

# Contrasting effects of exogenous cueing on saccades and reaches

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Previous studies have shown that eye and arm movements tend to be intrinsically coupled in their behavior. There is, however, no consensus on whether planning of eye and arm movements is based on shared or independent representations. One way to gain insight into these processes is to compare how exogenous attentional modulation influences the temporal and spatial characteristics of the eye and the arm during single or combined movements. Thirteen participants ( $M = 22.8$  years old,  $SD = 1.5$ ) performed single or combined movements to an eccentric target. A behaviorally irrelevant cue flashed just before the target at different locations. There was no effect of the cue on the saccade or reach amplitudes, whether they were performed alone or together. We found no differences in overall reaction times (RTs) between single and combined movements. With respect to the effect of the cue, both saccades and reaches followed a similar pattern with the shortest RTs when the cue was closest to the target, which we propose reflects effector-independent processes. Compared to when no cue was presented before the target, saccade RTs were generally inhibited by the irrelevant cue with increasing cue-target distance. In contrast, reach RTs showed strong facilitation at the target location and less facilitation at farther distances. We propose that this reflects the presence of effector-dependent processes. The similarities and differences in RTs between the saccades and reaches are consistent with effector-dependent and -independent processes working in parallel.

## Introduction

In our daily life, we are constantly making coordinated eye and arm movements, such as pointing to an object that we are looking at. Numerous studies have demonstrated that simultaneous eye and arm movements are coordinated both spatially and temporally, suggesting a shared representation for planning movements of the eyes and the arms (Carey, 2000; Crawford, Medendorp, & Marotta, 2004; Dean, Marti, Tsui, Rinzel, & Pesaran, 2011; Fischer & Rogal, 1986; Fisk & Goodale, 1985; Frens & Erkelens, 1991; Gribble, Everling, Ford, & Mattar, 2002; Herman, Herman, & Maulucci, 1981; Jeannerod, 1988; Land & Hayhoe, 2001; Neggers & Bekkering, 2002; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Sailer, Eggert, Ditterich, & Straube, 2000; Song & McPeck, 2009). The shared representation implies that motor commands for the eyes can also influence the arm, and vice versa (Lee, Poizner, Corcos, & Henriques, 2014; Sailer, Eggert, Ditterich, & Straube, 2002; Sailer, Eggert, & Straube, 2002; Soechting, Engel, & Flanders, 2001; Vazquez, Federici, & Pesaran, 2017). There are other studies that show little or no correlations between the timings (onsets) of eye and arm movements, suggesting independent representations for the different effectors (Guitton & Volle, 1987; Tweed, Glenn, & Vilis, 1995; Vercher, Mages, Prablanc, & Gauthier, 1994). Studies utilizing decoupled eye and arm movements also argue for independent representations of the effectors, with decoupling occurring in tasks where targets for the two effectors are spatially separated

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(Jonikaitis & Deubel, 2011), or when expectations are violated for learned visuomotor behaviors (Foerster, 2016). Moreover, combined eye and hand movements appear to be planned differently compared to single-effector movements, implying perhaps an additional and separate representation for combined movements (Lee et al., 2014; Nissens & Fiehler, 2017; Sailer, Eggert, Ditterich, et al., 2002). In sum, the underlying processes for eye and arm coupling still remain poorly understood.

One way to gain insight into these processes is to compare how attentional modulation influences the temporal and spatial characteristics of eye, arm, or combined eye–arm movements. Attention plays a major role in movement planning and can be either disruptive or beneficial (Gray, 2011; Wulf & Prinz, 2001). Exogenous attentional stimuli (e.g., a flash of lightning) have been shown to influence movement parameters for the eye (Fecteau, Bell, & Munoz, 2004; Khan, Blohm, McPeck, & Lefevre, 2009; Khan, Heinen, & McPeck, 2010; Khan, Munoz, Takahashi, Blohm, & McPeck, 2016; Maylor & Hockey, 1985; Posner & Cohen, 1984; Walker, Kentridge, & Findlay, 1995). Exogenous stimuli also influence arm movements in a specific and consistent manner (Galletti et al., 2010; Riggio & Kirsner, 1997). Moreover, exogenous attentional effects have also been observed in cases where saccades and reaches were investigated separately (Briand, Larrison, & Sereno, 2000) or in combination with each other (Hilchey, Klein, & Satel, 2014). The effect of the exogenous stimuli on movement characteristics (timing and amplitude) can be exploited to test for independent versus shared movement planning representations. For instance, when a behaviorally irrelevant exogenous cue is presented at the same location slightly before the target (20–200 ms), saccadic reaction times (SRTs) are decreased (Fecteau et al., 2004; Fecteau & Munoz, 2005; Khan et al., 2010; Khan et al., 2016). This decrease in RTs to cued targets is commonly known as attentional facilitation or capture (Jonides & Irwin, 1981; Klein, 2000; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). In contrast, there are also conditions under which cues tend to increase SRTs (Bompas & Sumner, 2009). We have previously shown that behaviorally irrelevant cues flashed at various locations just before a target resulted in a specific pattern of SRTs: a gradual decrease in RT as the cue approached the target (Khan et al., 2010; Khan et al., 2016).

In addition to the well-documented effects of attention on RT, there is also evidence for attentional capture effects on saccade amplitudes and trajectory (Cavegn, 1996; Crawford & Muller, 1992; Godijn & Theeuwes, 2002). Fewer studies have demonstrated exogenous attentional effects on reach movement parameters (Briand et al., 2000; Chang & Ro, 2005;

Hilchey et al., 2014). In summary, it has been shown that a cue preceding the target (presented during the early stages of movement planning) influences saccade and reach movement parameters in a specific manner. What remains unknown is whether the effect on saccades and reach movements are the same even when the movements are performed separately. To our knowledge, there have not yet been any studies using a pre-cue to compare the influence of irrelevant attentional cues on eye and arm movements performed either together (requiring hand–eye coordination), or separately. This comparison would aid in understanding the underlying independent or dependent mechanisms for eye and arm planning.

Here, we presented exogenous cues at different locations just prior to the target (Khan et al., 2010; Khan et al., 2016) to investigate how attentional mechanisms affect eye and hand RTs and amplitudes when performed separately or together. On the one hand, if movement planning of the eyes or the hand is based on a shared representation, we should observe similar spatial and temporal attentional cue effects on both effector movements. On the other hand, if movement planning of the effectors is based on independent representations, we should observe different patterns of RTs and amplitudes in response to the exogenous cue. Additionally, different patterns during combined movements compared to single effector movements would suggest a separate representation for combined movements.

## Materials and methods

### Participants

Thirteen participants ( $M$  age = 22.79 years,  $SD$  = 1.45, 10 females) took part in the experiment. All participants except one (author AM) were naive to the goal of the experiment. The experimental protocol was preapproved by the University of Montreal Health Research Ethics Committee. All participants had normal or corrected-to-normal vision and were right-handed.

### Apparatus

Participants were seated in a well-lit room at a distance of 35 cm from a 24-in. VIEWPixx three-dimensional (3-D) monitor (2.73 min arc/pixel, VPixx Technologies, Montreal, Canada) with a refresh rate of 60 Hz. The monitor background was dark gray (mean luminance of 2.07 cd/m<sup>2</sup>). Stimuli were presented using Eyelink Experiment Builder software (SR Research,

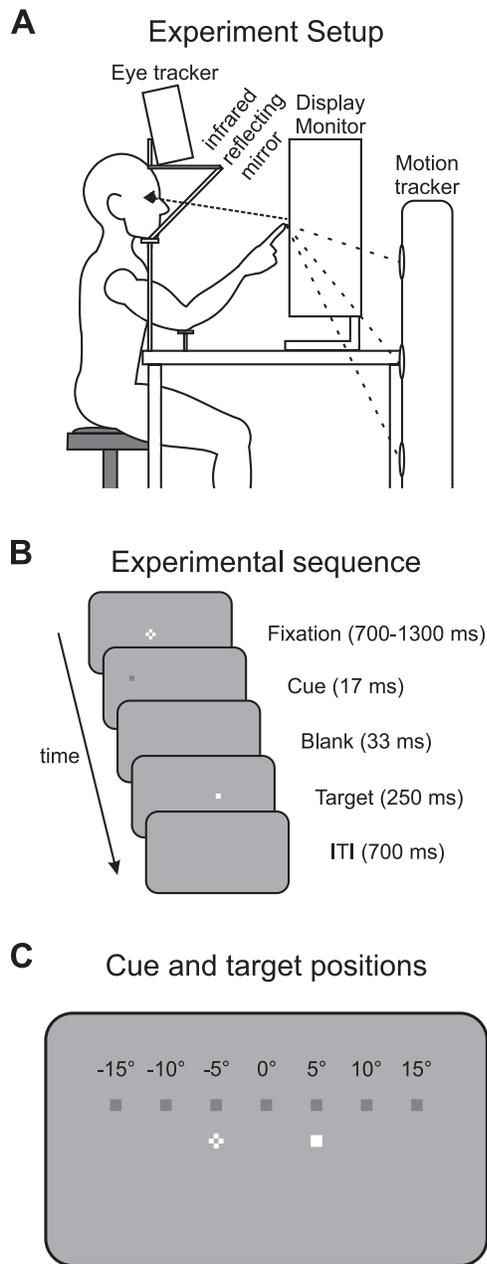


Figure 1. (A) Experimental setup. Participants sat in front of a computer display monitor on which stimuli were presented. An infrared-based eye tracker was used to measure the position of the right eye. A transparent infrared reflecting mirror was used to reflect infrared light from the eye tracker camera to the eyes, to enable eye position recordings. A motion tracker system recorded the 3-D positions of the markers placed on the right hand (dotted lines). (B) Experimental sequence. Each trial began with a fixation point at  $5^\circ$  to the left or right of the center of the screen (left demonstrated in the figure) for a random duration between 700 and 1,300 ms distributed at 100-ms intervals. A cue appeared at one of seven possible positions for 17 ms (leftmost position demonstrated). A blank screen followed for 33 ms, after which a target was presented at the mirror position of the fixation point (distance of  $10^\circ$  between them) for 250 ms.

Mississauga, Canada). Eye movement data were recorded from the participant's right eye at 1,000 Hz using an EyeLink 1000 Plus Tower Mount (SR Research), an infrared video-based eye tracker. A vertically adjustable chinrest and a forehead rest maintained the viewing distance and stabilized the head for accurate eye tracking. A half-reflecting mirror was fixed in front of the participant's face at a  $37.5^\circ$  to  $47.5^\circ$  angle (Figure 1A). The focus of the lens of the camera and the angle of the mirror were adjusted so that a clear and unobstructed corneal reflection and pupil image could be obtained for each participant.

Hand movement data were collected with a 3-D Investigator motion tracking system, First Principles motion capture software and markers (Northern Digital Inc., Waterloo, Canada) recording at 200 Hz with a 0.01-mm spatial resolution. The 3-D motion tracking system was factory calibrated and did not require additional calibration before or during testing to collect positional data. The markers were fixed with clear tape to the participant's right index finger and outer edge of the palm. Two markers were used to minimize spatial data loss in case one of the two was obstructed during testing.

## Procedure

Participants performed the experiment in three pairing conditions, (a) only eye movements, (b) only hand movements, and (c) combined eye and hand movements. There were 12 blocks of each of the three movement conditions, half of which were movements toward the right, and the other half to the left, in a randomized order. Within each block, only one movement condition and only one movement direction were used to minimize delays and errors associated with task switching (see Kiesel et al., 2010, for a review). During testing, participants were instructed to keep their right finger slightly below the fixation point to allow an unobstructed view of the target.

Before each block of trials, gaze position was calibrated and validated with a standard 5-point fixation sequence. The trial sequence (Figure 1B) was as follows: Participants fixated on a white checkered cross subtending  $1^\circ$  of visual angle, presented at  $5^\circ$  left or right from the center of the screen, for an interval of 700–1,300 ms (randomly selected from a uniform

The intertrial interval lasted 700 ms. (C) Cue positions. The cue was presented at  $-15^\circ$ ,  $-10^\circ$ ,  $-5^\circ$ ,  $0^\circ$ ,  $5^\circ$ ,  $10^\circ$  or  $15^\circ$  relative to the center of the screen, offset vertically by  $5^\circ$  above the horizontal meridian. For reference, the fixation point and target are also shown, but during a trial they would not be seen together.

distribution of 100-ms intervals). After fixation, a cue (light gray square of  $0.5^\circ$  diameter) was presented for 17 ms at one of seven possible positions at  $-15^\circ$ ,  $-10^\circ$ ,  $-5^\circ$ ,  $0^\circ$ ,  $5^\circ$ ,  $10^\circ$ , or  $15^\circ$  relative to the center of the screen, offset vertically by  $5^\circ$  above the horizontal meridian (Figure 1C). After the cue disappeared, a dark gray blank screen was presented for 33 ms. Next, a target (white square of  $0.5^\circ$  diameter) appeared at the mirror position from the fixation point (i.e., at  $-5^\circ$  if the latter appeared at  $5^\circ$  or vice versa). The stimulus-onset asynchrony, defined as the time period between the onset of the cue and the onset of the target, was 50 ms. Participants were instructed to make a movement from the fixation point to the target as soon as the target appeared. The intertrial interval was 700 ms, during which there was a dark gray blank screen. The location of the cue was randomized within each block. As a control, there was also a no-cue condition in which the cue was not presented, with otherwise the same timings.

Participants completed a minimum of 36 blocks (3 pairing conditions  $\times$  2 directions  $\times$  6 repetitions) with 56 trials each (8 possible cue positions  $\times$  7 repetitions), for a total of 2,016 trials per participant. A block was repeated if a considerable amount of eye tracking and/or motion tracking data was missing due to tracking problems, such as an obstructed marker. Because of the repetition, the average number of blocks per participant was 38.15,  $SD = 7.34$ . There was a 1–2 min break between the blocks. Participants performed the entire experiment in one session lasting approximately 3 hr.

## Preprocessing

A total of 27,776 trials were collected. All data were analyzed offline using custom-written software on MATLAB 9.1 (MathWorks, Natick, MA). Eye velocity was obtained through digital differentiation of the eye position signals and filtered to reduce noise (two-pole Butterworth filter, cut-off = 110 Hz). Saccade onsets and offsets were detected using acceleration and deceleration thresholds of  $1,000^\circ/s^2$ . Reach onsets and offsets were determined using a velocity threshold of 1 cm/s (Luciw, Jarocka, & Edin, 2014; Mason, Gomez, & Ebner, 2001; Messier & Kalaska, 1999). Two measures of interest were assessed for the movements: RT and amplitude. RT was defined as the time interval between the appearance of the target and the start of the effector's movement. Amplitudes were calculated by subtracting the horizontal end position values from the start position values; only horizontal position values were of interest.

To account for the overall differences in RTs and to investigate specifically the effect of cue position, we calculated normalized RTs (Khan et al., 2010). For each cue position and each participant, we subtracted

each RT from the mean of the no-cue trials within each single and combined effector conditions. RTs were normalized by subtracting the mean SRT of the participants' cued trials from their respective no-cue trial means. Normalized amplitudes were calculated in the same way.

Individual trials were manually removed when any of the following occurred: a blink before or during a saccade, if the participant moved either the hand or the eyes or blinked within 100 ms of the cue, if saccade amplitude was less than  $5^\circ$  (half of the target amplitude), if data from both markers were missing simultaneously, if a saccade occurred during a reach-only trial, or if one of the two movements did not take place during a combined saccade and reach condition. Across all participants and conditions, we removed all trials with saccade or reach onsets under 80 ms or over 500 ms (Bartz, 1962; Fischer & Ramsperger, 1984; Smeets, Hayhoe, & Ballard, 1996; White, Eason, & Bartlett, 1962). These criteria removed 5,977 trials (21.52%). Next, trials were excluded if either saccade or reach start positions fell outside of an elliptic filter. The two centers of the ellipses, one for each direction, were defined as the mean starting position of the effectors within each participant, and the diameter of the ellipses was defined by 5 and 4  $SDs$  for saccade and reach starting positions, respectively. This resulted in a rejection of 1,047 trials (4.8%). There remained 20,529 trials (74.27% of collected trials). Preliminary sorting and filtering of data was done with MATLAB 9.1 (MathWorks).

## Statistical analysis

Repeated-measures three-way analyses of variance (ANOVAs) were conducted with the following independent variables: effector (saccade and reach), pairing condition (single and combined), and cue position (position 1 to 7). In the case of a significant interaction, this was followed up with repeated-measures two-way ANOVAs for each pairing condition, with effector and cue position as the independent variables. Significant effects were followed up with  $t$  tests if there were only two levels, or a one-way ANOVAs for more than two levels. Greenhouse-Geisser corrected values are reported when Mauchly's test revealed that the sphericity assumption was violated. Further, one-sample  $t$  tests comparing the baseline-normalized values to 0 (no-cue trials) were used to demonstrate any inhibition or facilitation related to the cue at each position. All  $p$  values were Bonferroni-corrected for multiple comparisons. To assess the relationship between reach times and saccade times, we used a general linear model assuming an independent covariance matrix. In

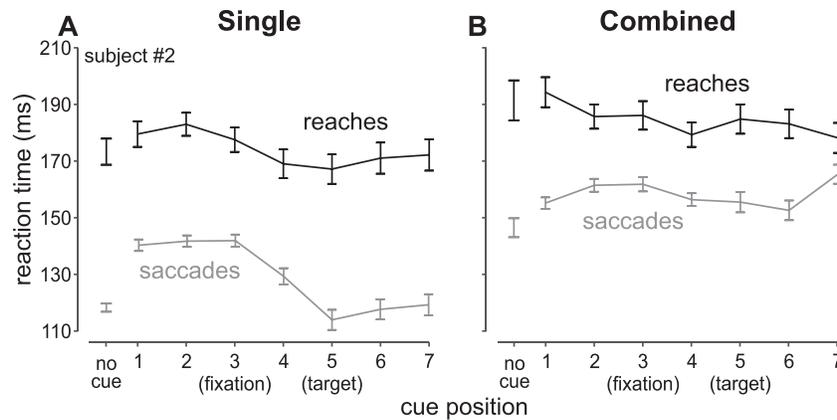


Figure 2. Representative participant RTs. The light gray bars represent saccades and the dark gray bars represent reaches. Error bars represent standard error of the mean. (A) Shows data from trials where movement was only performed with a single effector. (B) Shows data from trials where eye and arm movements were combined. On the x-axis is cue position, where 1 is the cue farthest on the left and 7 is the cue position on the far right. Although the fixation point was either on the left or the right, for ease of graphical representation, all data have been flipped so that the fixation point is always on the left (directly below Cue Position 3). Thus, Cue Position 1 and 2 were to the left of the fixation point, and Cues 4–7 were to the right of the fixation point. Cue 5 was directly above the target. There are 5° between each cue position.

addition to the independent participant variable, within-subjects independent variables included cue position and pairing condition (single vs. combined). The dependent variable was the average SRT for each participant, for each cue position, for each pairing condition. Predictors were reach reaction times (RRTs) and condition. Computations were carried out with SPSS Statistics, version 24 (IBM SPSS, Chicago, IL).

## Results

### Single subject overall results

The RTs for a typical subject are plotted in Figure 2 for saccades (gray lines) and reaches (black lines) for single effector (Figure 2A) and combined effector (Figure 2B) pairing conditions. RTs are plotted as a function of cue position (1–7). In addition, the baseline RTs are also plotted for the trials in which no cue was presented. A number of observations can be made. First, it can be seen that SRTs were overall lower than RRTs, as expected. Second, it appears that SRTs and RRTs might change depending when they were performed by themselves (single condition) compared to when the two movements are combined. Third, cued SRTs tend to be the same or longer compared to the no-cue trials, whereas cued RRTs are sometimes faster than the uncued trials. Finally, there appears to be a systematic effect of cue position. We quantified these observations across all participants in the next section.

### Overall RTs of effector and pairing conditions

We first investigated overall RTs. As can be seen in Figure 3, SRTs were shorter overall than RRTs. This was confirmed with a two-way ANOVA with effector and pairing condition as factors, which revealed a main effect of effector,  $F(1, 12) = 6.894, p = 0.022, \eta_p^2 = 0.365$ ; overall SRTs:  $M = 162.53, SD = 20.98$ ; overall RRTs:  $M = 178.15, SD = 29.35$ . Although there was a slight tendency toward increased SRTs and decreased RRTs in the combined condition, relative to the single condition, as has been previously reported (Sailer, Eggert, Ditterich, et al., 2002), we did not find a main effect of pairing condition,  $F(1, 12) = 0.696, p = 0.421, \eta_p^2 = 0.055$ , nor an interaction between factors,  $F(1, 12) = 3.994, p = 0.069, \eta_p^2 = 0.250$ .

### The effect of cue position, effector, and pairing of effectors on RTs

Next, we investigated the effect of cue position across the different conditions on RTs. In Figure 4, we plotted the normalized mean RTs of saccades and reaches in single and combined conditions at different cue positions across all participants. The three-way ANOVA revealed a significant three-way interaction effect,  $F(6, 72) = 3.1, p = 0.009, \eta_p^2 = 0.205$ . To understand this interaction, we followed up with two-way ANOVAs separately for the single and combined conditions with effector and cue position (seven positions) as factors. In the single-condition (Figure 4A) two-way ANOVA, there was a main effect of effector,  $F(1, 12) = 44.018, p > 0.001, \eta_p^2 = 0.786$ . There

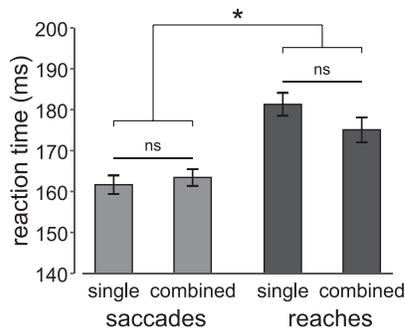


Figure 3. Overall mean RTs. The light gray bars represent saccades and the dark gray bars represent reaches. The mean RT data are plotted for the single condition (where a single effector moved to the target), and the combined condition (where both effectors moved together to the target). Error bars represent standard error of the mean across participants. \*  $p < 0.05$ .

was also a main effect of cue position,  $F(6, 72) = 25.147$ ,  $p > 0.001$ ,  $\eta_p^2 = 0.677$ ), affecting both SRTs and RRTs. The interaction effect was not significant ( $p > 0.05$ ), indicating similar changes in RTs as a function of cue position for both saccades and reaches. To investigate patterns of facilitation and inhibition, we performed one-sample  $t$  tests separately for saccades and reaches. Detailed results are reported in Table 1. For saccades: SRTs at Positions 1, 2 (opposite hemifield from target), 3 (fixation position), and 7 (farther away from target) were significantly slower than the no-cue trials (Position 1:  $t[12] = 5.403$ ,  $p = 0.001$ ; Position 2:  $t[12] = 5.546$ ,  $p > 0.001$ ; Position 3:  $t[12] = 3.825$ ,  $p = 0.017$ ; Position 7:  $t[12] = 3.805$ ,  $p = 0.018$ ). These results demonstrated

that the cue caused significant inhibition of SRTs at these locations. The cue did not cause any facilitation of SRTs, relative to no-cue, even when it was presented close to or at the target location. For reaches, we found the opposite pattern, with Positions 4–7 (close, or at the target location) showing significant facilitation compared to no-cue (Position 4:  $t[12] = -4.329$ ,  $p = 0.007$ ; Position 5:  $t[12] = -6.776$ ,  $p = 0.000$ ; Position 6:  $t[12] = -6.031$ ,  $p = 0.000$ ; Position 7:  $t[12] = -3.329$ ,  $p = 0.042$ ), and no inhibition for cues that were presented farther from the target.

The pattern of results was similar for the combined effector condition (Figure 4B). A two-way ANOVA revealed a main effect of effector,  $F(1, 12) = 39.545$ ,  $p > 0.001$ ,  $\eta_p^2 = 0.767$ ; a main effect of cue position,  $F(6, 72) = 8.303$ ,  $p > 0.001$ ,  $\eta_p^2 = 0.409$ ; and an interaction between the two,  $F(6, 72) = 4.553$ ,  $p = 0.001$ ,  $\eta_p^2 = 0.275$ . To tease apart the interaction, we followed up with two one-way ANOVAs, which revealed that combined reaches varied significantly with cue position,  $F(6, 72) = 11.848$ ,  $p > 0.001$ ,  $\eta_p^2 = 0.497$ , while combined saccades did not (although there was a trend,  $F[6, 72] = 2.517$ ,  $p = 0.071$ ). One-sample  $t$  tests at each cue position showed similar results for the combined condition as for the single condition. For SRTs in the combined condition, there were significant delays at Positions 1, 2 (opposite hemifield), 3 (fixation), and 6 (farther from target), compared to no-cue (Position 1:  $t[12] = 4.271$ ,  $p = 0.008$ ; Position 2:  $t[12] = 3.799$ ,  $p = 0.018$ ; Position 3:  $t[12] = 3.329$ ,  $p = 0.042$ ; Position 6:  $t[12] = 4.325$ ,  $p = 0.007$ ). In contrast, for RRTs that were performed at the same time as saccades, there was significant facilitation at Positions 4 and 5 (close or at

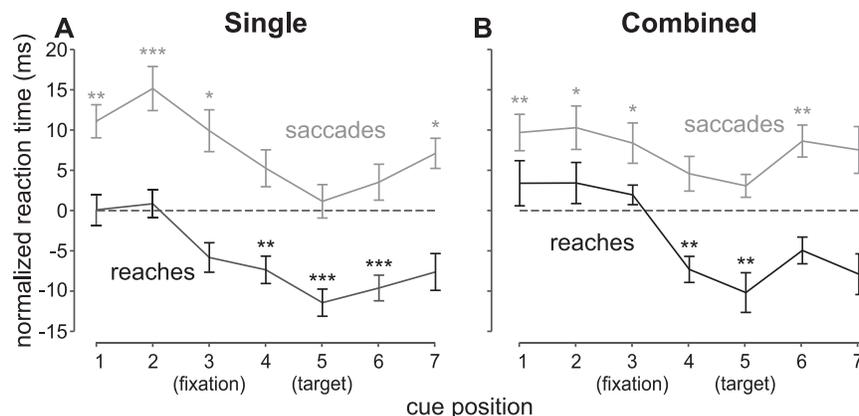


Figure 4. Mean RTs as a function of cue position. The light gray lines represent saccades and the dark gray lines represent reaches. (A) Shows data from trials where movement was only performed with a single effector. (B) Shows data from trials where eye and arm movements were combined. On the x-axis is cue position, where 1 is the cue farthest on the left and 7 is the cue position on the far right (conventions as in Figure 2). Thus, Cue Position 1 and 2 were to the left of the fixation point, and Cues 4–7 were to the right of the fixation point. Cue 5 was directly above the target. On the y-axis is the normalized RT, the difference between RT for each cue position trial and the RT for the no-cue trials. The dashed reference line at zero reflects reactions times in the no-cue trials. Negative normalized RTs are those that were faster than the no-cue trials, whereas positive indicates RTs slower than no-cue trials. Error bars represent SEM standard error of the mean. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

Effector × pairing	Cue position	<i>M</i>	<i>SEM</i>	<i>T</i> value	<i>p</i> value and significance
<b>Single saccades</b>					
1	1	<b>12.2</b>	<b>2.3</b>	<b>5.403</b>	<b>0.001</b> **
2	2	<b>16.7</b>	<b>3.0</b>	<b>5.546</b>	<b>0.001</b> ***
3	3	<b>10.9</b>	<b>2.9</b>	<b>3.825</b>	<b>0.017</b> *
4	4	5.8	2.5	2.302	0.280 NS
5	5	1.3	2.3	0.560	>0.999 NS
6	6	3.9	2.5	1.585	0.972 NS
7	7	<b>7.8</b>	<b>2.1</b>	<b>3.805</b>	<b>0.018</b> *
<b>Combined saccades</b>					
1	1	<b>10.7</b>	<b>2.5</b>	<b>4.271</b>	<b>0.008</b> **
2	2	<b>11.3</b>	<b>3.0</b>	<b>3.799</b>	<b>0.018</b> *
3	3	<b>9.2</b>	<b>2.8</b>	<b>3.329</b>	<b>0.042</b> *
4	4	5.0	2.4	2.105	0.400 NS
5	5	3.4	1.6	2.138	0.377 NS
6	6	<b>9.5</b>	<b>2.2</b>	<b>4.325</b>	<b>0.007</b> **
7	7	8.3	3.2	2.579	0.169 NS
<b>Single reaches</b>					
1	1	0.1	2.1	0.051	>0.999 NS
2	2	0.9	1.9	0.487	>0.999 NS
3	3	-6.4	2.0	-3.175	0.056 NS
4	4	<b>-8.1</b>	<b>1.9</b>	<b>-4.329</b>	<b>0.007</b> **
5	5	<b>-12.6</b>	<b>1.9</b>	<b>-6.776</b>	<b>&lt;0.001</b> ***
6	6	<b>-10.6</b>	<b>1.7</b>	<b>-6.031</b>	<b>&lt;0.001</b> ***
7	7	<b>-8.4</b>	<b>2.5</b>	<b>-3.329</b>	<b>0.042</b> *
<b>Combined reaches</b>					
1	1	3.7	3.1	1.198	>0.999 NS
2	2	3.7	2.8	1.326	>0.999 NS
3	3	2.1	1.3	1.570	0.997 NS
4	4	<b>-8.1</b>	<b>1.8</b>	<b>-4.537</b>	<b>0.005</b> **
5	5	<b>-11.3</b>	<b>2.7</b>	<b>-4.147</b>	<b>0.009</b> **
6	6	-5.5	1.8	-3.005	0.077 NS
7	7	-8.8	2.8	-3.138	0.060 NS

Table 1. Normalized reaction times (ms). Values in bold are significantly different from 0 (no-cue trials). \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ , Bonferroni-corrected.

the target location), compared to no-cue (Position 4:  $t[12] = -4.537, p = 0.005$ ; Position 5:  $t[12] = -4.147, p = 0.009$ ). In summary, saccades in both the single and combined conditions generally demonstrated an inhibition when the cue was presented far from the target’s position, in either direction, but no facilitation when the cue was presented at the target location. In contrast, reaches were generally facilitated by the cue when it appeared close to or at the target position, with no inhibition for cues that were presented far from the target’s position. There are also similarities in the changes in RTs as a function of cue position for saccades and reaches; the fastest normalized RT invariably occurred when the cue was presented at the target position, and the slowest normalized RT occurred when the cue was presented in the opposite hemifield from the target.

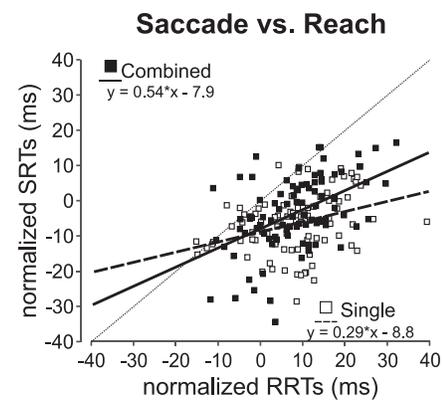


Figure 5. Correlations for SRTs and RRTs. Normalized SRTs are plotted as a function of normalized RRTs. The line of unity is drawn as a reference (gray dotted line). Empty squares represent the single effector pairing condition (dashed black line of best fit), where combined reaches and saccades are represented by filled squares (solid black line of best fit). Each participant has seven points, corresponding to the seven cue positions. The similar slopes and intercepts between SRTs and RRTs demonstrate that the changes in normalized RTs in response to the cue followed the same pattern for the two effectors.

We directly compared the pattern of normalized RTs for saccades and reaches. In Figure 5 we have plotted normalized SRTs against normalized RRTs (seven data points per participant = seven cue positions) for the single (open squares) and the combined (filled squares). Using generalized linear models to assess the relationship between SRTs and RRTs, we found a significant relationship between SRTs and RRTs ( $\chi^2_{(1, N=12)} = 7.5, p = 0.006$ ). The relationship between SRT and RRT appears to be somewhat stronger in the combined-effector condition (Pearson’s  $r = 0.490, p < 0.001$ ), compared to the single-effector condition (Pearson’s  $r = 0.337, p = 0.001$ ), but these linear models were not significantly different ( $\chi^2_{(1, N=12)} = 0.3, p = 0.584$ ). These findings demonstrate that the changes in normalized RTs in response to the cue were very similar for the two effectors.

### Overall amplitudes of effector and pairing conditions

For saccade and reach amplitude, we first analyzed overall amplitudes. As can be seen in Figure 6, saccade amplitudes were overall longer than reach amplitudes. This was confirmed with a two-way ANOVA with effector and pairing condition as factors, which revealed a main effect of effector,  $F(1, 12) = 5.564, p = 0.036, \eta_p^2 = 0.317$ ; overall saccade amplitudes:  $M = 10.00, SD = 0.53$ ; overall reach amplitudes:  $M = 9.33, SD = 0.99$ , and a significant interaction between the two

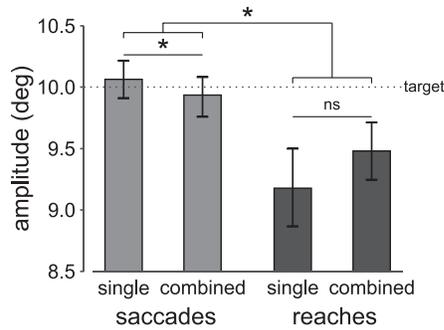


Figure 6. Overall amplitudes. The light gray bars represent saccades and the dark gray bars represent reaches. The mean amplitude data are plotted for the single condition (where a single effector moved to the target), and the combined condition (where both effectors moved together to the target). Error bars represent SEM. \*  $p < 0.05$ .

factors,  $F(1, 12) = 5.129$ ,  $p = 0.043$ ,  $\eta_p^2 = 0.299$ . To tease apart this interaction, we followed up with  $t$  tests, which revealed a significant difference between single and combined saccades,  $t(12) = 2.635$ ,  $p = 0.022$ ; single saccades:  $M = 10.06$ ,  $SD = 0.55$ ; saccades combined:  $M = 9.94$ ,  $SD = 0.53$ , but not between single and combined reaches,  $t(12) = 1.815$ ,  $p = 0.095$ ; single reaches:  $M = 9.18$ ,  $SD = 1.14$ ; reaches combined:  $M = 9.48$ ,  $SD = 0.84$ .

### The effect of cue position, effector, and pairing of effectors on movement amplitudes

We investigated whether amplitudes changed as a function of cue position. To evaluate the specific influence of the cue, we normalized saccade and reach

amplitudes as described in the Methods. Normalized amplitudes for the single (Figure 7A) and combined (Figure 7B) conditions are plotted. As with RTs, we investigated the effects of cue position and condition on movement amplitudes. We conducted a three-way ANOVA with the same independent variables and levels as in the RT analysis, with cue position (7), effector (2), and pairing conditions (2). This analysis revealed a significant three-way interaction effect,  $F(6, 72) = 4.097$ ,  $p = 0.001$ ,  $\eta_p^2 = 0.255$ . Therefore, we conducted two-way repeated-measures ANOVAs on each pairing condition independently. We found no significant main effects for either the single or combined ANOVAs, but there was a significant interaction effect between effector (saccade or reach) and cue position in the single effector ANOVA,  $F(6, 72) = 3.32$ ,  $p = 0.042$ ,  $\eta_p^2 = 0.217$ . We followed up this interaction effect with two one-way ANOVAs for each effector, to determine if the effect of cue varied the amplitude in the single reaches or the single saccades condition. However, neither ANOVA revealed a significant effect of cue (single saccades:  $F[6, 72] = 3.035$ ,  $p = 0.074$ ,  $\eta_p^2 = 0.202$ ; single reaches:  $F[6, 72] = 2.006$ ,  $p = 0.131$ ,  $\eta_p^2 = 0.143$ ). In summary, cue position did not reliably affect amplitudes in the single or combined conditions for saccades or reaches.

## Discussion

We investigated how the reorienting of exogenous attention affects eye and arm movements when they are performed separately or together. While saccade amplitudes were larger than reach amplitudes, we did

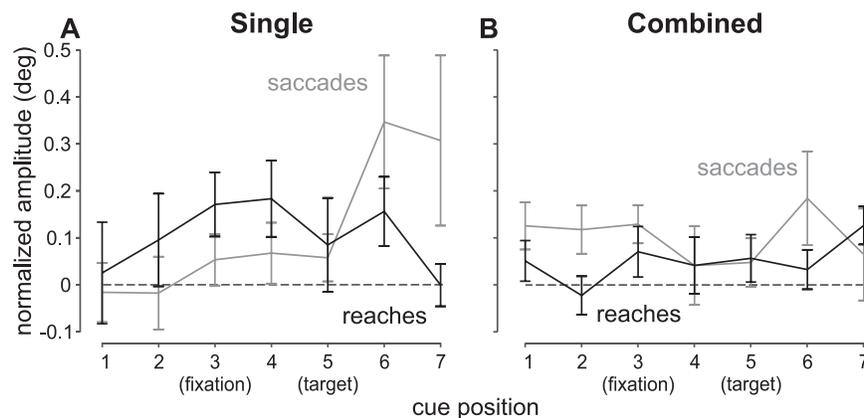


Figure 7. Mean normalized amplitudes as a function of cue position. The light gray bars represent saccades and the dark gray bars represent reaches. Error bars represent standard error of the mean. (A) Shows data from trials where movement was performed with a single effector. (B) Shows data from trials where eye and arm movements were combined. On the x-axis is cue position and on the y-axis is the normalized amplitude in degrees, which is the difference between the amplitude in a cue trial and the mean amplitude in the no-cue trials. The dashed reference line represents the amplitude for the no-cue trials. Negative numbers reflect amplitudes smaller than the no-cue trials whereas positive numbers reflect amplitudes larger than the no-cue trials.

not find any effect of cue position on amplitude. For RTs, we found no overall differences when movements were performed together compared to by themselves, regardless of cue presence. In addition, the pattern of relative changes in RTs as a function of cue position varied in a similar way across reaches and saccades. However, we also found differences in the patterns of facilitation and inhibition for saccades and reaches; reaches were facilitated when the cue was close to the target and were not inhibited by the cue at any position compared to the condition when a cue was not presented before the target. In contrast, saccades were not facilitated when the cue was presented close to the target, but were inhibited when the cue was presented away from the target in both directions. Taken together, our findings point toward a combination of effector-independent and -dependent processes in the initiation of goal-directed movements.

We did not find any differences in the overall RTs for either saccades or reaches when they were combined as opposed to when they moved alone; though we observed a slight tendency toward an increase in SRTs and a decrease in RRTs during combined movements (Figure 3). Previous studies show a broad spectrum of changes for combined movements to the same target compared to when the effector moves independently, from no changes to either effector such as in our study (Bekkering, Adam, Kingma, Huson, & Whiting, 1994; Bekkering, Adam, van den Aarsen, Kingma, & Whiting, 1995; Neggers & Bekkering, 1999), to changes in SRTs but not RRTs (Jonikaitis & Deubel, 2011), and to changes in both SRTs and RRTs (Lünenburger, Kutz, & Hoffmann, 2000; Niechwiej-Szwedo, McIlroy, Green, & Verrier, 2005; Sailer, Eggert, Ditterich, et al., 2002). It may be that our task, which required reaching or making a saccade to the exact same target location on each trial, may have become too automatic to demonstrate differences. Consistent with this hypothesis, overall RTs for both saccades and reaches were shorter than reported in other studies (Lee et al., 2014; Sailer et al., 2000).

In response to the exogenous cue, we found similar changes in RTs as a function of cue position for both saccades and reaches, but there was also an overall shift of RTs (with saccades not demonstrating the facilitation observed in the reaches when the cue was near the target). These findings are consistent with previous research suggesting both effector-dependent and -independent movement planning processes. As mentioned in the introduction, a number of studies have shown strong correlations between initiation times of the eye and the hand, consistent with a shared movement planning stage (Biguer, Jeannerod, & Prablanc, 1982; Bekkering et al., 1995; Gopal & Murthy, 2015; Lee et al., 2014; Neggers & Bekkering, 1999; Sailer et al., 2000; Suzuki, Izawa, Takahashi, &

Yamazaki, 2008; Tao, Khan, & Blohm, 2018). An effector-independent stage reflecting shared outcomes for different effectors has been suggested previously in terms of a shared target selection stage for both the eye and the hand (Song & McPeck, 2009). Target selection has been proposed to occur through a priority map directed by visual attention (Fecteau & Munoz, 2006; Zelinsky & Bisley, 2015), which combines bottom-up inputs (i.e., the physical distinctiveness of objects in the scene) and top-down inputs (i.e., the goals and motivations of the observer; see Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Serences, Yantis, Culberson, & Awh, 2004). When combined, these two types of inputs are used to create an integrated map (Itti & Koch, 2001; Treue, 2003), which is presumably used to select objects of interest for saccades and reach movements. In addition, we and others also show evidence for effector specific planning processes that result in different behavioral outcomes for the different motor systems. In our study, we observed that SRTs were mostly inhibited, while reaches were mostly facilitated. Previous studies have also proposed differential processing of eye and arm movement initiation (Briand et al., 2000; Sailer et al., 2000; Sailer, Eggert, Ditterich, et al., 2002). Differences have also been shown in the allocation of attention to eye and arm goal locations during movement planning, presumably reflecting a later effector-independent stage (Deubel & Schneider, 2003; Jonikaitis & Deubel, 2011; Khan, Song, & McPeck, 2011). Shared attentional resources during coordinated reaches and saccades were shown to be mainly guided by the eye, potentially as a synergistic mechanism to alleviate attentional demands, which in turn reduced the RTs of the effectors (Khan et al., 2011; Pelz, Hayhoe, & Loeber, 2001). This proposed effector-independent process of beneficial coordination can be disrupted by task-specific constraints (Pelz et al., 2001), suggesting that the hand and the eye rely, at least in part, on effector-specific processes when coordination is irrelevant or not possible.

A lack of attentional facilitation for SRTs in the presence of nearby exogenous cues, relative to the no-cue condition, has been reported before and is likely specific to the saccadic system (Crawford & Muller, 1992; Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007; Khan et al., 2016; van der Lubbe, Vogel, & Postma, 2005; Walker et al., 1995). One possible explanation is that eye movements involve a gating mechanism where omnipause neurons inhibit brain stem saccade generators from producing a saccade in response to activity in the superior colliculus reflecting the visual cue (Corneil, Munoz, Chapman, Admans, & Cushing, 2008; Everling, Pare, Dorris, & Munoz, 1998; Scudder, Kaneko, & Fuchs, 2002). This is in contrast to other motor systems such as head or reach movements that do not have such a gating mechanism (Corneil et

al., 2008; Kaufman et al., 2010; Kaufman, Churchland, & Shenoy, 2013). Consistent with this finding, Corneil et al. (2008) found neck muscle activation during cue presentation consistent with covert orienting (i.e., with no eye movement toward the cue). Thus, it could be that arm movements are more easily facilitated by nearby cues because their activity is not limited by a gating mechanism, whereas eye movement activity is downregulated by the saccadic gating mechanism.

In terms of neuronal correlates, there are many neurophysiological studies showing evidence for target selection and movement planning processes that are both effector-independent and -dependent. It is well established that there are separate networks for eye versus arm movement planning, consistent with effector dependent processing. Specifically, regions within the posterior parietal cortex (PPC), the frontal eye fields (FEF), the superior colliculus, and brainstem areas are involved in eye movement planning (Bruce & Goldberg, 1985; Goldberg & Bushnell, 1981; Schall, 1991; Schiller & Tehovnik, 2005; Sparks & Barton, 1993) while different regions of the PPC, the premotor, and motor cortices have been shown to be primarily involved in reach planning (Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003; Buneo & Andersen, 2006). However, in line with a target selection effector independent stage, neurons in areas in the PPC such as the lateral intraparietal area (LIP) and in the frontal cortex, such as FEF, have been shown to respond to both eye and reach movements (LIP: Buneo & Andersen, 2006; Lawrence & Snyder, 2006; Oristaglio, Schneider, Balan, & Gottlieb, 2006; FEF: Lawrence & Snyder, 2006; Levy, Schluppeck, Heeger, & Glimcher, 2007; Thura, Hadj-Bouziane, Meunier, & Boussaoud, 2008). Indeed these are two of the areas that have been proposed to represent a priority map (Bisley & Goldberg, 2010; Goldberg, Bisley, Powell, & Gottlieb, 2006; Liu, Yttri, & Snyder, 2010; McPeck & Keller, 2002; Thompson & Bichot, 2005). Moreover, the superior colliculus has also been demonstrated to be involved in target selection and covert attention for both eye and arm movements (Gandhi & Katnani, 2011; Krauzlis, Lovejoy, & Zénon, 2013; Khan et al., 2016; Lünenburger, Kleiser, Stuphorn, Miller, & Hoffman, 2001) and thus also proposed to be a candidate for a priority map (Boehnke & Munoz, 2008; Fecteau & Munoz, 2006; Song, Rafal, & McPeck, 2011). Interestingly, LIP was recently shown to be involved in eye-hand coordination, with inactivation of the region impairing combined saccades and reaches (Yttri, Liu, & Snyder, 2013).

The exogenous cues did not seem to affect amplitudes in the same way it did RTs in that there was no effect of cue. This is in contrast to Sailer, Eggert, Ditterich, and Straube (2002), who showed an amplitude difference between effectors depending on cue's

distance; when the cue was presented closer to the fixation point than the target, only saccade amplitudes decreased, whereas when it was presented farther than the target, both effectors' amplitudes increased. Moreover, while we found a systematic influence of cue position on RTs, Sailer, Eggert, Ditterich, and Straube (2002) did not. We believe the difference lies in the timings of the cue and the target. A number of studies have investigated how cues appearing at the same time or after the target influence eye, arm, and combined movements. Studies comparing single effector movements of the eyes and arms have demonstrated that saccades are consistently influenced by late cues (Bompas, Hedge, & Sumner, 2017; Buonocore, 2010; Sailer, Eggert, Ditterich, et al., 2002; Sailer, Eggert, & Straube, 2002). While the amplitudes of reach movements were similarly affected by cues, the latencies were either not affected, or affected by a smaller amount (Bompas et al., 2017; Buonocore, 2010; Sailer, Eggert, & Straube, 2002). Sailer, Eggert, Ditterich, et al. (2002) tested combined movements in addition to single effector movements and again found relatively unchanged patterns of responses to cues compared to single effector movements. In our study, we presented the cue before target onset, whereas in their study, they presented the cue and the target at the same time. It may be that the different timings affect different processes (e.g., attentional) in a different manner, where pretarget cues influence RTs more, whereas post- or simultaneously presented cues influence kinematics to a greater degree compared to initiation (McPeck, Han, & Keller, 2003; McSorley, Haggard, & Walker, 2005, 2006; Sailer, Eggert, & Straube, 2002; Theeuwes & Godijn, 2004). It remains unclear whether the simultaneous presentation of a cue involves attentional mechanisms to the same degree as attentional capture, as their influence on eye movements appears to be different (Bompas & Sumner, 2009; Walker et al., 1995), and simultaneous presentations appear to influence amplitudes more than RTs (Sailer, Eggert, & Straube, 2002).

To conclude, we found changes in RTs in reaches and saccades in response to an exogenous cue at different locations relative to the target. Our findings are in line with other research that has shown that oculomotor and reaching systems share certain attentional mechanisms (Briand et al., 2000; Sailer et al., 2000; Sailer, Eggert, Ditterich, et al., 2002), but are also independently driven (Deubel & Schneider, 2003; Jonikaitis & Deubel, 2011; Khan et al., 2011). Taken together, our results provide evidence for both shared and independent movement planning processes driving reaches and saccades.

*Keywords: exogenous attention, eye movements, reach movements, hand-eye coordination*

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