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Influence of arm movements on saccades in humans

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Abstract

When reaching for an object we usually look at it before we touch it with the hand. This often unconscious eye movement prior to the arm movement allows guiding of the final part of the hand trajectory by visual feedback. We examined the temporal and spatial coordination of this control system by psychophysical measurements of eye and arm movements of naive human subjects looking or looking and pointing as fast as possible to visual targets in physical and virtual-reality setups. The reaction times of saccades to a step-displaced target were reduced, and the number of corrective saccades decreased, when the subject had to produce a corresponding simultaneous hand movement to the same target. The saccadic reaction time was increased when saccade and hand movement went in opposite directions. In a double-step task the reaction time for the second saccade was longer than for the first. Co-use of the hand leads to an additional increase of saccadic reaction time. Taken together this study shows an improvement in initial saccades if they are accompanied by hand movements to the same target. This effect might ensure that the reach target is foveated early and accurately enough to support the visual feedback control of the hand near the target. Longer reaction times for the second saccade to double-step displaced targets might reflect a saccadic refractory time intensified by simultaneous arm movements. These results are discussed in the light of recent findings from our laboratory on saccade- and reach-related neurons in the superior colliculus of macaque monkeys.

Introduction

Orientating movements with the eyes or with eyes and hand towards a visible target, such as to grasp an object with the hand or, in our times, to press a button, are common behaviours in everyday life. Usually we first make a rapid gaze shift (eye-head-body movement) to the target and fixate it until the hand arrives, although we would be able to reach without vision of the hand, as we do in many routine tasks or in the dark. Eye movements consist in this context mainly of a sequence of saccades and fixation. When orientating gaze and hand, the hand movement will usually follow the gaze shift.

Such visually guided behaviour relies strongly on the coordination of gaze and limb movement. To achieve optimal performance, gaze has to arrive at the target before the hand (timing), has to go there as directly and precisely as possible (accuracy) and has to stay there until the hand has reached its goal (stability). These three aspects allow effective visual guidance of the hand (Prablanc *et al*., 1979; Biguer et el., 1982; Mather & Fisk, 1985; Prablanc *et al*., 1986; Vercher *et al*., 1994). Important for the temporal coordination between eye and hand is the arrival of the hand movement at the target rather than the start (Helsen *et al*., 1997, 1998).

To examine the oculomanual interference Mather & Fisk (1985) presented visual and auditory stimuli as targets to their subjects. The subjects were asked to orientate their gaze and/or hand from the central visual or auditory target to a peripheral visual or auditory target as quickly and accurately as possible. An increased reaction time of the saccades was reported for trials in which the subject had to move eyes and hand compared to trials with only eye movements. Later Bekkering *et al*. (1994; 1995) obtained similar results, whilst Megaw & Armstrong (1973) and Neggers & Bekkering (1999) did not, although both latter studies describe an interaction of eye and hand in other parameters. These controversial findings and their contradiction to the biological advantages of earlier target fixation during a reach lead to our study.

A temporal gap between switching off the visual fixation target and switching on the saccade target has long been known to reduce saccadic reaction times – the 'gap effect' – (Saslow, 1967; Fischer & Ramsperger, 1984). This gap also has a reducing effect on manual reactions times (Fischer & Rogal, 1986; Bekkering *et al*., 1996; Pratt *et al*., 1999), yet the influence of a simultaneous arm movement on the gap effect was only peripherally touched on by Bekkering *et al*. (1996) and will be addressed again in this study.

Also, the influence of arm movements on the precision of the saccades has not been described so far and is another subject of this investigation.

Furthermore, effects of interference between eye- and arm-control systems are so far unknown when a single target is displaced during the ongoing reach movement. Under these circumstances both eye and hand trajectories have to be corrected for the new position of the target. Earlier studies (Feinstein & Williams, 1972) showed that for a sequence of saccadic eye movements the reaction time for the second saccade is longer in a systematic way for different interstimulus intervals. The question of our present study about the interplay of eye and arm movements was studied previously by looking at online hand trajectory corrections (Prablanc & Martin, 1992) and perception of object constancy (Blouin *et al*., 1995). The possibility that ongoing hand movements could improve gaze stability by preventing the initiation of saccades was only recently examined by Neggers &

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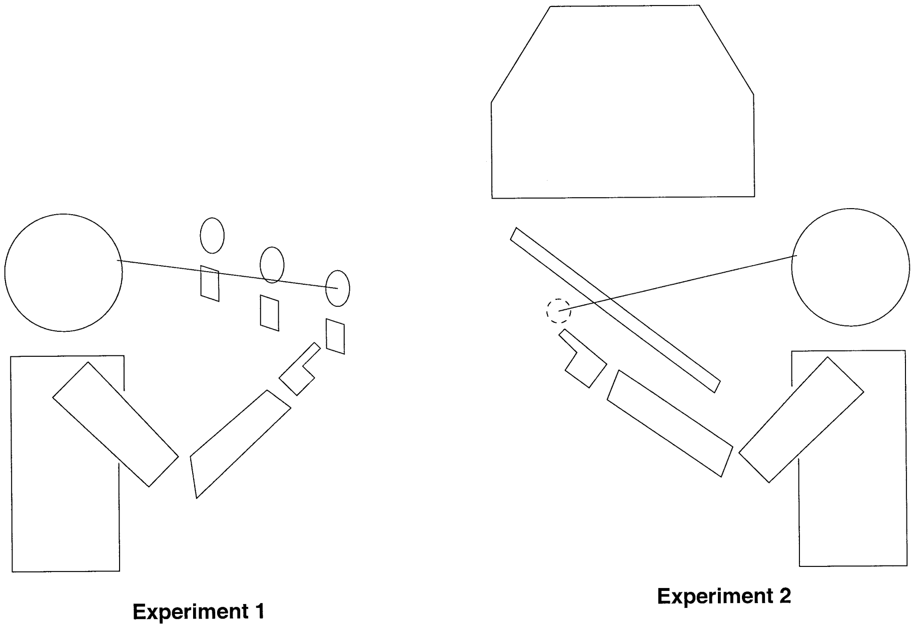

FIG. 1. Subjects had to produce goal-directed movements with their eyes (saccade task, ST) or with their eyes and hand (saccade–reach task, SRT). (Experiment 1) In the single-step experiment the targets consisted of red LEDs for eye movements and were located 3 cm above Morse buttons as targets for arm movements. The central target was straight ahead, the peripheral targets 29 ° eccentric. (Experiment 2) In the double-step experiment the subject viewed a monitor via a half-silvered mirror. The computer-generated targets (red balls of 1.2 cm diameter) appeared to the subject to be in the space behind the mirror. Subject's head movements were restricted by a chin rest in both experiments. In the control experiment a wooden plate was placed vertically such that the targets appeared on its surface.

Bekkering (2000). It was shown that subjects did not make an eye movement away from this target until their hand movement to it was completed.

The dominant brain structures controlling saccadic eye movements are the cortical frontal eye fields as well as the lateral intraparietal cortex and the subcortical superior colliculus (SC) (for review see Wurtz & Goldberg, 1989; Sparks & Mays, 1990). While no modulation of frontal eye field neurons by arm movements is reported so far, such modulations are known in the parietal cortex (Batista *et al.*, 1999) and SC (Werner, 1993; Werner *et al.*, 1997a,b; Stuphorn *et al.* 2000).

Preliminary data of this study has been published previously in abstract form (Kutz *et al.*, 1998; Lünenburger *et al.*, 1999).

Materials and methods

Experimental setup and data acquisition

Single-step experiment

The experimental setup consisted of a table with a chin rest to limit head movements. Three vertically mounted Morse buttons (3 cm diameter) were placed on the table in a frontoparallel plane 42 cm from the chin rest and an LED was attached 3 cm above each button (Fig. 1, Experiment 1). The central button was straight ahead on the midline. The other two buttons had a distance of 21 cm from the central button, corresponding to a 29 ° visual angle. Subjects did not perceive the LED and the button as different targets for eye and arm. This experiment was carried out in a dark room under visual open-loop conditions for arm control. Horizontal eye movements of both eyes were recorded by the infrared cornea reflection system OBER2 (Permobil Meditech AB, Sweden) at a rate of 600 Hz. Events of pressing and releasing a button were electronically detected and stored by the eye-tracking system.

Double-step experiment

In the double-step experiment subjects reached for virtual objects generated by a graphics workstation and displayed on a monitor with the screen tilted downwards (Fig. 1, Experiment 2). The screen with the target pictures (red balls of a diameter of 1.2 cm) was viewed via a half-silvered mirror, such that the image appeared in a fronto-parallel plane 44 cm in front of the subject. The virtual balls seemed to float in the space behind the mirror. This virtual reality approach allowed placement of targets at arbitrary positions and their instant displacement. Furthermore, the perception of object constancy was improved; it was the one ball which jumped around and not different balls/LEDs that lit up occasionally. A small light behind the mirror allowed visual feedback of the hand. With this light the targets, the subject's right hand and the black lab wall (at a distance of ≈ 80 cm) were visible. Horizontal eye movements of both eyes were recorded by the infrared cornea reflections system OBER2 at a rate of 600 Hz. Head movements were constrained by a chin rest. The position of the fingertip of the index finger of the preferred right hand was determined by the magnetic motion tracker miniBIRD (Ascension Technology Corp., USA) operating at a rate of 100 Hz. The lightweight sensor was fixed to the ventral side of the fingertip whilst the cable was taped to the subject's right arm near the wrist, elbow and shoulder joints and did not disturb the movements. All data were stored on computer hard disks and processed off-line by custom-made software (see Analysis).

To examine the influence of somatosensory feedback a control experiment was conducted in which a black wooden plate was placed vertically in the plane of the virtual target such that the subjects experienced some tactile feedback when reaching the target distance. In this experiment the motion tracker was fixed to the fingernail of the index finger.

Subjects

Fourteen subjects (five male, nine female, aged 21–31) participated in the single-step and seven (five male, two female, aged 21–33) in the double-step experiment; some participated in both experiments. All subjects were naive with respect to the experiments (except one in the double-step experiment). Subjects were students from the neurobiology classes given at the institute or members of the institute. All subjects were right-handed and participated voluntarily after giving informed consent. Eight subjects normally wear glasses of optical correction, which could not be used during the experiment except for one. Results did not differ for these subjects.

Tasks

Single-step experiment

In the saccade task (ST) the subject had only to move the eyes. The trial started with fixation on the illuminated central LED. After 1500–1700 ms the central LED was switched off and a peripheral LED was switched on randomly to the left or to the right of the extinguished fixation LED. The subject had to make a saccade to the illuminated target as fast as possible and fixate on it until it went off and the central LED came on again. In half of the trials a gap of 200 ms was inserted between fixation-off and target-on.

The coupled saccade–reach task (cSRT) was similar to the ST but included movements of the right hand to press the buttons. During initial fixation the subject had to press and hold the central button with the right hand. When the target was displaced to the peripheral position the subject had to make the saccade to the LED and to press, as fast as possible, the corresponding button and hold it until the end of the trial.

In the uncoupled saccade–reach task (uSRT) the trial started again with fixation on the illuminated central LED and holding of the central button, but now the subject had to self-paced initiate a hand movement to the right and press the right button as fast as possible with the right hand. When the subject's hand left the central button the computer switched off the central LED and illuminated randomly one of the peripheral LEDs. The subject had therefore to make a saccade, either to a target their hand was already travelling to or in the opposite direction. Preliminary tests with a 200-ms gap showed that subjects responded randomly with anticipatory saccades in the gap period, so we used no gap in uSRT (i.e. target-on coincided with fixation-off) in the trials reported here.

The subjects did blocks of 40 trials of ST, cSRT and uSRT and were instructed to act as fast as possible.

Double-step experiment

At the beginning of each trial a central circular red target appeared in the middle of the computer screen and was displaced after a fixation period of 1500–1700 ms randomly to the left or to the right by 10.2 cm (13.1°). After a delay of 300 or 500 ms the target was either moved back medially 5.1 cm (6.5°; 'step –1'), moved further peripherally 5.1 cm (6.0°; 'step +1') or stayed in place ('step 0') with equal probability of 0.33. After 1500 ms the target disappeared and after a blank screen for 100 ms the next trial began with the fixation target in the middle. This amplitude ratio of 0.5 is larger than the typical size of corrections (≈ 20%) and ensures individually programmed responses together with the delays of 300 ms (about manual reaction time) and 500 ms (hand travelled about halfway) (Becker & Fuchs, 1969; Prablanc & Jeannerod, 1975). In the saccade task (ST) the subjects were instructed to look at the current position of the target at any time and therefore make saccades when the target was displaced. In the saccade–reach tasks (SRT) they had to additionally point at the target at its current position with the extended right index finger. (There was no task similar to uSRT in the double-step experiment so we refer only to SRT in this experiment.) During ST subjects could lay their right hand comfortably on their knee, whilst during SRT it constantly remained in the target space. ST and SRT trials were performed alternatingly in blocks of 48, 36 and 36 trials, such that a total of 240 trials per subject were recorded, i.e. 10 trials in each condition.

In the control experiment with the tactile feedback from the wooden plate the target was only single-step displaced from the central to a 15.3-cm eccentric position (19°) to the left or right. Subjects had to look or look and point to them without vision of their hand, similarly to ST and cSRT in the single-step experiment.

Analysis

The recorded horizontal eye traces were smoothed by convolution with a Gaussian function of width $\sigma = 12$ ms, visually inspected and erroneous trials (because of blinks or anticipatory responses) discarded (< 4% of all trials). A higher proportion (17%) had to be excluded during later inspection because of improper fixations.

For each trial we performed relative velocity threshold detection for the saccades [similar to Neggers & Bekkering (1999) and Meyer *et al.* (1988)]. The saccade start was defined as the first of three continuous samples for which the velocity was > 10% of peak velocity in a manually selected window around this saccade. Similarly saccade end was the first of three samples where velocity stayed < 10% of peak velocity. The primary saccade and up to two correction saccades in the single-step experiment, and in the double-step experiment one or two primary saccades (depending on task) and up to five correction saccades were detected per trial. The primary saccade is understood here as the voluntary saccade made according to the target step.

The distribution of saccadic reaction times was skewed in most conditions (difference between mean and median up to 10%), so the medians of saccadic reaction times were calculated and compared by the Wilcoxon rank-sum test. Remarks on significant differences and probabilities refer always to this Wilcoxon rank-sum test unless otherwise stated.

For analysis of the precision on a trial-by-trial basis the relative amplitude of the correction saccade was calculated as the difference between the size of the primary saccade and the total eye position change distance in that trial divided by this total eye position change distance (cf. Fig. 2). Undershoots of the primary saccade lead to negative, overshoots to positive results. A relative amplitude of the correction saccade of –0.2 means that the primary saccade covered only 80% of the total distance.

Results

Single-step experiment

Example traces from one subject

Example eye traces from an ST and a cSRT of one subject in the same session are plotted in Fig. 2 for movements to the right without gap between fixation-off and target-on. Above the cSRT traces, arrows indicate the times of release of the central button and pressing of the peripheral button. These cSRT traces show that after fixation-off and target-on at 0 ms the eye started to move and arrived at the target before the hand released the central button. It is already obvious from this raw data set that the saccadic reaction time in ST (≈ 200 ms) was longer than in cSRT, where it was ≈ 190 ms.

Saccadic reaction times

This observation is supported by calculation of the reaction times for the 562/720 valid trials in ST and 567/720 valid trials in cSRT. The remaining recorded trials had to be discarded because of blinks, anticipatory responses and, mainly, improper fixation. The median saccadic latency was 182 ms in ST and 177.5 ms in cSRT without gap, which shows a facilitation of 4.5 ms due to the hand movement ($P < 0.05$). Calculated separately for movements to the left and the right, the median latencies were, respectively, 180 vs. 178 ms and 186.5 vs. 175 ms (Fig. 3A and B, and Table 1) which indicates that

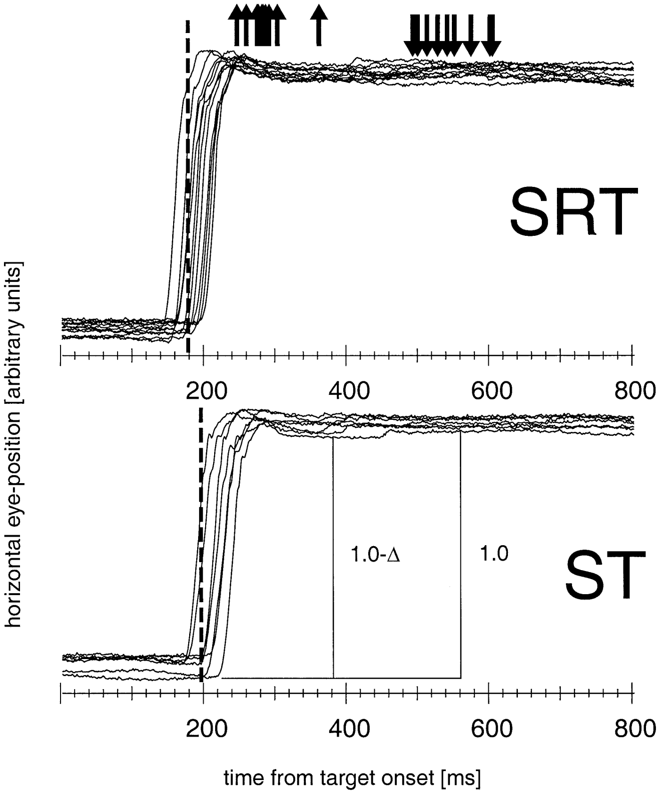

FIG. 2. Examples of horizontal eye traces from a naive subject in the single-step experiment. At time 0 the central fixation point went off and the right target appeared. The lower set of traces recorded in ST trials show a median latency of ≈200 ms (dotted line). The upper set of traces come from cSRT trials (reaction time ≈190 ms). The marks above the traces show the release of the central button (upward arrow) and pressing of the right target button (downward arrow). The eye started and completed the movements even before the hand started to move. It is already visible in these raw data that saccadic reaction time is shorter in SRT than in ST. The calculation of the relative size of the correction saccade is illustrated for one of the ST traces. For trials with correction saccades the size of the correction saccade was divided by the total eye position change.

the effect was more dominant for movements to the right (in right-handed subjects) ($P = 0.58$ and $P < 0.01$ for movements to the left and right, respectively).

The distribution of reaction times for these four conditions was not normal (Kolmogorov–Smirnov, $P < 0.0002$).

Gap effects of saccadic reaction times

The gap of 200 ms between fixation-point-off and target-on lead to shorter median saccadic latencies of 155 ms in ST and 146 ms in cSRT compared to the no-gap condition. This shows again a decrease of 9 ms with the simultaneous arm movement ($P < 0.05$). Again use of the right arm shows the larger difference in the medians for saccades to the right with 15 ms (162–147 ms; $P = 0.08$) than to the left with 3.5 ms (148.5–145 ms; $P = 0.33$) (Fig. 3C and D).

Proportion of correction saccades

In ST, 213 of 562 trials contained exactly the required saccade, 286 contained one detected and 63 two detected correction saccades. Hence in 349 ST trials the first saccade was incorrect. In cSRT, 318 of 567 trials contained exactly the required saccade, in 225 we detected one and in 24 two correction saccades. Therefore in 249 cSRT trials the first saccade was incorrect (Fig. 4A). The proportion

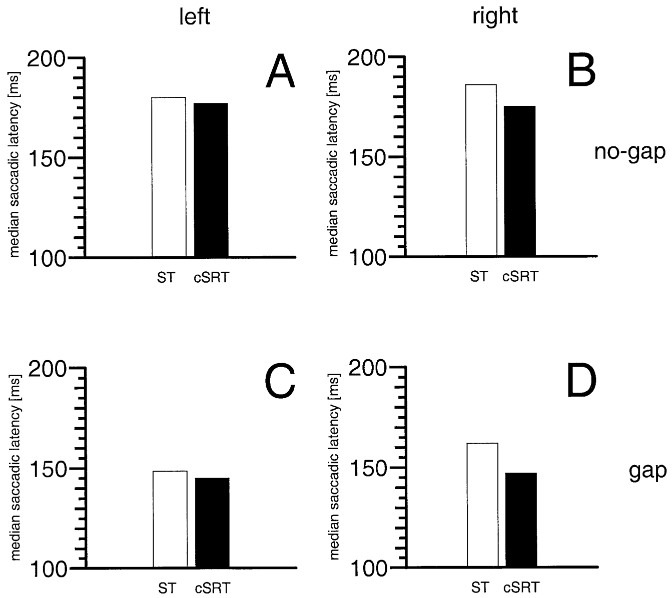

FIG. 3. Median saccadic reaction times in the saccade test (ST, outlined bars) and coupled saccade–reach task (cSRT, solid bars) for movements to the left (A and C) and to the right (B and D). No gap appeared in the trials depicted in A and B, whilst trials in C and D had a gap of 200 ms between fixation-point-off and target-on. The reaction time is in general shorter in cSRT than in ST. *P*-values were: A, 0.58; B, <0.01; C, 0.33; D, 0.08.

of 43.9% of trials with correction saccades in the cSRT trials (249 of 567) is significantly lower than the proportion of 62.1% (349 of 562) in the ST trials (z-test, $P < 0.01$).

Precision of primary saccade

The median relative size of the correction saccades over all subjects in trials with exactly one correction saccade was –4.15% in ST and –3.62% in cSRT trials (Fig. 4B). That means subjects undershot in both tasks, but less when they also had to move their hand to the same target ($P < 0.01$). Individual analysis showed this effect in 10 out of 13 subjects, whilst for three subjects the median was larger for cSRT than ST. One subject had only one trial with one correction saccade in the ST task and was excluded from this analysis.

However, the scatter of the endpoints of the first saccades (measured as interquartile distance) was in most subjects (9 of 13) larger in cSRT than in ST (cf. Fig. 4C). This means that although the first saccade landed more often nearer to the target its endpoints were more scattered.

Gap effects on manual reaction times and movement times

The reaction times for the arm movements in cSRT were calculated as time from target-on to release of the electrical contact in the central button. This reach reaction time was 214 ms for gap and 270 ms for no gap. This shows a significant facilitation effect of a gap on the reach latency ($P < 0.01$). However, the movement time for the hand, i.e. the time from releasing the central button to touching the peripheral button, was shorter in the no-gap task than in the gap task, 448 vs. 480 ms ($P < 0.01$). Arm movements to the left button took longer than to the right in the gap (466.5 vs. 423 ms, $P < 0.01$) as well as in the no-gap condition (491.5 vs. 465 ms, $P < 0.05$).

Adding up manual reaction and movement time to give the total response time we obtained 694 ms (214 + 480 ms) in the gap condition and 718 ms (270 + 448 ms) without gap. The saccadic movement time (saccade duration) was ≈70 ms in both conditions. Thus the hand

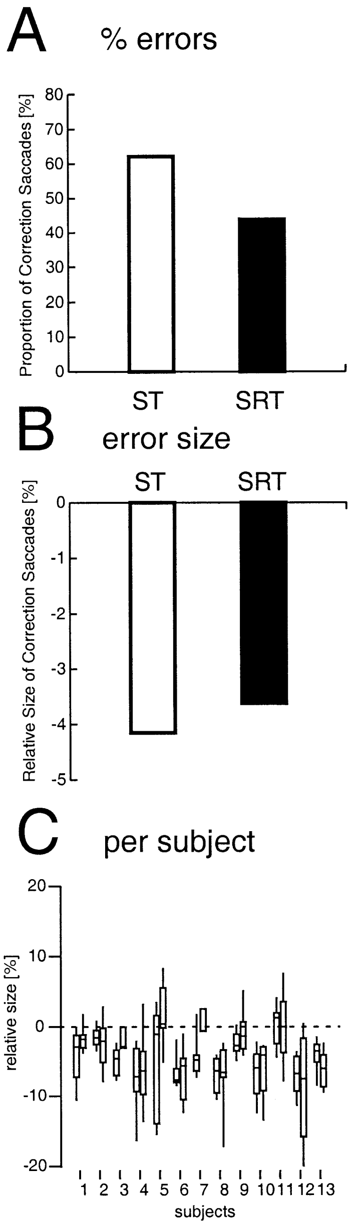

FIG. 4. (A and B) Errors made by naive subjects in the saccade task (ST, outlined bars) and the coupled saccade–reach task (cSRT, solid bars). (A) The percentage of trials containing correction saccades. (B) The median size of the correction saccades in these trials as a percentage of the size of the total eye position change. Both plots show a superior performance in the cSRT. (C) A more detailed presentation of the error size for all subjects. The left column for each subject is ST, the right column cSRT. The lower, middle and upper lines of each box depict the 25, 50 (median) and 75 percentiles. The bars extend to the 10 and 90 percentiles. Of the remaining 13 subjects, 10 showed an improved accuracy (concerning the median), although 9 of 13 had a larger interquartile distance in cSRT than in ST. One of the 14 subjects only contributed one trial in ST to this analysis and was excluded.

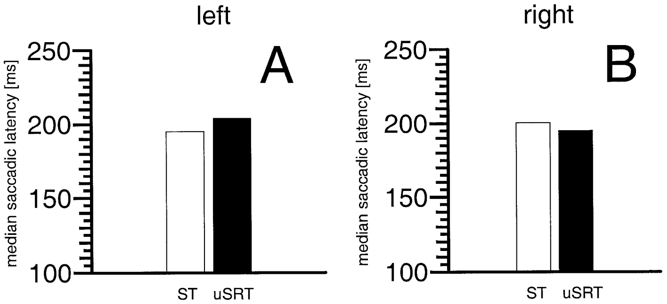

FIG. 5. Median saccadic reaction times in the saccade test (ST, outlined bars) and uncoupled saccade–reach task (uSRT, solid bars). (A) For eye movements to the left (opposite direction to arm) the reaction time was longer in uSRT than in ST ($P < 0.01$). (B) It was shorter for eye movements to the right (same direction as arm) ($P < 0.01$).

always arrived at the target ≈475 ms (gap, 478; no gap, 470.5 ms) after the eye.

Uncoupled saccade–reach task

In the uncoupled saccade–reach task the target was presented after the subject had started a hand movement to the right. Target-on immediately followed the fixation-point-off triggered by the subject's release of the central button. The median saccadic reaction times were higher in the uSRT than in ST (200 vs. 198 ms; see Table 2). However, calculating the medians separately for the two directions, i.e. the eyes moving in the same or in the opposite direction to the hand, we obtained different effects (Fig. 5). For eye movements to the left side, i.e. opposite to the hand movement, the median saccadic latency was 204 ms whilst it was 195 ms when only the eyes had to move ($P < 0.01$). In contrast, the median saccadic latency for eye movements to the right, i.e. in the direction the hand was already travelling, was 195 ms in uSRT and 200.5 ms in ST ($P < 0.01$). Eye movements to a target were facilitated when the hand was already moving to it and delayed when the eyes had to move to a target on the opposite side to the hand target.

In 9 of 11 subjects the movement of the hand, still being the same for both conditions in the task, took longer when the eyes had to move in the direction opposite to the hand. However, the difference between the medians over all available subjects of 483 ms to the left and 475 ms to the right fail to reach significance ($P = 0.08$).

Looking for influences on saccadic errors by arm movements already on their way to a target, again the proportion of trials with one or more correction saccades was lower in uSRT (313 of 672, 46.6%) than in ST (317 of 564, 56.2%) (z-test, $P < 0.01$). This improvement in uSRT was almost entirely evoked by the saccades in the same direction as the hand with only 124 out of 333 saccades (37%) needing a correction in comparison to 137 out of 277 in ST (49.5%). In contrast, when saccades had to be made in the opposite direction to the hand movement 189 out of 337 (56.1%) needed to be corrected in uSRT vs. 180 out of 287 (62.7%) in ST, a difference that was not significant ($P = 0.11$). We also found that the error size was reduced significantly more for saccades to the right, i.e. in the direction of the hand movement, than for saccades to the left, i.e. against the direction of the hand movement (–0.56 vs. –3.43%; $P < 0.01$). Nevertheless, both saccades during an ongoing arm movement were more precise than during the saccade-only condition with an error of –3.94% to the right and –4.15% to the left ($P < 0.01$ in both directions when compared to the values from uSRT).

Virtual setup validation

The obvious difference between the double-step and the single-step experiment is the availability of somatosensory feedback when the finger reaches the target. The tactile feedback was given by the button in the single-step experiment, but not during pointing to virtual targets in empty space during the double-step experiment. However, in this double-step experiment subjects received visual feedback from their hand. In a control experiment an invisible wooden plate at the position of the targets delivered additional tactile feedback. The target was single-step displaced similarly to the single-step experi-

TABLE 1. Reaction times in the saccade test (ST) and coupled saccade–reach test (cSRT) in the single-step experiment

	Median reaction times (ms)					
	Left direction		Right direction		Both directions	
Task	ST	cSRT	ST	cSRT	ST	cSRT
Saccadic reaction time						
no gap	180	178	186.5	175	182	177.5
gap	148.5	145	162	147	155	146
Reach reaction time						
no gap	–	276.5	–	267.5	–	270
gap	–	228	–	206	–	214
Hand movement time						
no gap	–	466.5	–	423	–	448
gap	–	491.5	–	465	–	480

Values are the medians over all subjects for each direction separately or pooled over both directions. $n = 14$ naive subjects.

ment. The resulting median saccadic reaction time in ST was 174 ms. In SRT the reaction time was 12 ms shorter at 162 ms ($P < 0.01$). Thus this experimental setup is comparable to the conditions in the single-step experiment and gives the similar reduction of saccadic reaction time when the arm is moved to the same target as the eyes (Compare values in Tables 1 and 3).

Double-step experiment

In this experiment the subjects had to move their eyes or eyes and hand to double-step displaced virtual targets. When pointing to double-step displaced targets subjects followed the target movement faster and quicker with the eye than with the hand. Two sets of three example SRT trials are displayed in Fig. 6. After the first step the target stayed at that position for 300 ms and then was displaced back medially (Fig. 6B) or further peripherally (Fig. 6A). The eyes followed the steps of the target rather ballistically, while the hand produced a smoother trajectory. In all these examples both gaze and hand first moved to the first target position before they moved to the final target position, even if the hand did not really stop in some of the trials with the 300-ms delay.

Reaction time of first saccade

For further evaluation, the only trials used were where the subjects did both required saccades to the two target displacements without correction saccades, which assured full attention during the selected trials. The following data came from seven subjects in a visually closed-loop condition. The median saccadic reaction time for the first saccade was 169 ms in ST and 161 in SRT. This again shows the reaction time decrease by hand movement ($P < 0.01$).

Reaction time of second saccade

In ST the median reaction times for the saccade after the second target step were 196 ms for the 300-ms delay and 171 ms for 500-ms delay. The times differed significantly ($P < 0.01$) and were longer than the reaction time (169 ms) for the saccade after the first target step ($P < 0.01$). In SRT the median saccadic reaction time to the second target step increased to 205.5 ms in the 300-ms delay and 184 ms in the 500-ms delay condition. Again the two reaction times differed and were significantly different from the latency of the first saccade (161 ms) ($P < 0.01$) in these trials. The median saccadic reaction times to the second target steps were thus 10 ms shorter in ST than in SRT for 300-ms delays and 13 ms shorter in ST than in SRT for 500-ms delays. These differences are significant ($P < 0.01$) but they are in the opposite direction than for the first saccade (169 ms in ST vs. 161 ms in SRT).

TABLE 2. Saccadic reaction times in the saccade test (ST) and uncoupled saccade–reach test (uSRT) in the single-step experiment

	Median reaction times (ms)					
	Left direction		Right direction		Both directions	
Task	ST	uSRT	ST	uSRT	ST	uSRT
Saccadic reaction time	195	204	200.5	195	198	200
Hand movement time	–	490	–	479	–	483

Values are the medians over all subjects for each direction separately or pooled over both directions. $n = 14$ naive subjects.

Separated into trials in which the second target displacement was either back medial or further peripheral, both previous statements were still valid (see Fig. 7 and Table 3). The reaction time for the second saccade in ST was increased by 29 ms compared to the first saccade (198 vs. 169 ms) when the target was displaced back medially and 17 ms (186 vs. 169 ms) when the target was displaced further peripherally, both times with a delay of 300 ms (open bars in Fig. 7A and B). With a delay of 500 ms after the first target step the saccadic reaction times to the second target displacements were 7 ms longer for further peripheral and not increased for back medial steps in comparison to the first saccade.

When the subject had to move eyes and hand together the reaction times for saccades to targets displaced further peripherally after 300-ms delays were 12 ms (198–186 ms) longer and after 500-ms delays they were 13 ms (189–176 ms) longer compared to trials without arm movements ($P < 0.01$). For back medially displaced targets the SRT reaction times were ≈ 17 ms (214.5–198 ms) longer with 300-ms delays and 12 ms (181–169 ms) longer with 500-ms delays than the reaction times in ST ($P < 0.01$).

Comparing the saccadic reaction times for the two possible directions of the second target step after 300-ms delays the medians were longer for back medial second saccades than for further peripheral second saccades (198 vs. 186 ms; $P < 0.01$). However, with 500-ms delay the difference was not significant ($P = 0.11$ and $P = 0.17$, respectively).

Trials with correction saccades

In some trials in open-loop conditions the naive subjects made the first saccade, corrected it with one correction saccade and then did the second saccade (Table 3). Of these 226 trials, 124 were ST (54.9%) and 102 were SRT trials (45.1%). In ST the median saccadic reaction time of the first saccade was 156 ms, which is shorter than the median of 169 ms in the above-described trials without correction saccades. The second saccade had a reaction time of 263 ms for the 300-ms delay and 186 ms for the 500-ms delay. Therefore when a correction saccade was performed the second saccade was initiated 67 ms (300-ms delay) and 15 ms (500-ms delay) later compared to the 196 and 171 ms, respectively, in trials without a correction saccade. The same was found for SRT (Table 3). The temporal delay between the initiation of the first saccade and its correction was longer in ST than in SRT trials (medians: 254 vs. 241 ms, $P < 0.01$).

This means that subjects started a correction of the first saccade earlier when they also had to move their arm. However, after a correction saccade the second saccade came earlier in ST than in SRT trials. For the 300-ms delay this difference was 18 ms (182 ms in ST vs. 200 ms in SRT, $P < 0.01$). For the 500-ms delay the median latency between the start of the correction saccade and the start of the

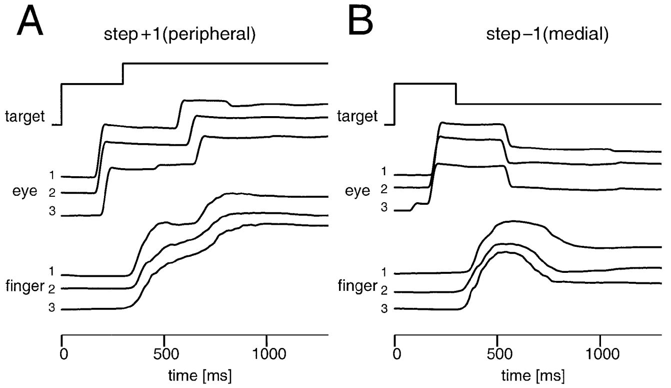

FIG. 6. Sample gaze and hand trajectories (three of each) in a double-step saccade reach test (SRT) session of one subject under closed-loop conditions. (A) Trials in which the target was displaced further peripherally (to the right; step +1) in a second step 300 ms after the first target presentation (displayed in the top third). The horizontal eye trace of the right eye (shown in the middle) follows the target movement with two saccades and possibly correction saccades. The position of the tip of the index finger in the horizontal-frontoparallel direction of the target movement (in the lower third) is much slower. (B) Trials from the same block with second target displacements back medially (step –1) after a 300-ms delay. Eye traces show again two saccades whilst the fingertip makes a slower smooth movement to the final target.

second saccade differed by 12 ms between ST (263 ms) and SRT (275 ms), which is significant ($P < 0.01$).

Discussion

To explore the modification of eye movements by simultaneously performed arm movements, subjects made saccades or combined eye and arm movements to single- and double-step displaced targets. The median reaction time of saccades in single-step trials and the first saccades in double-step trials were in general reduced when the subject had to simultaneously perform a straight arm movement to the same target as quickly as possible. When the subjects had to move their eyes to another target than the hand the saccadic reaction time was increased. In double-step trials the reaction times for the second saccade were increased compared to the first or to those in single-step trials. This increase became smaller with longer delays between the two steps, yet it was further increased by simultaneous hand movements to the same targets for both delays.

Facilitation for primary saccade

The coupled saccade–reach tests (cSRT) in the single-step experiment and the control experiment as well as the first saccade in the double-step experiment showed a robust reduction in saccadic reaction time by simultaneous arm movement (Figs 3 and 7).

These findings seem to be in contrast to some of the earlier research (Mather & Fisk, 1985; Bekkering *et al.*, 1994, 1995). However the analysis and the experimental tasks in these studies have been different. Mather & Fisk (1985) report a higher saccadic reaction time when the subject had also to move their hand to point to the target compared to only eye movements. The targets here were not differentiated into the auditory and visual targets they used, yet they also reported that saccadic reaction time to auditory targets was much higher than for visual targets. Their effect thus might be caused by pooling these data sets. Bekkering *et al.* (1994, 1995) asked the subjects to move a stylus over the surface of an *x–y* tablet when requiring eye and arm movements. The subject had to place the stylus over the fixation target and to look at it. When the movement target appeared the subjects had to look to it (saccade) and move the stylus over the surface of the tablet to the target. This movement similar to drawing a line is linear and continuous and not like the ballistic movements we used (releasing one button and pressing the other). The movement of Bekkering's subjects is therefore similarly constrained as in the condition CF (constrained free path) in Desmurget *et al.* (1997), while the movements in our present study are similar to condition UF (unconstrained free path). Desmurget *et al.* (1997) showed that reaction and movement times are shorter in the UF than in other conditions. They conclude that this would not have been expected if both movements involve the same underlying control strategies. Hence different types of simultaneous arm movements are likely to have different effects.

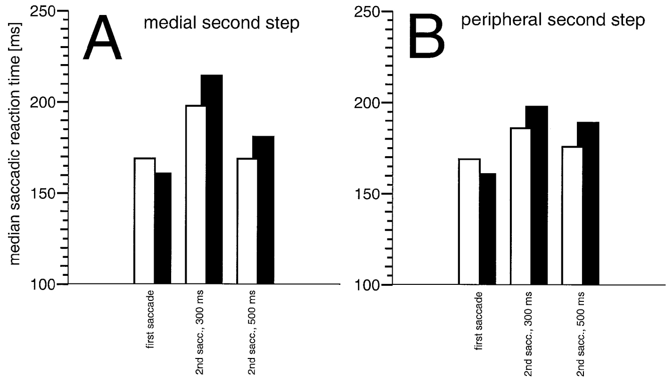

FIG. 7. Saccadic reaction times for all seven subjects in the double-step experiment. (A) The second target step was directed back medially (A) and further peripherally (B) from the target position for the first saccade. The median saccadic reaction times of the first saccade (left pair of bars), the second saccade for 300-ms delay (middle pair) and for 500-ms (right pair) in the saccade-test (ST, outlined bars) and the saccade–reach task (SRT, solid bars) are shown. Note that saccadic reaction time is always increased for the second saccade for 300-ms delay compared to the first ($P < 0.01$).

Helsen *et al.* (1997, 1998) report that the end of the gaze movements of their subjects coincided well with the moment of peak hand velocity in a task where the subjects made speeded aiming movements from a central to a peripheral target. Furthermore, the ratio between gaze and hand response times, which are the times to arrive at the target, is 50%. This means that the eye movement is timed to arrive in a specific temporal relationship to the end of the hand movement to the same target. Because the saccades have a stereotyped movement time the coordination occurs via the reaction time. This would predict slow saccadic reaction times together with slow arm movements whilst fast arm movements give fast saccades (Helsen *et al.*, 2000). We asked our subjects to move eyes and arm as quickly as possible to the new target, thus minimizing response time. Taking the given proportion of eye and hand response time we arrived at the explanation that our quick arm movements come with quick saccades. In earlier studies the slow-down of hand movements by more complex transformations from auditory coordinates or by slower kinematics of drawing with a stylus might also have slowed down the saccadic reaction time.

Therefore the reduction of saccadic reaction times in the cSRT compared to ST is a rather robust effect. Apart from this effect on the reaction times the number of correction saccades and the median size of these correction saccades is reduced in cSRT. Hence the performance of the oculomotor system (timing, accuracy, precision) is improved when the subjects had to look at a target they want to point to as quickly as possible. However, the scatter in the size of the correction saccades is larger in cSRT. This might be provoked by

TABLE 3. Saccadic reaction times in the saccade test (ST) and saccade–reach test (SRT) in the double-step experiment

			Median reaction times (ms)					
		Task:	ST	SRT	ST		SRT	
Experiment	*n*	Saccade:	First	First	Step +1	Step –1	Step +1	Step –1
Single-step control, wooden plate	5		174	162	–	–	–	–
Double-step experiment, closed-loop trials without correction saccades	7							
300-ms delay			169	161	186	198	198	214.5
500-ms delay			–	–	176	169	189	181
226 trials (one correction of first saccade)					(both steps)		(both steps)	
300-ms delay			156	144	263	–	252	–
500-ms delay			–	–	186	–	202.5	–

Values are the medians over all subjects for each direction separately or pooled over both directions; *n*, number of naive subjects.

the shorter reaction time, i.e. shorter planning phase of the first saccade.

Gap effects

The reduction of reaction time in tasks where the fixation spot was switched off before the target spot was illuminated (gap-effect) has been long known for saccades (Saslow, 1967; Fischer & Ramsperger, 1984) and has more recently also been reported for hand movements (Fischer & Rogal, 1986; Bekkering *et al.*, 1996; Pratt *et al.*, 1999). The results of our single-step experiment (Fig. 3) corroborate these findings. Furthermore the reduction of saccadic reaction times when the subjects also had to point to the target of the saccade was still present in trials with a 200-ms gap. This shows that simultaneous arm movements can still make the saccadic system faster even when it is already accelerated by the gap.

Inhibition for saccade to second target step

For the second saccade to a double-step displaced target the latency was increased compared to the first saccade. Co-use of the hand lead to an additional increase (Fig. 7).

This finding has to be seen in relation to earlier studies in humans (Feinstein & Williams, 1972) and recent studies in monkeys (Dorris *et al.*, 1999) on sequences of saccades. Feinstein & Williams (1972) report the variation of system delay (i.e. the increase of the second reaction time of a sequence compared to the first) with the interstimulus interval between the target displacements. The system delay, sometimes referred to as refractory time, decreased monotonically with increasing interval. It was ≈ 25 ms for an interval of 300 ms. However, the saccadic sequence always consisted of one horizontal and one vertical saccade, therefore allowing no direct comparison with our experiment. The monkey in the study of Dorris *et al.* (1999) made a saccade from a central fixation spot to a peripheral target and back to the central spot before the reaction time was measured for a saccade to a target at the same, opposite, or orthogonal location to the previous target. The reaction time is largest if the tested target was opposite to the previous target, which is in contrast to our present results.

Neuronal implementation

Our results show a robust interference effect between eye and arm movements. This interference cannot be mechanical like the dynamics of fore- and upper-arm. The arm and eyes have no mechanical coupling and it was long thought that at least the final stages of neuronal control are also uncoupled. The superior colliculus (SC) in the primate mid-brain is known as a crucial part of the oculomotor system (Wurtz & Goldberg, 1971; Schiller *et al.*, 1987; Sparks & Hartwich-Young, 1989) and is involved in eye and head movements to direct gaze (Guitton, 1992; Cowie & Robinson, 1994; Paré *et al.*, 1994; Freedman *et al.*, 1996; 1997). The interplay between different classes of oculomotor neurons in the SC turned out to be important (Munoz & Wurtz, 1992; 1993a,b; 1995a,b). Activity in the retinotopic map of build-up saccadic neurons is thought to be counterbalanced with the activity of fixation neurons in the rostral pole of the SC. An oncoming possible saccadic target will lead to an activation of build-up neurons at its specific location in the map which will lead to a reduction of fixation activity, eventually overcome a threshold and provoke a burst in the class of burst neurons which will drive the brainstem oculomotor system. A temporal gap between switching off the visual fixation target and switching on the saccade target leads to a decrease in activity of the fixation neurons prior to the complete inhibition during the saccade and to a steeper rise of the activity in the built-up neurons (Dorris *et al.*, 1997; Everling *et al.*, 1999).

However, the SC not only controls gaze; it has also been reported to contain neurons with activity related to goal-directed arm movements (Werner, 1993; Werner *et al.*, 1997a,b; Stuphorn *et al.* 2000). The close distance of neurons coding eye and arm movements might allow an interaction in this structure. For the facilitation of the first saccade one could think of an excitatory input to the build-up neurons from the activated reach neurons. For the inhibition of the saccade to the second target we can think of two explanations: (i) the reach neurons could excite the fixation neurons and thereby increase the saccadic trigger threshold and thus the reaction time; (ii) the additional input of the reach neurons on the build-up cells leading to the quicker first saccade might also lead to a deeper inhibition in the saccadic initiation map (build-up neurons) thus increasing the reaction time of the next saccade. The main difference between these two hypotheses is that the latter predicts a localized deficit for saccades with approximately the same size. This is consistent with the findings of Dorris *et al.* (1999). The dynamic implementation of hypothesis (i) would also predict a dependence on a current arm movement rather than on the previous one as in hypothesis (ii).

Electrophysiological recording of neurons, especially fixation and build-up neurons in the SC, in an awake monkey working on tasks similar to those in this study should give more insight into the specific role of the SC for modulation of saccade parameters by arm movements.

Parallel vs. serial tasks

We now have to compare our results in the double-step experiment with those of Neggers & Bekkering (2000). Neggers and Bekkering asked the subjects to look and point to a fixation target. When a new target appeared the subject had to move the gaze and the finger to it. Whilst gaze had already reached and fixated this target the fingertip moved slower. When the fingertip reached peak velocity a further target was presented. The subject had to complete the finger movement to the first target and make an eye movement from the first to the second target as fast as possible. Though the task was to make the saccade as soon as possible, subjects usually completed the hand movements before starting the saccade. Thus, reaction times for the second saccade were increased and depended on the duration of the previous arm movement. Then the task is not a parallel but a serial one. Our double-step experiment required the parallel control of eyes and hand towards the displaced target and reaction times for the second saccade are slightly lengthened in all cases, even though subjects were not asked to, nor did they necessarlily, complete the first pointing movement. This suggests that in our experiment the simultaneous presence of a parallel motor plan is what causes the second saccade to have a longer latency, rather than the serial completion of competing tasks.

Peripheral vs. medial or onward vs. reversal

In this paper the second target step so far was described as medial or peripheral displacement from the target position after the first step. Alternatively it can be seen as either a reversal in movement direction or an onward movement. It cannot be discriminated whether this means a disadvantage for movements towards the saggital plane or an inhibition of return. A further experiment to examine this question is to have the target and response movements started from a peripheral position and placing the first step on a straight-ahead target. Both possible second steps will then be away from the body axes, but still requiring reversal or onward correction. These experiments are currently in progress.

Saccadic modulation by goal-directed vs. independent arm movement

In the uSRT of the single-step experiment (Fig. 5) subjects moved their hand to a target and could initiate a saccade to that target earlier than without the arm movement. However, saccades in the opposite direction than the hand movement had longer reaction times. This shows the presence of an interaction although no relationship between the two movements could be inferred from instruction. Our experiments show a robust influence on the saccadic system when coordination was necessary (Figs 3–5 and 7).

In this study all examined movements were visually guided goal-directed movements. It is thus impossible to predict the effect of arbitrary arm movements from these findings. Although without obvious biological advantage it is possible that eye movements are changed during lifting a cup, yet during task-dependent, but not spatially related, movements (moving the cursor on the computer screen with the mouse) a coordination could be desirable. Thus experiments have to be designed to explore the influence of arm movements on saccades when the task requires no or only weak coordination of these movements.

Conclusions

In the present experiments we have shown that a target to which you prepare to move your hand as quickly as possible is reached earlier by a saccade than is a target to which you are not reaching. In a double-step paradigm the second saccade is delayed by a simultaneous arm movement, although this second reaction time is longer than for the first anyway. Both effects are, at least partly, explainable by the discharge properties of cells in the superior colliculus.

Correction saccades are smaller (median value), though with greater scatter, when the hand is also moving towards the single-step displaced target. This may be the price for the shorter reaction time.

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Abbreviations

cSRT, coupled saccade–reach task; SC, superior colliculus; SRT, saccade–reach task; ST, saccade task; uSRT, uncoupled saccade–reach task.

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