The influence of distractors on express saccades

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It is well known that regular target-driven saccades are affected by the presence of close and remote distractors. Distractors close to the target affect the saccade landing position (known as the *global effect*), while remote distractors prolong saccade latencies to the target (known as the *remote-distractor effect*). Little is known about whether a different population of saccades known as *express saccades* (saccades with very short latencies between 80 and 130 ms) is similarly affected by close and remote distractors, as these saccades are considered to be the result of advanced preparation of an oculomotor program toward the target. We designed a task in which we were able to generate a large number of express saccades, as evidenced by a separate and very early peak in the saccade-latency distribution—a distribution that was different from that of regular saccades. Our results show that irrelevant and unexpected visual input had a large effect on express saccades. We found a global and a remote-distractor effect which were similar to those seen in regular saccades. Even though our findings confirm the existence of very-short-latency saccades in humans, it is questionable whether they represent a different population of saccades, as they were equally affected by the presence of distractors as are regular saccades.

Introduction

Our decision where to move our eyes is influenced by many factors, such as knowledge about the visual world, expectations of what will happen next, and visual input from the world around us. Although many objects around us compete for selection, we can only make one eye movement at a time. Oculomotor selection is the process that resolves the competition between prospective goals and input from the environment. It is well known that the presence of irrelevant distractors affects our ability to make regular target-driven saccades. In the spatial domain, saccades are particularly affected when a distractor is presented close to the target. When two elements are presented in close proximity (polar distance of less than 35°), even when one of the elements is explicitly marked as the target, saccades to these elements tend to land at an intermediate location between the elements. This effect is known as the *global effect* or *saccade averaging* (Coren & Hoenig, 1972; Deubel, Wolf, & Hauske, 1984; Findlay, 1981, 1982; Findlay & Brown, 2006; Glimcher & Sparks, 1993; He & Kowler, 1989; Heeman, Theeuwes, & Van der Stigchel, 2014; Ottes, Van Gisbergen, & Eggermont, 1985; Van der Stigchel, Heeman, & Nijboer, 2012; Van der Stigchel & Nijboer, 2013; Van Opstal & Van Gisbergen, 1989; R. Walker, Deubel, Schneider, & Findlay, 1997). Saccade averaging has been explained in terms of a weighted average

(Tipper, Howard, & Jackson, 1997), which assumes that each element evokes a peak of activity within a common saccade map. The landing point of the next saccade is the result of the lateral interaction between the peaks of activation. When potential goals are positioned in close alignment, the peak of activity of the distractor cannot be fully inhibited without also affecting the target's activity. Distractor- and target-related activity thus merge into one resultant vector which directs the saccade to a weighted average location between the elements (see also Godijn & Theeuwes, 2002).

When a distractor is positioned at a remote location from the target, target and distractor interact in a different way. This is reflected in the well-known remote-distractor effect and results in elevated saccade latencies to the target (Born & Kerzel, 2008; Griffiths, Whittle, & Buckley, 2006; Honda, 2005; Levy-Schoen, 1969; M. F. Walker, Fitzgibbon, & Goldberg, 1995; R. Walker et al., 1997; White, Gegenfurtner, & Kerzel, 2005). Several mechanisms have been proposed to account for the remote-distractor effect. The dominant view is that it is the result of lateral inhibition between target and distractor. It has been suggested that lateral inhibition suppresses the buildup of oculomotor activity coding for the target location 60 to 110 ms after the onset of a distractor, which delays the speed at which a saccade is initiated (Born & Kerzel, 2008; Buonocore & McIntosh, 2008; Findlay & Walker, 1999; Godijn & Theeuwes, 2002; Griffiths et al., 2006; Honda, 2005; McCoy & Theeuwes, 2016; Reingold & Stampe, 2002; Trappenberg, Dorris, Munoz, & Klein, 2001; R. Walker et al., 1997; White et al., 2005). However, according to another view, remote distractors indirectly influence saccade initiation by inhibiting disengagement from fixation, causing a slowing of saccade initiation (McSorley & Cruickshank, 2010).

Much is known about distractor interference for regular eye movements with typical latencies of about 160 ms and up. Under specific circumstances, however, the latency of some saccades can be much shorter than the latency of regular saccades (see, e.g., Amatya, Gong, & Knox, 2011; Bibi & Edelman, 2009; Fischer & Weber, 1990, 1993; Knox & Wolohan, 2015; Matsue et al., 1994). These saccades are called *express saccades*. Express saccades are very-short-latency saccades that are visually driven and are considered to be the result of advanced preparation of an oculomotor program toward the target (Marino, Levy, & Munoz, 2015). They are supposed to reflect the fastest visually triggered eye movements, as their latencies approach the minimum afferent (~30 to 60 ms) and efferent (~20 to 35 ms) conduction delays that are required to transform sensory retinal input into an oculomotor response (Dorris, Pare, & Munoz, 1997;

Fischer & Boch, 1983; Fischer & Weber, 1993; Pare & Munoz, 1996). Behaviorally, express saccades are defined as saccades with latencies between 80 and 130 ms after the stimulus onset (Fischer & Boch, 1983; Fischer & Ramsperger, 1984). Whereas the lower bound of this latency range is based on neurophysiological evidence and behavioral research showing that responses within approximately 80 ms after the onset of a visual event cannot be the result of the visual onset (Fischer et al., 1993; Fischer & Boch, 1983; Fischer & Ramsperger, 1984; Wenban-Smith & Findlay, 1991), the upper bound is somewhat more arbitrary. The upper limit is mainly based on studies that show a bimodal latency distribution, with the dip between the first and the second peak occurring around 130 to 140 ms (e.g., Fischer et al., 1993; Fischer & Ramsperger, 1984; Jüttner & Wolf, 1992). Although most dominantly observed in monkeys, express saccades in humans have also been observed as a peak in the latency distribution that is separate from "regular" saccades (Carpenter, 2001; Fischer et al., 1993; Fischer & Ramsperger, 1986; Reuter-Lorenz, Hughes, & Fendrich, 1991; Weber, Aiple, Fischer, & Latanov, 1992). Most saccades that we make fall outside the latency range of express saccades, but it is estimated that about 10%–20% of all saccades are express saccades (e.g., Amatya et al., 2011; Knox & Wolohan, 2015; Sprenger et al., 2015). The percentage of express saccades increases when there is a temporal gap between the offset of a fixation point and the onset of a visual target (first described by Saslow, 1967). When a visual target is presented while the fixation point is still on, the latency of the saccade reflects the competition between remaining fixated at the fixation point and the strength of the signal produced by the new stimulus. In contrast, when there is a temporal gap between fixation offset and target onset, disengagement from fixation is easier, resulting in a decrease in saccadic latency (Edelman & Keller, 1996; Fischer & Ramsperger, 1984, 1986; Fischer & Weber, 1993).

Within the area of neurophysiology it has been found that in order to elicit express saccades, observers should be prepared maximally to respond as fast as possible. Premotor activity at the target location moves the oculomotor system closer to the response threshold (Marino et al., 2015). Upon stimulus onset, the stimulus-related visual activity is then added to the premotor activity, which drives the saccade generator over the response threshold (Munoz, Dorris, Pare, & Everling, 2000). Because the premotor activity is spatially aligned with the prospective target location, it is possible that the weight of activity of the target position in saccade averaging is much larger than the weight of distractors positioned at unexpected locations. Therefore, one expects a smaller global effect (if

any) and a smaller remote-distractor effect for express saccades than for regular saccades. This hypothesis is supported by the competitive integration model, which states that eye movements are the result of competitive integration of information originating from different brain areas (e.g., occipital, parietal, and frontal cortex) on the basis of which the endpoint of a saccade is computed (Godijn & Theeuwes, 2002; Meeter, Van der Stigchel, & Theeuwes, 2010; White et al., 2013). Knowledge about the target location possibly elevates the target-related baseline activity in the superior colliculus (Furlan, Smith, & Walker, 2015), tuning the system for a fast rise above the response threshold once the stimulus is presented. Given this model, the location-based preactivation in the saccade map may make express saccades less vulnerable to distractors than regular saccades, as the threshold to launch a saccade may be reached before the distractor-related activity reaches the saccade map.

In order to investigate distractor influences on express saccades, we designed two experiments triggering very-short-latency saccades. In the first experiment we used a standard target–distractor gap task without providing prior knowledge about the upcoming target location. This experiment served as a baseline, as we expect little to no premotor activity at the location of the target, implying that target and distractor activity could equally affect saccade execution. In the second experiment, participants were informed before each trial about the location of the target, allowing a buildup of target-related premotor activity, which is assumed to facilitate the production of express saccades. Participants were not informed about the location of the distractor. We investigated the time course of the effect of a distractor on express and regular saccades. A distinction was made between three categories of saccades: anticipatory, express, and regular. Anticipatory saccades are triggered before target information has been processed. It is generally assumed that saccades with latencies below 70 to 80 ms are not based on the processing of external signals, as accuracy for these saccades is usually at chance level if the target location is not known beforehand (Munoz et al., 2000; Sprenger et al., 2015). Therefore, any saccade with a latency shorter than 80 ms was regarded as an anticipatory saccade (Fischer et al., 1993; Wenban-Smith & Findlay, 1991). Since these saccades are not based on the processing of external signals from the outside world, no effect of distractors is expected. In contrast, express saccades with latencies over 80 ms fall within the time frame of saccades that can *potentially* be updated by new visual information (Carpenter, 1981; Fischer & Weber, 1993; Marino et al., 2015).

Materials and methods

We investigated the basic spatial and temporal characteristics of express saccades using the gap paradigm. We contrast two conditions in order to distinguish between spatial and temporal effects: a distractor close to the target that is expected to mainly impact the spatial characteristics of the saccade, and a distractor remote from the target that is expected to impact the temporal characteristics of the saccade. In Experiment 1 there were two target locations presented along the horizontal axis. Experiment 2 was identical to Experiment 1 except that we encouraged participants to be extremely fast. We did this by adding a location cue to each trial indicating the location of the target with 100% validity, a warning signal to announce the impending target, and qualitative feedback to the paradigm. The timing in both experiments was identical.

Participants

Experiment 1 had 11 participants (age: 18–33 years; $M = 23$; nine women, two men; all Caucasian), and Experiment 2, 15 (age: 18–37 years; $M = 25$; nine women, six men; 14 Caucasian, one Asian). The differences in number of participants between the experiments were of a practical nature and did not arise from a stopping rule. For each experiment we had approximately one week of lab time available, and for Experiment 2 we were able to test more participants within that week. All participants were unaware of the purpose of the experiment. All had normal or corrected-to-normal visual acuity. Participants were given either money or course credit for participating. Written informed consent was obtained from all individual participants in the study. This study has been carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans.

Apparatus

Participants performed the experiment in a dimly lit, sound-attenuated room, viewing a widescreen LCD monitor (1680 × 1050 pixels; Syncmaster 2233RZ; Samsung, Seoul, South Korea) at a distance of 70 cm. Selection of the LCD monitor was based on its good timing qualities. The average overall system lag is 17.5 ms ($SD = 2$; minimum = 14 ms; maximum = 22 ms; data from Saunders & Woods, 2014). This makes it a suitable monitor for our experiments (also see Wang & Nikolic, 2011). Eye movements were recorded using the

EyeLink 1000 desktop system (SR Research, Kanata, Canada), an infrared video-based eye tracker with a 1000-Hz temporal resolution and a spatial resolution of 0.01°. Each participant's head was stabilized with a chin rest. The left eye was monitored. An eye movement was considered a saccade when either eye velocity exceeded 35°/s or eye acceleration exceeded 9500°/s^2.

Stimuli and procedure

Each trial started with a dark display containing a gray cross (1° × 1°) in the center of the display, which was used as a fixation point. After a random interval of 800 to 1100 ms, the fixation cross was removed. The offset of the fixation cross was followed by a blank display. After a random period (gap) of 150 to 250 ms, a target appeared either to the left or to the right of fixation along the horizontal axis. Participants had to make one eye movement to the target as fast and accurately as possible. In 72.7% of the trials, the target was accompanied by a distractor that appeared simultaneously. The distractor could be located above or below the target at a polar distance of 15° (close) or 50° (remote). Target and distractor had the same shape and size (gray filled circle, 1° diameter) and were presented at an eccentricity of 10° visual angle from the location of the central fixation cross. (See Figure 1a for all possible stimulus configurations.) To discourage participants from making a saccade before the target was displayed, 9.1% of the trials were catch trials in which no target or distractor was presented. In the remainder of the trials (18.2%), only the target was presented. After 1000 ms, all objects were removed from the display and replaced by feedback in milliseconds regarding the saccade latency for the trial.

In Experiment 2, three additional components were integrated in the basic paradigm to encourage participants to respond fast. First, a location cue was presented 300 ms after the start of each trial which consisted of an angle bracket < or > added to the left or right side (respectively) of the fixation cross. This location cue revealed with 100% validity the location of the upcoming target. Second, a warning signal (pure tone of 2 kHz) of 100 ms announced the appearance of the target. The offset of the warning signal coincided with the offset of the fixation cross. Finally, the participants received qualitative feedback that rated their saccade latency according to four levels: a red screen with the text "wait for the target" for trials with a latency of less than 60 ms; a black screen with the text "great speed!" printed in green for trials with a latency between 60 and 150 ms; "faster" printed in orange on a black screen for trials with a latency between 150 and 200 ms; and "too slow" printed in red on a black screen for trials with a latency of more than 200 ms. "Wait for the target" and "too slow" were accompanied by a 100-ms pure tone of 250 Hz. Figure 1b and c show the schematic representation of the trial sequences of Experiment 1 and 2, respectively.

Participants were instructed to remain fixated on the location of the fixation cross until the target appeared left or right of the central fixation point, and to make an eye movement to the target as fast and accurately as possible.

The experiment started with 22 practice trials followed by two blocks of 264 trials. The different conditions (Close Distractor, Remote Distractor, No Distractor, and Catch) were intermixed and randomized across trials. Each block started with a nine-point grid calibration procedure.

Data analysis

Preprocessing

Saccade latency was defined as the interval between target onset and the initiation of the first saccadic eye movement. Saccades with a latency below 80 ms were regarded as anticipatory saccades; express saccades were those with a latency between 80 and 130 ms. Saccades with a latency over 130 ms were regarded as regular saccades. Because the saccade-latency data are not normally distributed, we used the average of the individual median saccade latencies.

The saccade endpoint deviation (φ) describes the distance between the saccade target and the actual landing point of the saccade, in polar angle (Figure 2). Each participant's mean saccade endpoint deviation in the No Distractor condition served as a baseline to compensate for idiosyncratic differences such as a consistent saccade endpoint landing above or below the target. Saccade endpoint deviation *toward* the distractor was marked as positive, and *away* from the distractor was marked as negative.

Saccade amplitude was defined as the distance between the start of the saccade and the saccade endpoint, in degrees of visual angle.

Before analysis, trials were filtered and excluded if they contained a technical error or blink. Trials were also excluded if the initial eye movement was to the nontarget hemifield or if the saccade latency or saccade amplitude exceeded 2.5 standard deviations from the participant's mean.

Statistical analysis

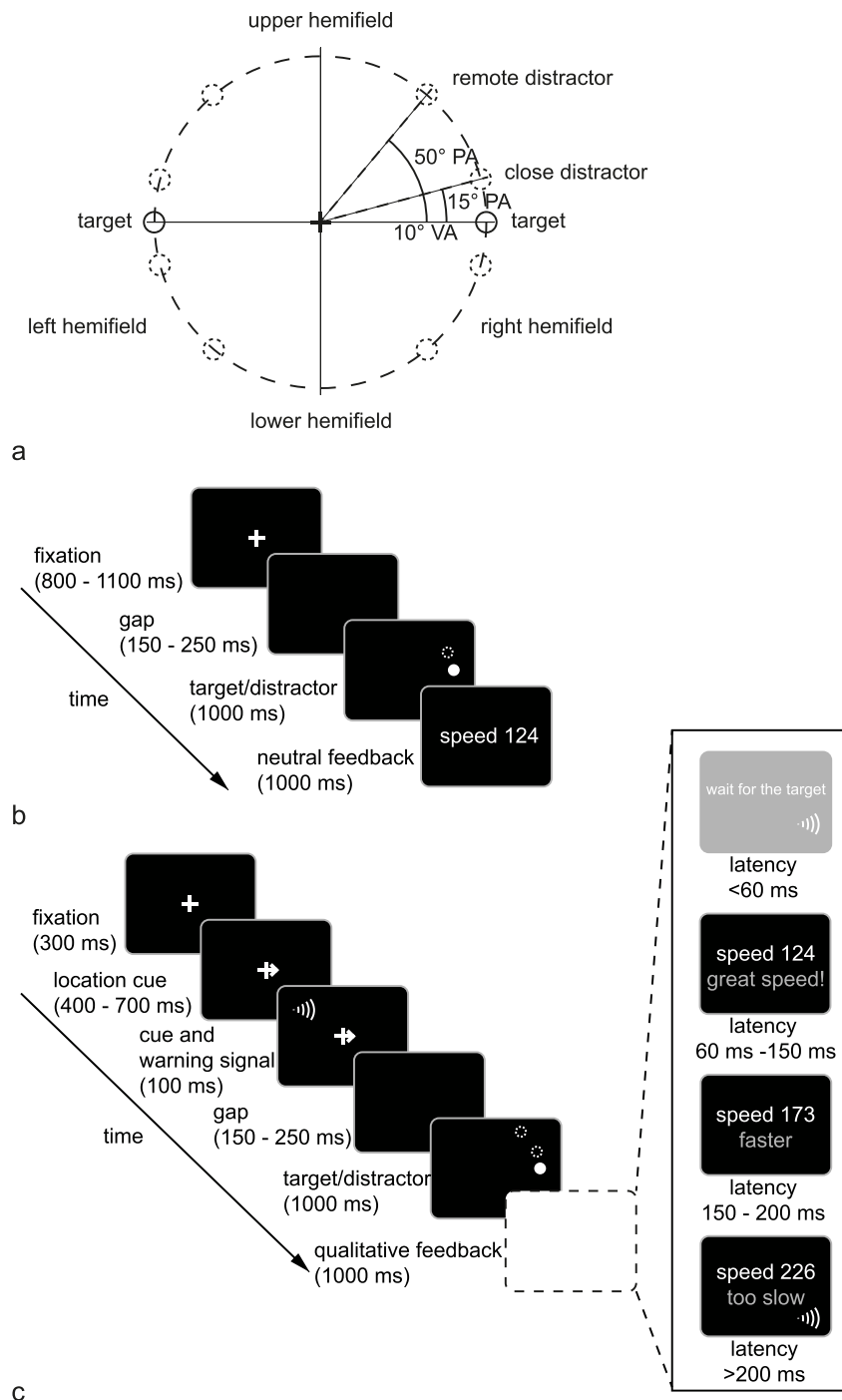The aim of the current study was to establish the time window of competition between target and

Figure 1. Template of possible target and distractor locations and trial sequence for Experiments 1 and 2. (a) The target and distractor configuration used in both experiments. Distances are indicated in visual angle (VA) or polar angle (PA). Target and distractor always appeared in the same hemifield. Circles indicate possible stimulus locations. (b) A schematic representation of the trial sequence and timing of Experiment 1. (c) The trial sequence in Experiment 2.

distractor. Therefore, we first analyzed the saccade latency. Trials were categorized as either anticipatory, express, or regular saccades according to the latency of the saccade in order to gain insight into whether the paradigm induced short-latency saccades. Also, to visualize the distribution of trials over time, the proportion of trials was plotted per 10-ms bin. Subsequently, we analyzed the temporal distractor effect (i.e., remote-distractor effect) by conducting a repeated-measures analysis of variance (ANOVA) on saccade latency with distractor location as a factor (No Distractor, Close Distractor, Remote Distractor).
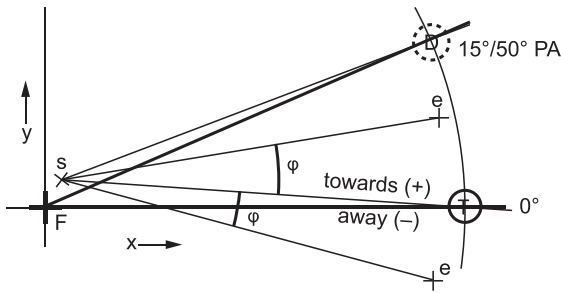
Figure 2. Saccade endpoint deviation (φ) as the polar distance between the target (T) and the end of the saccade (e), as seen from the start of the saccade (s). A shift of the endpoint toward the distractor (D) is marked as positive (+), and a shift away as negative (−).

Three post hoc paired-sample *t* tests were used to compare the three experimental conditions with each other. We corrected for multiple comparisons using the Holm–Bonferroni correction method.

Second, we analyzed the spatial distractor effect (i.e., global effect) by analyzing the saccade endpoint deviation in polar angle with a paired-sample *t* test between the Close Distractor and Remote Distractor conditions. Also, using a one-sample *t* test, we tested whether the saccade endpoint deviation for each condition (Close Distractor and Remote Distractor) deviated from zero (which indicates no shift from the saccade to the target in the No Distractor condition).

Since the impact of a distractor is closely related to the time frame in which the eye movement is made, we also analyzed the effects of latency on saccade endpoint deviation. Per condition, the trials of each participant were sorted from short- to long-latency saccades and divided into six bins, each bin containing one sixth of the trials. The mean saccade endpoint deviation of each bin was calculated and analyzed with an ANOVA using distractor location (Close Distractor, Remote Distractor) and latency bin (1 through 6, short through long) as factors. To investigate the buildup of saccade endpoint deviation over time, each bin was tested post hoc using a *t* test against test value 0 (which indicates no shift from the saccade to the target in the No Distractor condition). Additionally, a separate post hoc analysis of the saccade endpoint deviation was conducted in the latency range from 40 to 110 ms. This latency range is the time window in which the transition from anticipatory to express saccades takes place.

In cases where Mauchly's test of sphericity for repeated-measure ANOVAs showed a violation of the assumption of sphericity, we used the Greenhouse–Geisser corrected values for the results. The *p* values of all *t* tests were adjusted according to the Holm–

Bonferroni method for multiple comparisons (Holm, 1979).

Results

Exclusions

The exclusion criteria led to a loss of 15.3% of the trials in Experiment 1 and 16.3% of the trials in Experiment 2. Technical errors were responsible for a loss of 3.9% in Experiment 1 and 2.7% Experiment 2. Blinks or eye movements to the wrong hemifield led to 7.4% loss in Experiment 1 and 10% loss in Experiment 2. Based on the outlier criteria (trials may be excluded based on more than one criterium), 4.0% of the trials in Experiment 1 were removed from the analysis (latency: 1.8%; amplitude: 1.1%; saccade endpoint deviation: 1.3%). In Experiment 2, the outlier criteria led to the removal of 3.6% of the trials (latency: 1.5%; amplitude: 1.2%; saccade endpoint deviation: 1%).

Saccade latency

Experiment 1

Overall, saccade latencies were very short. The average of the median saccade latency[1] was 146 ms ($SEM = 7.917$). The fastest saccadic responses, as is clear from Figure 3a, had a latency of 80 ms, and there were almost no anticipatory saccades. The peak of the distribution for Remote Distractor trials occurred at a later latency range compared to the Close Distractor trials, which is indicative of a remote-distractor effect. Because between-subjects variation can greatly determine the shape of the distribution, we plotted all trials for individual participants in Figure 4a to illustrate that Figure 3a and d are an adequate representation of the overall latency distribution in Experiment 1. We did not observe a separate peak in the distribution for express saccades (see Figure 3c and d).

We found a main effect of distractor location, $F(1.236, 12.356) = 19.05$, $p < 0.001$, $\eta_p^2 = 0.656$, $\varepsilon = 0.618$. As shown by post hoc paired-sample *t* tests, saccade latencies in the Remote Distractor condition ($M = 152.7$ ms, $SEM = 7.45$) were longer than in the No Distractor ($M = 139.9$ ms, $SEM = 8.66$) or Close Distractor ($M = 142.3$ ms, $SEM = 8.04$) conditions— Remote Distractor versus No Distractor: $t(10) = 4.354$, $p = 0.001$, $d = 1.313$; Remote Distractor versus Close Distractor: $t(10) = 5.547$, $p < 0.001$, $d = 1.672$). The paired-sample *t* test between the No Distractor and Close Distractor conditions showed that saccade latencies in these conditions did not differ, $t(10) = 1.521$, $p = 0.159$, $d = 0.459$ (see Figure 5).
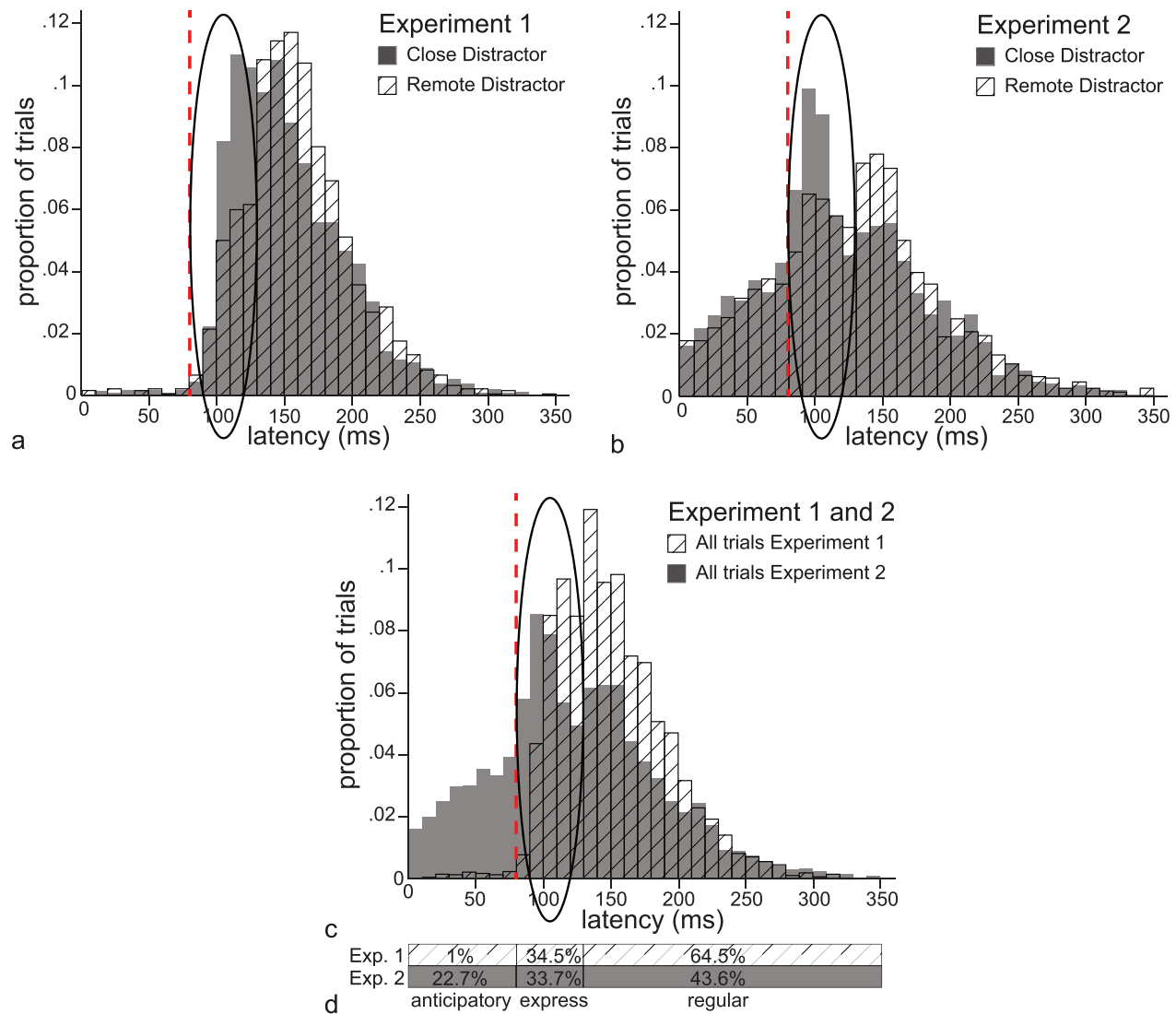
Figure 3. Saccade-latency distribution indicating the proportion of saccades within each 10-ms bin for (a) Experiment 1 and (b) Experiment 2. Saccades were divided according to condition: Close Distractor (gray) or Remote Distractor (striped). The dashed line indicates the 80-ms boundary between anticipatory and express saccades. Saccades between 80 and 130 ms (in ellipse) are regarded as express saccades; any saccades with a latency over 130 ms are considered regular saccades. (c) Saccade-latency distribution for all trials in Experiments 1 and 2, to allow comparison of the distributions. (d) Percentages of anticipatory, express, and regular saccades that were produced in Experiments 1 and 2.

Experiment 2

With an overall average median saccade latency[2] of 118.7 ms ($SEM = 4.9$), latencies in Experiment 2 were nearly 24.3 ms shorter than those in Experiment 1. Similar to Experiment 1, one third of the saccades in Experiment 2 were initiated within the latency range of express saccades (Figure 3c). There was, however, a drastic increase in the proportion of trials between 80 and 100 ms (see Figure 3b). As is clear from Figure 3b, express saccades are represented by a separate peak in the saccade-latency distribution, which occurs earlier than the peak in the saccade-latency distribution for regular saccades.

The differences in height of the peaks in the saccade-latency distribution show the effect of distractor location (Figure 3b). The express-saccade peak in the Close Distractor condition is higher than the express-saccade peak in the Remote Distractor condition, which means that a larger proportion of the saccades in Close Distractor trials fell within the express-saccade latency range compared to saccades in Remote Distractor trials. The peak for regular saccades showed the opposite pattern: Fewer saccades were made in response to targets in Close Distractor trials compared to targets in Remote Distractor trials. This difference also indicates that the remote-distractor effect was present in Experiment 2.
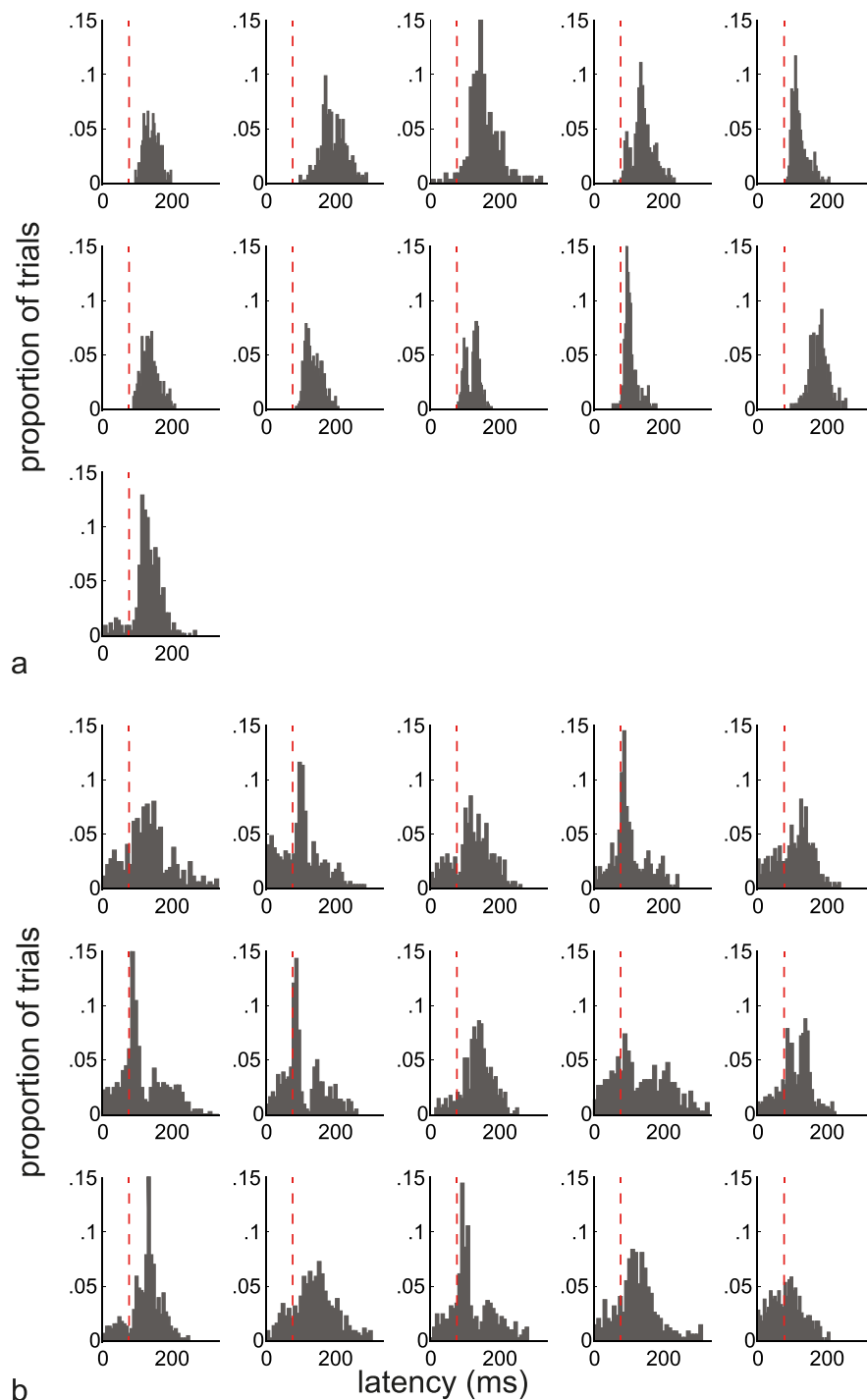
Figure 4. Saccade-latency distribution per participant, indicating the proportion of trials within each 10-ms bin for (a) Experiment 1 and (b) Experiment 2. The vertical dashed line indicates the 80-ms boundary between anticipatory and express saccades.

It has to be noted that the observed bimodal distribution of the pooled data can arise from pooling the data of "fast" and "slow" responders. In order to assess the contribution of the individual participants, Figure 4b shows the saccade-latency distribution per participant. Although the distributions are noisier than the pooled data, it is clear from the plots that the participants do not represent a "slow" and a "fast"

group. Therefore we conclude that the bimodal distribution observed in Experiment 2 is not the result of individual differences. Additionally, the individual plots make it apparent that for quite a few participants the "early" peak corresponds to what we have defined as anticipatory saccades.

We found a main effect of distractor location, $F(2, 28) = 5.834$, $p = 0.008$, $\eta_p^2 = 0.294$. As was shown by post
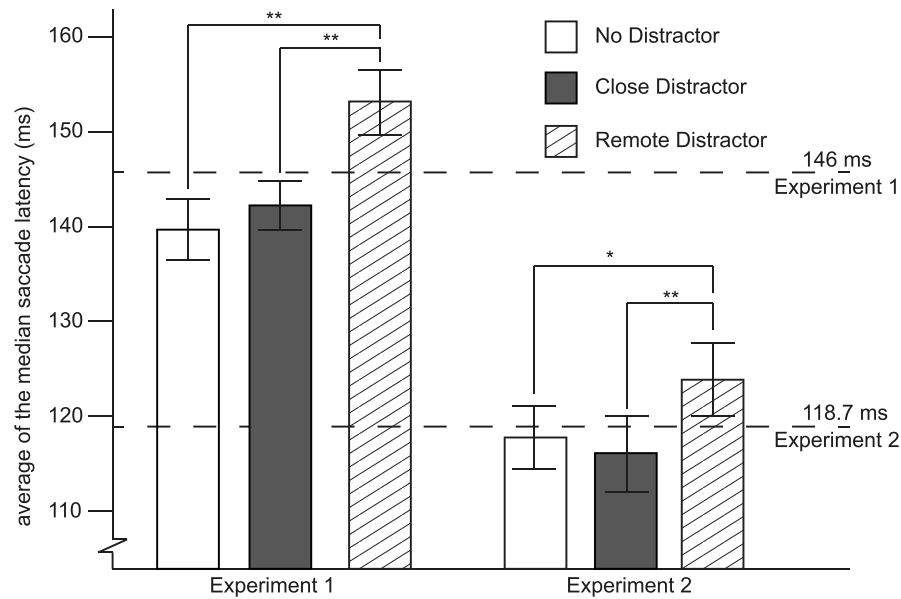
Figure 5. Average of the median saccade latencies for each of the three conditions: No Distractor (dashed fill), Close Distractor (white), and Remote Distractor (gray). The dashed line shows the overall average median latency of Experiments 1 and 2. Error bars indicate 95% confidence intervals.

hoc paired-sample t tests, saccade latencies in the Remote Distractor condition ($M = 123.8$ ms, $SEM = 4.86$) were slower than in the No Distractor ($M = 117.7$ ms, $SEM = 5.46$) and Close Distractor ($M = 115.9$ ms, $SEM = 5.14$) conditions—Remote Distractor versus No Distractor: $t(14) = 2.962$, $p = 0.03$, $d = 0.706$; Remote Distractor versus Close Distractor: $t(14) = 2.734$, $p = 0.032$, $d = 0.764$ (see Figure 5).

Saccade endpoint deviation

Experiment 1

There was a difference in saccade endpoint deviation between the Close Distractor and Remote Distractor conditions, $t(10) = 10.06$, $p < 0.001$, $d = 3.032$. The saccade endpoint deviation in the Close Distractor condition ($M = 2.7°$, $SEM = 0.41$) was larger than in the Remote Distractor condition ($M = 0.04°$, $SEM = 0.362$). Comparing both conditions to zero (indicating no deviation) showed that saccades in Close Distractor trials deviated significantly toward the distractor, while saccades in Remote Distractor trials did not deviate toward or away from the distractor—Close Distractor: $t(10) = 6.637$, $p < 0.001$, $d = 2$; Remote Distractor: $t(10) = 0.121$, $p = 0.906$, $d = 0.04$ (Figure 6, left).

Experiment 2

In Experiment 2 there was also a difference in saccade endpoint deviation between the Close Distractor and Remote Distractor conditions, $t(14) =$ 4.792, $p < 0.001$, $d = 1.237$. This is explained by the larger saccade endpoint deviation in the Close Distractor condition ($M = 1.5°$, $SEM = 0.23$) than in the Remote Distractor condition ($M = 0.233°$, $SEM = 0.16$). As was shown by a comparison of the different conditions with zero, only saccades in Close Distractor trials deviated significantly from the direct route from start of the saccade to the target saccades *toward* the distractor, $t(14) = 6.554$, $p < 0.001$, $d = 1.692$. Saccades in the Remote Distractor condition deviated neither toward nor away from the distractor (Figure 6, right).

Saccade endpoint deviation by latency

Experiment 1

The ANOVA with distractor location (Close Distractor, Remote Distractor) and latency bin (1 through 6, short through long) as factors showed a main effect of distractor location, $F(1,10) = 100.3$, $p < 0.001$, $\eta_p^2 = 0.909$. There was no effect of latency bin, $F(2.9, 29.2) = 1.049$, $p = 0.384$, $\eta_p^2 = 0.095$, $\varepsilon = 0.583$, and no interaction, $F(2.854, 28.544) = 1.29$, $p = 0.297$, $\eta_p^2 = 0.114$, $\varepsilon = 0.571$. As is clear from Figure 7, the effect of location is explained by differences in saccade endpoint deviation between Close Distractor and Remote Distractor trials. Saccades in the Close Distractor condition deviated from the No Distractor baseline *toward* the distractor, while saccades in the Remote Distractor condition did not (they landed close to the target). See Figure 7 for results.
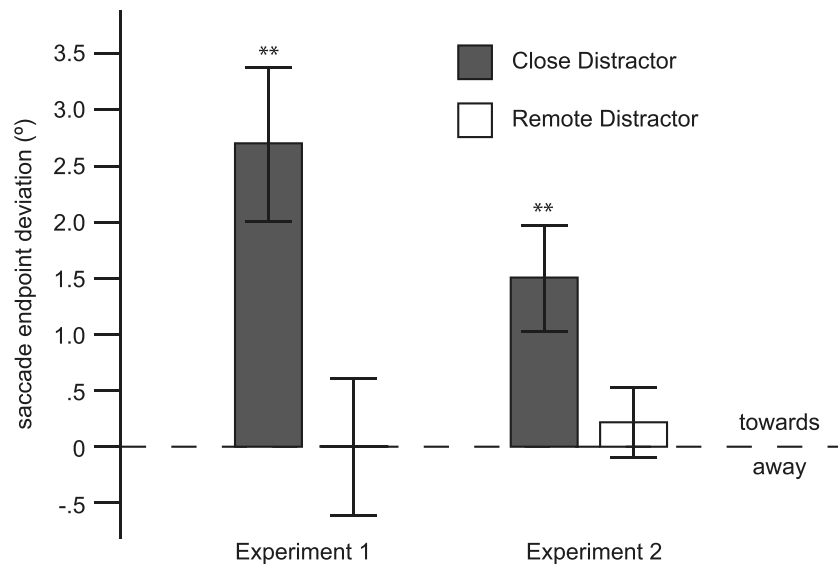
Figure 6. Saccade endpoint deviation as the polar distance between target (0°) and saccade endpoint in the Close Distractor (white) and Remote Distractor (gray) conditions in Experiments 1 and 2. Double asterisks indicate a *p* value of less than 0.001. Error bars indicate 95% confidence intervals.

Experiment 2

The repeated-measures ANOVA with distractor location (Close Distractor, Remote Distractor) and latency bin (1 through 6, short through long) as factors showed a main effect of location, $F(1, 14) = 22.593$, $p < 0.001$, $\eta_p^2 = 0.617$. There was no main effect of latency bin, $F(3.112, 15.76) = 1.605$, $p = 0.201$, $\eta_p^2 = 0.103$, $\varepsilon = 0.622$. Crucially, however, the interaction was significant, $F(3.195, 70.06) = 5.927$, $p = 0.001$, $\eta_p^2 = 0.294$, $\varepsilon = 0.639$. As is clear from Figure 8a, the interaction is explained by the saccade endpoints in the first two bins of the Close Distractor condition, containing the

shortest latency saccades, as these did not deviate from the target, whereas the longer latency bins (3 through 6) deviated significantly *toward* the distractor, as indicated by the post hoc *t* test (Figure 8a). In the Remote Distractor condition, such an increase of distractor influence over time was not present. Saccade endpoints in the second latency bin deviated marginally *toward* the distractor, while saccades in the other latency bins were not affected by the presence of the distractor (Figure 8a).

As shown by the previous analysis of the whole latency range, the distractor affected only saccades in
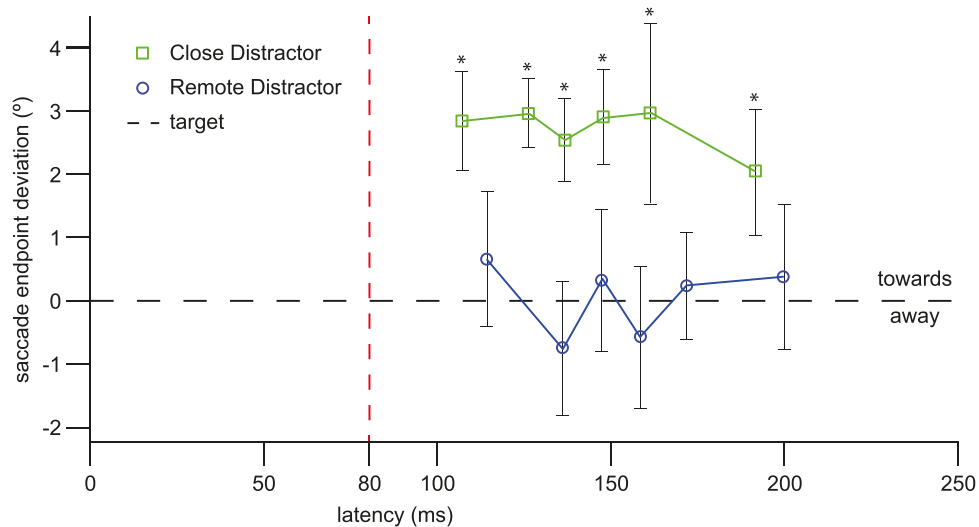

Figure 7. The baseline corrected saccade endpoint deviation of Experiment 1 in polar angle as a function of time for the Close Distractor (○) and Remote Distractor (□) conditions, divided into six latency bins. The vertical dashed line indicates the 80-ms boundary between anticipatory and express saccades. Error bars indicate 95% confidence intervals.
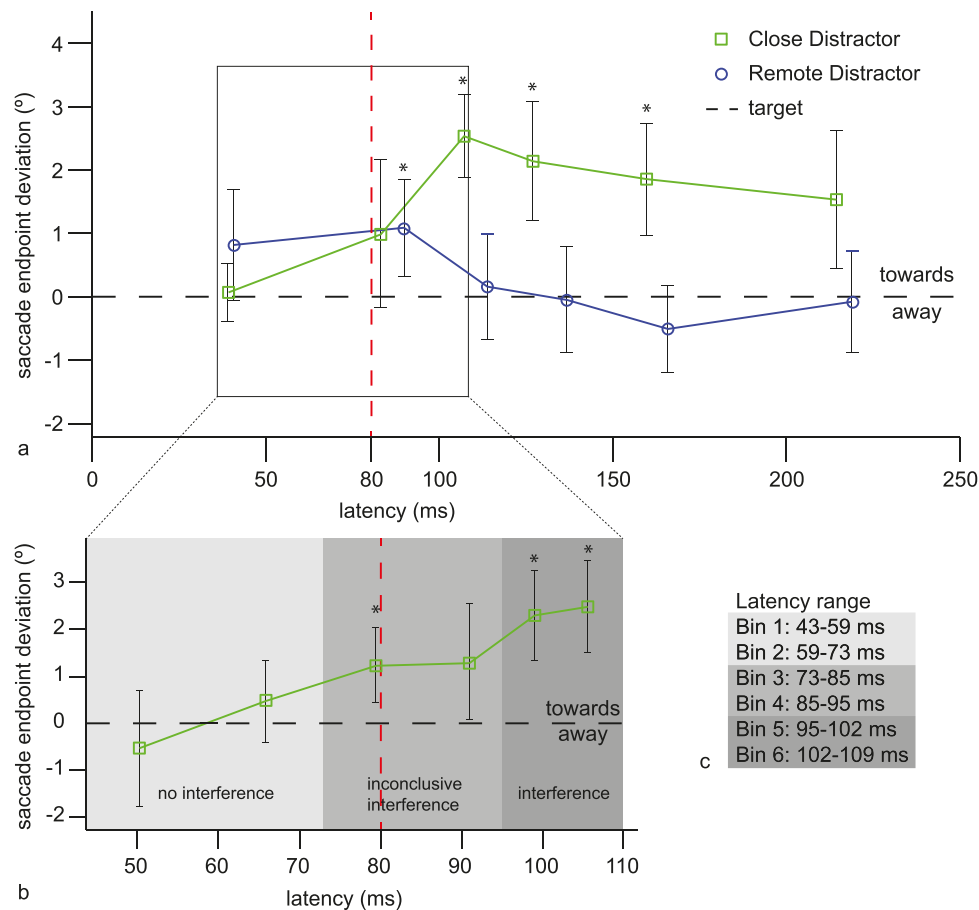
Figure 8. (a) Baseline corrected saccade endpoint deviation of Experiment 2 in polar angle as a function of time, divided into six latency bins in the Close Distractor (□) and Remote Distractor (○) conditions for the whole latency range. (b) The latency range from 40 to 110 ms for the Close Distractor condition, showing the transition from no interference to significant interference (as indicated by the asterisks) of the distractor on the target-directed saccade. Three levels of distractor interference are shown: no interference (light gray), inconclusive interference (medium gray), and interference (dark gray). (c) Bin times are shown in the latency-range inset. The vertical dashed line indicates the 80-ms boundary between anticipatory and express saccades. Error bars indicate 95% confidence intervals.

the Close Distractor trials. So in order to get a grasp of the exact latency at which the distractor starts to have an impact on the saccade endpoint, we separately analyzed the transition from anticipatory to express saccades in the Close Distractor condition. The transition is expected to take place around 80 ms (e.g., Sprenger et al., 2015; Wenban-Smith & Findlay, 1991). As shown by the previous analysis of the whole latency range, this expectation was corroborated by our data from the first three latency bins. Saccades in Bin 1 had a latency of well below 80 ms, saccades in Bin 2 had a mean latency of around 80 ms, and Bin 3 saccades had latencies of more than 80 ms. In order to extract a more detailed insight into the transition from no distractor influence to distractor influence on saccade endpoints, we performed a deviation-by-latency analysis for the Close Distractor condition on the first three bins (Figure 8b). Trials in this latency range were again sorted by latency and divided into six bins, each bin

containing at least 17 trials per participant (see Figure 8c for latencies). Per bin, a one-tailed t test was used to test the deviation from the target (test value 0) and thus quantify the distractor impact. The analysis of the Close Distractor condition showed that the first two latency bins (Bin 1: $M = -0.43°$, $SEM = 0.57$; Bin 2: $M = 0.53°$, $SEM = 0.43$), containing the fastest responses, did not deviate significantly from the target—Bin 1: $t(14) = 0.758$, $p = 0.461$, $d = 0.196$; Bin 2: $t(14) = 1.225$, $p = 0.482$, $d = 0.316$. Saccades in the latency range around and just beyond 80 ms (Bin 3: $M = 1.29°$, $SEM = 0.42$; Bin 4: $M = 1.36°$, $SEM = 0.6$) showed inconclusive interference because saccades in Bin 3 deviated significantly toward the distractor, while the slower latency saccades in Bin 4 did not—Bin 3: $t(14) = 3.033$, $p = 0.036$, $d = 0.783$; Bin 4: $t(14) = 2.255$, $p = 0.123$, $d = 0.582$. Starting from Bin 5 (Bin 5: $M = 2.33°$, $SEM = 0.57$; Bin 6: $M = 2.5°$, $SEM = 0.43$), deviation was *toward* the distractor, which means that the presence of

the distractor interfered significantly with the saccade to the target—Bin 5: $t(14) = 4.129$, $p = 0.005$, $d = 1.066$; Bin 6: $t(14) = 5.851$, $p < 0.001$, $d = 1.511$.

General discussion

The aim of the present study was to systematically investigate the time course of distractor influences on express saccades. In two experiments using a gap paradigm, peripheral targets were presented along with either a close or a remote distractor. Participants were instructed to make an eye movement to the target as fast as possible while ignoring any distractor. The paradigm was successful in triggering high percentages of express saccades in both experiments: About one third of the trials were initiated during the express-saccade interval (80–130 ms). Following Experiment 1, we were able to further reduce saccadic response times in Experiment 2 by adding a location cue and a warning signal, and by providing qualitative feedback. These manipulations resulted in a decrease of the percentage of regular saccades (43.6%) and an increase in the percentage of anticipatory saccades (22.7%), while the percentage of express saccades (34.5%) remained about the same compared to Experiment 1 (anticipatory: 1%, express: 34.5%, regular: 64.5%). Notably, we were able to generate two separate and distinct peaks in the latency distributions of Experiment 2: one representing express saccades and the other representing regular saccades. Even though these separate peaks in the distribution may suggest that we are dealing with possibly two separate processes (Dorris et al., 1997; McDowell, Dyckman, Austin, & Clementz, 2008; Sprenger et al., 2015), our data clearly show that the saccade endpoints of even the fastest visually guided saccades, which are certainly in the express-saccade range (around 80 ms), are affected by the presence of distractors. Unlike previous claims that have suggested that express saccades are fundamentally different from regular saccades (Broerse, Crawford, & den Boer, 2001; Chen, Liu, Wei, & Zhang, 2013; Everling & Johnston, 2013; Schiller & Tehovnik, 2005; Tinsley & Everling, 2002), the current findings do not support this notion, as there is basically no difference between express and regular saccades in the way they are affected by the presence of distractors.

In both Experiments 1 and 2, we found the expected global effect when a distractor was presented in close proximity to a target. Although the saccade averaging was relatively small, the oculomotor vectors toward the target and the distractor merged into one resultant oculomotor vector. This merging resulted in a saccade toward a location in between the target and distractor that reflected the weighted average of target and distractor. When the distractor was presented remote from the target, its presence no longer influenced the saccade endpoint. In the presence of a remote distractor, saccade endpoint deviation was about zero across the whole latency range of Experiments 1 and 2. The remote distractor, however, did affect the latency of the saccade, and both experiments demonstrated the classic remote-distractor effect. In addition, in Experiment 2 the remote-distractor effect resulted in a lower peak in the proportion of express saccades and a higher peak in the regular-saccade latency range, while the presence of a close distractor showed the reverse pattern (i.e., high peak of express saccades, low peak of regular saccades).

The distractor interference with the saccade endpoint starts to take effect as early as 70 to 90 ms after stimulus onset (Experiment 2). This means that it requires 70 to 90 ms before distracting information can have an effect on the oculomotor vector to the target and cause a deviation of the saccade endpoint. This is in line with the assumption that the minimum time needed to translate visual input into action is around 80 ms, as has been shown by several neurophysiology studies in nonhuman primates and by neuroimaging and behavioral studies in humans (Carpenter, 1981; Fischer & Weber, 1993; Kirchner & Thorpe, 2006; Marino et al., 2015; McDowell et al., 2008).

Saccade latencies in Experiment 2 were overall shorter than in Experiment 1. We argue that this decrease in latency is due to the crucial difference that the eye movement in Experiment 1 could not be prepared in advance, while in Experiment 2 participants were cued before each trial as to where the target would appear. This enabled participants to prepare the eye movement well before the onset of the target and enabled a buildup of preparatory premotor activity. The competitive integration model (Godijn & Theeuwes, 2002; Meeter et al., 2010) can account for short saccade latencies in situations in which there is high anticipatory input and a temporal gap between fixation offset and target onset. The foreknowledge of the target location induces an anticipatory signal, which increases anticipatory activity in the saccade map at the target location. Because of this increased baseline, the signal reaches threshold earlier in time, launching with very short saccade latencies (i.e., express saccades). Besides the prior knowledge about the target location, Experiment 2 also included a warning signal which is known to impact the saccade map in the superior colliculus (Meredith, Nemitz, & Stein, 1987; Ross & Ross, 1981; Trappenberg et al., 2001), as well as motivational feedback. The warning signal and feedback features could have further reduced saccade latencies in Experiment 2 compared to Experiment 1. Similar suggestions have been made

by Marino et al. (2015), who suggested that previsual activity increases depending on the amount of foreknowledge about the onset and location of the target, which correlates with the increase of express-saccade occurrence.

Given the model that knowledge about the target location possibly elevates the target-related baseline activity, tuning the system for a fast rise above the response threshold once the stimulus is presented, we predicted that express saccades may be less vulnerable to distractors than regular saccades. The current results, however, are not necessarily in line with this prediction, as express saccades were sensitive to both close and remote distractors. For the close distractor, we see the rise of a global effect starting as early as 80 ms. We assume that even though foreknowledge about the target location may have given the saccade-related activity toward the target a head start, due to its close proximity, the distractor-related activity cannot be sufficiently suppressed to prevent the occurrence of a global effect. This is in line with the notion underlying the global effect that activity of visual targets presented in close proximity will likely overlap and merge into one resultant peak of activity (Anderson, Keller, Gandhi, & Das, 1998; Edelman & Keller, 1998; Marino, Trappenberg, Dorris, & Munoz, 2012). Considering our findings, it is likely that due to its close proximity to the target, the distractor-related activity may even have gained from the anticipatory activity related to the target location.

For the remote distractor, lateral inhibition may have been effective; this is also possible for express saccades, as saccades were executed slightly later in time when a remote distractor was present relative to when a close distractor was present. This can be explained by the notion that lateral inhibition starts to build up as soon as the distractor is presented (Meeter et al., 2010). It is therefore not surprising that even the fastest saccades in the presence of remote distractors will be delayed. The target and distractor in the current experiments were presented simultaneously, and although the target location has an advantage due to the location cue, this advantage does not extinguish the development of the distractor-related activity. After the first 80 ms, lateral inhibition due to the presence of a remote distractor is fully developed and target and distractor have an equal opportunity to affect the saccade, thus showing a remote-distractor effect.

Taking a closer look at the distributions of both experiments, it is clear that in Experiment 2 the bulk of saccades that make up the express-saccade peak occurred between 80 and 100 ms, whereas there were very few saccades with these latencies in Experiment 1. The whole range of latencies of Experiment 1 appears to have shifted toward longer latencies, possibly

masking the occurrence of separate peaks in the distributions. This observation also explains the dichotomy in results that has been found in many experiments investigating express saccades, where some studies show a clear bimodality similar to our results in Experiment 2 (Fischer & Weber, 1993; Weber et al., 1992) but others do not (Edelman & Keller, 1996; Reuter-Lorenz et al., 1991; Wenban-Smith & Findlay, 1991). Therefore, we assume that Experiment 1 still contained a high percentage of express saccades but that they are not separable from the regular saccades.

The exact neuronal mechanism underlying express saccades is very much debated. Traditionally, express saccades have been thought to be mediated by a separate and more direct neuronal route than the slower regular saccades (Broerse et al., 2001; Munoz, Armstrong, & Coe, 2007; Schiller, Sandell, & Maunsell, 1987; Weber et al., 1992). The dominant view is that express-saccade generation involves a posterior pathway that leads through the lateral intraparietal sulcus via the superior colliculus to the oculomotor neurons in the brainstem (Chen et al., 2013; Schiller et al., 1987; Schiller & Tehovnik, 2001, 2005). A more anterior pathway is thought to mediate regular saccades and also involves the prefrontal cortex and the frontal and medial eye fields projecting to the superior colliculus (Everling & Johnston, 2013; Schiller & Tehovnik, 2005; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Tinsley & Everling, 2002). This "two pathway" view, however, has been challenged by evidence that frontal eye-field activity directly correlates with express-saccade latencies (Dias & Bruce, 1994; Everling & Munoz, 2000), which is evidence that the anterior pathway is also involved in express-saccade generation. Our findings that express and regular saccades have the same distractor properties supports this view of a more distributed network for express saccades that overlaps with the network that gives rise to regular saccades.

Given these considerations, it is feasible that express saccades do not represent a different class of saccades but instead are nothing else than very early regular saccades (see also Sparks, Rohrer, & Zhang, 2000). One would therefore also expect that these rapidly initiated saccades are affected by visual distractors even more than saccades with longer latencies (e.g., Heeman et al., 2014). Indeed, various models assume that when there is more time, top-down control allows saccades to become more and more goal directed, reducing the effect of close and remote distractors (Godijn & Theeuwes, 2002; Meeter et al., 2010). The current data are consistent with this notion that the effect of the close distractor decreases for saccades with a latency of more than 200 ms.

Conclusion

In conclusion, even though we report a large proportion of express saccades which were different from regular saccades (as evidenced by a separate very early peak in the distribution), we also show that these very early express saccades are affected by the presence of distractors in a similar way as regular saccades. Even though we did observe separate peaks in the latency distribution, we conclude that express saccades may not represent a special class of saccades, but can be considered to be very early and rapidly initiated regular saccades.

Keywords: express saccades, bimodality, global effect, remote-distractor effect, time course

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Footnotes

[1] Analysis of the mean saccade latency instead of the mean of the median latency results in the same conclusions. Main effect of condition: $F(2, 20) = 19.720$, $p < 0.001$, $\eta_p^2 = 0.664$. Planned comparisons: No Distractor versus Close Distractor: $t(10) = 0.815$, $p = 0.434$, $d = 0.247$; No Distractor versus Remote Distractor: $t(10) = 4.235$, $p = 0.002$, $d = 1.277$; Close Distractor versus Remote Distractor: $t(10) = 5.853$, $p < 0.001$, $d = 1.765$.

[2] Analysis of the mean saccade latency instead of the mean of the median latency results in the same conclusions. Main effect of condition: $F(2, 28) = 4.979$, $p = 0.014$, $\eta_p^2 = 0.262$. Planned comparisons: No Distractor versus Close Distractor: $t(14) = 0.247$, $p = 0.808$, $d = 0.064$; No Distractor versus Remote Distractor: $t(14) = 2.723$, $p = 0.017$, $d = 0.703$; Close Distractor versus Remote Distractor: $t(14) = 2.764$, $p = 0.015$, $d = 0.714$.

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