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Arm movement and gap as factors influencing the reaction time of the second saccade in a double-step task

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Abstract

To guide our hand for reaching, we explore our visual environment by sequences of saccades. In the present paper, we studied the eye and hand movements of human subjects looking or looking and pointing at a target that is instantaneously displaced two times (double-step task). It was previously shown that the second saccade has a much longer reaction time than the first one [Feinstein & Williams (1972) *Vision Res.*, **12**, 33–44]. The second reaction time is even longer if the subject also has to point to the target with the hand [Lünenburger *et al.* (2000) *Eur. J. Neurosci.*, **12**, 4107–4116]. The conditions and objective for these effects are further examined in the present paper. It is shown that vision of the hand reduces the first and second saccadic reaction times in parallel. The second reaction time is prolonged for shorter delays between both target steps as well as for larger amplitudes of the second saccade. However, the long second reaction time does not reflect an absolute saccadic refractory period, because a gap before the second target step reduces the second reaction time to a value similar to the first. Hand response time and average hand velocity were increased when the second target step was larger. The response time for the eyes was about 30% of the response time of the hand. We argue that the observed effects reflect the coordination of eye and hand movement to allow a precise and efficient reaching behaviour.

Introduction

To make use of the enormous capabilities of our hands we rely heavily on visual information. It is important to gain this information efficiently by precise and stable eye movements, usually by saccades to, and fixations of, the targets to be grasped or reached. The common behaviour of looking at the target before the hand arrives has the strategical advantage of a stable view of the target and the approaching hand (Prablanc *et al.*, 1979). To achieve this advantage a fast hand movement can actually lead to a reduction of the saccadic reaction time (Lünenburger *et al.*, 2000).

The reaction time of the second saccade in a rapid sequence of two visually guided saccades (double-step) is always much longer than that of the first saccade (Feinstein & Williams, 1972; Becker & Jürgens, 1979; Lünenburger *et al.*, 2000). This increase occurred not only for a second saccade back towards the initial fixation point, which might relate to inhibition of return (Posner & Cohen, 1984; for recent reviews see Taylor & Klein, 1998; Klein, 2000), but also when both saccades had the same direction. Inhibition of return is thought to prevent repeated movement of gaze or attention to one location. It can thus improve sampling of the environment. However, for very short delays the return to a location can be facilitated. One problem in our previous experiments preventing the clear conclusion that the relative direction of the saccades is important for the second reaction time was that initial fixation was at a central location, such that the second saccade was either centrifugal or centripetal (Lünenburger *et al.*, 2000). To allow for comparability of the second saccades, these saccades have to be the same in retino-, head- and allocentric coordinates, i.e. start and end point of the saccade have to be the same on the screen, irrespective of the first saccade. We solved this in experiment A of the present paper by having the subject make the first saccade from a peripheral position (either left or right) to the centre of the screen. The second saccade, e.g. to the right, now could have the same direction as the first (if this started on the left side of the screen) or the opposite (if the first saccade started on the right). The second saccade is the same in both cases, but is preceded by a first saccade with either the same or the opposite direction.

In their double-step experiment, Feinstein & Williams (1972) varied the time the target was present at the first location, and found for shorter periods systematically longer second reaction times for the second saccade. The reaction time difference, termed system delay, was described as a monotonously decreasing function of the delay between both target displacements. Deubel *et al.* (1982) plotted the reaction time of the second saccade depending on the time from the end of the first saccade until the second target displacement and obtained similar curves as Feinstein & Williams (1972) apart from constant shifts in both axes. However, when Ron & Berthoz (1991) looked at the relation of the delay from second target displacement until start of the first saccade and the intersaccadic interval, the data points could be described by a linear function with a slope close to unity. The dependence of the second reaction time, which is the sum of these two values, still is linear, yet with a much smaller slope. Therefore, this measure is more sensitive to nonlinearities, as the other studies suggest. All these studies only involved gaze shifts, in part with free head. Some experiments on double-step saccades by

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Prablanc & Jeannerod (1975) and Goossens & Van Opstel (1997) and on eye-hand coordination by Prablanc & Martin (1992) as well as work by Blouin *et al*. (1995), using intrasaccadically displaced targets, which should be acquired by saccades and reaching with the hand, revealed very short reaction times for the saccade compensating for the target displacement. 'Compensatory saccades' with reaction times of about 100 ms could be considered to be 'express saccades' (Boch *et al*., 1984; Fischer *et al*., 1984; Fischer & Ramsperger, 1984). To look for such short reaction times in a saccade-only task on the one hand and extending the earlier experiments of Feinstein & Williams (1972), Deubel *et al*. (1982) and Ron & Berthoz (1991) to a saccade-reach task on the other hand, we performed experiment B of the present paper. From the studies described above three different results could be expected: (i) the second saccadic reaction time is a monotonous (hyperbolic or linear) function of the stimulus delay in the saccade-only as well as in the saccade-reach task; (ii) the function is not monotonous. Similar to the time course of inhibition of return (e.g. fig. 3 of Klein, 2000), the reaction time of the second saccade is short for very long as well as for very short stimulus delays. For the correction of arm movements, this possibility has been shown (Goodale *et al*., 1986; Prablanc & Martin, 1992; Desmurget *et al*., 1999); and (iii), the dependence of second reaction time on the stimulus delay bifurcates for decreasing stimulus delays and the reaction time distribution becomes bimodal for a short delay, the second saccade is either a fast correction saccade or strongly delayed.

The increased reaction time for the second saccade in a sequence could be caused by a refractory period in the saccadic system, such that saccades cannot be initiated briefly one after another. However, this hypothesis is falsified by the previous work of Goossens & Van Opstal (1997) using sequences of two memory-guided saccade where inter-saccadic intervals were observed down to about 40 ms. However, the restricted hypothesis that two visually guided saccades in a sequence suffer refractoriness has to be addressed. It is known that temporal and spatial events around the target can modify the saccadic reaction time. A strong decrease in reaction time is produced by extinguishing the fixation point about 200 ms before the target appears (gap-effect, Saslow, 1967; Fischer & Weber, 1993; Bekkering *et al*., 1996). Can such a gap bring the reaction times of the second saccade back to normal, i.e. to the reaction time of the first? Is the coordination of eyes and hand changed by the gap? These questions are answered by experiment C.

Taken together, experiment A will examine the relative direction of first and second saccade as a factor for the reaction time of the second saccade, experiment B the timing and amplitude of the second target displacement, and experiment C the influence of noncontinuous visibility of the target (by use of a gap).

Materials and methods

Subjects and set-up

Three experiments were performed by healthy human subjects who participated voluntarily after giving informed consent. In total, 30 subjects (14 female, 16 male; age 17–37 years) participated. The numbers of subjects performing in each of the three experiments are given in Table 1. Some of the subjects participated in more than one of the three experiments. The subjects had normal or corrected-to-normal vision except three who normally wore glasses, but not for vision at the distance of the targets used. One of the authors (L.L.) participated in experiments B and C.

The setup and recording have been described in detail previously (Lünenburger *et al*., 2000) and are only outlined briefly here. The subjects looked at the downward facing monitor (20 inch CRT monitor operating at 72 Hz; Silicon Graphics Inc., Mountain View, USA) of a graphics workstation (SGI O2 or Octane; Silicon Graphics Inc.) via a 45-degree tilted half-silvered mirror such that they could see the virtual image of the screen in front of them. The visual target was a small red ball of luminance density 2.3 cd/m^2; it was displaced along a horizontal line in a frontal plane 44 cm in front of the subject. This virtual reality approach allowed the placement of the targets at arbitrary positions and their instantaneous displacement. It improved also the perception that the tasks contained one single target that was displaced (object constancy), not a sequence of different targets. In the saccade task (ST) the subject had to look at and fixate the target. In the saccade-reach task (SRT) the subject was required to look at the target and intercept or 'touch' it with the tip of the right index finger. When small lights behind the mirror were switched on, the subject could see their hand and parts of the lab wall too (closed-loop visual feedback control of the hand). When the lights were switched off only the targets without any external reference were visible (open-loop).

TABLE 1. Number, age, and sex of subjects in the double-step experiments

Experiment	Subjects	Female	Male	Age (years)
A	12	6	6	22–37
B	10	4	6	25–29
C	14	6	8	17–37

Eye movements were recorded with an EyeLink video system (SMI Sensorimotor Instrumentation, Germany). This system compensates for head movements such that no head restraint was necessary. However, in experiment B an adjustable neck-rest was provided. The movement of the tip of the right index finger and the right elbow was tracked with a magnetic miniBIRD system (Ascension Technology Inc., Burlington, USA). The cables of the sensor from the finger to the elbow was taped to the forearm, and this cable and the cable from the sensor at the elbow were taped to the upper arm and to the shoulder. This allowed the subjects to move their arms freely without disturbance. Data were stored by computers and analysed with computers using our own programs under Yorick (David Munro, Regents of the University of California). Whereas the onsets of saccades were determined online by the EyeLink, those of the arm movements were determined offline with the Yorick program (onset = three consecutive samples over 10 cm/s) together with other key figures of the trajectories (time and eccentricity of trajectory reversal, average and peak velocity). To improve the latter measures, arm traces were smoothed by

$$x'_i = 0.25x_{i-1} + 0.5x_i + 0.25x_{i+1}$$

where x_i is the ith sample of the finger position. The nonlinear regressions were calculated with SigmaPlot (SPSS, Chicago, IL, USA).

Two different tasks were given to the subjects in all experiments. 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 to the target at its current position with the extended right index finger. Subjects were instructed to move as fast as possible. During ST, subjects could lay their right hand comfortably on their knee, whereas during SRT it constantly remained in the target space. We used only horizontal displacements of the target to avoid artifacts from interaction of the horizontal and the vertical/torsional component of the saccades. These components are controlled by separate systems in the brainstem.

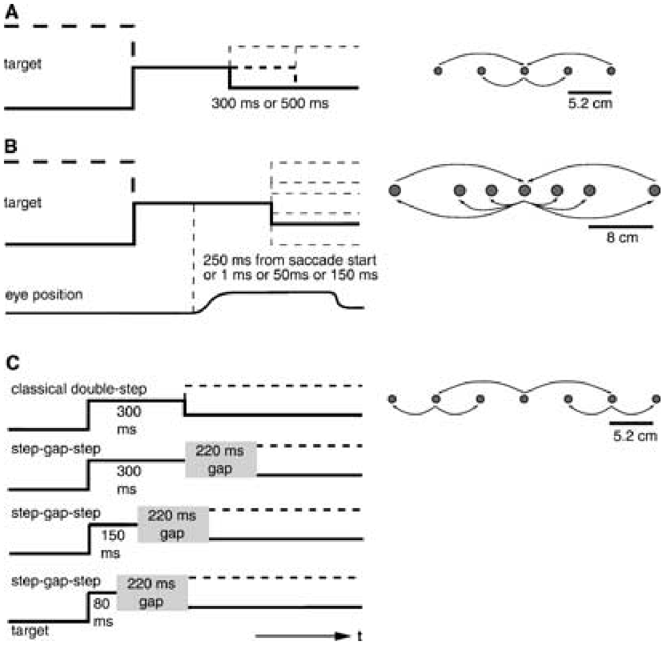

FIG. 1. The timing (left column) and the spatial layout (right column) of the target displacements in the double-step experiments. For details see text.

Experiment A

At the beginning of the trial, the target (a red ball of diameter 1.2 cm) was presented at a peripheral location 10.2 cm from the centre of the screen, randomly to the left or the right (Fig. 1A). After 1500 ms or 1700 ms it was displaced to the centre of the screen and remained there for a delay of 300 ms or 500 ms. After that delay it was displaced 5.1 cm either to the left or the right with equal probability. With this paradigm it was possible that the second saccade from the centre of the screen to the left was a 'reverse' saccade if the first saccade started from the left periphery, while the same saccade was an 'onward' saccade if the first saccade started at the right periphery.

These delays were chosen such that the second displacement occurred before or after the average start of the hand movement in SRT. In experiment A, the amplitude of the second target displacement of 5.1 cm was half the amplitude of the first displacement (10.2 cm). This amplitude ratio of 50% is larger than the typical amplitude ratio of correction saccade to primary saccade (about 20%) and ensures individually programmed responses in combination with the chosen stimulus delays (Becker & Fuchs, 1969; Prablanc & Jeannerod, 1975).

In experiment A, all subjects carried out two sessions (order was counterbalanced among the subjects). In one session, the lights behind the mirror were switched on such that the subjects could see their hand (closed-loop). In the other session, the lights were switched off (no vision of the hand; open-loop). Six files were recorded in each session; ST and SRT alternated and counterbalanced across subjects (e.g. 48 ST, 48 SRT, 32 ST, 32 SRT, 32 ST, 32 SRT; 224 trials in about 20 min) were recorded to get a total of 448 trials from both sessions. This gave 14 trials in each of the 32 conditions. 32 conditions result from two possibilities in each of the five parameters, which are two feedback conditions (open-loop/closed-loop), two different tasks (ST/SRT), two different directions of the first saccade (left/right) and the second saccade (onward/reverse), as well as two different stimulus delays (300 ms/500 ms).

Experiment B

In experiment B, timing and amplitude of the second displacement of the target (1.0 cm diameter) was varied (Fig. 1B). The light behind the mirror was switched off, such that the subjects could only see the targets (open loop). The initial fixation was either 16 cm to the right or to the left and the first target appeared at the centre. The second target could appear 4 cm, 8 cm or 16 cm in an onward or backward direction. Apart from trials with a constant delay of 500 ms between the target displacements, the onset of the second target was related to the start of the first saccade. The presentation of the second target was triggered 1 ms, 50 ms, 150 ms or 250 ms after the start of the first saccade, which was detected online by the EyeLink. The actual appearance of the target was delayed by the computer latency (especially video refresh). The spread of saccadic reaction time and computer response latency lead to a more or less uniform sampling of delay time between the two target displacements from about 200 ms to about 600 ms. Trials with delays smaller than 160 ms, reaction times longer than 500 ms, or incorrect first saccades were discarded.

Experiment C

Experiment C contained the step–gap–step trials. Fourteen subjects contributed to this experiment. Four different timings were used for the stimulus (Fig. 1C). A centre-out sequence was used to prevent predictability of the first saccade direction. The classical double-step with 300 ms delay was included for comparison. The target (1.2 cm diameter) was displaced horizontally from a central initial position to the first target position 10.2 cm left or right and after 300 ms 5.1 cm back medially or onward peripherally. The remaining three conditions included a gap before the second target displacement in which the screen was black. The target was visible for 80 ms, 150 ms, or 300 ms at the first target position before a gap of 220 ms. The timings were chosen to be similar to the classical double-step in which the target was visible for 300 ms, or the second target displacement occurred 300 ms after the first target displacement. The target was visible for the same duration in the 300 ms step–gap–step (the second target displacement occurred 520 ms after the first). In the 80 ms step–gap–step, the second target displacement occurred 300 ms after the first; however, the target was visible for only 80 ms at its first location. The 150 ms step–gap–step was chosen to have intermediate timing. Because these many conditions would have caused exaggerated recording sessions, we conducted two types of session that contained the classical double-step (300 ms) and the step–gap–step with 300 ms visibility, as well as either the step–gap–step with 80 ms or with 150 ms. Ten subjects performed one session type (randomly) and four subjects performed both session types. The hand was visible (closed-loop) in each session of six blocks (48,48,36,36,36,36 trials) of ST and SRT alternating, counterbalanced between the subjects.

Results

Experiment A: variation of direction and feedback

The saccadic reaction times recorded while the subjects looked (saccade-task, ST) or looked and pointed (saccade-reach task, SRT) to the targets were pooled over right and left movement directions for the first movement. In this experiment, the target was displaced first from a peripheral to the central position and then again to an eccentric position. The subject's hand was illuminated in half of the sessions to examine the necessity of visual feedback. The medians across all subjects are displayed in Fig. 2 and listed in Table 2. The significant differences (Wilcoxon rank-sum, $P < 0.05$) are described in the following.

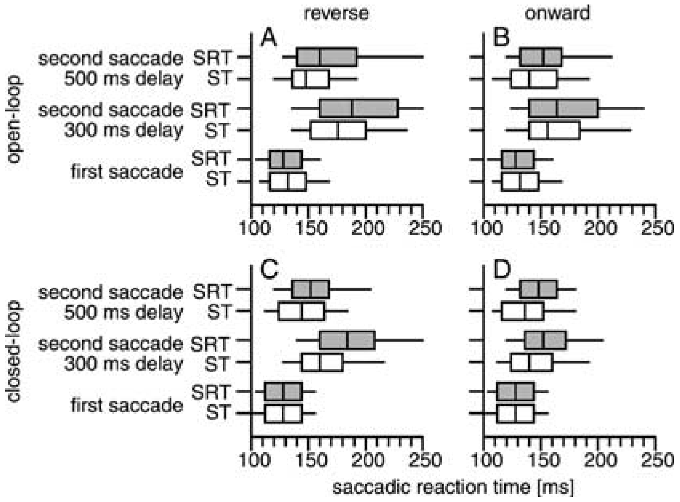

FIG. 2. Saccadic reaction times for all subjects performing classical double-step tasks (experiment A). The second target displacement had the reverse direction in the left column (A and C), and the onward direction in the right column (B and D) compared to the first target step. The subjects could not see their hand in the upper row (A and B; open-loop), whereas in the bottom row (C and D) a light behind the mirror was illuminating the subjects hand (closed-loop). The boxes extend between the 25% and 75% quartiles and are separated by a line for the median. The horizontal lines extend to the 10% and 90% percentiles. The reaction time of the first saccades is longer in ST (open boxes) than in SRT (grey boxes). The reaction times of the second saccades are longer than of the first, and further increase in SRT compared to ST. A delay of 300 ms between the first and second target step increases the reaction time more than a delay of 500 ms. Visibility of the hand (closed-loop) reduces all reaction times.

The reaction time for the first saccade was about 130 ms in all conditions. In the open-loop condition, the first saccade had a shorter reaction time in the SRT than in ST. The saccade and the arm movement in the SRT start from the same peripheral position and begin to move to the same target at the central position. In the closed-loop case the first reaction time is equal for ST and SRT. The reaction time for the second saccade is larger than for the first saccade in all conditions. This increase is larger (about 35 ms) for the 300 ms delay compared to the 500 ms delay (about 20 ms). The second reaction time is longer in SRT than in ST. This increase is about 20 ms for the shorter (300 ms) delay and still about 8 ms for the longer (500 ms) delay confirming the results of Lünenburger *et al*. (2000). Comparing onward and reverse second saccades, it is apparent that a reversal of direction leads to longer reaction times. This is statistically significant in 7 of 8 conditions, i.e. except closed-loop SRT with 500 ms delay. Comparison between the blocks with open-loop and closed-loop control shows shorter reaction times in all cases with visibility of the hand (closed-loop), which is statistically significant except for the conditions with the longest and the shortest SRT reaction times (reverse with short delay: 188 ms vs. 184 ms, and onward with long delay: 152 ms vs. 148 ms).

TABLE 2. Saccadic reaction time in the double-step experiment A

	Saccadic reaction time (ms)					
			ST		SRT	
	ST First	SRT First	Onward	Reverse	Onward	Reverse
Open loop						
300 ms delay	132	128	156	174	162	188
500 ms delay			140	174	152	160
Closed loop						
300 ms delay	128	128	140	160	152	184
500 ms delay			136	144	148	152

Values are the medians in saccade task (ST) and saccade-reach task (SRT) over all subjects pooled over both directions of the first saccade.

Applying a three-way analysis of variance (ANOVA) to the numbers of Table 2 with factors: task (ST/SRT), feedback condition (open/closed loop) and saccade type (first, second onward 300 ms, second reverse 300 ms, second onward 500 ms, second reverse 500 ms) shows significant effects of all factors. This confirms the results presented above which used nonparametric statistical tests. The saccadic reaction time depends on whether it is the first or the second saccade, on the presence of the simultaneous hand movement as well as on the visual feedback ($F_{1,4} = 24.96$, $P < 0.01$; $F_{1,4} = 10.34$, $P < 0.05$; and $F_{4,4} = 22.31$, $P < 0.01$, respectively). No interaction between the three factors was statistically significant.

Experiment B: variation of amplitude and timing

To describe the dependence of second reaction times in ST and SRT on the delay between both target displacements and the amplitude of the second displacement, we varied these parameters systematically. The target moved to its new location at some temporal interval after the start of the subject's saccade to the first target position. Furthermore the amplitude of the second target displacement could be a quarter, half, or full amplitude of the first target displacement in either the same or in the opposite direction as the first saccade.

Saccadic reaction times

The reaction times of all subjects are displayed in Fig. 3 along with the sliding medians. The reaction time of the second saccade (black diamonds, black line) is longer and depends on the stimulus delay, as well as the amplitude of the second target displacement. The second reaction time is longer for larger second amplitudes (Fig. 3, right panels). The reaction time of the first saccade (open symbols, grey line) is independent of the second amplitude.

The second reaction time increases clearly when the stimulus delay decreases (Fig. 3, left). The reaction time in SRT is about 200 ms for 500 ms stimulus delay and approaches 300 ms for 100 ms stimulus delay. It should be again pointed out that the time between the first saccade and the appearance of the second target was not always equal to the predetermined delays (1, 50, 150, 250 ms) because the stimulus was displayed on a CRT monitor. The stimulus appeared at its new position after the next frame refresh that could occur at different times relative to the first saccade. However, this does not have an influence on the effects reported here. The first reaction time is not influenced by the stimulus parameters. To examine the influence of a simultaneous arm movement, the upper and lower row of Fig. 3 have to be compared. For SRT (Fig. 3, upper row), the reaction time of the second saccades increased more strongly at short delays than for ST (Fig. 3, lower row). The plots on the right of Fig. 3 show that for large amplitudes the reaction time of the second saccade was longer and increased more strongly in SRT than in ST. This means that a simultaneous arm movement to the same target increases the effects of the double-step on the second saccadic reaction time.

The assumed hyperbolic dependence of reaction time of the second saccade on the delay was tested by fitting a function $RT = RT_0 + (a \cdot b)/(b + t)$ with second reaction time RT, stimulus delay t and parameters a, b and RT_0. RT_0 is the reaction time for infinitely long, $RT_0 + a$ that for zero stimulus delay; b is the time constant of decay. However, this gave a bad fit with $R = 0.292$ for $n = 409$ SRT trials compatible with the reaction time constraints. A linear fit, described by $RT = RT_0' + a' \cdot t$, with parameters RT_0' (reaction time

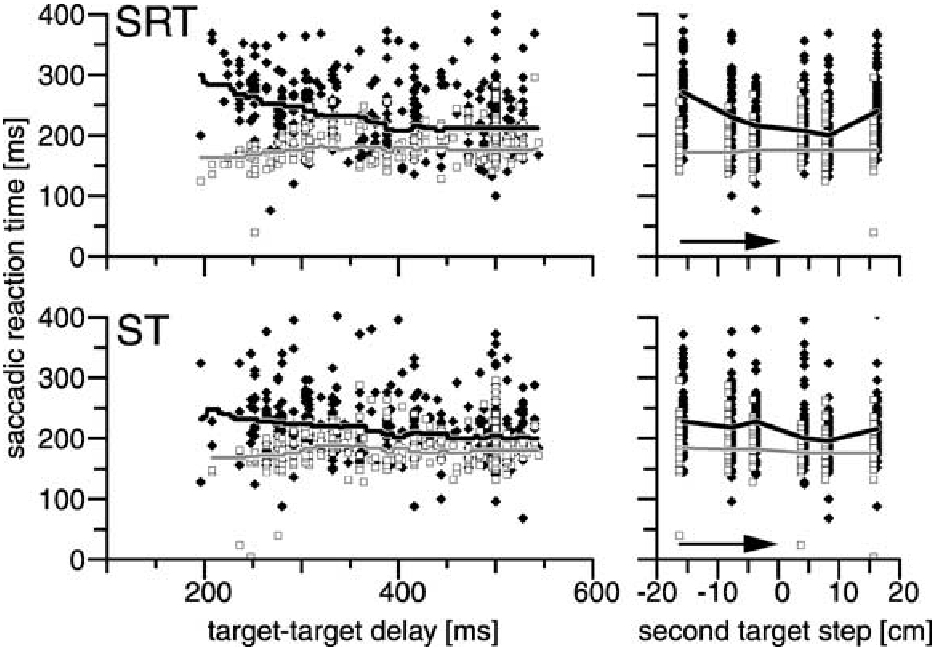

FIG. 3. The reaction time of the second saccade (black diamonds with thick black line from sliding median) in the saccade reach task (top row) and the saccade task (bottom row) depends on stimulus delay (left column) and amplitude of the second target displacement (right column) in experiment B. The reaction time of the first saccade (open squares and grey line) does not. The amplitude of the first saccade is represented by the arrow in the right column. Positive amplitudes correspond to onward trials, negative to reverse. Data of first and second saccade have been shifted slightly apart horizontally for better visibility.

for zero stimulus delay) and a' (transfer gain of delay to reaction time) was even worse (R-value 0.264). An exponential fit $[RT = RT_0'' + a'' \exp(-t/\tau)]$ gave the best R-value of 0.335 for the three fitted functions, where RT_0'' is the reaction time for infinitely long , $RT_0'' + a''$ for zero stimulus delay, and τ is the decay time constant. Although this value is still low, ANOVA revealed significance ($F = 25.6$, $P < 0.0001$). For ST correlations were lower (ST: $R = 0.193$ for hyperbolic, $R = 0.190$ for linear, $R = 0.194$ for exponential, $n = 429$). A 'per-person' fit with more trials per subject might be a direction worth pursuing.

Hand movement analysis

The reaction time of the hand movement, i.e. the time from appearance of the target until the finger velocity exceeded 10 cm/s for three consecutive samples, did not depend on the target delay, nor did the response time (second target-on until target reached) or the average or peak absolute velocities (Fig. 4). Although reaction time and peak hand velocity did not depend on the amplitude of the second target step, hand response time and average absolute hand velocity had larger values for larger amplitudes. In onward trials the correction of the ongoing movement had to be done in the same direction, which would have been detectable only in the velocity or acceleration signal. Indeed only few trials appeared visibly separable into two submovements. This is completely different for reversal trials, where the hand movement had to be stopped and re-accelerated into the opposite direction. This online correction gave a unique trajectory for which the time and location of the reversal point of the trajectory can be clearly determined. The time from the second target displacement until the time of trajectory reversal is a kind of reaction time for the correction (correction time in Fig. 5A). It is not dependent on the amplitude of the second step but depends on the stimulus delay. The shorter the stimulus delay was the longer the subjects needed to correct their arm movements. For short stimulus delays, the location of the reversal point of the trajectory undershoots the first target step (Fig. 5B). The amplitude of the first submovement, which is measured by this variable, increases for increasing stimulus delay. For the longest delays tested, the first submovement overshoots. However, a dependence on the second amplitude was not detectable.

Experiment C: step–gap–step

The rationale to introduce the step-gap-step paradigm was to verify whether the increased second reaction time reflects an absolute refractory time for saccades. The gap before the second target displacement was introduced to probe for reaction time decreases similar to those in single-step experiments. No subject has been clearly aware of the gap, yet some reported *post hoc* a possible presence of the gap when explicitly questioned after the experiment. This reflects the subconscious effect of the gap. In the following, we will again point out only the significant differences (Wilcoxon rank-sum, $P < 0.01$).

The second saccade in the classical double-step task (without gap) shows the now well-established increase of reaction time over the first (Fig. 6, Table 3). In all four conditions of this experiment, this reaction time in the task without gap was about 35 ms longer than in any of the step-gap-step tasks. Some dependence of the second reaction time on the stimulus delay is visible for reverse trials (Fig. 6, left column), the increase of about 10–15 ms for stimulus delay 80 ms (plus gap) reduces for stimulus delay 150 ms and vanishes for stimulus delay 300 ms. However, all second reaction times after the gap in the onward trials are shorter, in general shorter than the first reaction time. In the saccade task (ST), the second reaction time is shortest for the 80 ms delay (about 35 ms shorter than the first saccade) and is longer for 150 ms and 300 ms delay, but still shorter than the reaction time of the first saccade. In conclusion, the gap before the second target displacement could abolish the delay of the second saccade, i.e. there is no intrinsic saccadic refractory time.

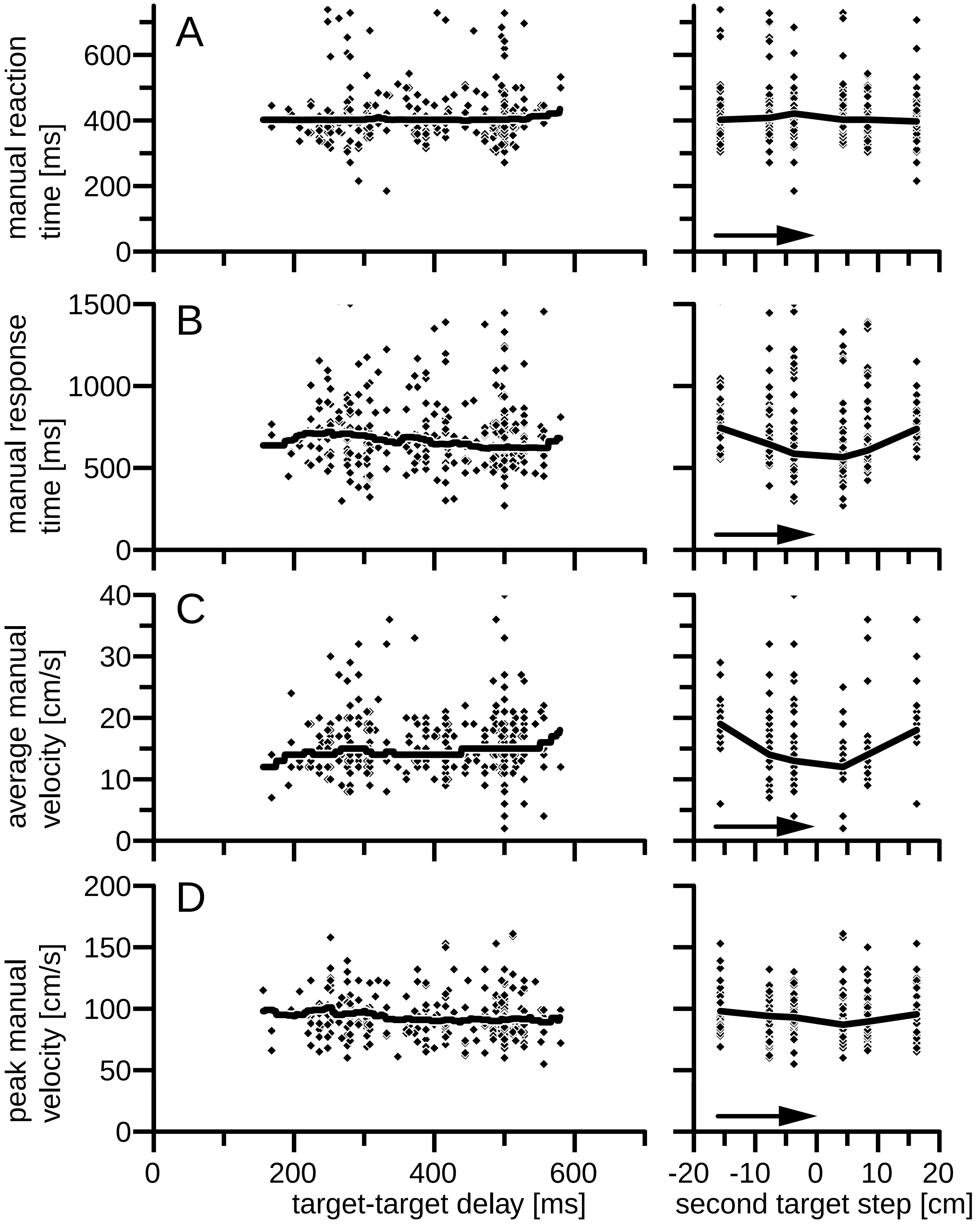

FIG. 4. Hand reaction time (A) and hand response time (B), as well as hand average and peak velocities (C and D) are plotted in dependence of stimulus delay (left column) and amplitude of the second target step (right column). None of these four quantities showed a clear dependence on stimulus delay. Hand response time and average hand velocity depend obviously on the amplitude of the second target step (B and C right panels). Manual reaction time and peak absolute velocity do not.

The finger trajectories of experiment C were analysed similarly to experiment B, yet only the result from the reversal trajectories will be presented. In these trials, the finger-tip had a unique time and location at its largest horizontal eccentricity. The locations were most eccentric for the step-gap-step with 300 ms delay (Fig. 7A). These reversals occurred at similar times after the beginning of the trial, i.e. the first target displacement (Fig. 7B). The time necessary for the correction of the trajectory was calculated by subtracting the stimulus delay and the gap from the reversal time (Fig. 7C). The correction times for the hand trajectory became shorter with longer delays in the step–gap–step trials. The correction time in the classical double-step (with 300 ms delay) is similar to that of the step–gap–step with 80 ms and

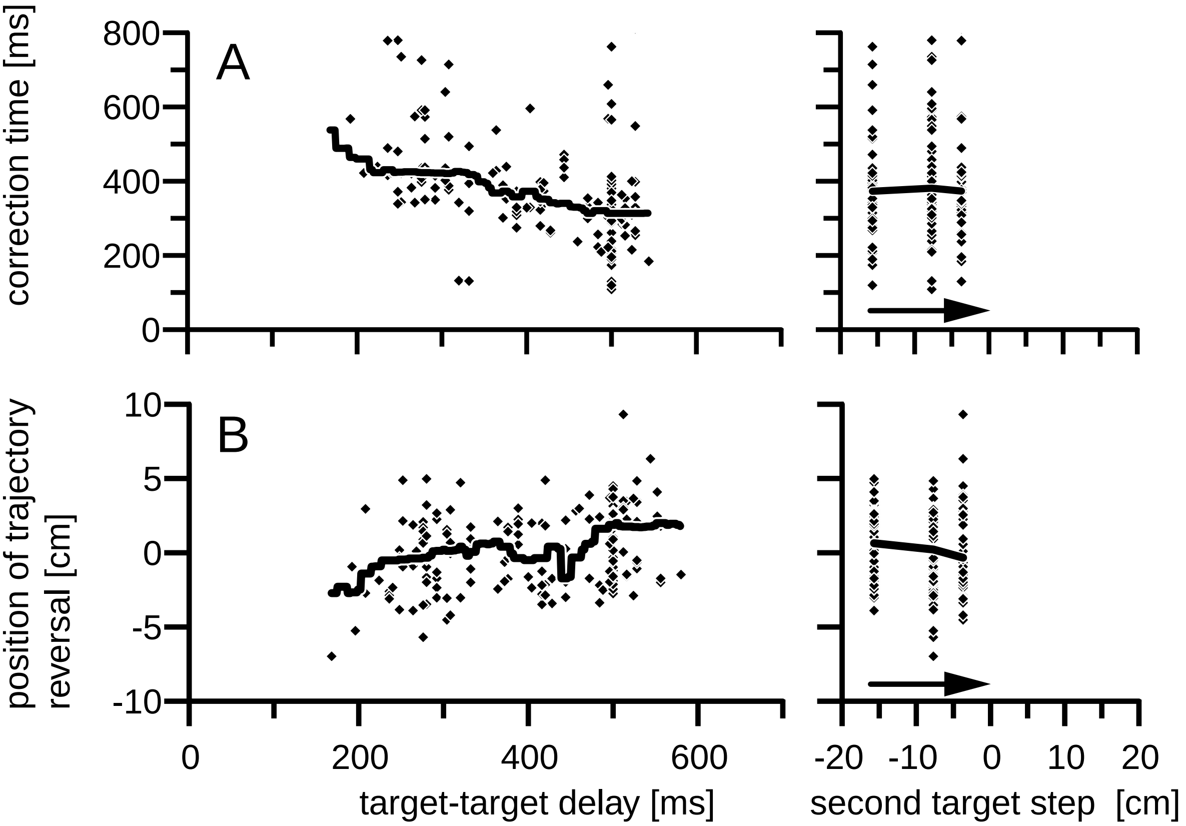

FIG. 5. Dependence of the trajectory reversal on stimulus delay (left column) and amplitude of the second target step (right column) in the reversal trials. The correction time (time from second target displacement to reversal of trajectory, A) is independent of the amplitude of the second target step. However, it decreases with increasing stimulus delay. The location of the reversal point (B) of the trajectory undershoots (negative values) the first target position for short delays and overshoots (positive values) for long delays.

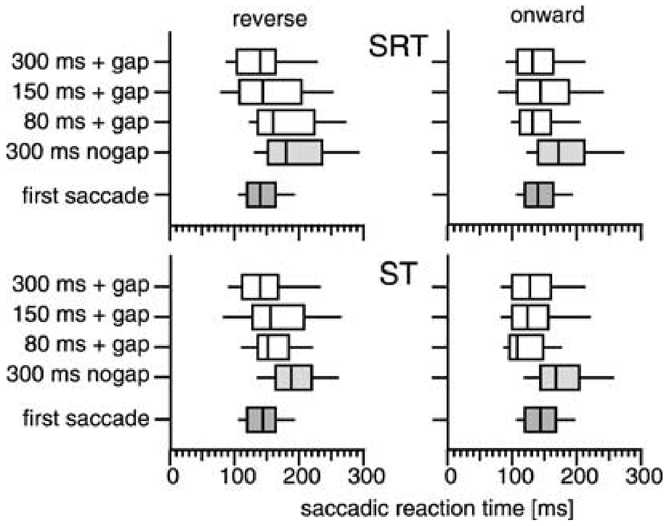

FIG. 6. Saccadic reaction times for all subjects in the step-gap-step task experiment C for saccade-reach task (SRT, top row) and saccade-only task (ST, bottom row). The boxes extend between the 25% and 75% quartiles and are separated by a line for the median. The horizontal lines extend to the 10% and 90% percentiles. The second target displacement had the reverse direction in the left column and the onward direction in the right column. The second saccades in the step-gap-step tasks have shorter reaction times than those of the classical double-step task, and are in part similar to those of the first saccade.

TABLE 3. Saccadic reaction times ms in the step–gap–step experiment C

	Saccadic reaction time (ms)					
			ST		SRT	
	ST First	SRT First	Onward	Reverse	Onward	Reverse
300 ms no gap	144	140	168	188	172	180
80 ms + gap			108	152	132	160
150 ms + gap			122	156	142	144
300 ms + gap			128	140	132	140

Values are the medians in saccade task (ST) and saccade-reach task (SRT) over all subjects pooled over both directions of the first saccade. The subjects could see their hand (closed loop).

150 ms delay (plus gap). This means the gap had an effect on the spatial but not on the temporal properties of the hand movement's correction.

The response time is the time from target appearance until completion of the movement to this target. Helsen *et al.* (1997, 1998, and 2000) report that, in a single-step saccade-reach task, the eye response time is 50% of the hand response time. We are able to calculate these figures for the second submovement in the present double-step experiment. The time from the appearance of a target until the completion of the movement to this target is called the response time. The response times for eyes and hand are plotted in Fig. 8A and B, respectively.

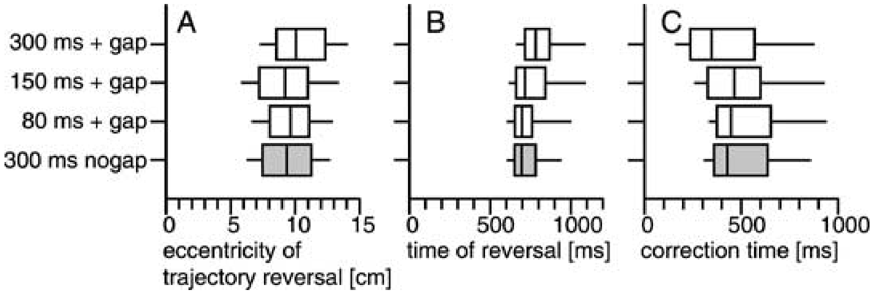

FIG. 7. Movement parameters of the finger trajectory of reversal trials in the step-gap-step task (experiment C). The reversal point has the maximal eccentricity of the trajectory. See text for details.

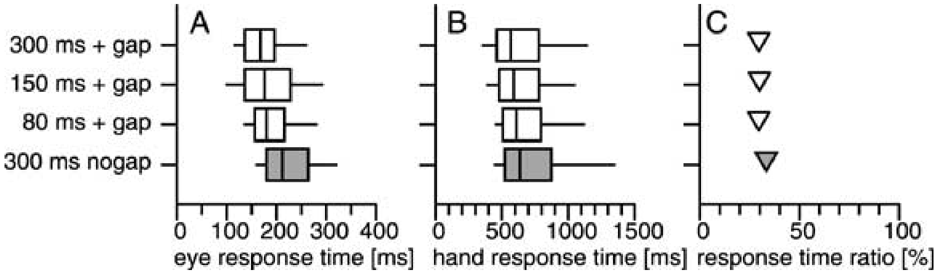

FIG. 8. Response times (time from target appearance until completion of the movement) to the second target step for eye (A) and hand (B), which were recorded in the step-gap-step tasks (experiment C). The eye response times are longest in the classical double-step. The ratio of eye response time divided by hand response time (C) is about 30% in all conditions.

Those for the eyes show the longest values in the classical double-step (as could be expected from the reaction times, as saccades have constant movement times). These strong variations vanish after calculation of the quotients of the medians of the response times of the eyes and the hand (Fig. 8C). The eye response times are about 30% of the hand response times in all four conditions (30.6%; std 1.6%; range: 29.6–33.3%). Calculating the difference of eye and hand response times also gives a value that is rather constant (417 ms; std 11 ms). This difference measures the time from stable foveal vision of the target until arrival of the hand.

Discussion

The present study shows that the reaction time of the second saccade in a rapid sequence of two visually guided saccades is increased compared with the first because of a variety of factors: (i) there was a stronger increase in reaction time when the second saccade had to change direction compared with the first; (ii) the reaction time of the second saccade is longer when the subject had to point to the target in addition to looking at it; (iii) the increase in reaction time for the second saccade was stronger for shorter delays between the two target displacements as well as for larger amplitudes; (iv) when the lights behind the mirror illuminated the subject's hand, the reaction times were shorter than without this illumination; and (v), however, a gap before the appearance of the target at the second position can reduce the described increases of the second reaction time. The gap can actually abolish the effect for onward saccades. The reaction time of the second saccade is then similar to that of the first saccade.

Onward vs. reversal, not medial vs. peripheral

The second saccades, the reaction times of which were assessed in experiment A, were always from the centre of the screen to a position 5.1 cm either to the left or to the right. The difference between onward and reverse conditions was given by the direction of the first saccade. The compared second saccades were therefore identical in retinocentric, egocentric and allocentric coordinates. This is the essential extension of our previous study (Lünenburger *et al*., 2000), where we used a kind of centre-out task. In that task the first saccade was from the centre to a location to the left or to the right and then either half-way back centrally or half-way further peripherally. The difference in reaction times of the second saccades in these two conditions could not clearly be attributed to a change in movement direction or to eccentricity. Although the saccades were the same in retinocentric coordinates (5.1 cm left or right of current gaze position), they were either in the left or right half-space from the subject's or the screen's midline. The onward condition always led to a larger eccentricity, whereas the reverse condition always led to a smaller eccentricity. This problem was overcome in the present study. It can now be stated clearly that the relation of the directions of the two saccades provokes the differences in reaction time. Reverse saccades have an approximate 40-ms longer reaction time in comparison with the first saccade; onward saccades have only a 20-ms longer reaction time. A brain area that might play an important role for this behaviour is the lateral intraparietal area (LIP). Duhamel *et al*. (1992) and Hamed *et al*. (2001) have described the shift of the visual receptive field of LIP neurons briefly before and during a saccadic eye movement (for review see Schlag & Schlag-Rey, 2002).

It should be noted that in the experiments A and B in the present paper the first target displacement is predictable. The target moves in 100% of the trials to the central position. In contrast, the second displacement moves the target to the right in 50% of the trials and to the left in the remaining 50%. It has been reported that higher target probability has a decreasing effect on saccadic reaction time (and on the neural activation in superior colliculus; Megaw & Armstrong, 1973; Pare & Munoz, 1996; Dorris & Munoz, 1998). However, in Lünenburger *et al*. (2000), we reported the results when first and second step target locations have 50% probability. As stated above, the second saccadic reaction time was longer than the first. The median saccadic reaction times of the first saccades in that study were longer (about 170 ms for ST and 160 ms for SRT) than in the present study (about 130 ms) reflecting the different probabilities.

Relevance of visual feedback

Experiment A allows the comparison of the sessions with closed loop and open loop visual feedback control of the hand. The saccadic reaction times were in general shorter in the closed loop condition when the lights behind the mirror were switched on, compared with the open loop condition in which only the targets were visible. This was the case also in the ST in which the subjects rested their hands on their knee that was out of sight. The lights did not only illuminate the hand (if near to the target), but also parts of the lab wall and the mirror/monitor mounting. Thus, external visual references were present in the closed loop condition but not in the open loop condition. This visual frame might have made the task easier leading to the shorter reaction times. Because a shifted frame leads to a mislocalization of a target within this frame (Bridgeman *et al*., 1997), a static frame can certainly make the localization of the target easier. The work of Deubel *et al*. (1998) indicates that visual information that is present in a defined (short) time window after a saccade is used to update the map of the visual world and to detect possible errors made while performing the saccade.

Dependence of timing and amplitude

We had three hypotheses for the dependence of the second reaction time on the delay between the two target displacements: (a) the second reaction time increases when delay decreases; (b) the second reaction time is increased for intermediate delays; it decreases towards the first reaction time for longer delays and drops to express reaction times for very short delays; and (c), intermediately between (a) and (b), for short delays the reaction time distribution might become bimodal containing short reaction time 'correction' saccades and longer reaction time 'delayed' saccades. This means the relation of second reaction time and stimulus delay bifurcates. The results from experiment B show that the reaction time increases monotonously with decreasing delay. This is only compatible with hypothesis (a). However the exponential fit was better than the hyperbolic fit. A group of short reaction time 'corrective' responses was not observed. The reason why other studies, e.g. Prablanc & Martin (1992) observe much shorter reaction times is not obvious. The relative amplitudes of first and second target displacement used might lead to different effects. The ratios of 25%, 50% and 100% used in the present study might be too large to be accounted for as error and hence are not compensated by an online correction system (Desmurget *et al*., 1999). In Prablanc & Martin (1992), the size of the second target displacement was small (about 11 cm) compared with the total distance of 65 cm. The fact that the second target displacement in Prablanc & Martin (1992) was not parallel to the first step is not likely to allow very short reaction times; the first displacement was centrifugal from a near starting point to a target on a circle around the subject, the second from one target on the circle to another. However, Feinstein & Williams (1972) used nonparallel first and second displacements (first horizontal, second vertical) but did not find short reaction times. Another parameter might help to understand the difference: The timing of the two target displacements in the present study allowed conscious perception of the second displacement, as it did in the studies of Feinstein & Williams (1972) and Becker & Jürgens (1979). In contrast, Prablanc & Martin (1992) and Desmurget *et al*. (2001) use very short delays such that the second displacement of the target occurs during the first saccade, and thus is not perceived consciously (saccadic suppression). In the latter case, the target did not project onto the fovea immediately after the saccade, which would also happen when the first saccade was erroneously short. For this error situation a mechanism should exist to correct the eye position by a corrective saccade quickly. We hypothesize that the second target displacement was handled by this short-latency correction mechanism as in Prablanc & Martin (1992) and Desmurget *et al*. (2001), whereas in the present study, as well as in Feinstein & Williams (1972) and Becker & Jürgens (1979), the longer target delays prohibited this mechanism but allowed the conscious detection of the target displacement.

In Fig. 3 presenting the dependence on stimulus delay and second amplitude both factors are examined separately. The problem with these two one-dimensional approaches is that they demand a separability of both effects (reaction time increase by short stimulus delay and by large amplitude of the second target displacement) and homogeneous sampling of the stimulus domain. This presentation of the data would look the same if large second amplitudes had been tested in trials with long stimulus delays and the dependence on the stimulus delay was the only real effect. That the data do not contain such an artifact can be seen in various ways. One possibility is to plot the second reaction time in three dimensions depending on second amplitude and stimulus delay. This presentation of the data (which can be downloaded in three-dimensional VRML format on http://www.ruhr-uni-bochum.de/neurobiol/publications/luenenburger_ejn2003/) supports the view that amplitude and delay effect are independent.

The reaction times for second saccades were longer in the saccade-reach task than in the saccade task. In addition the slope of increase due to delay and amplitude effect is larger. It is not clear how a simultaneous arm movement can influence saccadic reaction times. A possible neural correlate in the superior colliculus is discussed in Lünenburger *et al*. (2003). However, behavioural observations might shed light on the advantages of this behaviour. The purpose of a saccade to a visual target that has to be reached is quite obviously the easier control of the hand by foveal vision briefly before the contact. This means the saccadic reaction time should covary with the end of the arm movement. Given that assumption and the fact that the arm has much larger inertia and needs therefore longer to correct the trajectory, we might have a reason why the second saccade is delayed.

Gap effect in the double-step

In a recent paper, Boulinguez *et al*. (2001) reported changes of the second reaction time in an eye–hand coordination task in which the subjects made pointing movements away from their body to targets on a horizontal table. The radial displacement of the target was triggered by hand movement onset. A gap was introduced by removal of the first target after 100 ms resulting in a gap depending on hand reaction time of 237 ms on average. Unfortunately, no regard was given by Boulinguez *et al*. (2001) to a comparison of the reaction times of the first and the correction saccade, which might have corroborated our results. Furthermore, the longer hand movement time in the gap compared to the no-gap condition, not explicitly explained in that paper, might result from a longer trajectory, which manifests itself in the reversal trials of our experiment in more peripheral reversal points of the finger trajectory with gap than without. We would speculate that the loss of visual reference during the gap has to be compensated for by fixation of the final target position prior to correction of the hand trajectory.

In the classical double-step tasks (experiments A and B), the reaction time of the second saccade becomes shorter for increasing delays between the target displacements. It can be assumed that the second reaction time decreases to the level of the first saccade for sufficiently long delays. Actually, when the target appears at the beginning of the trial a saccade is required to fixate this target. The first target displacement occurs after 1500–1700 ms. This means, the reaction time of the first saccade would correspond to a stimulus delay of 1500–1700 ms. However, the reduction of the reaction times back to normal (first) reaction times in the step-gap-step task occurs already for shorter delays than without gap. Even more, for onward target displacements, the three stimulus timings used did not lead to different second reaction times. The apparent loss of the reaction time-delay relation might indicate that a completely different mechanism comes into play in the step-gap-step experiment. As an important consequence of the gap effect for the second saccade, it should be noted that the increased reaction time cannot be attributed to an absolute refractory time for visually guided saccades.

Apart from increased detectability thresholds during saccades (saccadic suppression), briefly presented visual stimuli are mislocalized when they appear around the time of a saccade (saccadic compression, e.g. Matin & Pearce, 1965; Hallet & Lightstone, 1976a, b; Dassonville *et al*., 1992b). Already before the start of the saccade, targets are perceived at shifted locations, usually towards the saccade end point. Saccades to the location of the second flash have different endpoints depending systematically on the timing of that flash (for review see Schlag & Schlag-Rey, 2002). This effect might be an artifact of a dynamic smooth distortion of the representation of the visual world, that is needed to maintain a smooth updating from the stable eye position before the saccade during the almost instantaneous step of the saccade to the stable eye position after the saccade. Neurons in the lateral intraparietal area are known to shift their receptive fields compatible to this idea (Duhamel *et al*., 1992; Colby *et al*., 1995; Colby & Goldberg, 1999; Kubischik *et al*., 1999).

The experiments with electrical microstimulation in the SC and frontal eye fields (FEF) briefly after a natural saccade (colliding saccades) (SC: Schlag-Rey *et al*., 1989; Schlag *et al*., 1989, 1998; Schlag & Schlag-Rey, 1990; Nichols & Sparks 1995; Kustov & Robinson, 1995; FEF: Dassonville *et al*., 1992a) show that the endpoints of electrically evoked saccades systematically depend on the temporal relation of the stimulation and a natural saccade. This might reflect the updating of the motor maps because of the first saccade.

Applied to the experiments presented in this paper, this means that the first saccade leads to the updating of the spatial maps degrading the accuracy of the map during this time. It appears plausible that a new saccade will only be started after the distortion ended and the accuracy is sufficiently restored. We propose that this led to the increased reaction time for the second saccade in a double-step. In the step–gap–step task, the second saccade might be triggered irrespective of the distortions in the maps that remain from the first saccade. The effect on the accuracy of the second saccades still has to be studied.

Aspects of eye–hand coordination

Although we explicitly instructed our subjects to do hand and eye movements in the saccade-reach task, we would expect similar behaviour when the instruction would have been to reach to the target without mentioning the eye movement because the coordinated sequence of an eye and the arm movement is what we practice every day. Situations in which we dissociate eye and arm movements are very rare, occur only in familiar contexts and often, yet not always, require conscious control. Efficient control of the eyes to ‘visually grasp’ the target before the reach of the hand is essential.

Recent papers by Helsen *et al*. (1997), (1998) and (2000) propose that the ratio of hand response time and eye response time (point of gaze in their terminology) is the key parameter in eye–hand coordination. They report that this ratio is 50% in their single-step saccade-reach task. In the step–gap–step experiments C, the ratio is about 30% for the second movements in a double-step paradigm (Fig. 8). This shows that the saccade occurs relatively earlier during this submovement compared with a single step. Helsen and colleagues furthermore state that the saccade temporally coincides with the time of peak acceleration of finger, elbow, and shoulder. These findings seem to propose a coupling of eye and hand movement based on dynamic parameters. However, the eye also arrived at the target with a quite constant lead before the hand in our experiments. This measure would point to a sensory-based or perceptional, temporal coupling of eye and hand movement. Furthermore, because the ratio was the same with and without gap, the eye–hand coordination is not changed by the presence of the gap.

The reaction time to correct the hand movement after the second target step (Fig. 5A) might reflect concurrent processing. Because the hand movement has a long, but quite constant, reaction time to the first target displacement (Fig. 4A) it is still on the way to the first target location when the target is displaced the second time. The ongoing hand movement still has to be controlled while the new target has to be processed. When the second target displacement occurs early during the first hand submovement, the reaction time is much longer compared with the case where the hand already moved for a while (Fig. 5A). This might indicate that planning is not completed at movement onset, but instead extends into the first movement phase. In this way, resources may be occupied at the beginning of the movement, inhibiting a quick correction (Becker & Jürgens, 1979).

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Abbreviations

FEF, frontal eye fields; LIP, lateral intraparietal area; SC, superior colliculus; SRT, saccade reach task; ST, saccade task.

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