The eye dominates in guiding attention during simultaneous eye and hand movements

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Prior to the onset of a saccade or a reach, attention is directed to the goal of the upcoming movement. However, it remains unknown whether attentional resources are shared across effectors for simultaneous eye and hand movements. Using a 4-AFC shape discrimination task, we investigated attentional allocation during the planning of a saccade alone, reach alone, or combined saccade and reach to one of five peripheral locations. Target discrimination was better when the probe appeared at the goal of the impending movement than when it appeared elsewhere. However, discrimination performance at the movement goal was not better for combined eye–hand movements compared to either effector alone, suggesting a shared limited attentional resource rather than separate pools of effector-specific attention. To test which effector dominates in guiding attention, we then separated eye and hand movement goals in two conditions: (1) cued reach/fixed saccade—subjects made saccades to the same peripheral location throughout the block, while the reach goal was cued and (2) cued saccade/fixed reach—subjects made reaches to the same location, while the saccade goal was cued. For both conditions, discrimination performance was consistently better at the eye goal than the hand goal. This indicates that shared attentional resources are guided predominantly by the eye during the planning of eye and hand movements.

Keywords: attention, detection/discrimination, eye movements, reach movements, eye–hand coordination


Introduction

Many tasks in daily life, such as reaching for a coffee cup, involve both eye and arm movements, and a number of studies have shown that the hand and the eyes typically show stereotyped patterns of coordinated movement (Crawford, Medendorp, & Marotta, 2004; Land & Furneaux, 1997; Land & Hayhoe, 2001; Prablanc, Echallier, Komilis, & Jeannerod, 1979). In general, eye and hand movements are highly coordinated both spatially and temporally (Bekkering, Abrams, & Pratt, 1995; Carey, Coleman, & Della Sala, 1997; Fisk & Goodale, 1985; Gielen, van den Heuvel, & van Gisbergen, 1984; Jackson, Newport, Mort, & Husain, 2005; Johansson, Westling, Bäckström, & Flanagan, 2001; Neggers & Bekkering, 2000, 2001; Sailer, Eggert, Ditterich, & Straube, 2000; Song & McPeek, 2009; Vercher & Gauthier, 1988, but see Bekkering & Sailer, 2002).

Studies investigating the relationship between attention and saccades have shown that attention is typically shifted to the goal of a saccade just before the onset of the eye movement (Baldauf & Deubel, 2008a; Deubel & Schneider, 1996, 2003; Gersch, Kowler, & Dosher, 2004; Hoffman & Subramaniam, 1995; Peterson, Kramer, & Irwin, 2004). Indeed, it has been suggested that a saccade cannot occur without a preceding attention shift (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Schneider & Deubel, 2002). These findings imply a strong linkage between attention and saccades (Awh, Armstrong, & Moore, 2006; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Rizzolatti, Riggio, & Sheligia, 1994; Schneider & Deubel, 2002; Shepherd, Findlay, & Hockey, 1986). Specifically, there is evidence that saccadic commands may direct attention to the eye goal location (Figure 1A), thereby improving perceptual discrimination at that location (Cavanaugh & Wurtz, 2004; Moore, Armstrong, & Fallah, 2003; Moore &
Other behavioral studies have shown that attention is shifted to the goal of a reaching movement even when the eyes remain fixated (Baldauf & Deubel, 2008b; Baldauf, Wolf, & Deubel, 2006; Deubel & Schneider, 2003; Deubel, Schneider, & Paprotta, 1998); perceptual discrimination is better at the reach goal compared to any other spatial location, suggesting that, as for saccades, there is an obligatory attention shift to the reach goal just before the reaching movement begins (Figure 1B). These findings raise the question of how attention is allocated during simultaneous eye and hand movements. One possibility is that there are separate attentional resources dedicated to each effector, and that those attentional resources summate when both effectors’ movement goals coincide. Alternatively, there may be a single common attentional resource that is shared across different effectors, such that the amount of attention allocated to a given location is independent of the number of movement commands.

To answer this question, we first asked how attention is directed during simultaneous eye and hand movements to the same location. If there are separate attentional resources for the two effectors, allocation of attention to the movement goal may be enhanced when multiple movement commands are issued, compared to one (Figure 1C). We also asked how attention is directed when the eyes and the hand move to different locations. If attentional resources are separate for the two effectors, we would predict no decrease in the allocation of attention at either effector goal (Figure 1D). Alternatively, if attentional resources are shared across effectors, we would predict a decrease in attentional allocation at one or both goal locations, as depicted in Figure 1E.

Previous studies have established that shifting attention to a location in the periphery improves shape discrimination for objects at the attended location (e.g., Palmer, 1994; Shaw, 1984; Sperling & Dosher, 1986). To gauge the allocation of attention during the preparation of eye and hand movements, we measured performance in discriminating the shape of a peripheral target that was presented briefly, and then masked, before the execution of the eye and/or hand movement. The particular task that we used was modified from Deubel and Schneider (2003). A number of studies have used this type of dual-task paradigm with either eye or reaching movements alone (Baldauf & Deubel, 2008a; Deubel & Schneider, 1996; Deubel et al., 1998; Hoffman & Subramaniam, 1995; Kowler et al., 1995). These studies have found that discrimination performance is consistently better at the intended saccade or reach goal than at any other location regardless of the probability with which the discrimination target appears at that location (Deubel & Schneider, 2003; Hoffman & Subramaniam, 1995; Kowler et al., 1995).

Here, we determined (1) whether perceptual discrimination of a peripheral target at the movement goal is enhanced during simultaneous eye and hand movements to the same goal compared to single effector movements.


Figure 1. Schematic of current findings and hypotheses. (A) It has been shown that attention is directed to the location to which an eye movement will occur. (B) This has also been shown to be true for reach movements. (C) If attentional resources are specific to the effector, both a reach and an eye movement to the same location could result in an enhancement of attention at that location. In addition, if the reach and eye movement are directed to different locations (D), effector-specific attentional resources would predict no detriment in attentional allocation at either location. However, if attentional resources are shared across effectors, then attentional allocation should be reduced at one (as shown in (E)) or both goal locations when the goals are at different locations.
and (2) how perceptual discrimination varies between effectors during simultaneous eye and hand movements to different goals.

## Methods

### Subjects

Five subjects (ages: 24 to 34) participated in the experiment. Three subjects were naive to the goal of the experiment. The experimental protocol was pre-approved by the Smith-Kettlewell Institutional Review Board in compliance with NCPHS, US. All subjects had normal or corrected-to-normal vision.

### Apparatus

Subjects were seated in front of a 17-inch high-resolution Eizo Nanao Flexscan T565 CRT (Eizo Nanao Corporation, Ishikawa, Japan) color monitor (1.76 min arc/pixel) with a refresh rate of 60 Hz that was controlled by a Macintosh computer and viewed from a distance of 48 cm. Stimuli were presented using Matlab (The Math Works, Natick, MA) and functions from the PsychToolbox (Brainard, 1997; Pelli, 1997). Eye position was recorded at 1000 Hz using a video-based tracker (EyeLink 1000; SR Research, Mississauga, Canada). Finger position was recorded using a Keytec Magic touch screen (Keytec, Garland, TX). A chinrest maintained the viewing distance and stabilized the head for accurate eye tracking. Prior to each block of trials, the eye tracker was calibrated by having the subject fixate a series of 9 positions on the display (8 surrounding the periphery of the display and the center) while the gains and offsets were set.

### Procedure

Subjects performed trials in 5 separate conditions, (1) saccade only, (2) reach only, (3) combined saccade and reach to the same goal, (4) cued reach/fixated saccade to different goals, and (5) cued saccade/fixated reach to different goals. All paradigms had almost identical trial sequences. Figure 2 depicts a typical trial sequence for the saccade only condition modified from Deubel and Schneider (2003). The screen background was black and the stimuli were white (polarity is inverted in the figure). Each trial began with the presentation of a central white fixation dot (0.22° diameter) surrounded by stimuli consisting of figure 8s in 5 locations equally spaced along an invisible semicircle centered on the fixation dot (radius = 5°). The figure 8s (height = 0.15°, width = 0.3°, arrow pointed to one of the five figure 8s). Subjects were asked to saccade to the figure 8 corresponding to the arrow as soon as possible. The direction of the arrow was randomly chosen. After 100 ms, the figure 8s changed, one of them changed into one of four target characters: "d", "r", "q", "b" (see Figure 2), whereas the other 4 changed into either a "2" or a "5." The target character appeared at the saccade goal location (indicated by the arrow) 50% of the time. In the other 50% of trials, it could appear at any other location (pseudo-randomly selected). The duration of this shape change varied randomly from 33 to 133 ms (2 to 8 frames). After 500 ms, the four possible target characters appeared below the fixation location (spaced 3.75° apart) and subjects were asked to indicate which of the four had been presented by touching it with their fingertip. Once they made their choice, a new trial began.

All other effector conditions had the same stimuli and timing except for the following differences: (1) the target characters appeared below the fixation location when the finger was detected at the goal location, rather than at the fixed interval of 500 ms, (2) for the cued reach/fixated saccade and the cued saccade/fixated reach conditions, the arrow never indicated the 12 o’clock location; it pseudo-randomly pointed toward one of the 4 other target locations.

For the reach only condition, subjects were asked to maintain fixation at the central dot/arrow during the entire trial and to reach with their index finger from slightly below the fixation dot to the goal location indicated by the arrow as soon as possible. For the combined saccade and reach condition, subjects were asked to both reach and saccade to the goal location indicated by the arrow as soon as possible. For the cued reach/fixated saccade condition, subjects were asked to always saccade to the 12 o’clock location and to reach to the location indicated by the arrow. The go signal for the saccade was the arrow appearance. For the cued saccade/fixated reach condition, subjects were asked to always reach to the 12 o’clock location and to saccade to the location indicated by the arrow. The reach go signal was the arrow appearance.

Each block consisted of 140 trials (20 trials for each of 7 discrimination target durations). Subjects performed training blocks until they felt comfortable with the task. They trained on both the discrimination of the target and on executing the movements within certain criteria limits (see Data analysis section). After training, each subject completed 5–6 blocks for each condition.

All subjects began with the saccade only condition to learn the basic task. They then completed 3–4 experimental blocks. Thereafter, they performed training and experimental blocks one condition at a time. The order of
Figure 2. Task. Each trial began with the presentation of 5 figure 8s with a central fixation dot. Subjects fixated on the central dot and placed their index finger slightly below the fixation dot. After 1.2 s, the fixation dot became an arrow indicating the movement goal location. After 100 ms (within the movement latency), four of the five figure 8s became distractors ("2" or "5") and one became one of the 4 possible discrimination targets ("d", "P", "q", "b") for a random duration of 33–133 ms (2 to 8 frames). Thereafter, the distractors and target became figure 8s again for 500 ms. In the saccade only condition, subjects were asked to saccade to the location indicated by the arrow (movement goal location) while keeping their finger at the fixation location. In the reach only condition, they were asked to maintain fixation while reaching to touch the movement goal location. In the combined saccade and reach condition, they were asked to saccade and to reach to the movement goal location. In the cued reach/fixed saccade condition, subjects were asked to always saccade to the 12 o’clock position and to reach to the movement goal location at arrow onset. In the cued saccade/fixed reach condition, subjects were asked to always reach to the 12 o’clock position and to saccade to the movement goal location at arrow onset. At the end of each trial, subjects indicated which of the four possible discrimination targets (shown at the bottom of the final frame) they perceived.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Saccade only (4200 total)</th>
<th>Reach only (4060 total)</th>
<th>Saccade and reach (3920 total)</th>
<th>Cued reach/fixed saccade (4200 total)</th>
<th>Cued saccade/fixed reach (3920 total)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Omission type (in order of removal)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eye/reach landed on MG before DT offset</td>
<td>N/A</td>
<td>N/A</td>
<td>18 (0.4%)</td>
<td>N/A</td>
<td>921 (21.9%)</td>
</tr>
<tr>
<td>Choice was ambiguous</td>
<td>71 (1.7%)</td>
<td>141 (3.4%)</td>
<td>68 (1.7%)</td>
<td>83 (2%)</td>
<td>107 (2.7%)</td>
</tr>
<tr>
<td>Saccade occurred</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Reach latencies less than 100 ms or greater than 500 ms</td>
<td>N/A</td>
<td>345 (8.5%)</td>
<td>159 (4.1%)</td>
<td>284 (6.8%)</td>
<td>96 (2.4%)</td>
</tr>
<tr>
<td>Reach duration less than 100 ms or greater than 400 ms</td>
<td>N/A</td>
<td>N/A</td>
<td>143 (3.6%)</td>
<td>674 (16%)</td>
<td>212 (5.4%)</td>
</tr>
<tr>
<td>Saccade reaction times less than 80 ms or greater than 500 ms</td>
<td>18 (0.4%)</td>
<td>N/A</td>
<td>5 (0.1%)</td>
<td>11 (0.3%)</td>
<td>41 (1%)</td>
</tr>
<tr>
<td>Saccade landed outside 1.5° or reach landed outside 2° of respective MG</td>
<td>921 (21.9%)</td>
<td>160 (3.9%)</td>
<td>891 (22.7%)</td>
<td>794 (18.9%)</td>
<td>709 (18.1%)</td>
</tr>
<tr>
<td>Total remaining trials</td>
<td>2805 (66.8%)</td>
<td>2714 (66.8%)</td>
<td>2356 (60.1%)</td>
<td>2004 (47.7%)</td>
<td>2646 (67.5%)</td>
</tr>
</tbody>
</table>

Table 1. Omitted trials. Notes: *Number of trials removed (percent of total trials).
conditions was counterbalanced across subjects. After the experimental blocks for all the other conditions were completed, subjects then completed 2 additional experimental blocks of the saccade only condition. The total number of trials per subject per condition was 700–840.

Data analysis

All data were analyzed using Matlab 7.3 (The Math Works, Natick, MA). Saccade onset and offset timing and position were calculated offline using a saccade detection algorithm with a velocity criterion of 25°/s. We measured the time and position of fingertip offset from the fixation position, time and position of fingertip landing at the goal location, and the position of the fingertip at the choice locations. Correct trials were determined to be those in which the correct required movement was made as follows: the required reach and/or saccadic movements landed at their respective goal locations after the figure 8s reappeared on the screen (Figure 2), saccade latencies were greater than 80 ms and less than 500 ms, reach latencies were greater than 100 ms and less than 500 ms, reach durations were greater than 100 ms and less than 400 ms, subjects’ saccades landed within 1.5°, and subjects’ reaches landed within 2° of the movement goal location(s). In the reach only condition, we excluded trials in which subjects broke fixation. We only selected those trials in which the fingertip position indicating shape choice was unambiguous (within 3° horizontal or 5° vertical of any of the 4 choice locations). Details of omitted trials are listed in Table 1. After applying these criteria, there remained 218 to 776 trials per subject per condition. We performed repeated-measures ANOVAs across subjects to analyze both discrimination performance and movement latencies.

Results

Discrimination performance

Single and combined effector conditions—Overall performance

We first tested whether discrimination performance was better in the combined eye and reach condition compared to either effector alone. Performance was analyzed for each of the three conditions (eye only, reach only, combined eye and reach) according to whether the discrimination target (DT) appeared at the movement goal (MG) location or whether it appeared at a non-MG location, for each of the 5 individual subjects (Figures 3A–3E) and across all subjects (Figure 3F). A two-factor repeated-measures ANOVA with condition and DT location showed a significant effect of location ($F(1,4) = 105.9, p < 0.01$) but not of condition ($p > 0.05$). This can be seen in the figure; performance for all three conditions was consistently better when the DT appeared at the MG location than when it appeared at a non-MG location. This pattern of results was expected from previous work examining the allocation of attention during eye or hand movement planning (e.g., Deubel & Schneider, 1996; Deubel et al., 1998; Hoffman & Subramaniam, 1995; Kowler et al., 1995), as well as from the fact that the DT was more likely to appear at the MG than at other locations. There was also a significant interaction effect ($F(2,8) = 5.7, p < 0.05$), likely due to the performance during the reach only condition compared to the other two conditions; performance when the DT was at the MG location was slightly worse in this condition than in the other conditions, while performance when the DT was at a non-MG location was slightly better in this condition than in the other conditions. However, separate sets of $t$-tests on discrimination performance at the MG and non-MG locations revealed no significant differences among the three conditions ($p > 0.05$). These findings show that when both the eyes and hand are directed to the same location, discrimination performance at the MG is no better than performance for either an eye or hand movement alone.

Single and combined effector conditions—Performance as a function of DT duration

As mentioned in the Methods section, in each trial the DT appeared for one of seven different durations. In order to investigate whether different effectors directed attention with different time courses, we analyzed the patterns of performance across the 7 DT durations for each condition. In addition, since overall performance was relatively good when the DT was at the movement goal, there may have been a ceiling effect, which could explain the lack of enhanced performance in the combined saccade/reach condition. Examining performance across the different DT durations allowed us to examine this possibility as well. Figure 4 shows discrimination performance as a function of DT duration across all subjects. We performed a two-way repeated-measures ANOVA on performance at the MG location, with condition and duration as factors. There was a significant effect of DT duration ($F(6,24) = 19.5, p < 0.01$) but no main effect of condition ($p > 0.05$), nor was there an interaction effect ($p > 0.05$). To summarize, performance increased as DT duration increased for all three conditions in the same manner and there was no difference among the three conditions even at lower performance levels. These results indicate that attentional resources are likely shared across effectors, rather than specific to each effector. If there were separate attentional resources specific to each effector, we would expect an additive effect on discrimination when both effectors are directed to the same location.
To further investigate this question, we measured performance when the eye and hand were directed to different locations. Figures 5A–5F depict performance for the two conditions with separate eye and hand goals, for individual subjects (Figure 5A–5E) and across all subjects (Figure 5F). Performance is plotted as a function of DT location relative to MG location for the cued reach/fixed saccade condition (purple bars) and the cued saccade/fixed reach condition (yellow bars). For the cued reach/fixed saccade condition, a one-way repeated-measures ANOVA with DT location as a factor revealed significant differences among DT locations (DT at cued MG vs. DT at fixed MG vs. DT at a non-MG location—F(2,8) = 12.7, p < 0.01). Holm–Bonferroni corrected post-hoc paired t-tests revealed significantly better performance when the DT was at the cued or fixed MG locations compared to when it was at a non-MG location, but no significant differences between the cued and fixed MG locations.
performed two-way repeated-measures ANOVAs with across different durations and different DT locations, we dashed). To test whether performance was different (dark gray dotted), and at a non-MG location (light gray cued MG location (black solid), at the fixed MG location performance for the different DT locations—DT at the fixed saccade and reach task. Next, we examined performance in the cued saccade/fixed reach condition. Performance overall was significantly different across DT locations \((F(2,8) = 40.5, p < 0.001)\), with discrimination performance significantly better at the cued MG location than at the fixed MG location or at a non-MG location (Holm–Bonferroni corrected paired \(t\)-tests, \(p < 0.01)\). Furthermore, discrimination performance was not significantly better at the fixed MG location than at non-MG locations \((p > 0.05)\). In summary, it appears that in the cued saccade/fixed reach condition, more attention is directed to the saccade goal (cued) than to the reach goal (fixed).

**Separate eye and hand goal conditions—Performance as a function of DT duration**

In Figure 6, performance is plotted as a function of DT duration for the cued reach/fixed saccade (Figure 6A) and the cued saccade/fixed reach (Figure 6B) conditions across all subjects. The differently shaded lines represent performance for the different DT locations—DT at the cued MG location (black solid), at the fixed MG location (dark gray dotted), and at a non-MG location (light gray dashed). To test whether performance was different across different durations and different DT locations, we performed two-way repeated-measures ANOVAs with duration (7) and DT location (cued vs. fixed) for each of the two conditions separately. For the cued reach/fixed saccade condition, we found a significant effect of duration \((F(6,24) = 7.7, p < 0.01)\), but no significant effect for location \((p > 0.05)\) and no interaction effect \((p > 0.05)\), showing that performance at both the fixed (saccade) location and the cued (reach) location improved as duration increased (Figure 6A). For the cued saccade/fixed reach condition (Figure 6B), we found significant effects of DT location \((F(1,4) = 81, p < 0.01)\) and duration \((F(6,24) = 5.4, p < 0.01)\), and a significant interaction effect \((F(6,24) = 5.6, p < 0.01)\). Separate analyses of performance at the saccade and reach goals showed that while performance improved significantly for longer durations for the cued (saccade) goal (repeated-measures one-way ANOVA—\(F(6,24) = 9.9, p < 0.05)\), it did not for the fixed (reach) goal \((p > 0.05)\). When we compared performance when the DT was at the fixed reach goal with performance when it was at a non-MG location, we found that there was no significant difference at any duration (repeated-measures ANOVA, paired \(t\)-tests—\(p > 0.05)\). Taken together, the results suggest that in this condition, very little attention was allocated to the fixed reach location; the amount of attention allocated to the fixed reach goal was no more than that allocated to a location that was not an effector goal.

**Comparison of discrimination performance for saccades vs. reaches**

In order to compare performance for saccades and reaches separately, we replotted performance for DTs appearing at saccade and reach goals separately across the different conditions (Figures 7A and 7B). To compare discrimination performance during different conditions involving saccades (Figure 7A), we performed a repeated-measures ANOVA on performance for the 4 conditions and found no significant differences \((F(3,12) = 1.7, p > 0.05)\). These results suggest that significant attentional resources were always directed to the saccade goal, including in the cued reach/fixed saccade condition, in which the DT was less likely to appear at the saccade goal than at the reach goal. Next, we analyzed discrimination performance at the reach goal (Figure 7B) and found significant differences across the 4 conditions (Greenhouse–Geisser corrected repeated-measures ANOVA, \(F(3,12) = 15.6, p < 0.001)\). Holm–Bonferroni corrected post-hoc paired \(t\)-tests revealed that discrimination performance was significantly worse for the fixed reach goal in the cued saccade/fixed reach condition compared to the reach alone condition or the combined saccade and reach conditions \((p < 0.01)\). Importantly, discrimination performance was also significantly worse at the cued reach goal in the cued reach/fixed saccade condition compared to the condition in which a saccade and reach were made to the same goal \((p < 0.01)\). The DT appeared at the reach
MG with the same likelihood in both of these conditions, yet performance was significantly worse when a saccade was made elsewhere. In summary, when the reach goal was cued in each trial, the requirement to make a concurrent saccade to a fixed location significantly reduced discrimination performance at the reach goal. An even greater reduction was seen when the reach goal was kept fixed and the saccade goal was cued: in this condition, target discrimination at the reach goal was no better than at non-goal locations. This is in stark contrast to performance at the saccade goal, which was uniformly good across all conditions, even in the two conditions in which the saccade and reach goals were dissociated.

**All conditions—Latencies**

To ensure that discrimination performance was not influenced by differences in saccade and reach latencies,
we compared saccade and reach latencies across different DT locations and conditions. Within each condition, we found no significant differences across the two (or three) DT locations for either saccade (one-way repeated-measures ANOVAs, \( p > 0.05 \)) or reach (\( p > 0.05 \)) latencies. There were also no significant differences across the four (or two) conditions for each DT location (\( p > 0.05 \)). Mean saccade latencies across subjects ranged from 232 to 264 ms whereas reach latencies ranged from 297 to 327 ms.

**Discussion**

We measured the allocation of visual attention before the execution of simultaneous eye and hand movements to the same or different locations to investigate whether there are separate attentional resources specific to each effector or whether attentional resources are shared across effectors. We found evidence for shared attentional resources that are predominately linked to saccades (Figure 1E).

**Attention is predominately allocated to saccade goals**

As shown in Figure 7, perceptual discrimination at the saccade goal was consistently high across all conditions; discrimination performance was similar regardless of whether the task involved only saccades to a certain location or whether it involved saccades with reaches to the same or other locations. Performance was also similar across conditions.
Attention at the reach goal depends on task conditions

In contrast to saccades, our findings for reaches suggest that the amount of attention allocated to the goal of a reaching movement depends on the task conditions. When the eyes remained at fixation or when the eyes accompanied the reach, discrimination performance at reach goals was good. It declined when the reach was cued to one location and a saccade was made elsewhere (cued reach/fixed saccade condition), even though the discrimination target was more likely to appear at the reach goal than at any other location. Finally, discrimination performance at the reach goal during the cued saccade/fixated reach condition was no better than performance at locations that were not movement goals. These results imply that, unlike saccades, reaching movements do not necessarily require a concomitant shift of spatial attention. Indeed, there does not seem to be a fixed amount of attention specifically allocated to reaching movements, as there appears to be for saccades. In the cued saccade/fixated reach condition, the smaller amount of attention at the reach goal could be due to the fixed, repetitive reaching movement, which could be pre-planned. This would be consistent with previous studies that have shown that delayed reach movements (unlike delayed saccades) do not require the allocation of attention at the movement goal, presumably because the reach has already been pre-planned (Deubel & Schneider, 2003).

Discrimination performance at the reach goal was lower in the cued reach/fixed saccade condition than in the reach only condition. This suggests that the allocation of attention to the reach goal was reduced by the requirement to make an eye movement elsewhere, even though the eye movement was always directed to the same goal. Moreover, in this condition, attentional performance was good at the repetitive eye movement goal, in contrast to what was seen for repetitive reaches in the cued saccade/fixated reach condition.

It should be noted that in this study, we measured only visuospatial attention. Thus, it is possible that reaching movements may entail some other type of attentional demand, such as attention to posture or proprioception. If this were the case, then our results would imply that these other reaching-related attentional demands draw upon separate attentional resources and do not interfere with the allocation of visuospatial attention.

Eye–hand coordination and attention

Our finding that spatial attention is directed predominantly by the eyes may have some implications for eye–hand coordination. Studies have shown that subjects tend to fixate the location to which they will eventually reach (Fisk & Goodale, 1985; Frens & Erkelens, 1991; Gielen et al., 1984; Prablanc et al., 1979; Sailer et al., 2000). Furthermore, time-critical eye–hand coordination studies have shown that although most fixations are directed to the current reach location, some are directed toward locations relevant to future actions (Mennie, Hayhoe, & Sullivan, 2007; Pelz & Canosa, 2001). Our results suggest that these strategies may be related to directing attention to appropriate locations in order to process the properties of objects that will be goals of future reaching movements.

We note, however, that our findings are not related to a specific observation in some eye–hand coordination studies, namely that the eyes remain fixated at a reach goal until the end of the reach, before making a subsequent saccade elsewhere (Johansson et al., 2001; Neggers & Bekkering, 2000, 2001; Pelz & Canosa, 2001). Our study investigates the allocation of attention before the eyes arrive at a certain location, not after. Presumably, the tendency of the eyes to remain at the reach goal is due either to an attentional requirement at the reach goal or to the need for foveal acuity in order to guide the hand to its goal (Crawford et al., 2004; Johansson et al., 2001).

Neural mechanisms

As can be seen in Figures 1C and 1E, we propose that an endogenous saccade and/or reach plan directs attention. This could take the form of reach and saccade command signals sent to areas involved in perception that are modulated by attention such as V4 or MT (Motter, 1993; Reynolds, Pasternak, & Desimone, 2000; Spitzer, Desimone, & Moran, 1988; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996). It has been suggested that the attentional signal that modifies the activity of neurons in these areas originates from higher order areas in frontal or parietal cortex (Reynolds & Chelazzi, 2004). For example, the frontal eye field (FEF) has been shown to be involved
in both eye movement planning and attention (Moore & Armstrong, 2003; Moore & Fallah, 2004; Schall & Boucher, 2007; Thompson, Biscoe, & Sato, 2005) and is connected to higher visual areas (Moore & Armstrong, 2003; Moore & Fallah, 2004; Neggers et al., 2007). Alternatively, endogenous saccade command signals may be sent from FEF to the posterior parietal cortex (Khan et al., 2009; Moore & Armstrong, 2003; Neggers et al., 2007; Schall, Morel, King, & Bullier, 1995; Stanton, Bruce, & Goldberg, 1995), a key area involved in attention (Colby & Goldberg, 1999). Specifically, it has been proposed that the lateral intraparietal area (LIP) in the posterior parietal cortex (PPC) contains a saliency/relevance map that determines specific locations to be attended (Fecteau & Munoz, 2006; Goldberg, Bisley, Powell, & Gottlieb, 2006; Gottlieb, 2007; Steinmetz & Constantinidis, 1995). It may be that saccade command signals from FEF are used in LIP to determine where attention should be allocated. These signals are in turn sent back to higher visual areas involved in perception (Buffalo, Fries, Landman, Liang, & Desimone, 2010).

We suggest that a similar process could occur for reach plans. The dorsal premotor area (PMd) has been implicated in generating reaching movements and in reach-related target selection (Cisek & Kalaska, 2002, 2005; Pesaran, Nelson, & Andersen, 2008; Song & McPeek, 2009; Westendorff, Klaes, & Gail, 2010) and a number of studies have demonstrated attentional signals in this area as well (Boussaoud, 2001; Boussaoud & Wise, 1993; Lebedev & Wise, 2001). Anatomically, PMd has reciprocal connections to an area of PPC (Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003) sometimes known as the parietal reach region (PRR), which has also been shown to be involved in reach target selection (Pesaran et al., 2008; Scherberger & Andersen, 2007; Westendorff et al., 2010). This area, in turn, has reciprocal connections to higher visual areas such as V4 (Galletti et al., 2003).

Our findings suggest that attentional resources are shared to a certain degree, and, therefore, the attentional signals for the eye and hand movement goal locations presumably must converge at some level. One possibility is that they converge at the level at which perceptual discrimination takes place (e.g., V4). In this case, attentional signals for the eye and hand movement goal locations would remain separated at the level of FEF and PMd or at the level of PPC, with eye-related attentional signals occurring in LIP (Bisley & Goldberg, 2003a, 2003b, 2010; Goldberg, Bisley, Powell, Gottlieb, & Kusunoki, 2002) and reach-related attentional signals occurring in PRR (Pesaran et al., 2008; Quian Quiroga, Snyder, Batista, Cui, & Andersen, 2006; Scherberger & Andersen, 2007). Alternatively, the attentional signals could converge at the level at which attention is allocated to certain regions in space (e.g., PPC). For example, it has been suggested that the salience/relevance map in LIP is effector independent (Berman & Colby, 2009; Gottlieb, 2007; Oristaglio, Schneider, Balan, & Gottlieb, 2006; Wardak, Olivier, & Duhamel, 2004) and has activity that is related to the locus of attention rather than just saccades (Bisley & Goldberg, 2003b; Quian Quiroga et al., 2006), just as it has been proposed to be feature independent (Itti & Koch, 2001). LIP could thus act as an effector-independent supervisory attentional control map in the brain.

Relationship to previous studies

There have been very few studies that have directly compared attentional allocation during simultaneous eye and hand movements to the same or different locations. Recently, Jonikaitis and Deubel (2009) showed evidence for independent attentional resources for the eye and hand; discrimination performance did not decrease at either movement location when they were separated. In contrast, we propose shared attentional resources since discrimination performance decreased (for the hand) when the hand and eyes were directed to different locations. These differences in results may be due to task difficulty: we required subjects to perform a 4 AFC, while their task used a 2 AFC. It is likely that we would have observed performance similar to what was observed by Jonikaitis and Deubel (2009) if our task had been easier. Taking both studies together, we conclude that attention can be directed separately, to a certain extent, to reach and saccade goals. We also propose that the attentional resources involved in saccades and reaches are limited and shared, but that the amount of attention available may be sufficient for good shape discrimination performance at both the reach and eye goals, depending on the difficulty of the task.

Conclusions

We measured perceptual discrimination performance when saccades and reaches were made alone, together to a common goal, or together to different goals. We found that performance was consistently good at the saccade goal across irrespective of the task condition, whereas performance at the reach goal varied across conditions. Based on these results, we conclude that attentional resources are shared between the eyes and hand, and that attention is more strongly linked to the saccade goal than to the reach goal.

Acknowledgments

We thank Dr. G. Blohm for comments and discussion on the manuscript. AZK was supported by Canadian
Institutes for Health Research (CIHR, Canada) and Heart and Stroke (Canada) fellowships. RMM and JHS were supported by NIH EY04885.

Commercial relationships: none.

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References


Gersch, T. M., Kowler, E., & Dosher, B. (2004). Dynamic allocation of visual attention during the execution of


