

The spatial and temporal properties of attentional selectivity for saccades and reaches

Emma E. M. Stewart

School of Psychology, University of Adelaide,
Adelaide, Australia

Preeti Verghese

The Smith-Kettlewell Eye Research Institute,
San Francisco, CA, USA

Anna Ma-Wyatt

School of Psychology, University of Adelaide,
Adelaide, Australia



The preparation and execution of saccades and goal-directed movements elicits an accompanying shift in attention at the locus of the impending movement. However, some key aspects of the spatiotemporal profile of this attentional shift between eye and hand movements are not resolved. While there is evidence that attention is improved at the target location when making a reach, it is not clear how attention shifts over space and time around the movement target as a saccade and a reach are made to that target. Determining this spread of attention is an important aspect in understanding how attentional resources are used in relation to movement planning and guidance in real world tasks. We compared performance on a perceptual discrimination paradigm during a saccade-alone task, reach-alone task, and a saccade-plus-reach task to map the temporal profile of the premotor attentional shift at the goal of the movement and at three surrounding locations. We measured performance relative to a valid baseline level to determine whether motor planning induces additional attentional facilitation compared to mere covert attention. Sensitivity increased relative to movement onset at the target and at the surrounding locations, for both the saccade-alone and saccade-plus-reach conditions. The results suggest that the temporal profile of the attentional shift is similar for the two tasks involving saccades (saccade-alone and saccade-plus-reach tasks), but is very different when the influence of the saccade is removed. In this case, performance in the saccade-plus-reach task reflects the lower sensitivity observed when a reach-alone task is being conducted. In addition, the spatial profile of this spread of attention is not symmetrical around the target. This suggests that when a saccade and reach are being planned together, the saccade drives the attentional shift, and the reach-alone carries little attentional weight.

Introduction

Eye and hand movements are often directed to the same location, particularly when reaching rapidly to a visually defined target (Land & Hayhoe, 2001; Ma-Wyatt, Stritzke, & Trommershäuser, 2010; Neggers & Bekkering, 2001). This close coupling seems to make intuitive sense, given evidence that the same visual information is used to drive eye and hand movements both in planning a reach and during online updating (Gegenfurtner & Franz, 2007; Ma-Wyatt & McKee, 2006, 2007; Ma-Wyatt et al., 2010; Stritzke & Trommershäuser, 2007). This is also the case in naturalistic tasks involving sequences of movements, in which the eye tends to precede the hand, indicating visual information is important in the guidance of sequences of hand movements (Land & Hayhoe, 2001). Subsequent benefits to hand movement planning and guidance comes not only from the new visual information acquired by foveating the target but also the proprioceptive information from the position of the eye (Prablanc, Echallier, Komilis, & Jeannerod, 1979; Ren, 2006).

The visual environment that we interact with is complex, so we need attention to filter the relevant information from the irrelevant, and to select targets for upcoming movements. A shift in attention often accompanies a saccade (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995), and is directed toward upcoming saccade and reach locations as people make eye and hand movements to interact with the world. The close link between eye and hand movements observed for rapid tasks and for slower, more naturalistic tasks is reflective of the attentional guidance that accompanies eye movements and is also

Citation: Stewart, E. E. M., Verghese, P., & Ma-Wyatt, A. (2019). The spatial and temporal properties of attentional selectivity for saccades and reaches. *Journal of Vision*, 19(9):12, 1–19, <https://doi.org/10.1167/19.9.12>.

<https://doi.org/10.1167/19.9.12>

Received January 23, 2018; published August 21, 2019

ISSN 1534-7362 Copyright 2019 The Authors



present when one is making a hand movement alone (Stewart & Ma-Wyatt, 2015). It seems that this attentional guidance plays a role in the planning and execution of both saccades and any concurrent hand movements.

Many studies have sought to determine how this shift in attention works, and have tested both the spatial extent of the attentional shift, and its time-course. Some evidence suggests that, for saccades, attention can shift as early as 50–100 ms after a cue (Deubel, 2008; Rolfs & Carrasco, 2012), while others observe this shift happening on a longer timescale of approximately 100–200 ms after a cue (Castet, Jean-jean, Montagnini, Laugier, & Masson, 2006; Jonikaitis & Deubel, 2011; Montagnini & Castet, 2007). With respect to saccade onset, Rolfs and Carrasco (2012) found that attentional facilitation built up at the saccade target from 100 ms before the saccade, while White, Rolfs, and Carrasco (2013) found that attention built up at the impending saccade location 50 ms before saccade onset. Preparing a hand movement has also been shown to elicit a similar attentional shift, and the time-course and spatial spread of this shift seems to be comparable to that of pre-saccadic attention (Jonikaitis & Deubel, 2011; Rolfs, Lawrence, & Carrasco, 2013).

In terms of the spatial properties of the premotor attentional shift, there is some diverging evidence on whether, and how tightly, pre-saccadic attention is locked to the saccade target. Many studies point to pre-saccadic attention being specific to the saccade target: for example Deubel and Schneider (1996), Hoffman and Subramaniam (1995), Kowler et al. (1995), and White et al. (2013) have found that attentional facilitation was higher at the saccade location than neighboring non-saccade locations, and Jonikaitis, Klapetek, and Deubel (2017) showed that attention was biased toward the choice of a future saccade target. However, there is some evidence to suggest that attention may be allocated in a broader manner around a saccade target: Castet et al. (2006) reported that locations neighboring the saccade target location also showed a benefit in performance when participants were required to attend to those locations, and Stewart and Ma-Wyatt (2017) showed an asymmetrical spread of attention based on the direction of hand movement. For reaches, Rolfs, Lawrence, and Carrasco (2013) found that discrimination performance was better at the reach target compared to a location on the opposite side of the screen, and Jonikaitis and Deubel's (2011) results showed that attention shifted to the location of the reach before reach onset, but did not spread to locations around the reach target. Similarly, when sequential movements were being planned, attention was allocated to multiple upcoming movement targets in parallel, but not to locations between these targets (Baldauf, Wolf, & Deubel, 2006). Additionally, in a

task where a reach alone was conducted while the eye was fixated, there was attentional facilitation around the reach endpoint, suggesting that reaching alone can trigger a broad shift in attention around the reach target (Stewart & Ma-Wyatt, 2015).

This suggests that the planning and execution of both saccades and reaches can elicit a shift of attention that may be flexible depending on the task being performed (White et al., 2013), and that the facilitation may not be spatially limited to the movement target, but may spread around the target, or to multiple locations, depending on the demands of the task. Since the deployment of eye and hand can differ depending on task demands, it is important to study the spatiotemporal profile of this shift and how the accompanying shift of attention may differ, and especially whether the planning and execution of saccades and reaches results in a different spread of attention around a movement target due to the different motor requirements for each movement. In this study we also wanted to compare the amount of attentional facilitation associated with overt action compared to covert attention. Previous studies have generally used a neutral or invalid-cued baseline (Hanning, Aagten-Murphy, & Deubel, 2018; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012; Rolfs et al., 2013; White et al., 2013); we show here that the baseline measure affects the relative amount of attentional facilitation that can be measured at any stimulus onset asynchrony (SOA) or location.

Previous studies have compared the spatiotemporal profile of saccades and reaches in an attempt to determine whether the underlying attentional mechanisms driving these shifts are similar for both movement types. There is, however, diverging evidence on this issue: for example, during simultaneous eye and hand movements to different locations, the amount of attention allocated to the reach goal is reduced in favor of the saccade location (Khan, Song, & McPeck, 2011). It was also found that spatial selection for saccade and reach targets is tightly coupled (Song & McPeck, 2009), while the temporal coupling is less rigid as attentional facilitation can be tied to both saccade and reach onset latency. This suggests that the attentional allocation to the eye and the hand may be linked. However, studies by Jonikaitis and Deubel (2011) and Jonikaitis, Schubert, and Deubel (2010) both show that attentional resources can be independently allocated to saccade and reach goals, suggesting that eye and hand movements have different underlying attentional mechanisms. Recent work also suggests that the spatiotemporal profile of premotor attention around the target for a reach alone can involve both suppression and facilitation of performance (Stewart & Ma-Wyatt, 2015), similar to findings for covert attention (Koenig-Robert & Van Rullen, 2011).

While this approach of comparing saccade and reach, or quantifying the spatial and/or temporal profile of attention has indicated that attentional allocation to the eye and hand may be linked, it is still not clear how the spatiotemporal profile of the reach differs when the eye and hand are acting alone or when a combined movement is being made. As yet, there has been no direct comparison of the spatiotemporal profile of attention at the target and around the target, using the same task. Investigating the spatiotemporal profile of these attentional shifts is an important step in understanding how attention is allocated during planning and guidance of movements when interacting with the environment. In the current study, we directly compared the attentional contributions of each motor effector on the spatiotemporal profile of attention at and around a movement target when a saccade-alone, reach-alone, or a saccade-plus-reach is being made. We compared performance to a valid-cue baseline to distill any effects of movement planning from pure covert attention driven by a cue, as well as to measure a more naturalistic deployment of attention. It is difficult to translate findings related to premotor attention studied in the lab to real-world scenarios where there are complex scenes and multiple objects. In the lab, while movement-relevant locations are cued, in the real world, the target of an upcoming eye or hand movement is likely first selected by covert attention before a movement is planned to that location. The mechanisms for deployment of saccades seem to underlie these shifts in covert attention (for a review, see Moore & Zirnsak, 2017); however, studies have shown that overt attentional shifts elicit greater neural activity than covert attentional shifts (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; de Haan, Morgan, & Rorden, 2008), suggesting that overt processes may elicit an additional attentional processing advantage. Using a valid baseline is thus analogous to measuring any additional premotor attention that is allocated on top of the covert attention used to select a target in the first instance.

We used a perceptual discrimination task during a saccade-only, reach-only, and saccade-plus-reach task to map the temporal and spatial properties of the attentional shift relative to both eye and hand movements. In each condition, the goal of the movement was identical for the eye and the hand. In addition to the target, three locations around the saccade-plus-reach target were probed to determine the spatial spread of attention around this target: one probe location was between the fixation point and the target, one was beyond the target, and one was above the target, so that it was orthogonal to the direction of movement. The temporal properties of the attentional shift were explored by changing the onset of a perceptual probe during both eye and hand movements. The aim of this design was to quantify how

planning each of these movements may trigger a shift in attention, and allows us to see whether attention plays a different role in the planning and guidance stages of saccades and reaches.

Method

Participants

There were five participants: one was an author, and four were naïve as to the purposes of the study. Three were experienced psychophysical participants. All participants had normal or corrected-to-normal vision, and used their right hands to point; all participants were right-hand dominant as classified by the Edinburgh handedness test. Ages ranged from 20 to 43. Ethics approval was obtained from the School of Psychology, and the work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki, 1964). Participants were free to withdraw at any time without penalty. Participants completed approximately 8 hours of data collection in 1-hour blocks.

Equipment

Stimuli were presented on a 17-inch ELO touchscreen monitor, with a resolution of 1024×768 pixels and a screen refresh rate of 75 Hz. The monitor was calibrated to ensure that contrast levels remained consistent across sessions, and to ensure that the monitor's nonlinear gamma function was corrected to be linear. Eye movements were measured using a SR Research EyeLink 1000 eye tracker to record eye position during the task. Eye position was sampled at a rate of 1000 Hz with a spatial precision of 0.25° . The experiment was run using custom software written in MATLAB (MathWorks, Natick, MA) using routines from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A mouse was located central to the touch screen, in front of the chin rest. Participants started a trial by depressing the mouse button. Touch responses were recorded when participants pointed to stimuli on the touch screen monitor. A keyboard to the left was used to collect participant responses.

Experimental design

The experimental design is based on Stewart and Ma-Wyatt (2015), and aimed to measure the perceptual facilitation around and at a movement target location in the visual field, during a saccade-only task, a reach-only

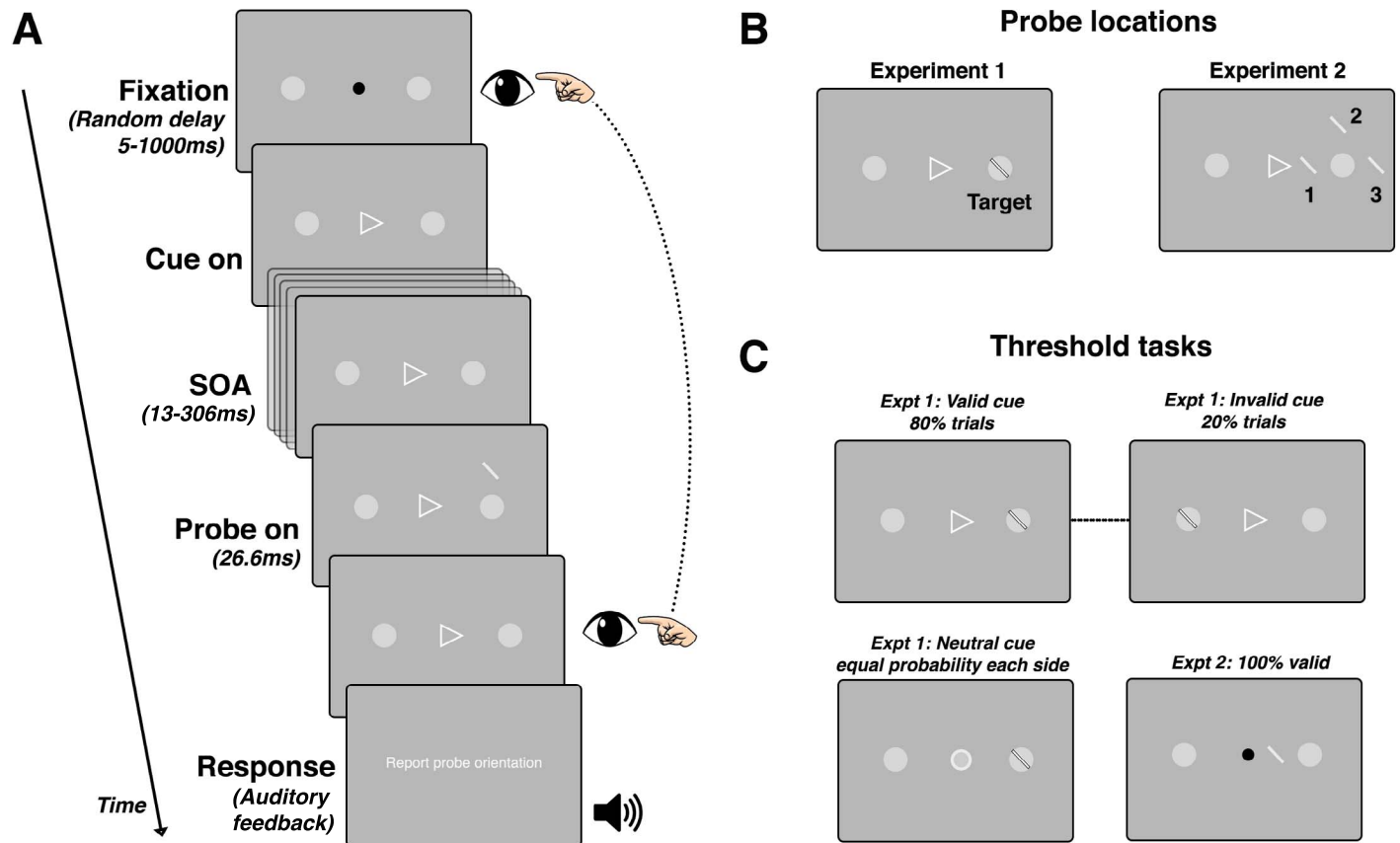


Figure 1. Events in a saccade-only, saccade-plus-reach, and reach-only task trial. (A) After a variable fixation period, a cue indicated the side of the screen to which the participant had to make a saccade, and/or reach. At a variable SOA after cue onset, a perceptual probe (oriented line) appeared at the target location (Experiment 1) or at one of three locations surrounding the reach target (Experiment 2). (B) Probe locations (not to scale). In Experiment 1, the probe appeared at the same location as the target, 10° from cue. In Experiment 2, the probe (oriented line) could appear at one of three locations surrounding the reach/saccade target on either side of the screen. Location 1 was 8° from the cue, Location 2 was 3° above the reach/saccade target and 10° from cue, and Location 3 was 12° from cue. All probes were lines of higher contrast than the background (Experiment 1) or movement target (Experiment 2). (C) Threshold tasks. Thresholds in Experiment 1 were measured at the target location with a neutral cue, or valid/invalid cue (80% cue validity). Thresholds in Experiment 2 for each location were tested separately with 100% valid cue.

task, and a saccade-plus-reach task. In the previous reach-only study (Stewart & Ma-Wyatt, 2015), we tested two distances from the target in each of the three directions mentioned above and found that the temporal profile of attention at locations before/beyond and above the reach target did not change with probe distance, so in this study we selected a subset of these locations to compare the spread of attention near a movement target for different effectors. We did not use locations below the target as these might have been obscured by reaching movements. In Experiment 1, the perceptual probe always appeared at the movement target; in Experiment 2 the perceptual probe location was selected randomly from the three surrounding locations on each trial. The perceptual probe could appear at one of seven temporal offsets relative to the cue, which allowed us to create a timeline of how attention acts over the course of the movement across locations. We also measured the

magnitude of attentional facilitation at the target compared to different baselines, to demonstrate that the amount of facilitation observed is dependent on the baseline used to measure this facilitation.

There were two experiments, each comprised of four separate tasks. For each experiment, we first measured a contrast threshold to determine the contrast of the stimuli presented to individual participants in the subsequent tasks. Participants then completed a saccade-only condition, a saccade-plus-reach condition, and a reach-only condition. In all conditions, a perceptual discrimination task was completed concurrent to the movement: in Experiment 1 participants had to discriminate the orientation of a probe at movement target and in Experiment 2, participants had to discriminate probe orientation at locations around the movement target (Figure 1B). The contrast threshold task was always completed first, and the subsequent

blocks of the saccade-only and saccade-plus-reach tasks were interleaved for all observers. The reach-only task was completed either before or after the two conditions involving saccades.

The experiment was a fully repeated-measures design, with all participants completing the four tasks in both experiments. This included 27 blocks of data in the threshold measurement tasks and 67 blocks across the three movement tasks. Each block contained 84 trials, for a total of 5,628 trials per participant recorded over multiple sessions (approximately 8 hours each participant).

Stimuli

The central fixation circle was 0.25° in size and darker than the background, with a Weber contrast of -0.34 . Saccade/reach targets were a circle 0.75° in diameter, with a Weber contrast of 0.27 with respect to the background. The cue was a triangular arrow of 0.5° size and 0.48 contrast, which pointed to either the left or right side of the screen. The perceptual probes were oriented lines 0.5° in length, oriented at an angle of 45° left or right, and were at a contrast level determined by an individual threshold task for each participant. The background luminance of the screen was 27.5 cd/m^2 . In Experiment 1, the probe appeared at the target in the movement conditions (see below for probe location in the threshold tasks). In Experiment 2, the movement target on the left or right of the screen was cued with equal probability (100% valid cue), and perceptual probes appeared at any one of three locations around the cued movement target (Figure 1B). Each side of the screen had two locations along the central horizontal axis, that were 8° and 12° from central fixation, and one location that was 3° above the saccade target at 10° eccentricity from fixation.

Preliminary measures: Contrast thresholds

Contrast thresholds were measured separately before the main experimental task, with the participant maintaining central fixation at all times. For each individual, we measured the contrast required to discriminate the orientation of the probe line at the movement target, with thresholds on either side of the screen being tested separately. Probes in the main experimental task were presented at these individual contrast threshold levels. In Experiment 1, we determined threshold at the target location in response to valid, invalid, and neutral cues, while observers fixated the central marker. Probe thresholds were measured for each target location (left or right of the screen) in separate blocks, and participants were informed where the probe would appear at the start of each block. Valid, invalid, and neutral thresholds were

also tested in separate blocks. For valid threshold trials, participants were informed that the probe would always appear on one side of the screen (e.g., always on the left). Participants pressed a key to start the trial. Upon key press, both the cue (arrow pointing to the tested side) and probe appeared (0 ms temporal delay). For invalid blocks, participants were informed that the probe would appear on the cued/tested side on 80% of trials, and on the opposite side of the screen on 20% of trials. For neutral threshold trials, a neutral cue (circle) appeared in the center of the screen upon key press, and participants were informed that the probe could appear on either side of the screen with equal probability.

For all threshold trials, the probe was displayed for a duration of 26.6 ms (per Stewart & Ma-Wyatt, 2015). Measurements for targets on the left and right side of the screen were tested separately using a QUEST procedure: participants reported the orientation of the line using the left or right arrows on the keyboard. Using a QUEST paradigm set to an 82% correct threshold (Watson & Pelli, 1983), the probe contrast was adjusted based on correct or incorrect answers. Fifty trials were used to obtain the threshold measurement, and each location was tested three times, with the final threshold being the average of the three values. Separate staircases calculated thresholds for valid and invalid trials. Separate QUEST staircases were used to determine the thresholds for the probe on either side of the screen. For Experiment 2, all preliminary contrast thresholds were measured with valid cues; participants were always aware of the location of the probe in these threshold measurements.

Main experimental procedure (Experiments 1 and 2)

Saccade-only

At the start of each trial, a fixation circle and two saccade targets appeared on the screen, one on either side of the fixation point, at 10° eccentricity. As shown in Figure 1A, the trial started when the participant depressed a key on the mouse, which was affixed to the desk 40 cm from the screen, central to the screen and the participant's body. After a random delay (between 5 and 1,000 ms, at 5 ms intervals calculated on a trial-by-trial basis using MATLAB's `randperm` function), a cue appeared at the center of the screen. The cue signaled the side to which the participant had to make a saccade and the side of the screen where the probe would also appear. The cue was 100% valid, and left and right cues occurred with equal probability. In Experiment 1, the probe appeared at the target location on the cued side of the screen, 10° eccentricity

from fixation. In Experiment 2, each side had two locations along the central horizontal axis, 8° and 12° from central fixation, and one that was 3° above the saccade target at 10° eccentricity from fixation. Perceptual probes appeared on the cued side, at any one of these three locations, with equal probability (Figure 1B).

Stimulus onset asynchrony (SOA) was measured from cue onset (Castet et al., 2006; consistent with Stewart & Ma-Wyatt, 2015), and could be one of seven different durations: 13.3, 53, 106, 146, 199, 253, and 306 ms. This range was chosen to capture the modulation in sensitivity that may accompany both the preparation and the completion of a saccade. After the saccade was completed, a line of text indicated that the subject had to report the orientation of the perceptual probe using the arrow buttons on the keyboard (left/right). Auditory feedback was given for correct and incorrect answers (“nice” beep for correct answers, “nasty” beep for incorrect answers).

Saccade-plus-reach

This task was exactly the same as the saccade-only task described above, except that in addition to a saccade, participants made a reach to the target on the cued side. Participants received negative auditory feedback (short beep) if the reach time exceeded 600 ms.

Reach only

All stimulus presentation and responses were identical to the saccade task; however, in this task participants maintained central fixation throughout the trial and made a reach to the target on the cued side.

Results

Data exclusions

Individual saccades were examined prior to analysis to exclude trials in which saccades were made to the wrong location, or in which the pupil was lost (e.g., due to blinking). Saccades were classified using criteria of velocity of $35^\circ/\text{s}$ and acceleration of $9,500^\circ/\text{s}^2$.

Saccade latency was measured as the time from cue onset until the time the saccade was initiated. For both saccade-only and saccade-plus-reach conditions, trials were also excluded based on the following saccade-related criteria: trials in which the saccade latency was below 100 ms were excluded as it was unlikely that the programming of these saccades was influenced by the visual target (He & Kowler, 1989). Saccades initiated

after 570 ms were excluded to avoid any trials where the probe would have appeared and disappeared before the movement had even been planned or initiated (calculations based on the longest SOA value of 306 ms plus the average total saccade completion time (saccade latency + duration)). Trials where the probe appeared between 50 ms before saccade onset and 25 ms after saccade onset were excluded to eliminate any potential effects of saccadic suppression (Volkman, 1962; Volkman, Riggs, White, & Moore, 1978). Trials were excluded where the saccade endpoint was more than 1.5 standard deviations from mean radial error from the target.

Additional exclusion criteria applied for the reaching task: trials in which the reach latency or reach time were ± 2 standard deviations from the mean were excluded, and reaches that landed more than ± 2 standard deviations from the mean reach endpoint were excluded (cut-off criteria differ for saccades and reaches due to greater variability of saccade landing points at surrounding probe locations). For Experiment 1, the following proportions of trials were included: for the saccade only condition: 67% (1,348 trials), for the reach-plus-saccade condition: 53% (1,063 trials), and for the reach-only condition: 89% (1,745 trials). For Experiment 2, for the saccade-only condition, 63% of trials were included for analysis (5,116 trials). For the reach-plus-saccade condition, 63% of trials were included after exclusions (5,000 trials). For the reach-only condition, 89% of trials were included (4,471 trials).

Reach latency was measured as the time from cue onset until the time the participant lifted their finger from the mouse button. Reach time was measured as the time interval between when the finger was lifted to when the screen was touched. Movement times were consistent across participants, as shown by Figure 2. Saccade latencies for individual participants are shown for both the saccade-only (Figure 2A) and saccade-plus-reach tasks (Figure 2B). Reach latencies (Figure 2C) and eye-hand latencies (Figure 2D) for individual participants are also shown in Figure 2. We tested the normality of the saccade latency and reach dynamics distributions using a Lilliefors test, which revealed non-normality for all conditions; hence, median values and interquartile ranges are reported in Table 1. It is worth noting that the saccade-latency distributions appear comparable between the saccade-only and saccade-plus-reach conditions, and the reach-latency distributions appear comparable between the reach-only and saccade-and-reach conditions. Saccade and reach endpoint accuracy was calculated as the radial distance from the centre of the movement target to the recorded endpoint (Figure 3; Table 1).

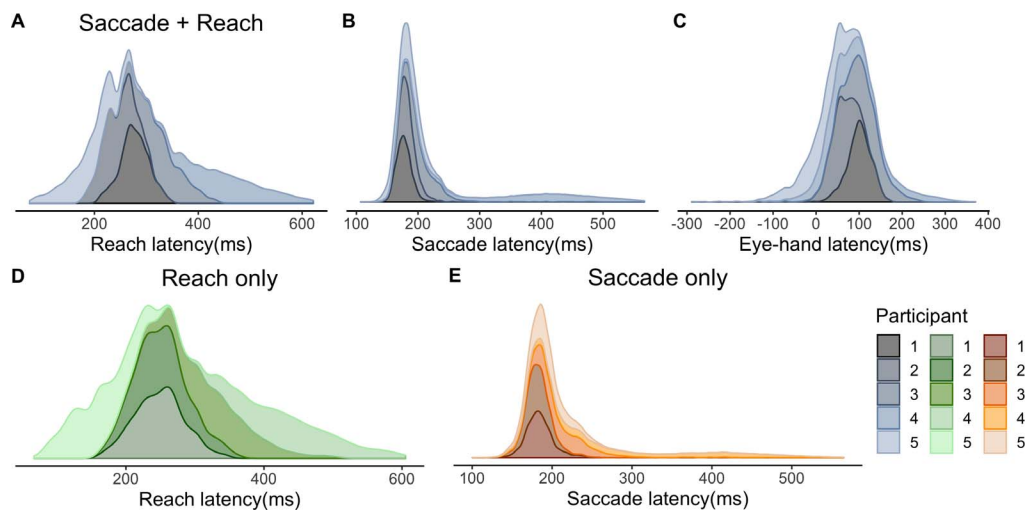


Figure 2. Stacked density plots of saccade latencies for each participant across both experiments (data has exclusion criteria applied). (A–C) Represent latencies for the saccade plus reach condition (A. reach latency, B. saccade latency, C. eye–hand latency). (D) Represents reach latencies for the reach-only condition, and (E) represents saccade latencies for the saccade-only condition.

	Saccade latency (ms)	Reach latency (ms)	Eye–hand latency (ms)	Saccade accuracy (degrees)	Reach accuracy (degrees)
Experiment 1					
Saccade-only	203 (51)	—	—	1 (0.48)	—
Reach-only	—	272 (56)	—	—	0.98 (0.51)
Saccade-plus-reach	186 (26)	296 (47)	107 (50)	1.03 (0.53)	0.8 (0.41)
Experiment 2					
Saccade-only	215 (60)	—	—	1.5 (0.47)	—
Reach-only	—	288 (68)	—	—	0.91 (0.46)
Saccade-plus-reach	232 (42)	299 (59)	66 (50)	1.2 (0.48)	0.78 (0.39)

Table 1. Median saccade and reach dynamics for each condition (medians and IQR reported). Mean landing accuracy for saccades and reaches (means and SD reported).

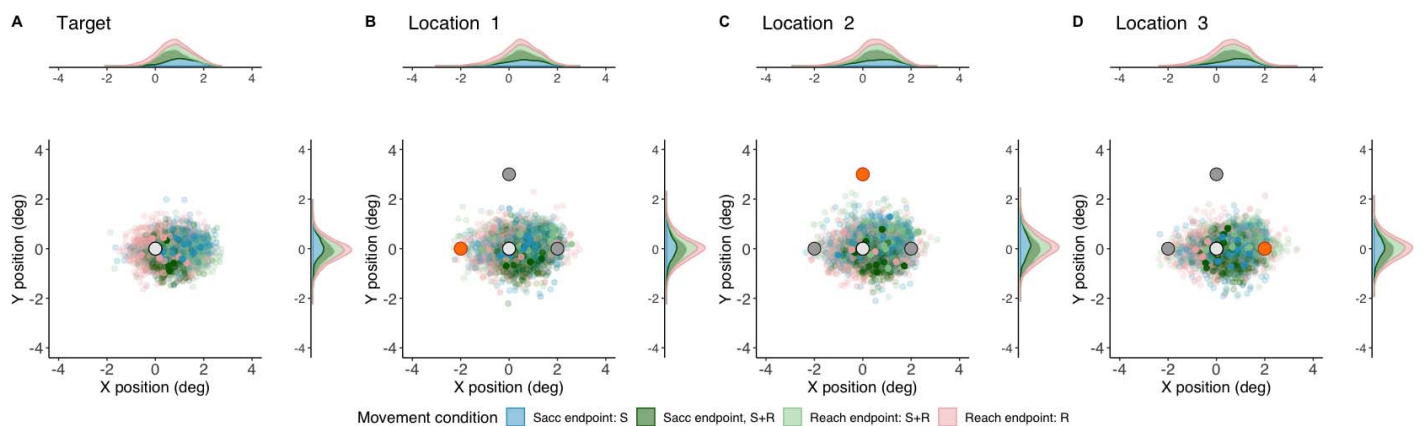


Figure 3. Saccade and reach endpoints for all participants. (A) Saccade and reach endpoints for Experiment 1. (B–D) Saccade and reach endpoints for Experiment 2. The movement target is shown in white, potential probe locations in gray, and the location where the probe appeared in each location condition is shown in orange (B. Location 1, C. Location 2, D. Location 3). Stacked density plots show corresponding distribution of x and y landing positions for each movement type and condition: saccade-only (blue); reach-only (pink); saccade-plus-reach, saccade endpoint (dark green); saccade-plus-reach, reach endpoint (light green).

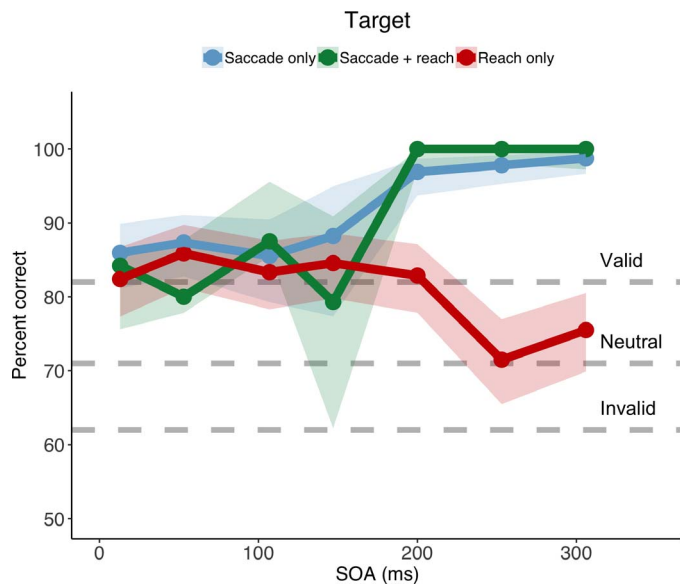


Figure 4. Performance as a function of SOA at the movement target for saccade only (blue), saccade-plus-reach (green), and reach-only (red) conditions. Error bars are Jeffrey’s interval, which provides a Bayesian calculation of confidence intervals in binomial data. Dashed horizontal lines represent baseline performance measurements for the valid, neutral, and invalid threshold measurements.

Perceptual performance at movement target

Figure 4 shows the temporal profile of sensitivity at the movement target for each movement condition (Experiment 1). Performance is measured as percent correct, and weighted means are shown. Weighted means were calculated using the amount of data at each SOA for each participant. Here we compare performance in each movement condition to the three baseline conditions measured: baseline performance with a valid cue, neutral cue, or invalid cue. To determine the baseline level for each cue condition we first determined the contrast corresponding to 82% correct for the valid-cue condition. We then determined the percent correct corresponding to this contrast for the invalid- and neutral-cue conditions. This was calculated for each participant by finding the percentage correct value on the psychometric curve for each type of cue that corresponded to the measured contrast threshold. Thus, the valid threshold measurement was always 82% correct, and the mean neutral threshold

level across all observers was 71% correct, and mean invalid threshold level was 62%.

We used paired-samples *t* tests with a Holm correction to compare overall performance in each condition to each of these baseline measures (Table 2). Overall performance was better than an invalid or neutral baseline for all movement conditions; however, reach performance did not differ from a valid baseline. This shows that, particularly in the case of the reach-only condition, the amount of facilitation measured in an attentional task can be very dependent on the baseline measure used (for example, compare to the baseline used by Hanning et al., 2018). In this study, we compare performance to the valid threshold level, as this was the task that we used to measure probe contrast for locations *around* the target. Additionally, by using a valid probe we could measure any additional attentional benefit caused by movement planning, beyond any effects of pure covert attention. By comparing pre-movement performance to an invalid or neutral cue, we would be over-estimating any effects of movement planning, as observed attentional enhancement would be a combination of covert and pre-movement facilitation. We took this approach as we are interested in understanding naturalistic deployment of attention.

Perceptual performance relative to SOA

Performance at the target location and three surrounding locations was calculated as the *d'* difference relative to the threshold level measured in the valid contrast-threshold task. Performance on the perceptual probe discrimination task is plotted as a function of SOA, for the saccade-only condition, the saccade-and-reach condition, and the reach-only condition for the target location and all surrounding locations (Figure 5). The profile of attentional facilitation for the tasks involving saccades is similar, with sensitivity increasing in the lead-up to mean movement onset time, with the higher level of sensitivity being sustained throughout the course of the movement. On the other hand, the reach-only condition shows constant sensitivity at each probe location at all values of SOA.

To compare performance across all conditions, linear mixed models were conducted to determine the effect of location (target + three surrounding locations), SOA and movement condition on performance for the

	Valid baseline	Neutral baseline	Invalid baseline
Saccade-only	* <i>t</i> (34) = 6, <i>p</i> < 0.001	* <i>t</i> (34) = 12.6, <i>p</i> < 0.0001	* <i>t</i> (34) = 9.54, <i>p</i> < 0.0001
Reach-only	<i>t</i> (34) = 0.304, <i>p</i> = 0.67	* <i>t</i> (34) = 5.11, <i>p</i> < 0.0001	* <i>t</i> (34) = 14.9, <i>p</i> < 0.0001
Saccade-plus-reach	* <i>t</i> (34) = 4.9, <i>p</i> < 0.0001	* <i>t</i> (34) = 10.4, <i>p</i> < 0.0001	* <i>t</i> (34) = 18, <i>p</i> < 0.0001

Table 2. Paired-samples *t* test comparing each movement condition to a valid-, neutral-, or invalid-cue baseline. Asterisks indicate significant comparisons.

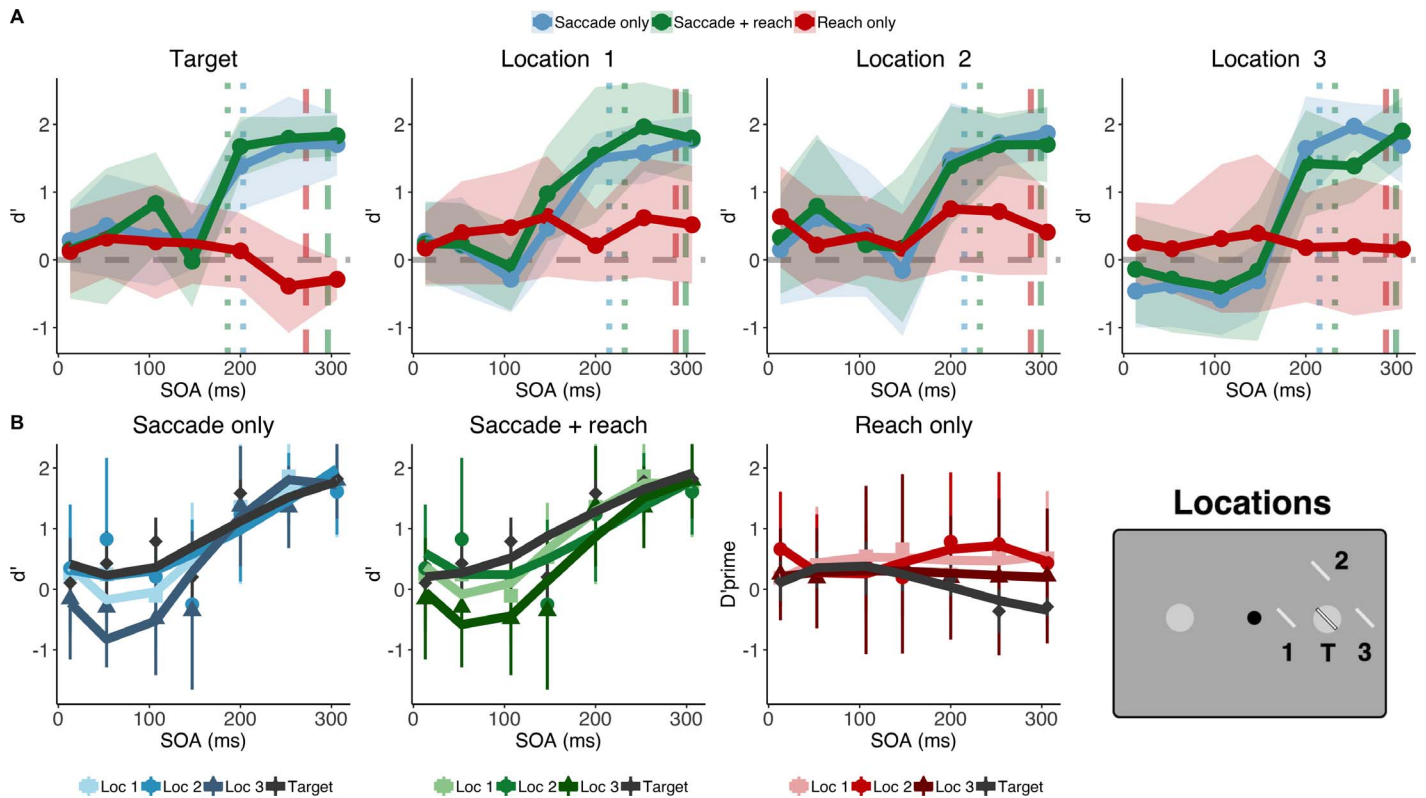


Figure 5. (A) Perceptual performance relative to cue onset (SOA) for the saccade-only task (blue), reach-only task (red), and saccade-plus-reach task (green). These data represent the weighted mean across all participants. The dotted lines represent the median saccade latency, and the dashed lines represent the median reach latency across participants for each condition (colors matched to movement condition). Error bars represent 95% confidence intervals. (B) Fitted model for growth curve analysis for each movement condition. The four curves in each plot represent the four locations: Location 1 (lightest shade, squares), Location 2 (medium shade, circles), Location 3 (dark shade, triangles), and target (darkest shade, diamonds). Error bars are 95% confidence intervals of the mean data for each time-point.

aggregate performance of all participants. The models used fixed effects of SOA, movement condition and location, and a random effect of participant. There was a significant main effect of SOA: $F(1, 348) = 211.72$, $p < 0.0001$, a significant main effect of movement condition: $F(2, 8) = 5.03$, $p = 0.039$, a significant interaction between location and SOA: $F(3, 348) = 3.5$, $p = 0.016$, and a significant interaction between SOA and movement condition: $F(2, 348) = 58.79$, $p < 0.0001$. This shows that attentional modulation differed based on probe location, movement condition, and SOA. This means that attention was not allocated in a uniform manner around the movement target across the measured time-course.

To further compare differences between locations, we used growth curve analysis (Mirman, 2014) to compare the differing time-courses of performance for each location versus the movement target. This approach uses a similar hierarchical regression approach to linear mixed models, but allows us to fit n th-order polynomials to the time-course data for each condition and participant, so it takes into account individual variability

in performance across time (see Mirman, Dixon, & Magnuson, 2008, and Supplementary File S1 for further methodological details). As with the mixed model analysis, we can then determine the overall difference in level of performance between conditions (intercept), as well as differences in each polynomial term of the fit: in this case, we are interested in whether the linear term of the fit is significantly different between conditions, as this shows us whether the rate of change across the time-course differs across conditions. The smallest order polynomial required to fit the s-shape of the d' versus SOA data was of order 3. So for each condition (location \times movement condition), we fit a third-order orthogonal polynomial to the data, with fixed effect of location, and random effect of participant (as in the mixed-model analysis above). We report estimates of the difference between the baseline condition (target location) and comparison condition (Locations 1 to 3) and the standard error of the fit. A normal approximation was used to determine significance. This approach allowed us to quantify both the magnitude of difference between each location compared to the target location,

	Estimate	Standard error	<i>p</i> value
Saccade-only			
Target versus Location 3			
Overall performance*	0.38	0.12	0.002
Linear change*	−1.02	0.33	0.002
Target versus Location 1			
Overall performance	0.13	0.13	0.32
Linear change	−0.30	0.34	0.36
Target versus Location 2			
Overall performance	0.04	0.15	0.79
Linear change	−0.14	0.40	0.72
Saccade-plus-reach			
Target versus Location 3			
Overall performance*	0.50	0.16	0.002
Linear change	−0.45	0.43	0.30
Target versus Location 1			
Overall performance	0.13	0.15	0.41
Linear change	−0.059	0.41	0.885
Target versus Location 2			
Overall performance	0.15	0.18	0.40
Linear change	0.41	0.48	0.40
Reach-only			
Target versus Location 1			
Overall performance*	−0.37	0.14	0.010
Linear change	−0.74	0.38	0.05
Target versus Location 2			
Overall performance*	−0.41	0.13	0.0019
Linear change	−0.65	0.35	0.066
Target versus Location 3			
Overall performance	−0.17	0.16	0.30
Linear change	−0.49	0.43	0.26

Table 3. Estimates, standard error and *p* value for growth curve analysis of differences within movement condition, between locations. Asterisks indicate significant comparisons.

and the performance change across time. Figure 5B shows the model fits to the data for each movement condition. For each comparison between locations, the target location was used as a baseline.

The saccade-only and saccade-plus-reach conditions showed similar performance at the target location compared to other locations, however for the reach-only condition overall performance is worse at the target than Locations 1 and 2 (Table 3). For both saccade-only and saccade-plus-reach, there was a significant difference in the overall level of performance between the target and Location 3, with Location 3 showing lower overall performance than the target. Additionally in the saccade-only condition, Location 3 showed a greater linear change over the time-course, suggesting a greater change from pre- to post-saccadic performance than at the target. For reach-only there was a significant difference in the overall level of performance between the target and Locations 1 and 2,

with both locations showing higher performance than the target, and Location 1 showing more linear change across time than the target. Taken together these results indicate that the spatial allocation of attention may not be symmetrical around the movement target for all movement conditions, and that the time-course of the build-up of sensitivity also depends on probe location.

Growth curve analysis was also used to compare the difference in performance between saccade-only versus saccade-plus-reach tasks, and reach-only versus saccade-plus-reach tasks to determine how the single-movement conditions differed from the combined movement condition at each location (Table 4). There were no significant differences between the saccade-only and saccade-plus-reach tasks for any location. The reach-only and saccade-plus-reach conditions were significantly different in the overall level of performance at the target and Location 1 only, with the reach-only conditions showing lower overall performance. The linear change between movement conditions was significantly different for all locations, with reach-only showing less change across time than the saccade-plus-reach condition. This indicates that the profile of attention is the same for conditions where a saccade is being made, but the profile differs between reach-only and saccade-plus-reach conditions.

Perceptual performance relative to movement onset

To examine how attention shifts relative to movement onset, probe performance for both conditions was binned relative to either saccade onset (Figure 6A) or reach onset (Figure 6B). For each trial, the bin was determined by calculating when the probe appeared (measured as probe offset time) relative to the movement onset. For example, if the probe was presented 100 ms before the initiation of the movement, that trial would be put in the −100 ms bin. For each trial, the difference between probe offset and movement onset was calculated, and the trial was put in the bin closest to this rounded difference value. Data were sorted into 50 ms bins from 150 ms before movement initiation to 150 ms after initiation. There were no data in the bin that fell at 0 ms relative to saccade onset, as we removed any data that would be subject to saccadic suppression (Volkman, 1962; Volkman et al., 1978). In the saccade-plus-reach condition binned relative to reach onset (Figure 6B), we removed trials where the probe appeared after saccade onset, to avoid any potential effects of elevated probe visibility due to eye position after the saccade. For comparison, Figure 6B also shows the saccade-plus-reach data without these exclusions applied (light green curves).

	Estimate	Standard error	<i>p</i> value
Reach-only versus saccade-plus-reach			
Target			
Overall performance*	−0.87	0.10	<0.0001
Linear change*	−2.16	0.27	<0.0001
Location 1			
Overall performance*	−0.38	0.12	0.0016
Linear change*	−1.48	0.32	<0.0001
Location 2			
Overall performance*	−0.31	0.14	0.028
Linear change*	−1.11	0.37	0.0028
Location 3			
Overall performance	−0.21	0.12	0.084
Linear change*	−2.12	0.32	<0.0001
Saccade-only versus saccade-plus-reach			
Target			
Overall performance	0.08	0.11	0.44
Linear change	0.23	0.29	0.42
Location 1			
Overall performance	0.083	0.11	0.45
Linear change	−0.018	0.29	0.95
Location 2			
Overall performance	−0.027	0.19	0.85
Linear change	−0.32	0.38	0.41
Location 3			
Overall performance	−0.028	0.11	0.80
Linear change	−0.34	0.29	0.24
Saccade-only versus reach-only			
Target			
Overall performance*	−0.79	0.10	<0.0001
Linear change*	−1.93	0.26	<0.0001
Location 1			
Overall performance*	−0.30	0.10	0.0044
Linear change*	−1.5	0.28	<0.0001
Location 2			
Overall performance*	−0.34	0.12	0.0043
Linear change*	−1.43	0.31	<0.0001
Location 3			
Overall performance	−0.24	0.13	0.068
Linear change*	−2.46	0.34	<0.0001

Table 4. Estimates, standard error, and *p* value for growth curve analysis of differences between movement conditions. Asterisks indicate significant comparisons.

The sensitivity profile is similar for both the saccade-only and saccade-plus-reach task when binned relative to saccade onset (Figure 6A). Sensitivity is low before the onset of the saccade, and increases markedly after the saccade is initiated. Furthermore, when sensitivity is binned relative to reach onset (Figure 6B), the profile of the enhancement in the saccade-plus-reach task does not differ from reach-only performance.

To examine the pre-saccadic fluctuation in performance before movement onset in the saccade conditions

(Figure 6A), we used a linear mixed model with fixed effects of location, movement condition (saccade-only vs. saccade-plus-reach) and time relative to movement onset (bins −150, −100, −50), and random effect of participant. There was a significant interaction between location and time bin: $F(3, 72) = 2.97, p = 0.037$. This indicates that variation in performance before saccade onset varied across locations, but not between the saccade-only and saccade-plus-reach conditions. This can be seen in Figure 6A, where the target and Location 1 show a greater linear increase than the other locations. A mixed model as above was used to compare the pre-reach performance for the reach-only and saccade-plus-reach conditions for the bins −200 to −50 (Figure 6B). There was a significant effect of movement condition: $F(1, 15) = 7.14, p = 0.017$, and a significant interaction between location, time-bin and movement condition: $F(3, 103) = 3.17, p = 0.027$. Post hoc pairwise comparisons with a Holm correction indicate however that the only significant difference between conditions was at Location 3: $t(15) = 3.56, p = 0.011$. This indicates that pre-reach performance was similar for reach-only and saccade-plus-reach conditions for all locations except for Location 3. This suggests that once the influence of the saccade is removed, the amount of attention carried by the hand alone differs very little to when a reach alone is being made. Saccade-plus-reach performance was lower at Location 3 than reach-only performance: this is consistent with the suppressed performance seen at Location 3 when performance is measured relative to saccade onset (Figure 6A). This suggests that the addition of the saccade produces an additional suppressive effect at this location compared to when a reach alone is being performed.

The post-saccadic enhancement for the saccade conditions is not entirely due to higher visibility due to the eye being closer to the probes, and may reflect an additional attentional effect: in an additional experiment we measured attentional facilitation with probe contrasts set to threshold values measured when the eye was at the saccade target, and a post-saccadic facilitation is still observed (consistent with Dorr & Bex, 2013; see analyses in Supplementary File S1). Although this facilitation was not as large as that observed in Figure 6A, it indicates additional post-saccadic sensitivity that cannot be accounted for purely by a covert attentional shift.

Heatmaps of sensitivity relative to SOA

Heatmaps of the spatiotemporal profile of attention for all movement conditions were created to compare the spread of attention across different motor effectors (Figure 5). Heatmap values were calculated at target and the three probe locations, and interpolated based on the weighted values of the nearest tested locations,

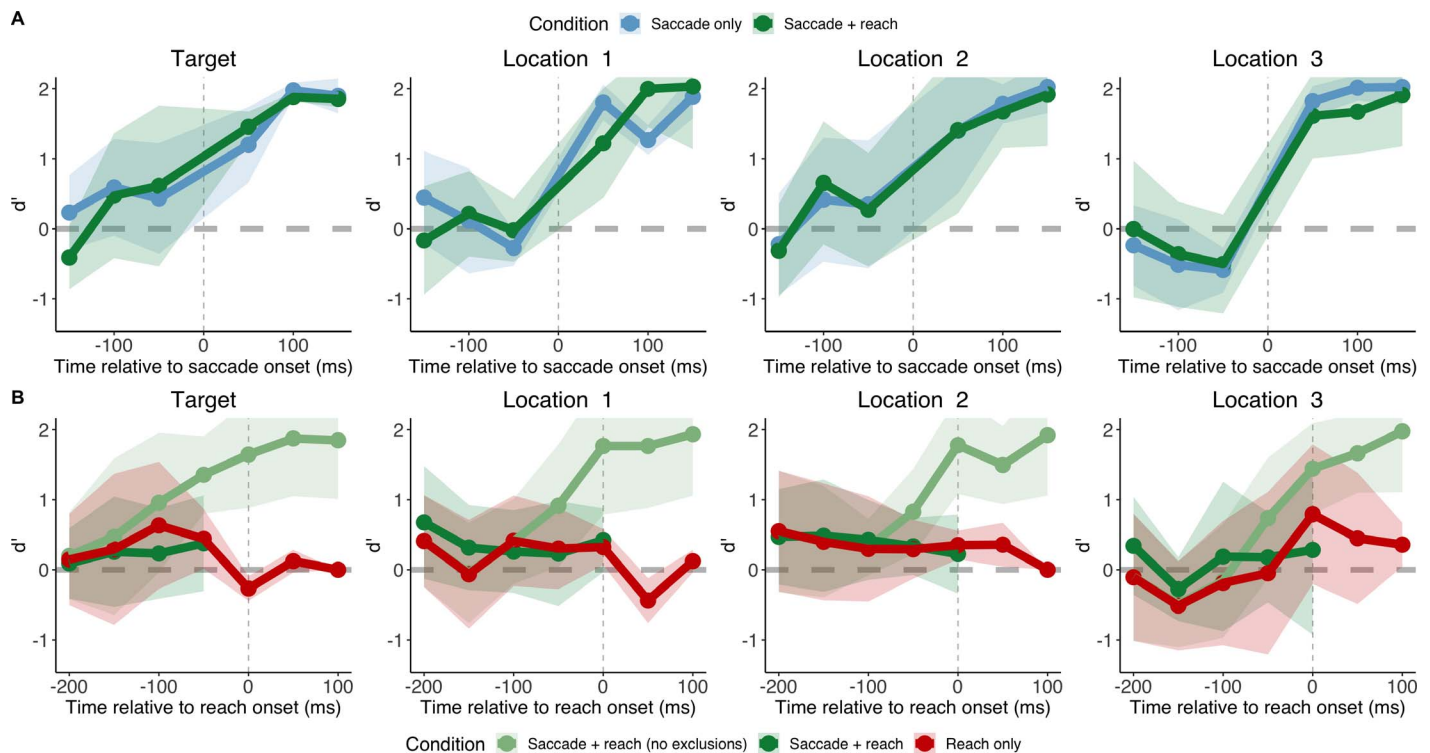


Figure 6. (A) Perceptual performance relative to saccade onset during the saccade-only task (light blue) and saccade-plus-reach task (dark green). (B) Performance relative to reach onset for the saccade-plus-reach condition including post-saccade data (light green), saccade-plus-reach excluding trials after saccade onset (dark green), and reach-only condition (red). Error bars are 95% confidence intervals, as in Figure 3.

and the distance between these points. This weighting meant that interpolated performance between tested locations was more dependent on performance at the closest tested location, with the influence of this location decreasing with distance. The heatmaps thus provide insight into the spatial spread of attention at the locations around the target.

It can be seen that for the conditions where a saccade is being made, the temporal profile of sensitivity is markedly different from the reach-only condition (Figure 5: compare Rows 1 or 2 vs. Row 3). Spatially, Location 3 (beyond the target) shows significantly reduced sensitivity for the saccade-only and saccade-plus-reach conditions, compared to the other locations (see also Table 1).

Discussion

The magnitude of attentional facilitation depends on the baseline measure used

In this study, we measured sensitivity relative to a valid-cued baseline. This allowed us to measure any additional attentional benefit that arises from movement planning, compared to the facilitation associated with

covert attention to a valid cue. Our results show little increase in sensitivity before movement onset in the saccade conditions relative to a valid cue, and only a small post-saccadic enhancement between fixation and target (Location 1) when we account for the post-saccadic retinal location (see Supplementary File S1). These results are different from previous studies that report a far greater pre-saccadic or pre-reach attentional enhancement using different baseline measures, or Deubel (2008) who showed no pre-saccadic enhancement relative to a valid cue. As Figure 4 shows, the amount of facilitation observed very much depends on the baseline measure used. If, as we do for the majority of the analyses in this paper, performance is measured as a modulation from a valid-cued threshold level, then performance does not deviate greatly from this baseline.

However, when performance is compared to either a neutral or invalid baseline, there is a much greater facilitation associated with the movement. Previous studies using a neutral or invalid-cued baseline (Haning et al., 2018; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012; Rolfs et al., 2013; White et al., 2013) have all showed enhancement relative to an invalid or neutral baseline. Recent studies have shown a saccade-related modulation at the target or on the surface containing the target that did not occur with mere covert attention (Ghahghaei & Verghese, 2017; Li, Barbot, & Carrasco, 2016; Li, Pan, & Carrasco, 2019).

In contrast, Khan et al. (2015) showed no saccade-related change at the target location relative to covert attention, although they found a saccade-related decline in sensitivity at distractor locations. The common thread in all of these studies is that movement causes a relative modulation of the target with respect to distractors that is above the level produced by covert attention alone. It should be noted that, in our study, the level of covert attention that was actually deployed in the baseline task could have been overestimated compared to the premotor tasks. Given that the probe appeared upon key press, at a time chosen by the participant, it is likely that covert attention was already fully deployed at the location in anticipation of the probe (participants were aware where the probe would appear in each block in the threshold task so there was no spatial or temporal uncertainty). This lack of spatial or temporal uncertainty, coupled with the probe appearing at a time-point chosen by the participant may have resulted in maximal attention deployment in our valid baseline measure compared to covert attention measured at one of seven SOAs relative to a cue. It is surprising that performance in the premotor conditions is still improved relative to a valid baseline, even though our results suggest that the amount of attention that is deployed in an overt task compared to covert attention is rather small.

These results also hold for our reach-only condition. While the performance in this condition did not differ from a valid-cued baseline measure, it did show significant enhancement relative to neutral and invalid cues measured at the reach target. This is consistent with previous work that has compared performance at a movement target with an invalid- or neutral-cued location (e.g., Deubel, 2008; Hanning et al., 2018; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012). This suggests that a hand movement can result in enhanced sensitivity around the target while the eyes are fixated elsewhere; however, when comparing sensitivity to a valid baseline, the hand does not seem to elicit any additional attentional power than pure covert attention would provide. As noted previously however, the threshold procedure had no spatial or temporal uncertainty so may have led to an over-estimation of performance in the baseline condition.

It is interesting to note that performance for all movement conditions where the cue indicates one of two targets is similar to the valid-threshold level where the target location was known. This is true even at the earliest SOAs. It is possible that improved visual memory at both potential movement targets contributes to performance at a movement-relevant location (Heuer & Schubö, 2018; Ohl & Rolfs, 2016, 2018), especially given this effect can also spread to locations neighboring action-relevant locations (Heuer, Crawford, & Schubö, 2017). This may explain why performance in the

movement condition is as good as that in the valid-threshold condition measured without eye movements, even at the earliest SOAs. However, the improvement in performance at later SOAs is unlikely to be due to memory, but more likely to be due to attention.

The temporal profile of attention is driven by the saccade

One consistent pattern of results across all locations is that the profile of the attentional shift differs markedly when a hand movement alone is made without a concurrent saccade. This is consistent with previous studies showing the same sustained pattern of attention when a reach alone is being made (Stewart & Ma-Wyatt, 2015), and demonstrates the large difference in the profile of attention before a reach depending on whether or not a saccade is being carried out. This can especially be seen when the influence of the saccade is removed from the saccade-plus-reach data, and the profile becomes similar to a reach being made alone (Figure 6B). This suggests that the primary driving force behind the attentional shift is the saccade rather than the hand, which is in line with previous research that suggests that the eye carries a greater attentional weighting than the hand (Khan et al., 2011). Given that these tasks involve a movement to a visually defined target, it is perhaps unsurprising that visually based attention may be dominant in this case, or that it may carry more weight in the guidance of this visually-guided hand movement. This is however contrary to other research suggesting that attention can be independently allocated to eye and hand (Jonikaitis & Deubel, 2011)—these discrepancies may arise from paradigm differences between studies which we address further in the latter parts of the discussion. The discrepancy in performance between the saccade and reach-only conditions suggest that there may be an additive effect when the two movements are enacted. Indeed, it may be the case that the planning and execution of an accurate hand movement requires different attentional guidance than a saccade. This could then result in the lower but more sustained level of attentional performance leading up to the reach onset when there is no eye movement available to provide any foveal information during the enactment of the reach (Stewart & Ma-Wyatt, 2015).

It must also be noted that the distinct pattern for movements that include saccades is evident only in the sensitivity plot, but not for saccade latencies. As noted in the Results section, saccade latencies are comparable across conditions with saccades (the saccade-only and saccade-plus-reach) and reach latencies that are comparable across conditions with reaches (reach-only and saccade-plus-reach). This pattern indicates that changes

in sensitivity between conditions that involve saccades and reach-only must be due to changes in perception, not to changes in movement dynamics.

Comparison of the temporal profile for reach and saccade to other studies

We measured the profile of attention relative to a saccade alone, reach alone, and a saccade with a concurrent reach. The pre-saccadic shift observed around the movement target in this experiment seems to occur around the same time as the saccade onset, which is later than the shift observed at target locations in previous studies, where shifts can occur as early as 50 ms (White et al., 2013) or 100 ms before saccade onset (Deubel, 2008; Hanning et al., 2018; Jonikaitis & Deubel, 2011; Jonikaitis et al., 2017; Jonikaitis & Theeuwes, 2013; Rolfs & Carrasco, 2012). Interestingly, when perceptual performance at locations around the target is plotted relative to SOA (13–306 ms), the pattern of enhancement observed in this study shows only a very shallow build-up of sensitivity before the initiation of a saccade when compared to the valid baseline (covert attention). The discrepancy between this and previous studies could be due to this baseline measure (as discussed previously). This pattern could, however, also be due to the spatial layout of the paradigm itself. In this study we measured sensitivity around the movement target separately from measures at the target, so that we could measure broader attentional performance without the target necessarily being given attentional priority due to the task instructions, as evidence suggests that attention is spatially selective for the intended saccade target only (Deubel & Schneider, 1996). Evidence also suggests that attention is selective for a movement target, but not locations in between targets in the case of multiple movement paradigms (Baldauf & Deubel, 2009). It could be the case that in our study, the measured areas surrounding the movement target did not receive attentional facilitation at the same time as the target, but the facilitation may spread from the movement target once the movement was initiated. This could suggest the need for a narrower window of attention to select a target for movement planning purposes, and for a broader attentional facilitation once the movement is underway, to accurately guide the movement to the target (Stewart & Ma-Wyatt, 2017).

The shift of attention in the saccade-plus-reach task, when measured relative to a reach, shows no increase prior to reach onset, consistent with the reach-only task that also shows little modulation in performance. This is interesting when compared to Jonikaitis and Deubel (2011) who saw a longer and more marked increase in performance before a reach, either with or without a

concurrent saccade. However, Rolfs et al. (2013) saw a similar pattern of results to this study, where there wasn't such a marked temporal evolution before reach onset when compared to a neutral baseline. In their data, an increase in sensitivity was observed only when performance was compared at a location on the opposite side of the screen. However, as noted previously, these studies compared performance to a neutral baseline, whereas our comparisons are relative to a valid-cue baseline.

There is a slight discrepancy in the timing of the attentional shift between studies, which may be due to the behavioral paradigms used, and the differences in the SOA lengths measured. For example, Jonikaitis and Deubel (2011) used SOAs ranging from –200 to 600 ms, and saw mean saccade latencies of 288 ms, compared with 203 ms in this study. Similarly, Deubel (2008) had an SOA spanning 800 ms and saw latencies of 259 ms. In contrast, the range of SOAs used here was shorter, so the movement times in our present study were quite fast. It is conceivable that in studies that measured a longer time-course, the shift in attention could reflect this more leisurely timescale, as constraints on movement times are slower. In fact, there is evidence to suggest that covert attention can be temporally cued, and deployed at different times, depending on the timing of stimulus onset (Coull, Frith, Büchel, & Nobre, 2000). It could be the case that premotor attention is similarly temporally cued by the particular movement latency or paradigm timing. Another possible explanation is that perceptual stimuli differed greatly between studies, which could affect how attention is allocated (Hanning et al., 2018). For example, tasks that require stimulus discrimination (such as “E” vs. “3”) may require a longer build-up of attention than our task, which was a simple orientation discrimination.

One other possibility is that unlike other studies (e.g., Deubel, 2008; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012), we did not mask our probe after it was presented; hence, the large difference between the pre- and post-saccadic performance could be due to the loss of iconic memory of the pre-saccadic probe. This effect may be particularly prominent at the locations around the movement targets (Ohl & Rolfs, 2016). However, we don't believe that the difference in pre- versus post-saccadic performance is due to any interference due to memory, as there is much evidence to suggest that a representation of the pre-saccadic object is retained across the saccade; for example, for form (Demeyer, De Graef, Wagemans, & Verfaillie, 2009, 2010), orientation (Ganmor, Landy, & Simoncelli, 2015; Melcher, 2005; Wolf & Schütz, 2015), location (Cicchini, Binda, Burr, & Morrone, 2013; Prime, Niemeier, & Crawford, 2005), and trans-saccadic memory can aid perceptual continuity (Ross & Ma-Wyatt, 2003; Stewart & Schütz, 2018b). Attention may even play a role in using pre-saccadic information for integration with a post-saccadic stimulus (Stewart & Schütz, 2018a).

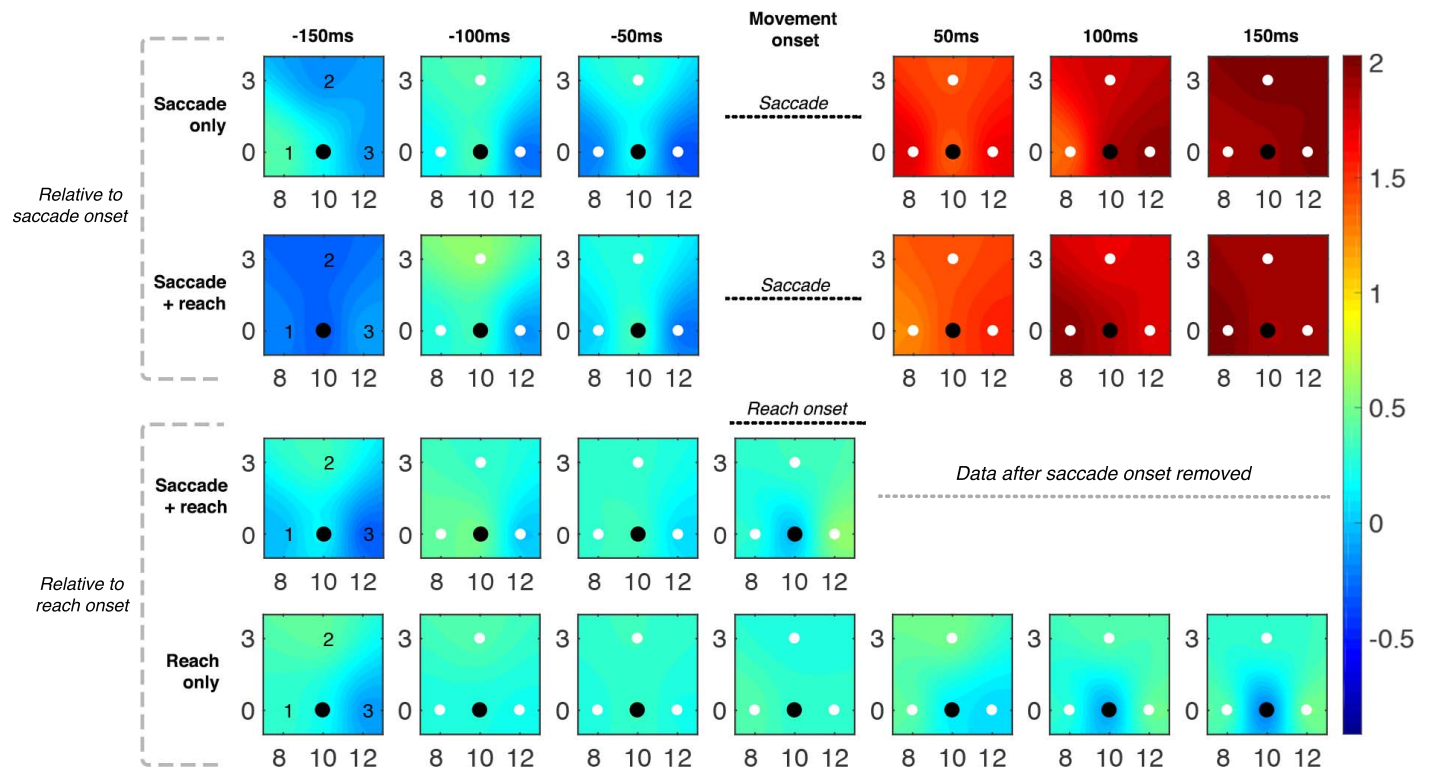


Figure 7. Heatmap of performance at all locations for each time-bin relative to movement onset for saccade-only and saccade-plus-reach conditions (performance relative to saccade onset) and reach-only and saccade-plus-reach conditions (performance relative to reach onset). The saccade-plus-reach condition relative to reach onset only includes trials before saccade onset. The movement target is displayed as a black dot, and surrounding probe locations as white dots. Color scale denotes d' performance relative to baseline (per Figures 5 and 6).

The spatial profile of attention at different locations

The second aspect of attention that this study aimed to examine was the spatial properties of the attentional shift for each movement. For all movement conditions, sensitivity increased at all locations around the time of the movement (see Figure 6); however, this shift was more pronounced at the movement target (Figure 7), compared to the surrounding locations. As is evident from these figures, this suggests that while attention may spread to locations surrounding a movement target, this shift is slower, with greater facilitation only occurring after movement onset. There was also a consistent pattern showing smaller facilitation for Location 3 (beyond the movement target). It is interesting to note that in our previous work (Stewart & Ma-Wyatt, 2015), when attention was measured relative to a reach, the analogous location above the target (Location 2) also showed a higher and more sustained attentional profile than the analogous locations between fixation and target and beyond the target (Locations 1 and 3). Furthermore, the analogous location beyond the target (Location 3) showed a similarly lower facilitation. This pattern of weaker facilitation at Location 3 could be due to its location beyond the saccade target being flagged as

behaviorally irrelevant. These results also suggest that for conditions in which a saccade took place, attention spreads differentially to locations in line with movement direction (Locations 1 and 3; both horizontally aligned with target) and orthogonal to movement direction (Location 2; above target; Stewart & Ma-Wyatt, 2017). Although we cannot claim that sensitivity at Location 3 is being inhibited (we did not measure an attention-free baseline for this condition), we can speculate that the lower sensitivity could also reflect findings that attention acts in a dual facilitatory/inhibitory manner. Studies have shown for example that there can be interference for objects close to the attended object (Bahcall & Kowler, 1999), that items neighboring the attentional focus may be suppressed (Caputo & Guerra, 1998), and that the attended location may be surrounded by a complimentary band of inhibition (Cutzu & Tsotsos, 2003; Hopf et al., 2006). It is possible that in testing the movement target and the surrounding locations separately we influenced the spread of attention; we used this method since we were primarily interested in the spread of attention around the target. It may be interesting in the future to compare these results to the profile when the probe could appear at either the target or surrounding locations in the same block.

This facilitation at locations around the saccade target supports previous suggestions that the locus of attentional deployment is not always constrained to the specific saccade target (Castet et al., 2006). This is especially true when sequences of movements are being made, with studies showing that attention can be spread to multiple impending locations for both saccades (Gersch, Kowler, & Doshier, 2004; Gersch, Kowler, Schnitzer, & Doshier, 2009; Zhao, Gersch, Schnitzer, Doshier, & Kowler, 2012), and hand movements (Baldauf et al., 2006). This spread of attention beyond a movement target may, however, depend on the task being carried out, and it could be the case that in this paradigm the screen layout was fairly simple, and thus attention could be spread in a broader fashion as there is no clutter to avoid, and our movement target locations were always fixed.

Do attention resources for the eye and hand interact?

Despite all its other attributes, attention also seems to be primarily linked to the planning and execution of a saccade. Attention resources for the eye and hand may be drawn from a common pool. Alternatively, there may be separate resources for the eye and hand that interact, such that the attention profile of the saccade modulates that of the reach. Our results are consistent with recent evidence that attention tends to go with the eye, even when there are competing target locations for the saccade and hand (Khan et al., 2011). However, while these results show that the hand might have different profile of sensitivity when no saccade is being enacted, in the real world we rarely reach to small targets without a concurrent eye movement. Hence, the pattern of sensitivity for the combined eye and hand movements is probably more generalizable to real-world tasks.

There is considerable evidence that parts of parietal cortex are involved in eye–hand coordination (e.g., Crawford, 2004) and that reaches are planned in eye-centered coordinates (e.g., Batista et al., 1999). The close association of neural representations for eye and hand movements offer several plausible options for a representation of target location that might be common to both effectors, or modulated by either effector. The spatial profile of sensitivity around a target may be linked to a type of priority map with a common representation of space, as has been suggested by several groups (e.g., Fecteau & Munoz, 2006; Itti & Koch, 2000). Of course, it is also possible that separate attention resources used for these effectors interact through feedback to earlier visual areas (Jonikaitis & Deubel, 2011; Moore & Fallah, 2001).

Conclusion

The aim of this study was to understand the spatiotemporal profile of attention when a saccade alone, reach alone, or saccade with concurrent reach are made to the same visual target. Performance was compared to a valid baseline to isolate effects of movement planning from cue-based covert attention. This study shows a similar spatial pattern of sensitivity for the two saccade-related conditions when considered relative to SOA. Attention spreads asymmetrically around the movement target, with greater sensitivity at the target than surrounding it, and decreased performance beyond the target. This suggests that attention is not allocated to all locations surrounding the target in a uniform manner, and this spread may reflect the spatial structure of the task. More importantly, this study shows that when a reach is made in addition to a saccade, perceptual sensitivity is modulated on a similar timescale to when a saccade alone is being produced and this differs markedly from when a reach alone is being made. When the influence of the saccade is removed from the combined movement, the reach alone carries little attentional weight, suggesting that the saccade drives the attentional shift in a combined movement.

Keywords: reaching, action, attention, saccade, eye movement

Acknowledgments

This project was supported by an Australian Postgraduate Award scholarship to EEMS, NIH 1R01EY027390 grant to PV, and a U.S. Department of Defense ITC-PAC grant to AMW.

Commercial relationships: none.

Corresponding author: Anna Ma-Wyatt.

Email: anna.mawyatt@adelaide.edu.au.

Address: School of Psychology, University of Adelaide, Adelaide, Australia.

References

- Bahcall, D. O., & Kowler, E. (1999). Attentional interference at small spatial separations. *Vision Research*, 39(1), 71–86.
- Baldauf, D., & Deubel, H. (2009). Attentional selection of multiple goal positions before rapid hand movement sequences: An event-related potential study. *Journal of Cognitive Neuroscience*, 21(1), 18–29, <https://doi.org/10.1163/156856897X00249>.

- Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research*, *46*(26), 4355–4374, <https://doi.org/10.1016/j.visres.2006.08.021>.
- Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999, July 9). Reach plans in eye-centered coordinates. *Science*, *285*(5425), 257–260.
- Beauchamp, M. S., Petit, L., Ellmore, T. M., Ingeholm, J., & Haxby, J. V. (2001). A parametric fMRI study of overt and covert shifts of visuospatial attention. *NeuroImage*, *14*(2), 310–321, <https://doi.org/10.1006/nimg.2001.0788>.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Caputo, G., & Guerra, S. (1998). Attentional selection by distractor suppression. *Vision Research*, *38*(5), 669–689.
- Castet, E., Jeanjean, S., Montagnini, A., Laugier, D., & Masson, G. S. (2006). Dynamics of attentional deployment during saccadic programming. *Journal of Vision*, *6*(3):2, 196–212, <https://doi.org/10.1167/6.3.2>. [PubMed] [Article]
- Cicchini, G. M., Binda, P., Burr, D. C., & Morrone, M. C. (2013). Transient spatiotopic integration across saccadic eye movements mediates visual stability. *Journal of Neurophysiology*, *109*(4), 1117–1125, <https://doi.org/10.1152/jn.00478.2012>.
- Coull, J. T., Frith, C. D., Büchel, C., & Nobre, A. C. (2000). Orienting attention in time: Behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia*, *38*(6), 808–819.
- Crawford, J. D. (2004). Spatial transformations for eye-hand coordination. *Journal of Neurophysiology*, *92*(1), 10–19, <https://doi.org/10.1152/jn.00117.2004>.
- Cutzu, F., & Tsotsos, J. K. (2003). The selective tuning model of attention: Psychophysical evidence for a suppressive annulus around an attended item. *Vision Research*, *43*(2), 205–219.
- de Haan, B., Morgan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, *1204*, 102–111, <https://doi.org/10.1016/j.brainres.2008.01.105>.
- Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2009). Trans-saccadic identification of highly similar artificial shapes. *Journal of Vision*, *9*(4):28, 1–14, <https://doi.org/10.1167/9.4.28>. [PubMed] [Article]
- Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2010). Parametric integration of visual form across saccades. *Vision Research*, *50*(13), 1225–1234, <https://doi.org/10.1016/j.visres.2010.04.008>.
- Deubel, H. (2008). The time course of pre-saccadic attention shifts. *Psychological Research*, *72*(6), 630–640, <https://doi.org/10.1007/s00426-008-0165-3>.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837.
- Dorr, M., & Bex, P. J. (2013). Peri-saccadic natural vision. *Journal of Neuroscience*, *33*(3), 1211–1217.
- Fecteau, J. H., & Munoz, D. P. (2006). Saliency, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences*, *10*(8), 382–390, <https://doi.org/10.1016/j.tics.2006.06.011>.
- Ganmor, E., Landy, M. S., & Simoncelli, E. P. (2015). Near-optimal integration of orientation information across saccades. *Journal of Vision*, *15*(16):8, 1–12, <https://doi.org/10.1167/15.16.8>. [PubMed] [Article]
- Gegenfurtner, K. R., & Franz, V. H. (2007). A comparison of localization judgments and pointing precision. *Journal of Vision*, *7*(5):11, 1–12, <https://doi.org/10.1167/7.5.11>. [PubMed] [Article]
- Gersch, T. M., Kowler, E., & Doshier, B. (2004). Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Research*, *44*(12), 1469–1483, <https://doi.org/10.1016/j.visres.2003.12.014>.
- Gersch, T. M., Kowler, E., Schnitzer, B. S., & Doshier, B. A. (2009). Attention during sequences of saccades along marked and memorized paths. *Vision Research*, *49*(10), 1256–1266, <https://doi.org/10.1016/j.visres.2007.10.030>.
- Ghahghaei, S., & Verghese, P. (2017). Texture segmentation influences the spatial profile of presaccadic attention. *Journal of Vision*, *17*(2):10, 1–16, <https://doi.org/10.1167/17.2.10>. [PubMed] [Article]
- Hanning, N. M., Aagten-Murphy, D., & Deubel, H. (2018). Independent selection of eye and hand targets suggests effector-specific attentional mechanisms. *Scientific Reports*, *8*, 1–8, <https://doi.org/10.1038/s41598-018-27723-4>.
- He, P. Y., & Kowler, E. (1989). The role of location probability in the programming of saccades: Implications for “center-of-gravity” tendencies. *Vision Research*, *29*(9), 1165–1181.
- Heuer, A., Crawford, J. D., & Schubö, A. (2017). Action relevance induces an attentional weighting of representations in visual working memory. *Memory & Cognition*, *45*, 1–15, <https://doi.org/10.3758/s13421-016-0670-3>.

- Heuer, A., & Schubö, A. (2018). Separate and combined effects of action relevance and motivational value on visual working memory. *Journal of Vision*, *18*(5):14, 1–14, <https://doi.org/10.1167/18.5.14>. [PubMed] [Article]
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, *57*(6), 787–795.
- Hopf, J. M., Boehler, C. N., Luck, S. J., Tsotsos, J. K., Heinze, H. J., & Schoenfeld, M. A. (2006). Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. *Proceedings of the National Academy of Sciences, USA*, *103*(4), 1053–1058, <https://doi.org/10.1073/pnas.0507746103>.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, *2*(3), 194–203, <https://doi.org/10.1038/35058500>.
- Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye–hand movements. *Psychological Science*, *22*(3), 339–347, <https://doi.org/10.1177/0956797610397666>.
- Jonikaitis, D., Klapetek, A., & Deubel, H. (2017). Spatial attention during saccade decisions. *Journal of Neurophysiology*, *118*(1), 149–160, <https://doi.org/10.1152/jn.00665.2016>.
- Jonikaitis, D., Schubert, T., & Deubel, H. (2010). Preparing coordinated eye and hand movements: Dual-task costs are not attentional. *Journal of Vision*, *10*(14):23, 1–17, <https://doi.org/10.1167/10.14.23>. [PubMed] [Article]
- Jonikaitis, D., & Theeuwes, J. (2013). Dissociating oculomotor contributions to spatial and feature-based selection. *Journal of Neurophysiology*, *110*(7), 1525–1534.
- Khan, A. Z., Blohm, G., Pisella, L., & Munoz, D. P. (2015). Saccade execution suppresses discrimination at distractor locations rather than enhancing the saccade goal location. *European Journal of Neuroscience*, *41*(12), 1624–1634, <https://doi.org/10.1111/ejn.12923>.
- Khan, A. Z., Song, J. H., & McPeck, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision*, *11*(1):9, 1–14, <https://doi.org/10.1167/11.1.9>. [PubMed] [Article]
- Koenig-Robert, R., & VanRullen, R. (2011). Spatio-temporal mapping of visual attention. *Journal of Vision*, *11*(14):12, 1–16, <https://doi.org/10.1167/11.14.12>. [PubMed] [Article]
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916.
- Land, M. F., & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research*, *41*(25–26), 3559–3565.
- Li, H. H., Barbot, A., & Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. *Current Biology*, *26*(12), 1564–1570.
- Li, H.-H., Pan, J., & Carrasco, M. (2019). Pre-saccadic attention improves or impairs performance by enhancing sensitivity to higher spatial frequencies. *Scientific Reports*, *9*, 1–10, <https://doi.org/10.1038/s41598-018-38262-3>.
- Ma-Wyatt, A., & McKee, S. P. (2006). Initial visual information determines endpoint precision for rapid pointing. *Vision Research*, *46*(28), 4675–4683, <https://doi.org/10.1016/j.visres.2006.08.009>.
- Ma-Wyatt, A., & McKee, S. P. (2007). Visual information throughout a reach determines endpoint precision. *Experimental Brain Research*, *179*(1), 55–64, <https://doi.org/10.1007/s00221-006-0767-1>.
- Ma-Wyatt, A., Stritzke, M., & Trommershäuser, J. (2010). Eye-hand coordination while pointing rapidly under risk. *Experimental Brain Research*, *203*(1), 131–145, <https://doi.org/10.1007/s00221-010-2218-2>.
- Melcher, D. (2005). Spatiotopic transfer of visual-form adaptation across saccadic eye movements. *Current Biology*, *15*(19), 1745–1748, <https://doi.org/10.1016/j.cub.2005.08.044>.
- Mirman, D. (2014). Growth curve analysis and visualization using R. New York, NY: Chapman and Hall/CRC. <https://doi.org/10.1201/9781315373218>.
- Mirman, D., Dixon, J. A., & Magnuson, J. S. (2008). Statistical and computational models of the visual world paradigm: Growth curves and individual differences. *Journal of Memory and Language*, *59*(4), 475–494, <https://doi.org/10.1016/j.jml.2007.11.006>.
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, *7*(14):8, 1–16, <https://doi.org/10.1167/7.14.8>. [PubMed] [Article]
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(3), 1273–1276, <https://doi.org/10.1073/pnas.021549498>.

- Moore, T., & Zirnsak, M. (2017). Neural mechanisms of selective visual attention. *Annual Review of Psychology*, *68*, 47–72.
- Neggers, S. F., & Bekkering, H. (2001). Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. *Journal of Neurophysiology*, *86*(2), 961–970.
- Ohl, S., & Rolfs, M. (2016). Saccadic eye movements impose a natural bottleneck on visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *43*, 736–748, <https://doi.org/10.1037/xlm0000338>.
- Ohl, S., & Rolfs, M. (2018). Saccadic selection of stabilized items in visuospatial working memory. *Consciousness and Cognition*, *64*, 32–44, <https://doi.org/10.1016/j.concog.2018.06.016>.
- Pelli, D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Prablanc, C., Echallier, J. F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biological Cybernetics*, *35*(2), 113–124.
- Prime, S. L., Niemeier, M., & Crawford, J. D. (2005). Trans-saccadic integration of visual features in a line intersection task. *Experimental Brain Research*, *169*(4), 532–548, <https://doi.org/10.1007/s00221-005-0164-1>.
- Ren, L. (2006). Proprioceptive guidance of saccades in eye–hand coordination. *Journal of Neurophysiology*, *96*(3), 1464–1477, <https://doi.org/10.1152/jn.01012.2005>.
- Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience*, *32*(40), 13744–13752a, <https://doi.org/10.1523/JNEUROSCI.2676-12.2012>.
- Rolfs, M., Lawrence, B. M., & Carrasco, M. (2013). Reach preparation enhances visual performance and appearance. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1628), <https://doi.org/10.1098/rstb.2013.0057>.
- Ross, J., & Ma-Wyatt, A. (2003). Saccades actively maintain perceptual continuity. *Nature Neuroscience*, *7*(1), 65–69, <https://doi.org/10.1038/nn1163>.
- Song, J. H., & McPeck, R. M. (2009). Eye–hand coordination during target selection in a pop-out visual search. *Journal of Neurophysiology*, *102*(5), 2681–2692, <https://doi.org/10.1152/jn.91352.2008>.
- Stewart, E. E. M., & Ma-Wyatt, A. (2015). The spatiotemporal characteristics of the attentional shift relative to a reach. *Journal of Vision*, *15*(5):10, 1–17, <https://doi.org/10.1167/15.5.10>. [PubMed] [Article]
- Stewart, E. E. M., & Ma-Wyatt, A. (2017). The profile of attention differs between locations orthogonal to and in line with reach direction. *Attention, Perception, & Psychophysics*, *79*, 2412–2423, <https://doi.org/10.3758/s13414-017-1400-z>.
- Stewart, E. E. M., & Schütz, A. C. (2018a). Attention modulates trans-saccadic integration. *Vision Research*, *142*, 1–10, <https://doi.org/10.1016/j.visres.2017.11.006>.
- Stewart, E. E. M., & Schütz, A. C. (2018b). Optimal trans-saccadic integration relies on visual working memory. *Vision Research*, *153*, 70–81.
- Stritzke, M., & Trommershäuser, J. (2007). Eye movements during rapid pointing under risk. *Vision Research*, *47*(15), 2000–2009, <https://doi.org/10.1016/j.visres.2007.04.013>.
- Volkman, F. C. (1962). Vision during voluntary saccadic eye movements. *Journal of the Optical Society of America*, *52*(5), 571–578, <https://doi.org/10.1364/JOSA.52.000571>.
- Volkman, F. C., Riggs, L. A., White, K. D., & Moore, R. K. (1978). Contrast sensitivity during saccadic eye movements. *Vision Research*, *18*(9), 1193–1199.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113–120.
- White, A. L., Rolfs, M., & Carrasco, M. (2013). Adaptive deployment of spatial and feature-based attention before saccades. *Vision Research*, *85*, 26–35, <https://doi.org/10.1016/j.visres.2012.10.017>.
- Wolf, C., & Schütz, A. C. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision*, *15*(16):1, 1–18, <https://doi.org/10.1167/15.16.1>. [PubMed] [Article]
- Zhao, M., Gersch, T. M., Schnitzer, B. S., Doshier, B. A., & Kowler, E. (2012). Eye movements and attention: The role of pre-saccadic shifts of attention in perception, memory and the control of saccades. *Vision Research*, *74*(C), 40–60, <https://doi.org/10.1016/j.visres.2012.06.017>.