baseline and no-saccade tasks. (A) Discrimination performance as a function of DS location for the baseline condition. The radial lines depict discrimination performance as percent correct, whereas the linear lines show the DS location in degrees. Performance is shown at each DS location in the solid black lines. (B) Discrimination performance as a function of DS location for the no-saccade task. Performance is shown for only the cued condition for the six different DS locations in the same manner as for A.

Fig. S2. Performance as a function of DS onset relative to saccade onset for successful go trials for main experiment and control dual-task. Discrimination performance is shown as a function of the DS onset relative to saccade onset for the main dual-task experiment as well as the control dual-task (no red arrow). The thicker lines (mean) and darker shading (SEM) represent the control dual-task experiment, whereas the thinner lines and shading represent the main dual-task experiment (with countermanding 25% of the time). SRTs were shorter for the control dual-task hence fewer 25 ms bins. Data are shown only for the eight participants that performed both tasks and for bins in which there were performance data from at least six of the eight participants. As can be seen, performance was very similar for the two tasks as a function of time.

## Abbreviations

DS, discrimination symbol; SRT, saccade reaction time; SSD, stop signal delay.

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