Hand Position Affects Saccadic Reaction Times in Monkeys and Humans

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Thura D, Boussaoud D, Meunier M. Hand position affects saccadic reaction times in monkeys and humans. J Neurophysiol 99: 2194–2202, 2008. First published March 12, 2008; doi:10.1152/jn.01271.2007. In daily life, activities requiring the hand and eye to work separately are as frequent as activities requiring tight eye–hand coordination, and we effortlessly switch from one type of activity to the other. Such flexibility is unlikely to be achieved without each effector “knowing” where the other one is at all times, even when it is static. Here, we provide behavioral evidence that the mere position of the static hand affects one eye movement parameter: saccadic reaction time. Two monkeys were trained and 11 humans instructed to perform nonde- layed or delayed visually guided saccades to either a right or a left target while holding their hand at a location either near or far from the eye target. From trial to trial, target locations and hand positions varied pseudorandomly. Subjects were tested both when they could and when they could not see their hand. The main findings are 1) the presence of the static hand in the workspace did affect saccade initiation; 2) this interaction persisted when the hand was invisible; 3) it was strongly influenced by the delay duration: hand–target proximity retarded immediate saccades, whereas it could hasten delayed saccades; and 4) this held true both for humans and for each of the two monkeys. We propose that both visual and nonvisual hand position signals are used by the primates’ oculomotor system for the planning and execution of saccades, and that this may result in a hand–eye competition for spatial attentional resources that explains the delay-dependent reversal observed.

INTRODUCTION

Psychophysical research has heretofore focused on skilled behaviors requiring tight eye–hand coordination toward a common goal (e.g., Prablanc et al. 1979). However, in daily life, activities requiring the hand and eye motor systems to work separately (driving, reading, typing, playing music, etc.) are as frequent, if not more. Also, we ceaselessly need to switch from one type of activity to the other. Such flexibility is unlikely to be achieved without each effector “knowing” where the other one is at all times, even if it is static and unneeded for the current task. There is some evidence that the static eye position affects hand movements (Blouin et al. 2002; Bridge- man and Stark 1991; Henriques et al. 1998). Here, we endeavor to provide behavioral evidence that this static effector influence is reciprocal.

The strongest support for a mutual influence of static effectors comes from recording studies in monkeys. In an early study, one of us showed that neuronal activity coding arm movements in the dorsal premotor area (Boussaoud et al. 1998; see also, e.g., Pesaran et al. 2006) varies according to the static eye position in the orbit. Recently (Thura et al. 2008), we addressed the converse issue by recording from the frontal eye field (FEF) of two monkeys performing delayed saccades while holding their hand either near or far from the eye target. Neurophysiological results were clear-cut: more than half of the saccadic neurons of this major oculomotor area integrate hand position signals to encode visually guided saccades. This was true irrespective of whether the animals could see their hand, indicating that FEF receives both visual and nonvisual information from the hand.

Behavioral data were less straightforward. Our prediction was that hand–target spatial congruency would reduce saccadic reaction times since 1) saccade latencies tend to decrease when a somatosensory stimulus is presented at the same spatial location as the visual target (Amflot et al. 2003; Groh and Sparks 1996) and 2) the hand presence near a stimulus enhances visual processes (Brown et al. 2008; di Pellegrino and Frassinetti 2000; Reed et al. 2006; Schendel and Robertson 2004). Data collected in the course of FEF recordings only partly fulfilled this prediction because congruency reduced saccadic latencies for only one specific preparatory delay (500 ms for one animal, 1,000 ms for the other).

The present behavioral study was thus undertaken 1) to ascertain that hand position, whether visible or nonvisible, reliably affects saccadic reaction times and 2) to elucidate the influence of the delay duration on this modulation. The effects of hand position on saccadic latencies were measured for the experimentally delayed saccades typically used to dissociate stimulus- from motor-related activity in neurophysiology, as well as for natural, nondelayed saccades. The exact same protocol was applied to the two monkeys involved in FEF recordings and to a group of 11 human volunteers. Because an influence of the static hand on saccadic reaction times has never been reported before, this cross-species comparison was necessary to determine to what extent findings from recording studies in monkeys can shed light on the human brain implementation of eye–hand interactions.

METHODS

Subjects

Two monkeys and 11 humans participated to the study. The monkeys were the same two adult males as reported in Thura et al. (2008): a Macaca fascicularis (monkey A) and a Macaca mulatta (monkey S). The behavioral data collected earlier during FEF recordings were included in the present results. All procedures involving the monkeys were in accordance with the European Community’s Council Directive for the Care and Use of Laboratory Animals (86/609/EC). The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
The humans were six female and five male adult volunteers, ranging in age from 24 to 54 yr (mean age 32.9 ± 10.5 yr). Ten were naïve with respect to the experiment. Nine were right-handed and two left-handed, as assessed by a French adaptation of the Edinburgh Handedness Scale (Oldfield 1971). Experiments were conducted in compliance with the French Law (Titer I and II du Code de la Santé Publique) and with the understanding and consent of each subject. Each of them was free from self-reported neurological impairments affecting ocular control and had normal or (for three of them) corrected-to-normal vision.

**Experimental setup and data acquisition**

Monkeys were trained and humans were instructed to perform visually guided saccades while holding their hand at one of two possible locations on a touch screen. All human subjects (whether right- or left-handed) and monkey A performed the task using their right hand, whereas monkey S used his left hand. Monkeys were trained and humans instructed to keep the other, nonacting hand at rest under the screen; during testing sessions, the actual behavior of the subject was monitored via a videocamera placed above his/her head. Monkeys were seated in a primate chair with the head fixed to the chair. Humans sat on a regular chair with head stabilized by use of a bite bar. Eye position was recorded at 250 Hz using an infrared camera (ISCAN). Subjects faced a resistive touch screen (36 × 27 cm) inclined at a 45° angle under a mirror onto which stimuli were projected from a computer monitor positioned above their heads (Fig. 1A). The semireflective properties of the mirror made the visual stimuli appear as if located on the underneath touch screen together with the hand. In this condition (“hand visible”), saccades were made while hand position was provided through both vision and proprioception. Insertion of a black paper board under the mirror made it fully reflective. Under this condition (“hand invisible”), visual stimuli still appeared on the touch screen, but the hand was invisible to the subjects. Saccades were thus made whereas hand position was felt only through nonvisual signals. Stimulus presentation and behavioral data acquisition were controlled using CORTEX software (http://www.cortex.salk.edu).

**Design**

A trial began with the presentation of a white square (2 × 2”) at the bottom left or the bottom right part of the screen. This stimulus instructed the subject to put his/her hand on the touch screen at that location (Fig. 1B) and was turned off when the hand contacted the touch screen. A fixation point (FP, white circle, 0.25° diameter) then appeared immediately at the (apparent) screen center, which the subject had to fixate without moving his/her hand. After 500 ms of fixation, a peripheral target (a white square, 1 × 1”) appeared at one of two possible locations, immediately above the hand positions at 10.3° from the screen center (two other targets located in the upper part of the screen were used in monkeys to study the sensory and/or motor fields of FEF neurons but these data were excluded from the present comparative study). Extinction of the FP served as a Go signal for saccade execution. In the nondelayed saccade task, target onset coincided with the Go signal. In the delayed saccade task, a delay period was introduced between target onset and the Go signal (Fig. 1C). Monkeys were submitted to two delays, 500 and 1,000 ms; humans to only one, 1,000 ms. Likewise, the stringent criteria used to define correct saccades for the extensively trained monkeys (duration <75 ms and 300-ms fixation within ±1.5° around the target center) were softened for naïve humans (duration <100 ms and 300-ms fixation with a ±2° precision). The hand vision condition and delay length were kept stable within each block of trials, varying only across blocks, whereas the target and hand positions changed on a trial-to-trial basis, based on a pseudorandom order within each block.

Monkeys received a liquid reward for each correct response. Their daily testing sessions varied in length depending on their motivation and included several blocks of nondelayed or delayed saccades, with or without hand vision. Before testing, humans were instructed to “make a saccade toward the target promptly at the Go signal and then fixate it as precisely as possible”; they received no response feedback during testing. Each human subject participated in two sessions on two separate days, one for the nondelayed and one for the delayed saccade task. Each session lasted about 40 min and consisted of a total of 144 trials separated in two blocks of 72 trials, one for each hand vision condition. Within each block, 18 trials were presented per hand–target configuration in a pseudorandom order. The order of sessions and blocks was balanced between subjects.

**Data analysis**

The ISCAN analog output was recorded in a CORTEX file and analyzed off-line with the use of a MATLAB routine (MathWorks, Natick, MA). The detection of saccade onset, used to determine the reaction time to the target, was based on a strict 1° threshold. For each condition and each subject, the average reaction time was calculated for each block of trials (18 trials) and for all blocks. The reaction times were then converted to a percent reaction time distribution for each condition. The mean reaction time for the nondelayed condition and the delayed condition of 500-ms delay, 90% was respectively 219 ± 27 ms and 230 ± 31 ms. The mean reaction time for the delayed condition of 1000 ms was respectively 232 ± 35 ms. The mean reaction time for the hand invisible condition was respectively 217 ± 32 ms for the nondelayed condition, 230 ± 35 ms for the delayed condition of 500 ms, and 234 ± 36 ms for the delayed condition of 1000 ms.
saccadic reaction times (SRTs), was performed by differentiating the eye position signals. The beginning of the saccade was defined as the first moment in time after the Go signal at which the eye velocity exceeded a fixed threshold, set at 50°/s for monkeys and as close as possible to 50°/s (generally 70°/s) for humans whose looser head fixation yielded a poorer signal-to-noise ratio. For both species, trials with SRTs <80 or >500 ms, i.e., early and late responses, respectively, were excluded from analysis.

For each target, two hand–target spatial configurations were possible: the “congruent” configuration, when the hand was near the target, and the “noncongruent” one, when the hand was far from it. ANOVAs were used to determine the effects of four factors on SRTs: hand vision (hand visible vs. hand invisible), delay duration (0, 500, 1000 ms in monkeys; 0 vs. 0.1000 ms in humans), target position (right vs. left), and hand–target spatial configuration (congruent vs. noncongruent). For humans, SRTs were averaged for each subject and each testing condition and analyzed using a four-way ANOVA with repeated measures for each factor, and paired t-tests for within-condition comparisons. For monkeys, ANOVAs and t-tests were performed separately for each animal, without repeated measures, due to highly variable numbers of trials across conditions.

RESULTS

Hand position effects on SRTs in monkey A

Monkey A performed an average of 192 ± 20 trials per condition (range: 61–405), with the right hand, for a total of 4,599 trials. Mean SRTs for each condition are illustrated in Fig. 2. The 2 × 3 × 2 × 2 ANOVA showed that all main effects, except hand–target configuration, were significant. Monkey A was slower to respond as the delay increased [131.8 ± 1.2, 231.2 ± 1.2, and 317.4 ± 2.2 ms for 0, 500, and 1,000 ms, respectively; \(F_{(2,4575)} = 2.299.8, P < 0.001\)], slower when he could not see his hand than when he could see it [253.7 ± 1.9 vs. 221.4 ± 1.8 ms, respectively; \(F_{(1,4575)} = 43.6, P < 0.001\)] and, to a lesser extent, slower for the right target, ipsilateral to his acting hand, than for the left one [237.9 ± 1.6 vs. 231.4 ± 2.4 ms, respectively; \(F_{(1,4575)} = 17.6, P < 0.001\)]. Consequently, monkey A’s longest SRTs occurred for saccades made to the right target after a 1,000-ms delay while the hand was invisible (321.0 ± 4.5 ms).

Interactions revealed that hand–target configuration also affected SRTs, but in different directions depending on the delay [configuration × delay: \(F_{(2,4575)} = 12.2, P < 0.001\)] and this delay-dependent reversal was most marked for the target ipsilateral to the acting arm [configuration × delay × target: \(F_{(2,4575)} = 7.2, P = 0.001\)]. By contrast, irrespective of whether the hand was visible did not significantly modify the impact of its position on SRTs [configuration × vision: \(F_{(1,4575)} = 0.0, n.s.;\] configuration × vision × target: \(F_{(1,4575)} = 0.0, n.s.;\] and configuration × vision × target × delay: \(F_{(2,4575)} = 0.4, n.s.\). Although somewhat attenuated (see Fig. 2), the hand position impact on saccade initiation persisted when the hand was invisible.

Separate t-tests were conducted for each delay and target on SRTs pooled across vision conditions to further specify hand–target configuration effects (Table 1). For the ipsilateral target, the congruent configuration produced a 13% increase in SRTs relative to the noncongruent one without delay and a 4% increase with 500-ms delay, whereas it yielded a 7% decrease with 1,000-ms delay. For the contralateral target, the same delay-dependent reversal occurred but the amplitude of the changes was reduced and only the 6% increase observed for nondelayed saccades reached significance.

Hand position effects on SRTs in monkey S

Monkey S performed an average of 219 ± 15 trials per condition (range: 96–359), with the left hand, for a total of 5,259 trials. The 2 × 3 × 2 × 2 ANOVA yielded the same three main effects (delay, hand vision, and target) as in monkey A. Like monkey A, monkey S was slower to respond as the delay increased [208.8 ± 1.0, 255.3 ± 1.0, and 286.9 ± 0.9 ms for 0, 500, and 1,000 ms, respectively; \(F_{(2,5235)} = 1.420.4, P < 0.001\)] and somewhat slower for the target ipsilateral to his acting hand than for the contralateral target [248.0 ± 1.0 vs. 241.3 ± 1.0 ms, respectively; \(F_{(1,5235)} = 38.1, P < 0.001\)].

![Fig. 2. Effects of hand–target spatial configuration on saccadic reaction times (SRTs) in monkey A. Mean saccadic latencies (±SE) are illustrated for the 2 possible hand–target configurations (i.e., congruent vs. noncongruent), for the left and right target locations (left and right columns, respectively), and the 0- and 1,000-ms delay durations (top and bottom rows, respectively), while the hand was either visible (solid line, black diamonds) or invisible (dashed line, open squares). The * symbol indicates a significant configuration effect as revealed by separate t-tests for each configuration and hand vision condition (P < 0.05).](image-url)
TABLE 1.  Mean saccadic reaction times (averaged across vision conditions) and hand–target (H-T) configuration effect

<table>
<thead>
<tr>
<th></th>
<th>Left Target</th>
<th></th>
<th>Right Target</th>
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<tbody>
<tr>
<td></td>
<td>Congruent</td>
<td>Noncongruent</td>
<td>H-T Configuration Effect, ms</td>
<td>Congruent</td>
</tr>
<tr>
<td><strong>A. Monkey A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No delay</td>
<td>127.5 ± 2.3</td>
<td>120.5 ± 1.9</td>
<td>+7.0**</td>
<td>147.9 ± 2.5</td>
</tr>
<tr>
<td>Delay, 500 ms</td>
<td>225.8 ± 3.7</td>
<td>229.8 ± 3.3</td>
<td>−4.0</td>
<td>238.4 ± 2.0</td>
</tr>
<tr>
<td>Delay, 1,000 ms</td>
<td>311.6 ± 4.3</td>
<td>317.3 ± 4.1</td>
<td>−5.7</td>
<td>308.7 ± 4.5</td>
</tr>
<tr>
<td><strong>B. Monkey S</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No delay</td>
<td>218.7 ± 2.1</td>
<td>209.9 ± 1.8</td>
<td>+8.7***</td>
<td>202.7 ± 2.2</td>
</tr>
<tr>
<td>Delay, 500 ms</td>
<td>249.8 ± 2.1</td>
<td>260.1 ± 2.0</td>
<td>−10.2***</td>
<td>257.2 ± 1.7</td>
</tr>
<tr>
<td>Delay, 1,000 ms</td>
<td>293.9 ± 1.7</td>
<td>290.9 ± 1.7</td>
<td>+3.0</td>
<td>282.1 ± 1.8</td>
</tr>
<tr>
<td><strong>C. Humans</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No delay</td>
<td>262.6 ± 11.2</td>
<td>251.0 ± 11.6</td>
<td>+11.6**</td>
<td>269.0 ± 12.2</td>
</tr>
<tr>
<td>Delay, 1,000 ms</td>
<td>263.9 ± 13.4</td>
<td>265.3 ± 12.9</td>
<td>−1.4</td>
<td>258.1 ± 12.3</td>
</tr>
</tbody>
</table>

Values are means ± SE; bold; *P < 0.05, **P ≤ 0.02, ***P ≤ 0.002.

Contrary to monkey A, though, monkey S responded faster when he could not see his hand than when he could see it [235.9 ± 1.2 vs. 250.1 ± 0.9 ms, respectively; \(F_{(1,5235)} = 119.0, P < 0.001\)]. Importantly, monkey S confirmed that hand position modified SRTs in opposite directions depending on the delay length [configuration × delay: \(F_{(2,5235)} = 3.9, P = 0.02\)] and that this delay-dependent effect concerns mostly the target located in the hemifield ipsilateral to the acting hand, i.e., the left one for this animal [configuration × delay × target: \(F_{(2,5235)} = 10.0, P < 0.001\)] irrespective of hand vision conditions [configuration × vision: \(F_{(1,5235)} = 0.05, n.s.; configuration × vision × target: F_{(1,5235)} = 2.1, n.s.; configuration × vision × target × delay: F_{(1,5235)} = 0.5, n.s.\)]. In the case of monkey S (Table 1), the congruent configuration yielded a 4% increase in SRTs to the left target without delay and a 4% decrease with 500-ms delay; all other changes failed to reach significance. Thus although the specific delay length triggering the reversal of the hand position effect differed across the two animals (1,000 ms for monkey A vs. 500 ms for monkey S), both displayed the same reversal affecting predominantly the ipsilateral target.

**Hand position effects on SRTs in humans**

GROUP PERFORMANCE. In humans, incorrect responses amounted to 5% of the nondelayed saccades and 12.8% of the delayed saccades and were excluded from the analyses. SRTs recorded during correct trials were averaged for each subject and each testing condition. Group means are illustrated in Fig. 3 for each condition. The four-way ANOVA yielded no main effect of delay [\(F_{(1,10)} = 0.4; n.s.\)], hand vision [\(F_{(1,10)} = 3.5; n.s.\)], or target [\(F_{(1,10)} = 0.05; n.s.\)] in naïve humans, suggesting that the global impact of these factors in monkeys reflects a species specificity and/or biases acquired through extensive training in the task. Also, unlike monkeys, humans showed a slight but significant main effect of the hand–target spatial configuration [\(F_{(1,10)} = 5.7; P = 0.04\)] because they were slower, overall, to initiate saccades when their hand was near the target than when it was far from the target.
(263.4 ± 4.4 vs. 258.5 ± 4.2 ms, for congruent and noncongruent trials, respectively).

Notwithstanding these differences, the four-way ANOVA yielded the same two interactions as those found in monkeys [configuration × delay: $F_{110} = 12.8; P = 0.005$; configuration × delay × target: $F_{110} = 11.5; P = 0.007$] indicating, respectively, that hand–target proximity either retarded or hastened saccade initiation depending on the delay length and that these changes were most salient for the target ipsilateral to the acting hand (the right one). No other interaction reached significance, confirming that, as in monkeys, precluding hand vision might reduce the impact of hand position on saccade initiation but did not suppress it. An example of this effect persistence across vision conditions is illustrated in Fig. 4 for nondelayed saccades to the right target in subject 6.

Separate t-tests for each delay and target on SRTs pooled across vision conditions (Table 1) yielded the exact same pattern of results as in monkey A. For the ipsilateral target, the congruent configuration produced an 8% increase in SRTs relative to the noncongruent one without delay; whereas it yielded a 4% decrease with 1,000-ms delay. For the contralateral target, the same delay-dependent reversal occurred but the magnitude of the changes was reduced and only the 5% increase observed for nondelayed saccades reached significance.

**INDIVIDUAL DATA.** Figure 5 provides, for each subject, the changes in mean saccadic latency (averaged across hand vision conditions) observed in the congruent hand–target spatial configurations relative to the noncongruent ones. These individual data confirm the different impact of hand position across targets. The deleterious effect of hand–target proximity on initiation of nondelayed saccade occurred in 9/11 participants (82%) and could reach an amplitude of +69 ms, for the right target, compared with 8 participants (73%) and a maximum of +30 ms for the left target. Likewise, the reversal produced by the 1,000-ms delay reached significance in 6/11 subjects (55%) and could amount to a gain of −43 ms for the right target, whereas it concerned only 3 subjects (27%) with a maximum gain of −26 ms for the left target (two subjects even showed opposite changes). Interestingly, the two left-handed subjects of the group (who nevertheless performed the task with their right hand) showed the same predominant impact on the right target. This suggests that the acting hand, rather than handedness, explains differences observed across targets.

**Hand position effects common to the two expert monkeys and naïve humans**

Despite the differences not only in species, but also in expertise in the task, similarities emerged between monkeys and humans, which are summarized in Fig. 6. In each of the two expert monkeys, as well as in the group of naïve humans, changes in SRTs due to hand position concerned mostly the visual target ipsilateral to the subject’s working arm and took opposite directions depending on the length of the delay. Nondelayed saccades were retarded by the congruent configuration. This deleterious effect of hand–target proximity was slightly attenuated when hand vision was prevented, but remained significant. When saccade initiation was delayed relative to target onset, the hand position effect was reversed in both species. Hand–target proximity then facilitated saccade initiation. This facilitation was also detectable when the hand was invisible, but this time the change observed in the absence of hand vision fell short of significance.

**DISCUSSION**

The present study had a threefold aim: 1) to confirm preliminary behavioral data suggesting that static hand position affects saccadic latency in monkeys; 2) to determine how hand vision, on the one hand, and delay length, on the other hand, modulate this effect; and 3) to delimit the extent to which overtrained monkeys constitute appropriate models of natural human eye–hand interactions. We found that the presence of the static hand in the workspace indeed affects saccade initiation. This interaction is still present and only partly reduced by...
the absence of hand vision. It is strongly influenced by the delay duration: hand–target proximity systematically retarded immediate saccades, whereas it could hasten delayed saccades. An additional, unexpected finding was that this delay-dependent impact of hand position on SRTs was most salient for the target ipsilateral to the acting hand. All the above-cited conclusions hold true for each of the two expert monkeys and for the group of naïve humans. We will discuss these findings in light of earlier psycho-physical and neuropsychological investigations of eye–hand co-ordination and visuospatial attention, before briefly evoking potential neurophysiological correlates of these findings.

Similar hand position effects in two expert monkeys and naïve humans

A major strength of the present study is the parallel testing of monkeys and humans using the same apparatus and quasi-identical procedures. Most of our knowledge about the neural underpinnings of eye–hand interactions rests on recordings obtained from macaque monkeys that have received extensive training on a single specific task. Thus potential pitfalls for neurophysiology are to study monkeys’ species-specific behaviors or idiosyncratic biases induced by overtraining, neither of which would likely shed light on human natural behavior.

In the present behavioral study, SRTs varied significantly with the delay, target, and hand vision condition only in monkeys. Species specificity may account for these monkey peculiarities. Also, it may well be that acquisition of a task through instruction (in humans) versus operant conditioning (in monkeys) is responsible for some of these differences. However, biases acquired over extensive training seem a more probable explanation, at least for the hand vision effect, because the two animals showed opposite patterns (monkey A responding more quickly for the visible hand, monkey S for the invisible hand). Overtraining-induced biases also likely explain the other idiosyncrasies of monkey S, i.e., 1) a reversal of the hand position effect occurring with preparatory delays of 500 ms, rather than 1,000 ms in monkey A and humans; and 2) the nonsignificant hand position effect for the target contralateral

![Figure 5: Impact of hand–target proximity on saccade initiation in each of the 11 human participants. SRTs averaged over both hand vision conditions are illustrated for nondelayed (open bars) and delayed (gray bars) saccades to the left and right targets. The bars represent the difference in SRTs in the congruent relative to the noncongruent configuration (in milliseconds) for each subject separately and for the group. Positive values mean that hand–target proximity lengthened SRTs, negative values that it shortened them (within-subject paired t-test, *P < 0.05, **P < 0.01). Immediate saccades were retarded, whereas delayed saccades were hastened. Whatever their direction, the changes observed for the right target, ipsilateral to the hand used by the participants, reached a greater amplitude and concerned a larger number of subjects than those observed for the left target. This asymmetry was not due to handedness because the two left-handed subjects (6th and 10th bars from left) also showed more prominent changes for the right target.]

![Figure 6: Comparison of the effects of visible (open bars) and invisible (gray bars) hand–target proximity on SRTs in monkeys (A and B) and humans (C). As in Fig. 5, the values were obtained by calculating the difference between mean SRTs in the congruent and noncongruent configuration, for the target ipsilateral to the subjects’ working hand, i.e., the right one for monkey A and humans, and the left one for monkey S. Monkeys A and S presented, like naïve human subjects, a delay-dependent reversal of the effect of hand–target proximity that was attenuated but not suppressed by the absence of hand vision (t-test, *P < 0.05).]
to the acting arm, again differing from both monkey A and humans.

Nonetheless, each of the two expert monkeys displayed, like naïve humans, a delay-dependent hand position effect for saccades to the target ipsilateral to the acting arm that was detectable in both vision conditions. This similarity confirms that monkey neurophysiology can provide valid insights into the neural bases of human eye–hand interactions.

Visual and nonvisual signals from the static hand affect saccadic latencies

Saccades characteristics were found to change when accompanied by an arm movement, both in humans (e.g., Epelboïm et al. 1997; Lünenberger et al. 2000; Mather and Fisk 1985; Neggers and Bekkering 2000) and monkeys (Snyder et al. 2002). The present study is the first behavioral evidence that, as surmised by Tipper et al. (2001), even when the hand is not performing a response toward the target, its mere position influences eye movement parameters.

Efferent motor signals (hand/arm commands) and afferent sensory signals (vision, touch, and proprioception) both contribute to the influence of arm movements on the oculomotor system (e.g., Ariff et al. 2002; Nanayakkara et al. 2003; Neggers and Bekkering 2001; Ren et al. 2006; van Donkelaar et al. 2004; Vercher et al. 1996). Here, the hand was static during saccade execution, but its position changed on a trial-to-trial basis and it had to be actively maintained on the screen during the trial. Efferent motor signals were therefore not nil, albeit less prominent than in the preceding studies combining arm movements with saccade execution. Among afferent sensory signals, vision predominated, the strongest influence being observed when subjects could see their hand. Yet, nonvisual signals, in particular perhaps proprioceptive inputs, also contributed since some changes in SRTs persisted when hand vision was prevented.

Delay-dependent hand–target configuration effects on SRTs: an eye–hand competition for attentional resources?

Direct interaction between oculo- and skeletomotor brain areas, as well as integration of sensory signals from the hand in oculomotor centers (see Fries 1984, 1985; Neggers and Bekkering 2002; Stuphorn et al. 2000; Werner 1993; Werner et al. 1997), surely contribute to the changes seen here, as evoked earlier. However, an additional mechanism is necessary to explain the delay-dependent reversal of the hand position effect. One possibility relates to the temporal dynamics of spatial attention orientation. The capture of a particular stimulus by attention is short-lived: it varies across tasks and species, but remains inferior to 500 ms (Posner and Cohen 1984). After that, attention is slower to return to the previously inspected location, favoring instead new locations (for a review see Klein 2000). This inhibition of return (IOR), classically described for visual stimuli (Posner and Cohen 1984), also exists for tactile cues (Spence et al. 2000; Tassinari and Campara 1996). In our case, hand position was determined anew at the start of each trial. Visual and/or somatosensory signals from the hand could thereby attract spatial attention toward the hand location for a short time after hand positioning. However, by the end of the 500-ms fixation separating hand positioning from target onset, the IOR phenomenon likely yielded a new spatial attention shift, this time away from hand location. Nondelayed saccades being initiated immediately at target onset would thus fall during this IOR to the hand location—thus the longer SRTs for the congruent hand–target configuration. By contrast, due to the additional (preparatory) 500- or 1,000-ms period, delayed saccades intervened about 1,000 or 1,500 ms after hand positioning. Such delay would at least release the IOR or even allow still another spatial attention shift, back to the hand position, and thus the SRTs that were either unchanged or shortened for delayed saccades in the congruent configuration.

Although speculative, this idea of a dynamic eye–hand competition for attentional resources is supported by the recent findings reported by Neggers and Bekkering (2000, 2001), showing that humans cannot initiate a saccade to a second target until their visible or invisible hand has reached a first one. This finding suggests that there exists a spatial attention enhancement around the hand movement target that precludes eye movements. The temporal dynamics of this competition could also explain the variability of arm movement effects on SRTs, some authors observing a decrease (Lünenburger et al. 2000), whereas others report no significant effect (Epelboïm et al. 1997; van Donkelaar et al. 2004), or an increase (in humans: Bekkering et al. 1994, 1995; Mather and Fisk 1985; in monkeys: Snyder et al. 2002). Finally, our proposal is not incompatible with the facilitation of visual processes (e.g., target detection) observed in the hand presence in both normal (Reed et al. 2006) and brain-damaged humans (Brown et al. 2008; di Pellegrino and Frassinetti 2000; Schendel and Robertson 2004). Indeed, in these experiments the hand was kept static both within and across trials; its presence thus may have acted as a steady spatial attention attractor, rather than triggering shifts of attention as in our paradigm.

Predilection of hand position effects for the target ipsilateral to the acting hand: a challenge for future studies

Hand position effects on saccadic latencies were more pronounced for the target ipsilateral to the acting hand in monkeys and humans alike. This difference was related to the hand involvement in the task, rather than to subjects’ handedness because both right- and left-handed humans, performing the task with the right hand, all displayed more marked effects for the right target. A similar behavioral bias was noted in one earlier study (Lünenburger et al. 2000), but remains unexplained.

Because most of our subjects (12/13) performed the task with their right hand, the possibility that this bias reflects a right-hand peculiarity cannot be ruled out. However, in light of recent neurophysiological evidence obtained by Oristaglio et al. (2006), an effector-specific effect seems more likely. Neurons in the lateral intraparietal (LIP) area, known to be involved in attentional and oculomotor processes, were found to be modulated by the active limb, irrespective of its spatial location. Moreover, some neurons were most responsive for visual cues appearing in the hemifield ipsilateral to the active limb. These neural properties, together with the present unexpected behavioral finding, raise the interesting possibility that sensory stimuli close to the effector currently involved in a task are processed differently in the brain. It may be worthwhile to
test this hypothesis in the future by comparing hand position effects in the same subjects depending on whether they perform the task with the right hand, the left hand, or both.

Neuronal implementation

Areas devoted to the planning of hand movements are known to contain neurons whose properties integrate signals from the eye, whether moving or static (e.g., Batista et al. 1999; Battaglia-Mayer et al. 2006; Boussaoud et al. 1993, 1998; Jouffrais and Boussaoud 1999; Mushiake et al. 1997; Pesaran et al. 2006; Snyder et al. 2000; Stuphorn et al. 2000). There is now growing evidence that, reciprocally, oculomotor areas, including the superior colliculus (Meredith and Stein 1986; Werner 1993; Werner et al. 1997), the supplementary eye field (Mushiake et al. 1996), and LIP (Oriostiglio et al. 2006), integrate signals from the hand, at least when it is moving. We recently demonstrated that another oculomotor area, the FEF, does integrate signals from the hand, even when static. Hand position modulates saccadic activity within the FEF (Thura et al. 2008) and preliminary data indicate that this holds true as well for FEF visual responses (Thura et al. 2007). Taken together with the present behavioral data, these neurophysiological findings suggest that the mere position of the hand influences visually guided saccades not only during the late preparatory phase preceding movement execution but also, very early on, during the presentation and encoding of the visual target. Hand position signals thus appear to influence neuronal processes underlying target selection and oculomotor exploration of space.

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