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Jürgen Krölller, Jozina B. de Graaf, Claude Prablanc, Denis Péliisson. Effects of short-term adaptation of saccadic gaze amplitude on hand-pointing movements. *Experimental Brain Research*, 1999, 124, pp.351-362. 10.1007/s002210050632 . hal-01454680

HAL Id: hal-01454680

<https://hal.science/hal-01454680>

Submitted on 22 Nov 2017

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RESEARCH ARTICLE

J. Krölller · J.B. De Graaf · C. Prablanc · D. Péllisson

Effects of short-term adaptation of saccadic gaze amplitude on hand-pointing movements

Received: 9 February 1998 / Accepted: 18 August 1998

Abstract We investigated whether and how adaptive changes in saccadic amplitudes (short-term saccadic adaptation) modify hand movements when subjects are involved in a pointing task to visual targets without vision of the hand. An experiment consisted of the pre-adaptation test of hand pointing (placing the finger tip on a LED position), a period of adaptation, and a post-adaptation test of hand pointing. In a basic task (transfer paradigm A), the pre- and post-adaptation trials were performed *without* accompanying eye and head movements: in the double-step gaze adaptation task, subjects had to fixate a single, suddenly displaced visual target by moving eyes and head in a natural way. Two experimental sessions were run with the visual target jumping during the saccades, either backwards (from 30 to 20°, gaze saccade shortening) or onwards (30 to 40°, gaze saccade lengthening). Following gaze-shortening adaptation (level of adaptation $79 \pm 10\%$, mean and s.d.), we found a statistically significant shift (*t*-test, error level $P < 0.05$) in the final hand-movement points, possibly due to adaptation transfer, representing 15.2% of the respective gaze adaptation. After gaze-lengthening adaptation (level of adaptation $92 \pm 17\%$), a non-significant shift occurred in the opposite direction to that expected from adaptation transfer. The applied computations were also performed on some data of an earlier transfer paradigm (B, three target displacements at a time) with gain shortening. They revealed a significant transfer relative to the amount of adaptation of $18.5 \pm 17.5\%$ ($P < 0.05$). In the coupling paradigm (C), we studied the influence of gaze saccade adaptation of hand-pointing movements *with* concomitant orienting gaze shifts. The adaptation levels achieved were $59 \pm 20\%$ (shortening) and $61 \pm 27\%$ (lengthening). Shifts in the final fingertip positions were congruent with inter-

nal coupling between gaze and hand, representing 53% of the respective gaze-amplitude changes in the shortening session and 6% in the lengthening session. With an adaptation transfer of less than 20% (paradigm A and B), we concluded that saccadic adaptation does not “automatically” produce a functionally meaningful change in the skeleto-motor system controlling hand-pointing movements. In tasks with concomitant gaze saccades (coupling paradigm C), the modification of hand pointing by the adapted gaze comes out more clearly, but only in the shortening session.

Key words Saccadic adaptation · Gaze · Short term adaptation · Transfer to hand movements · Human

Introduction

The metrics of saccadic eye movements need to be continuously adjusted or adapted to changing environmental conditions. Extraocular muscle paresis, for example, elicits a compensation of the reduced saccadic amplitude over a few days of weak eye viewing (Kommerell et al. 1976; Abel et al. 1978; Optican and Robinson 1980; Inchingolo et al. 1991). A much faster process of saccadic adaptation is induced when post-saccadic visual error is artificially modified by slightly displacing the saccade target during the ongoing movement, taking advantage of the saccadic suppression phenomenon [Bridgeman et al. 1975, 1994]. Repeating this double-step stimulation leads to a gradual modification of the primary saccade until, after some hundred trials, the primary saccade brings the eye directly onto the final target position. This short-term saccadic adaptation paradigm has mostly been used to increase or decrease saccade size (McLaughlin 1967; McLaughlin et al. 1968; Weisfeld 1972; Henson 1978; Mack et al. 1978; Miller et al. 1981; Snow et al. 1985; Deubel et al. 1986; Deubel 1987, 1995; Semmlow et al. 1989; Albano 1992, 1996; Goldberg et al. 1993; Frens and van Opstal 1994; Straube et al. 1997) and to modify saccade direction (Deu-

J. Krölller · J.B. De Graaf · C. Prablanc · D. Péllisson
INSERM, Unité 94, 16 avenue du Doyen Lépine,
F-69500 Bron, France

J. Krölller (✉)
Institute of Physiology, Freie Universität,
Arnimallee 22, D-14195 Berlin, Germany
Tel.: +49-30-8382512, Fax: +49-30-8382507

bel 1987; Chaturvedi and van Gisberger 1997). Recently, de Graaf et al. (in preparation) have observed that gaze shifts performed with the head unrestrained adapt in the same way as eye saccades studied in the head-fixed condition, which could suggest that adaptation is not an effector-specific process. Although short-term saccadic adaptation is a well-known phenomenon, the underlying neural mechanisms are still not understood and are the subject of intensive experimental investigations.

While a parametric adjustment of saccade gain was proposed to account for short-term adaptation of saccadic amplitude (McLaughlin 1967), increasing evidence argues for the existence of a "restricted adaptation field", within which adaptation strength decreases progressively as the target differs from the adapted one (Miller et al. 1981; Semmlow et al. 1989; Abrams et al. 1992; Frens and van Opstal 1994, 1997; Chaturvedi and van Gisbergen 1997).

A question that pertains to the nature of saccadic adaptation is whether adaptive readjustment of visually elicited saccades transfers to other types of eye movements. Recent investigations of this issue have revealed the lack of adaptation transfer from internally triggered to reflexively triggered saccades towards visual targets in man (Erkelens and Hulleman 1993; Deubel 1995) and vice versa. On the contrary, in rhesus monkeys transfer of adaptation among saccades of different types have been found (Fuchs et al. 1996). In addition, in man, a study dealing exclusively with reflexively triggered saccades showed a transfer between saccades towards a visual target and saccades towards an acoustic target (Frens and van Opstal 1994). The latter data suggest that adaptation occurs within the efferent limb of the sensory-motor pathways. It takes place at the level at which sensory signals from the visual and acoustic modalities have already converged, but, in humans, upstream the final common pathway (brainstem saccadic-pulse generator) involved in the execution of all saccade types. In any case, tests of saccadic adaptation transfer may provide information about both the locus of saccadic adaptation and the organization of neural systems involved in different types of saccades (Fuchs et al. 1996).

In the present study, our goal was to test the existence of any transfer or mediation of saccadic adaptation to movements of the hand while pointing at a visual target. We explored two cases: a pure transfer of adaptation and an adaptation shift to hand movements during coupled gaze and hand responses. In the course of the study, we modified some conditions of saccadic adaptation as well as conditions under which hand-pointing responses were tested. Under some we found a weak transfer, but not under others. Instead of the usually applied eye-saccade adaptation, we adapted the gaze amplitude. This enabled us to adapt visually fixating movements larger than 20°. Such large movements could be better related to arm movements of a size that were precisely measurable in our experimental set up. Some original data (paradigm B) were previously published as a short note (De Graaf et al. 1995); the raw data are now submitted to a defined quantitative approach for comparison with the other data.

By definition, transfer of short-term adaptation of saccadic gaze movements will be revealed when movements of body parts not involved during the adaptation phase are modified after adaptation, even when executed without concomitant gaze movements. Thus, transfer would indicate the existence of adaptation-induced modifications not only in neural circuits controlling gaze saccades specifically, but also in others. To our knowledge, McLaughlin et al. (1968) were the first to test the existence of saccadic adaptation transfer to hand pointing; however, they found none. The small number of repetitions (11) of the double-step stimulation, even if sufficient to induce a surprisingly large saccadic adaptation, may not have been sufficient to reveal any significant modification of hand pointing. Contrary to transfer of adaptation, the observation of adaptation transmission under coupled eye and hand responses may reveal a synergistic reading of the efferent oculomotor signals by the hand motor control system.

Materials and methods

Experimental set-up

Thirty-nine experimental sessions were performed in 18 subjects seated in a comfortable chair in front of a table (tilted 23° to the horizontal), on which images of LEDs were mirror-projected (Fig. 1A). The LEDs appeared on three circles concentric around a center point, C, (Fig. 1A,B) located roughly 40 cm below the eyes in the subjects' midsagittal plane. The LEDs of the intermediate circle (radius 62 cm) served as targets for gaze saccades and hand pointing. The LEDs of the outer and inner circles were only used with lower luminosity in paradigm C to provide a field stimulation (a set of three LEDs at the same eccentricity). The intermediate LED just in front of the subject (T_0) was the starting point for all gaze movements. In the following, the position of the LED images on the table will denoted in degrees with respect to C and T_0 . The distance eye- T_0 was also 62 cm.

Head- and eye-movement measurements

A helmet connected to a potentiometer measured head rotation about the yaw axis without preventing subjects from bending their head slightly (12–20°) to achieve a convenient position. Horizontal eye movements were recorded by means of the electro-oculography (EOG). Advantages of the EOG-technique were that it did not induce any discomfort to the subjects, even after long recording periods and, particularly, in a task requiring rapid head movements. The DC-EOG had been proved to be sufficiently suited for the recording of large, horizontal eye movements. Sensitive surface electrodes were placed bi-temporally near the external canthus of the orbitae. A DC-coupled amplifier was used, as well as a low-pass filter (cut-off frequency 30 Hz) and a 12-bit A/D converter for data acquisition. Calibrations were performed by measuring the EOG-signal when the subject accurately fixated nine targets between 40° left and right. The calibration was performed at the beginning and the end of the recording period. A polynomial was fitted to the measured calibration values to construct a look-up table (10-bits or 5° resolution), which was used to convert off-line the EOG-voltages of the whole experiment into a calibrated and linearized signal of the horizontal gaze component. Every 4–10 s (at the onset of a trial), the DC-drift was set to zero and the EOG-voltage was computerized only over the following 2 s. For further details and the calibration procedure see Prablanc et al. (1986) and Pélisson and Prablanc (1988). Calibrated eye and head signals

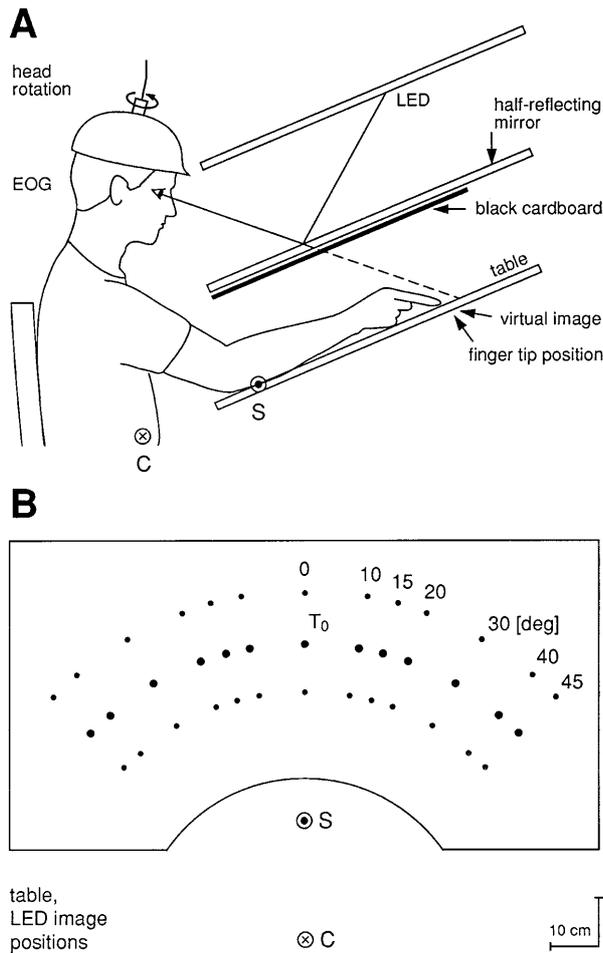


Fig. 1A, B Scheme of experimental set-up. **A** The position of head, hand, and table are shown. Yaw head rotation, horizontal electro-oculography (*EOG*) and the 2-D finger-tip position on the table were recorded. The target LEDs were mirror-projected onto the table. **B** The pointing table and the positions of the targets are shown. *S* Starting positions of egocentric finger movements, *C* center of the target circles

were added to provide the angular position of the gaze in the yaw direction.

As the location of the center point, *C*, of the LED circles and the position of the eyes differed (Fig. 1), the size of the horizontal component of the targeting eye movements were different from the indicated eccentricities of the LEDs. When indicating the target positions and the required gaze movement to reach them, we will speak of eccentricities with respect to T_0 and *C* (10, 15, 20, 30, 40, 45°) throughout the text. For the computations of movement amplitudes shown below (a_1 – a_4), we used the true horizontal eye, head, and gaze amplitudes. The horizontal gaze component necessary to fixate the respective targets were 9.9, 14.6, 19.6, 28.9, 37.6, 41.7°.

The position of the index-finger tip was continuously recorded by means of a 2-D infrared system (Urquizar and Pélisson 1992). An electric contact between finger tip and table marked beginning and termination of hand movements. Unless otherwise specified (see below), experiments were performed in a totally dark room and after the subjects had been dark adapted. In all experiments but two, the peripheral LEDs appeared on the right side, and the subject's right hand was used for pointing. Some data of a left-handed subject were obtained on the left side (sessions JK2, JK3) and were added to the others after mirror-imaging the results onto the right side.

Experimental protocols

Each experiment consisted of three phases: a pre-adaptation test of hand pointing, a period of gaze adaptation, and a post-adaptation test of hand pointing identical to the pre-adaptation test. The pre- and post-adaptation tests consisted of 30–50 hand movements each. For all three phases, a trial started with presentation of T_0 . The subjects then aligned their head with T_0 ($\pm 1^\circ$ tolerance range) and fixated T_0 , while the EOG signal was set to zero to eliminate any residual drift. For the hand-movement phases, the procedure was as follows: when T_0 was turned off, a peripheral target was simultaneously lit, and the subjects were requested to touch it with the tip of the index finger. In the following, such movements will be called pointing. At the end of a pointing trial, T_0 went on again, and the subjects had to return the finger to the starting position. In some experiments, the hand was illuminated during rest at the starting position, *S* (Fig. 1), but it could never be seen during the ongoing hand movement. During the saccadic-adaptation phase, subjects were instructed always to fixate the currently illuminated LED and to follow target-position changes immediately. When T_0 disappeared, a peripheral stimulus went on (target T_1). While the subjects were performing a gaze movement towards T_1 , it disappeared and another stimulus (T_2) was simultaneously turned on. The target jump from T_1 to T_2 was elicited during the primary saccade by an electronic threshold device fed with the gaze velocity signal. Each peripheral target (T_1 and T_2) consisted of either a single LED of the intermediate circle (transfer paradigms) or of three LEDs located on the three circles at the same eccentricity, defining a radial segment (coupling paradigm). Different paradigms were used to test whether gaze saccadic adaptation affected hand-pointing movements with (paradigm C) or without concomitant orienting gaze shifts (paradigms A and B).

Transfer paradigms

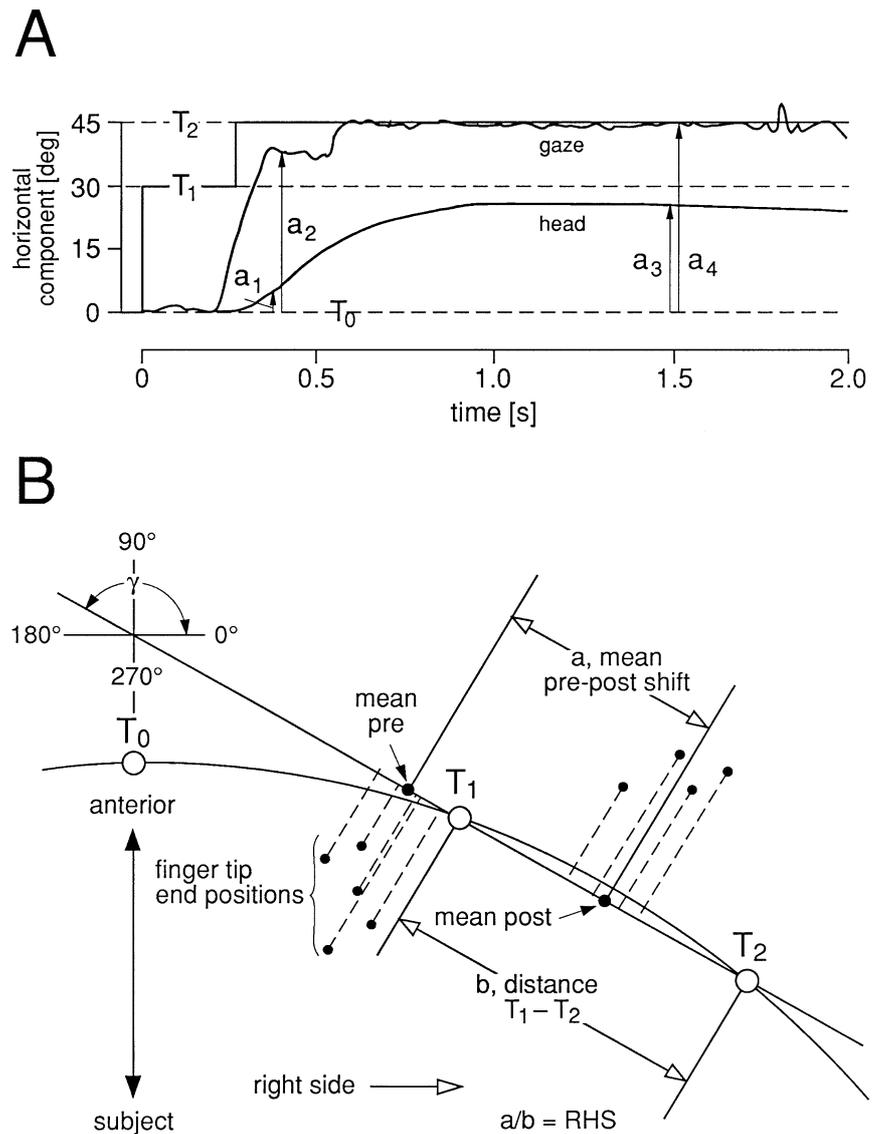
In paradigm A, only one double-step target was presented to the subjects in the adaptation phase, and, in paradigm B, three different double-step targets were presented. In both series, the subjects were instructed and trained not to move eye and head during hand pointing. When they did it inattentively, all LEDs were immediately turned off, the trial was omitted from the recording, and the next one initiated. For egocentric pointings, the starting point (*S*) of the index finger movements was located in the midsagittal line, 23.5 cm anterior to the center of the LED circles (Fig. 1).

Paradigm A. Seven subjects participated. Hand pointing in the pre- and post-adaptation period was performed to targets at 15, 20, 30 and 40°. During adaptation, LED-lights were displaced from 30 to 20° (saccade-shortening session) or 30 to 40° (saccade-lengthening session). The sessions are illustrated in the insets of Figs. 4 and 5.

Paradigm B. Six subjects participated. Pre- and post-adaptation hand pointings were performed to targets at 10, 15, 20, 30 and 45°. During adaptation, three double-step targets were presented: primary targets at 15, 30 and 45° and secondary targets at 10, 20 and 30°, respectively. Each target displacement was presented 30 times in random order. The paradigm is illustrated in Fig. 6. See De Graaf et al. (1995) for more details.

Paradigm C (coupling paradigm). Four subjects participated. In the pre- and post-adaptation periods, the subjects were asked to move their eyes, head, and hand towards the peripheral target in a way they usually would do when looking and pointing at a target simultaneously. To prevent disadaptation, the peripheral LED disappeared immediately at gaze movement onset. The starting point of the invisible hand movements was T_0 . In the adaptation phase, a total of 120–270 double-step trials was presented. In the saccade

Fig. 2 Determination of amount of adaptation (**A**) and relative hand shift (**B**). **A** Recording of the horizontal electro-oculography and head rotation (*ordinate*) during an adaptation trial with LED-perturbation from 30° (T_1) to 45° (T_2). a_1 – a_4 indicate amplitudes determined from gaze and head-position trajectories necessary to estimate the amount of adaptation: a_1 head displacement at the end of the primary saccade, a_2 gaze position at the end of the primary saccade, a_3 final head position, a_4 final gaze position (for further details see Methods). **B** Each finger-tip end position of the pre-adaptation and the post-adaptation pointings (*small filled circles*) was projected onto the T_1 – T_2 connection line, and then the average sites on this line were computed (*mean pre*, *mean post*). The distance between the two averages (a , *mean pre-post shift*) yielded a length that provided the relative hand shift (*RHS*), when expressed in relation to the T_1 – T_2 distance b . The direction of the T_1 – T_2 connection line on the table is given by the *angle* γ



shortening experiments, targets jumped from 20 to 10, 30 to 20, and 45 to 30° during the adaptation phase, and pre- and post-adaptation responses were required to 20, 30, and 45°. For the saccade-lengthening experiments, the adaptive double-step targets from 10 to 20, 20 to 30, and 30 to 45° and pre- and post-adaptation responses were required to 10, 20, and 30°. Sketches of the sessions are presented in Fig. 7.

Paradigm D (null-adaptation experiments). Control experiments were performed in nine subjects to assess the consistency of hand-pointing movements and, specifically, to test the possibility that a shift in the final hand-movement points was not related to saccadic adaptation, but, e.g., to repetitive execution of eye and head movements. For this purpose, hand pointing to visual targets was performed under the same condition as in the transfer paradigm A, but, instead of a displaced target, we presented a single stationary target at 30° during the pseudo-adaptation period.

Evaluation of gaze adaptation

During the primary gaze saccade, T_1 was replaced by T_2 , and subjects executed a corrective saccade to align the line of sight with

T_2 (Fig. 2A). a_2 designates the total amplitude of the gaze primary saccade and a_1 the head component amplitude obtained at the end of the primary saccade; similarly, a_4 and a_3 designate gaze and head angular deviations measured 1.5 s after the beginning of the trial when eyes and head were stationary and the subject, as requested, was accurately fixating T_2 . Recall that the EOG signal was set at zero before each trial. Due to possible EOG gain fluctuations along the length of an experiment, the measured gaze positions could slightly differ from the computed ones; however, a_4 provided an additional trial-by-trial calibration of gaze while the subjects fixated T_2 . Therefore, for each trial, the scaling factor $(a_4 - a_3)/(T_2 - a_3)$ was computed to finely correct the eye component. As the whole EOG recording was already scaled according to the calibration at the beginning and the end of the experiment, the additional scaling corrections varied only slightly between 0.9 and 1.1. A further correction factor, k , was introduced to account for the known systematic undershoot of saccadic responses to stationary targets. The amount of undershoot had been determined and used in an earlier study in ten subjects (six of which also participated in the present study) conducted under comparable conditions in the same laboratory (Kröllner et al. 1996). The associated average gain of the saccades was 0.971 (slightly larger than commonly observed) and, in Eq. 1, k is its inverse. Then, we put together these corrections in the following Eq. designed to provide

Table 1 Numerical results from all transfer and coupling experiments. Number of experiments (n) and the respective target jump (*Displ.*) are given for each paradigm (*A, B, C*) and the shortening and lengthening session. Overall averages for the mean and standard deviation of the amount of adaptation (*A*), relative hand shift

(*RHS*) and respective ratio (transfer rate: *TRF* or coupling rate: *CLR*) are given as percentages. Negative sign indicates *RHS* and *TFR* or *CLR* in the opposite direction to the transfer or coupling direction expected

	n	Shortening				Lengthening			
		Displ.	A	RHS	TFR or CLR	Displ.	A	RHS	TFR or CLR
Transfer									
A	8	30→20	79±10	11±10	15±16	30→40	92±17	-15±25	-19±28.5
B	6	15→10	58±26	15±16	33±48				
		30→20	82±23	15±13	18.5±17.5				
		45→30	102±31	9±8	10±8				
Coupling									
C	4	20→10	29±19	12.5±10	63±49	10→20	30.5±15	-2±5	-11±27.5
		30→20	59±20	28±12	52.5±26.5	20→30	47±37	11±7	68.5±94
		45→30	72±5	28.5±13	39±16	30→45	61±27	4±3.5	6±3

an estimate of adaptation for each trial. For saccade-lengthening and saccade-shortening sessions, the adaptation rate of a single trial was:

$$A_s = \frac{k \left[(a_2 - a_1) \frac{a_4 - a_3}{T_2 - a_3} + a_1 \right] - T_1}{T_2 - T_1} \quad (\text{Eq. 1})$$

A_s is zero if the primary saccade (being corrected for undershoot) ends at T_1 and has a value of unity if the primary saccade is targeting T_2 , which would mean full adaptation. For each adaptation period, A will define the final amount of adaptation achieved. It is the average of the A_s -values of the last five trials.

Evaluation of hand-pointing shifts

The hand-pointing task of touching a target required a positioning of the finger tip in two dimensions. To measure modifications in the hand pointings due to saccadic adaptation, we determined the difference in finger end positions between the pre-adaptation and the post-adaptation period (further called shift). Adaptation was expected to result in hand-position shift that parallels the saccadic gaze shift, and, therefore, we computed the mean component of hand position shift parallel to the line connecting T_1 to T_2 . Figure 2B illustrates the approach for a saccade-lengthening session: the line “subject - anterior” marks the body sagittal axis, only the right half of the pointing table is shown. First, the projection of each finger end position onto the T_1 - T_2 connection line was computed. By means of this computation, we reduced the pointings in two dimensions to a one-dimensional event. Then, the mean position on the connection line was computed separately for the pre- and post-adaptation period. Student's t -test (paired, two sided), was used to assess significance levels for the difference between the mean of the pre- and post-adaptation pointings.

Definitions of relative hand shift, transfer rate, and coupling rate

The ratio “shift along T_1 - T_2 -connection line/distance T_1 - T_2 ” provided the relative hand shift (*RHS*). A positive or negative *RHS* indicates a shift in the direction expected from an adaptation effect or in the opposite direction, respectively. The ratio “relative hand shift/adaptation rate” will be called transfer rate (*TFR*, paradigm *A* and *B*) or coupling rate (*CLR*) in paradigm *C*. All values will be given as percentages. Mean and standard deviation of *A*, *RHS*, and *TFR* or *CLR* computed over all subjects participating in a session (grand averages) are listed in Table 1.

Results

Transfer paradigm A

In this paradigm, we used one peripheral target (30°) during the adaptation phase that was displaced by 10° inwards or outwards when the saccade was performed. We first applied a direct approach to analyzing the data, which was simpler than computing *RHS* and *TFR* (Fig. 3).

This approach was based on the two-dimensional coordinates of the finger tip positions (given in mm). For each experiment, the differences between the mean finger end position of the pre-adaptation and the post-adaptation pointings were plotted in a posterior-anterior/left-right coordinate system (Fig. 3, upper diagram). In this diagram, data from all eight experiments (seven subjects) in the shortening and the lengthening session are given. In each case, the mean location of the pre-adaptation pointings was placed at the center of the coordinate system. Plotting the mean position of post-adaptation pointings (Fig. 3, open symbols) in this coordinate system directly illustrates the amount and direction of hand shifts. The distance between T_1 and T_2 was 108.1 mm. Filled symbols in Fig. 3 represent the averages computed across all eight experiments. For the saccade-shortening session, the grand average of the finger-movement terminations was shifted in the direction towards T_2 , as expected from adaptation transfer. The comparable shift for the saccade-lengthening sessions, however, was inconsistent with the assumption of adaptation transfer: T_2 was located to the right and posterior to T_1 (Fig. 1); the hand-position shift, however, was directed towards the left and anterior and was therefore antiadaptive. This discrepancy let us run a control paradigm in nine subjects (Fig. 3, lower diagram), in which the adaptation session was replaced by a series of non-jumping target presentations at 30° s, called the ‘null adaptation’ (paradigm *D*), while the experiment otherwise remained unchanged. The results show that the average final finger-movement position was slightly shifted to the left and towards the body. The mean shifts in final finger position of movements to all four targets did

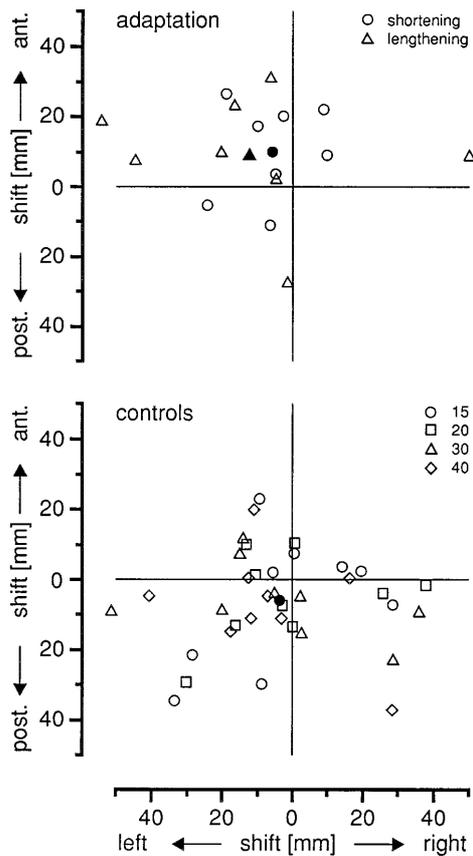


Fig. 3 Transfer paradigm A and control experiments; shift of finger-tip end positions between pre-adaptation and post-adaptation period. Shift in post-adaptation pointings to the left with respect to the pre-adaptation is directed towards the sagittal line; a shift forward (away from the body) extends in the anterior direction (*post.* posterior). For each experiment, the mean position of all eight or ten pre-adaptation pointings is placed in the center of the coordinate system; the mean position of post-adaptation pointings is indicated by *open symbols*. *Top panel* Only pointing movements towards the 30° target of paradigm A were encountered, eight experiments with the saccade shortening protocol (*open circles*) and eight experiments with saccade lengthening (*open triangles*). The *filled symbols* indicate the respective position averaged over all eight experiments. *Bottom panel* Data from nine control experiments; shift between pre- and post-adaptation hand pointings towards 15, 20, 30, 40° are shown. Instead of an adaptation period, gaze movements towards a non-jumping 30° target were required. The shift averaged over all subjects and the four pointing movements is marked by a *filled circle*. Number of gaze movements required in the adaptation period: 1 subject: 120, 6 subjects: 180, 2 subjects: 240

not deviate significantly from the mean shift computed only on the 30° pointings.

For an overall statistical evaluation on any possible effect due to adaptation in paradigm A, we compared the shift in the finger-movement termination (Fig. 3, upper diagram) between pre- and post-adaptation test to the respective shift of the nine controls (Fig. 3, lower diagram). A difference in these shifts would be a clear-cut indication whether an influence due to adaptation exists at all. Under the hypothesis of existing transfer, this difference should have a significant component in the direction of the T1–T2 connection line of the adaptation period. In

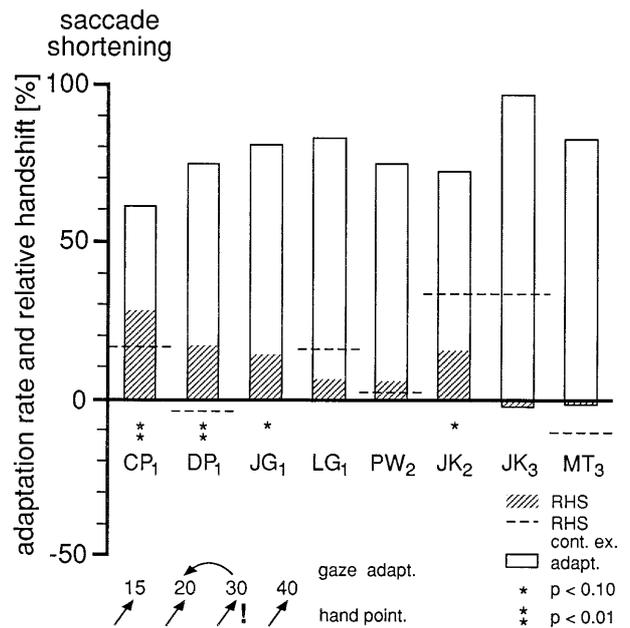


Fig. 4 Transfer paradigm A, saccade-shortening sessions. Results from each experiment displayed separately. Subject's initials (CP–MT) are given; meaning of the subscripts explained in the Results section. *Open bars* show the amount of adaptation achieved. *Hatched bars* show the relative hands shift (RHS), computed according to Fig. 2B. Both full adaptation and full right-hand shift would end at 100%. A significant shift between pre- and post-adaptation hand pointings in the direction of the expected transfer is indicated on the bars: *dashed lines* mark the “pseudo-transfer” computable from control experiments. A negative transfer indicates a shift between pre- and post-adaptation pointings in the opposite direction to the one expected for adaptation transfer. *Inset* at bottom illustrates the experimental conditions: *numbers* indicate LED eccentricities on the right side, *bent arrow* target displacement during adaptation, *oblique arrows* targets for hand movements starting from S (egocentric movements). Computation only from pointings towards 30° target (!)

other words, the data points, as seen in Fig. 3A and B, were placed in a common coordinate system. Then a computing procedure similar to the one explained in Fig. 2B was applied; i.e., the data points were projected onto the T1–T2 connection line in order to remove the radial components of the pointing. Shifts in control pointing were compared to shifts in pointing of the shortening session and the lengthening session. The result was a significant adaptation transfer in the saccade shortening session ($P=0.038$); whereas, in the saccade-lengthening sessions, the shift was in the anti-transfer direction and not significant ($P=0.15$).

The question whether some dependency of the hand-pointing shift on the degree of adaptation exists required a more detailed separate analysis for each subject. In the further analysis, we focused on the position difference between pre- and post-adaptation pointings of the adaptation data only, and we concentrated our analysis on the hand pointing to the 30° target. Therefore, the amount of saccadic adaptation and the relative hand shift (RHS as described in Methods) between the pre-adaptation and post-adaptation final finger-tip positions were computed.

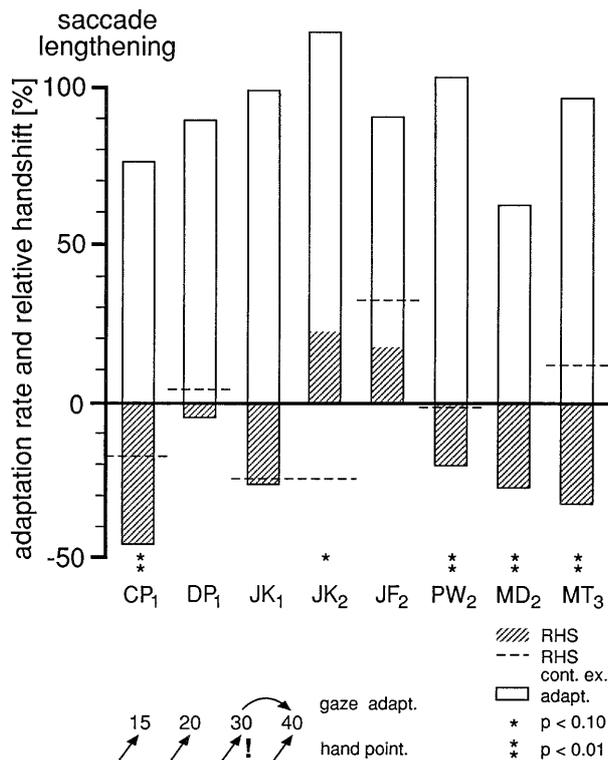


Fig. 5 Transfer paradigm A, saccade-lengthening sessions. Same conventions as in Fig. 4

For paradigm A, they are shown in Figs. 4 and 5. For relative hand shifts, the significance levels are reported in the figures. The transfer rates ($TFR = RHS/A$) averaged across all experiments are given numerically in Table 1. In Figs. 4 and 5, subscripts 1–3 indicate the following differences in protocols: subscript 1 denotes that, in the pre- and post-adaptation period, the hand resting at the starting position was illuminated by a dim spot light (Prablanc et al. 1979, Rosetti et al. 1994), which was immediately extinguished upon the onset of hand movement, ensuring that hand movement could not be controlled via visual feedback. When the subjects made involuntary gaze movements after the peripheral LED onset, the peripheral LED was immediately switched off and the trial repeated. In the adaptation periods, 240 trials were performed (120 trials for subject LG, Fig. 4). Subscript 2 denotes that subjects were trained not to move the eyes during the pre- and post-adaptation phases when the peripheral LED came on, and stability of the eyes was controlled through an on-line display of the EOG signal. The LED was not controlled by the gaze movement. 180 adaptation trials were performed. Subscript 3 denotes that same conditions as in subscript 1 prevailed, except for 180 adaptation trials.

On average, the amount of adaptation achieved was 79% for saccade shortening and 92% for saccade lengthening sessions. Regarding hand pointing, it became apparent that the subjects tended to displace the final finger positions towards the left (i.e., to the body sagittal plane), which was in the transfer direction, expected for saccade

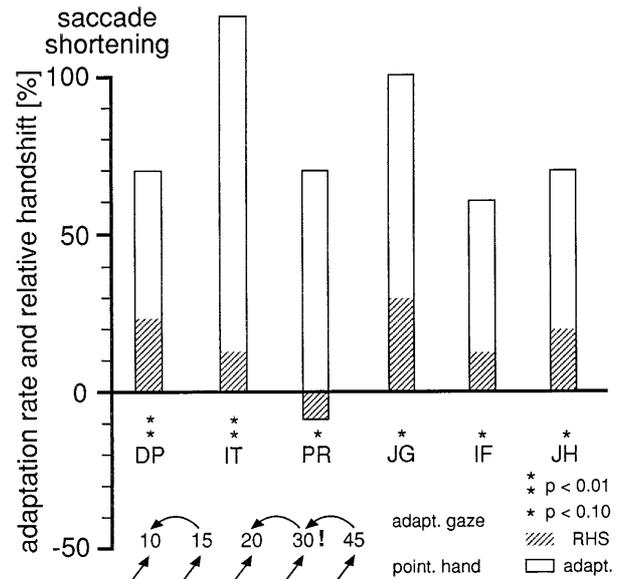


Fig. 6 Transfer paradigm B, saccade-shortening session, display of amount of adaptation and relative hands shift (RHS), as in Figs. 4 and 5. Selected data from De Graaf et al. (1995) processed in the same way as the raw data from paradigms A, C, and D. Paradigm indicated in the inset. Amount of adaptation computed from 30° to 20° target jump, hand pointing shifts towards 30° target. During the adaptation period, three displaced targets appeared with 30 trials per target jump. Same conventions as in Fig. 4

shortening adaptation, but in the opposite direction for saccade lengthening adaptation. On average, the relative hand shift of 11% (i.e., adaptive) for the saccade shortening was significant ($P=0.02$). It was -15% (i.e. antiadaptive) for the saccade-lengthening session, but was not significant ($P=0.135$). The respective average transfer rates (TFR) were about 15% and -19% . A correlation analysis between the amount of adaptation and the relative hand shift (dependent variable) yielded the following results: for saccade shortening, we found a significant ($P<0.01$) negative correlation (slope = -0.877 , $r = -0.879$); whereas, for saccade lengthening, the correlation did not deviate significantly from zero (slope = 0.274 , $r = 0.366$).

In Figs. 4 and 5, we could not detect clear effects dependent on the various conditions. Instead, the results seem to be influenced by some individual movement patterns. For example, subjects CP, DP, and PW exhibited a tendency to always point more to the left after the adaptation period of both the shortening and lengthening sessions. In CP and PW, this movement pattern was also observed in the control experiments. In contrast, subject MT's hand pointing was shifted more to the periphery in all three conditions.

The computation of relative hand shifts was also applied to the pointing to the 30° target of the control experiments. For each experiment of the “null adaptation” session, the component of the shift in the direction of the T1–T2 connecting line of paradigm A was computed. Note that the direction of the connecting line is different in the shortening and the lengthening sessions. Then, the shift between the pre- and the post-test was set in rela-

tion to the T1–T2 distance of 108.1 mm. The result was the “pseudo RHS”; its value for the corresponding subjects is indicated in Figs. 4 and 5 by dashed lines. For all nine subjects of this paradigm, the average pseudo-RHS was 0.7% (shortening) and 1.1% (lengthening). For the subgroup of subjects that participated in both the “null adaptation control” and the true transfer experiments, it was 9.4% or gain shortening and 1% in the gain lengthening direction.

Transfer paradigm B

We intended next to compare the present data with the shifts previously evaluated in final finger positions in a triple-displacement paradigm (De Graaf et al. 1995). Therefore, we submitted some of the raw data of this paradigm to the present computing procedures to determine the amount of adaptation and relative hand shift. From the five pointing movements, we selected those directed towards the T₁ targets. They were obtained under the same conditions as the data of the present single-target displacement. The results of the 10° target displacement were suitable for a direct comparison to paradigm A and are shown in Fig. 6. The graph shows the amount of adaptation and the relative hand shift averaged for all subjects; the latter value was 15%, yielding a transfer rate of 18.5%. The grand averages of all three adaptation levels and the respective relative hand shifts are listed in Table 1.

Coupling paradigm C

On examining the data obtained so far, we had some doubts as to a functionally meaningful modification of hand pointings under the strict conditions of adaptation transfer. Therefore, we performed an additional paradigm under conditions that were expected to facilitate hand-pointing modifications due to adaptation. Of course, these experiments were no longer suited to investigate adaptation transfer, as defined in the Introduction. In the pre- and post-adaptation periods, hand and gaze movements were required to be executed simultaneously, both starting from the same location in space (T₀) and aimed at the same peripheral target. The instruction to the subjects was that hand pointing and gaze shifts should be done in a quite natural manner, but visual feedback was still prevented and the peripheral target was switched off upon gaze-shift onset. During the adaptation phase, three double-step stimulations were used, with the target jumping either forwards or backwards during the saccade (saccade shortening and lengthening sessions, respectively). Furthermore, we tried to enlarge the expected “adaptation field” by making three LEDs of the eccentricities T₁ and T₂, located on the inner, middle, and outer circle of LEDs, jump (see Methods). Repetitions (40 to 90) of each target pair were presented in random order.

For each experiment, the amount of adaptation, A, and the RHS for all three target jumps are shown in Fig.

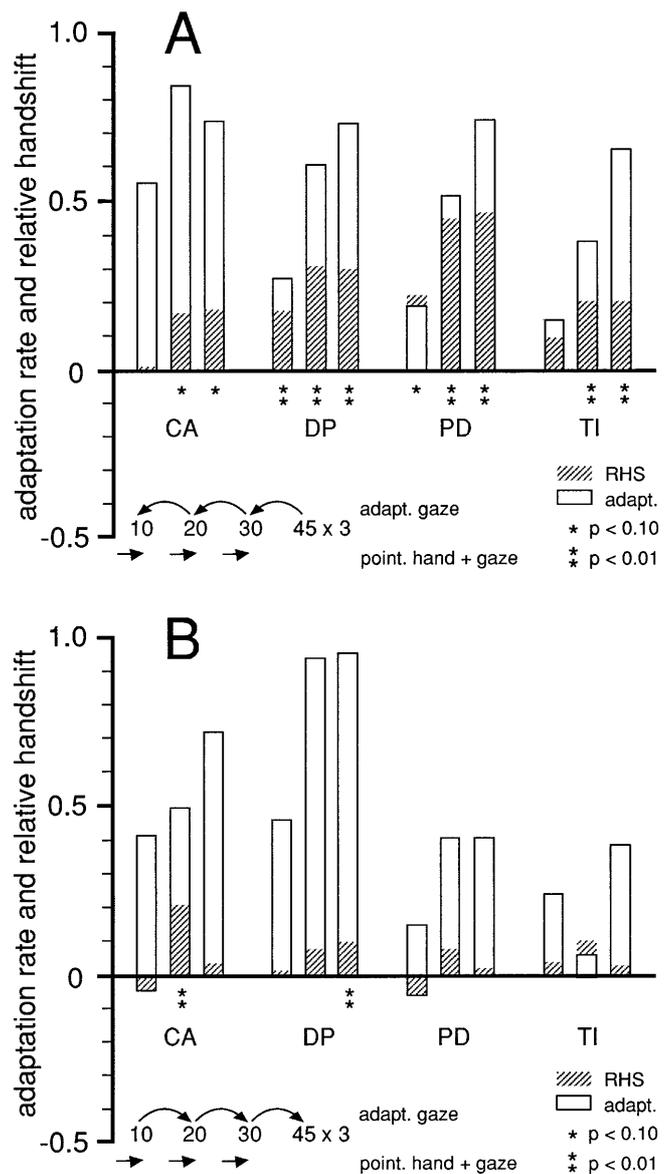


Fig. 7A, B Coupling paradigm C. In pre- and post-adaptation pointing, hand and gaze shifts were allowed. **A** Saccade shortening. Same display as in Figs. 4–6: the degree of adaptation obtained for each subject when targets were displaced from 20° to 10° (left), 30° to 20° (middle), and 45° to 30° (right). Relative hand shift (RHS) of hand pointing towards LEDs at 20° (left vertical bar), 30° (middle), and 45° (right) are shown. **B** Saccade lengthening. Adaptation to target displacement from 10° to 20° (left), 20° to 30° (middle), 30° to 45° (right) are shown. **A** and **B** illustrate experimental conditions; horizontal arrows indicate that the starting position of the hand movement was always T₀, ×3 indicates that during adaptation three LEDs of the same eccentricity were lit simultaneously. CA–TI Subjects, subject DP: 120 adaptation trials, 270 in subject CA in the lengthening session, otherwise 180 trials

7, grand averages are given in Table 1. The data show that the amount of adaptation seemed to increase with eccentricity, and in general it was lower and more variable than with the single-step stimulations used in the transfer paradigm. Because of the influence of target eccentricity

on adaptation rate and in order to compare transfer and coupling paradigms, we focused on the amount of adaptation in trials with target displacements from 30 to 20° and 30 to 45°, and on the RHS of hand pointings to the 30° target. Under these conditions, the mean adaptation level in the saccade shortening session was 59% and the mean RHS was 28% (the middle column for the data in each subject in Fig. 7A). The average coupling rate (CLR) was 52.5% of the amount of adaptation. In the saccade-lengthening session (displacement from 30 to 45°), the mean amount of adaptation was 61% and the RHS was 4% (right set of data for each subject in Fig. 7B). The respective percentage of hand pointing modified was again very low. The large value of 68.5% for the CLR at the target jump from 20 to 30° is strongly influenced by the deviating amount of adaptation in subject I (middle column in Fig. 7). It represents a meaningless result.

Discussion

The influence of short-term saccadic gaze adaptation on hand movement has been investigated to determine whether saccadic adaptation modifies goal-directed hand movements. If so, this would mean that adaptive processes are not restricted to the sensorimotor system exposed to the conflict, but lead to a larger perceptual reorganization or a reinterpretation of a general spatial map (Jeannerod 1988). Conversely, a lack of modification after adaptation would mean that adaptation is limited to the oculomotor system, at least under the conditions used to test hand pointing responses in the present report. Our general answer to this problem of intersegmental shift due to adaptation was that a weak adaptation transfer was present, but seemingly too small to have a clear functional meaning for gaze and hand coordination. A task requiring simultaneous gaze saccades and hand pointing movements provided the largest relative hand shift for a gain shortening adaptation but still failed to produce a consistent change in hand pointing for a gain lengthening adaptation.

Amount of adaptation

In the transfer paradigm with single stimulus adaptation (double-step stimulation at a single eccentricity), both saccade shortening and lengthening yielded adaptation of 80–90% within about 200 trials. Thus, the effectiveness of our adaptation protocol appears to be the same for increasing as for decreasing gaze-saccade amplitudes. This is in contrast to earlier findings showing that saccade-lengthening adaptation yielded a smaller effect or required many more trials than saccade shortening (Miller et al. 1981; Deubel et al. 1986; Semmlow et al. 1989), but see Albano (1996). The different time constants of adaptation have been explained by a putative role of adaptation mechanism in preventing saccadic overshoot, favoring saccade amplitude reduction (Deubel et al. 1986;

Becker 1991). Instead, the similar effectiveness of adaptation paradigms in producing saccade shortening and lengthening (Albano 1996; present data) and the existence of saccadic adaptation to directional changes (Deubel 1987) suggest a more general process.

Probably, short-term adaptation continuously readjusts saccade parameters to bring the target's retinal image in or close to the fovea by means of a single saccade. We have no definitive explanation for the discrepancies among the various investigations, but it appears that the time-course of saccadic adaptation may depend on experimental conditions. The fact that our subjects executed gaze and not solely eye movements during adaptation is one possible explanation. In another series of gaze shortening adaptation experiments (De Graaf et al., in preparation), we observed that the adaptation level achieved with the head unrestrained did not differ from that achieved in a head-fixed condition, but the comparison between head-fixed and head-free conditions has not yet been performed for gaze-lengthening adaptation. In our present study, the eccentricity of the stepping targets differed from that of previous investigations (mainly below 20°) and could favor saccade-lengthening adaptation towards values usually observed for saccade shortening. In some recordings, we checked whether the head component of gaze was altered along the adaptation period. The results seen so far showed no clear effect. A detailed study of this question, however, was beyond the scope of the present report.

Adaptation transfer

At first glance, our data show that hand pointing performed after saccade shortening periods were significantly different from pointing movements before adaptation. This was observed for both the single- and triple-step adaptation paradigms A and B. In both cases, the relative hand shift was in the direction expected from adaptation transfer, 11% in the single-step paradigm (A) and 15% in the triple-step paradigm (B) at the corresponding 10° target displacement. When computed with respect to the gaze adaptation level, the amount of transfer represented not more than 15% in the single-step paradigm and about 18.5% in the triple-step paradigm. The weakness of the effect under single-step conditions is not related to a narrow spatial range of adaptation, since data were analyzed from pointing movements directed to the initial position of the double-step stimuli.

Furthermore, in paradigm A, our results were totally asymmetric with respect to shortening and lengthening sessions, showing no transfer, at least, for lengthening. Searching for a reason, we conducted the control experiments (Fig. 2B) with null adaptation and computed the respective 'pseudo-RHS'. The experiments consisted of the same gaze movements as paradigm A, but without adaptation: if modifications in hand pointing would have been exclusively related to adaptation, hand shift should not have been observed. In fact, a slight leftward and

backward shift appeared. For the six (out of the nine tested) subjects that participated in both the null-adaptation paradigm and transfer experiments, on average, very similar values for the pseudo-RHS and the true RHS were obtained: 9.4% in null experiments and 10.7% in the transfer data. Practically, this would eliminate any hand pointing modification that can be attributed to transfer of saccadic adaptation under the single stimulus adaptation paradigm. The first tentative explanation for RHS in the null experiment is a possible fatigue effect. However, such an effect should mainly be observed on the amplitude of the egocentric pointings, which contrasts with the very small (1.6%) hand-movement shortening in the radial direction measured between pre- and post-test in the null adaptation paradigm. Regardless of the origin of this effect, one should be cautious when speaking of a transfer after the sole observation of a significant RHS in the transfer paradigm, and indeed no positive correlation between the amount of adaptation and RHS was seen.

In conclusion, based on the present approach with different kinds of paradigms, control experiments, and the computation of adaptation and relative hand shift, we found a weak transfer of short-term saccadic gain adaptation from gaze to the hand movements, but could not prove a consistent nature. In a recent study (Krölller et al. 1996), we could not find evidence of transfer of saccade shortening to orienting head movements. Therefore, the data available so far seem to indicate that adaptation of saccadic eye movements does not reliably affect the skeletomotor system under the transfer conditions, as defined in the Introduction. Surely, another explanation of our results could be that we have not yet found the experimental conditions under which a transfer could clearly be revealed. Then, one can only repeat that the number of jumping targets used for adaptation might be a relevant factor. One can consider that inter-segmental transfer requires some degree of spatial generalization or coherence, a condition that is better met in the triple-stimulation adaptation of paradigm B than in the single- or double-stimulation paradigm (Krölller et al. 1996). At present, this idea awaits further investigations using other adaptation tools, like magnifying lenses (Gauthier and Robinson 1975), allowing a broad spatial generalization.

According to the definition given in the Introduction, adaptation transfer is a special case of internal transmission of stored information from gaze to hand motor systems. After we did not see convincing and functionally significant adaptation-dependent modifications of the hand pointing movements under the transfer conditions described, we abandoned the narrow conditions of adaptation transfer and tried to find others suitable for enhancing modifications of hand-pointing movements by gaze adaptation.

Adaptation-related hand shift under coupling conditions

For this purpose, we tested the effect of gaze adaptation on the hand motor system when eye and hand movements

were simultaneously involved in pointing tasks. The question was whether, after saccadic adaptation, a coupling between the oculomotor and the hand motor response appeared when both were initiated synergistically. In particular, we wanted to know whether the difference between lengthening and shortening sessions remained. In other words, was the modified oculomotor output read out by the skeleto-motor system in initiating a hand movement towards the same stimulus that triggered the saccade? The answer was that a significant RHS of 28% was observed in the saccade-shortening paradigm. This can be interpreted as a meaningful shift under oculo-manual coupling, as the coupling rate was 52.5%. However, the respective RHS in the lengthening session was 4%, which, although in the direction anticipated, was still too small to have a functional impact. In these coupling experiments, we had enlarged the adaptation fields by letting three LEDs jump at a time. This could also explain the larger RHS observed, but nevertheless was unable to create a relevant RHS during lengthening. It seems that the gaze saccade-amplitude signal could be transmitted to the hand motor system, but why it was only for decreasing gain adaptation remains unexplained.

The only partial and non-systematic transmission of information from the gaze control system to that of the hand also contrasts with many previous studies (Hanson and Skavenski 1977; Prablanc et al. 1979; Biguer et al. 1984; Mather and Fisk 1985; Pélisson et al. 1986; Carnahan and Marteniuk 1994; Gentilucci et al. 1994; Vercher et al. 1994), which have shown that allowing eye and/or head movements greatly improves the accuracy of hand pointings without vision of the hand itself. However, this lack of clear coupling between eye saccade and hand pointing might be explained by a recent study that showed that the gaze-position signal without a foveal stimulus loses most of its accuracy (Blouin et al. 1995). If the ultimate role of foveation was to guide the hand to the target, independent from the hand visual reafferences, this could explain why we did not systematically observe a coupling between gaze and hand and a corresponding pointing shift after adaptation. On this basis, one could design a more sophisticated pre- and post-adaptation in a control experiment. Then, instead of cutting off the stimulus at saccade onset during the coupling responses, the stimulus would be replaced at the end of the saccade by a transient foveal stimulus, which would give its accuracy to the eye position signal. Independent from the technical complexity, this procedure could modify the normal state of the oculomotor system prior to the pre-adaptation test itself, but also mostly destroy the adapted state in the first trials of the post-test.

Concluding remarks

In contrast to our results, adaptation of smooth-pursuit eye movements has been shown to clearly transfer to hand movements (van Donkelaar et al. 1994). In this study, subjects manually tracked a visual target in peripheral vi-

sion while keeping their eyes fixated on a central target. The difference between these results and ours might be explained either by the type of eye movements (smooth pursuit versus saccades) or by the manual responses investigated (tracking versus pointing). Indeed, as the two oculomotor systems are differently organized and use different types of visual information (mainly velocity versus position signals), adaptation of these two ocular responses may be independent. Alternatively, a larger transfer of smooth-pursuit adaptation to hand tracking movements may reflect the possibility that eye and hand are usually coupled more strongly during a tracking task than during a pointing task. This second possibility could be tested by investigating whether smooth pursuit adaptation can also transfer to hand pointing movements.

Regarding the location of the adaptation-eliciting processes in humans and monkeys (Fitzgibbon et al. 1985; Goldberg et al. 1993; Frens and van Opstal 1994, 1997; Fuchs et al. 1996; Melis and van Gisbergen 1996), our data partly correspond to the considered downstream position along the oculomotor pathway: under strict transfer conditions, hand- and eye-control circuits are largely separated at the site of adaptation implementation. Then, adaptation-dependent shifts in the hand pointings should also not exist in the coupling paradigm; however, it does so at least partly. The observed hand pointing modification after shortening gaze adaptation under coupling conditions could give a hint that a cortical component could play a role; for inter-saccadic transfer, the FEF was considered to play a role (Fitzgibbon et al. 1985; Melis and van Gisbergen 1996). In transfer paradigms, modified vision and eye movements could affect the handpointing under two assumptions: The superior colliculi involved, and the impact of superior-colliculus-activity on hand movements, found in rhesus monkeys (Werner 1994) also exists in humans. Then, similar to the monkey (Fuchs et al. 1996), in humans transfer should also exist among different types of saccades. The lack of such inter-saccadic transfer in humans (Erkelens and Hulleman 1973; Deubel 1995), and as reported by others in monkeys (Melis and van Gisbergen 1996), however, still more complicates the findings obtained so far and could indicate differences between human and monkey collicular organization. Right now, further data are required to clarify these points before a full comprehension of short-term saccadic adaptation and its transfer is possible.

Acknowledgements We thank C. Urquizar and P. Monjaud for developing computer programs and for essential help in building the experimental set-up and Mrs. J. Dames for correcting the English manuscript. We also appreciate very much the friendly cooperation of 14 colleagues in the laboratory for helping us as subjects in the lengthy experimental sessions. J.B. de Graaf was supported by an INSERM fellowship, the work by INSERM unité 94 and the Deutsche Forschungsgemeinschaft (Kr 700/8-1).

References

- Abel LA, Schmidt D, Dell'Osso LF, Darof RB (1978) Saccadic system plasticity in humans. *Ann Neurol* 4:313–318
- Abrams RA, Dobkin RS, Helfrich MK (1992) Adaptive modification of saccadic eye movements. *Exp Psychol Hum Percept Perform* 18:922–933
- Albano JE (1992) Rapid saccadic adaptation is conjugate. *Invest Ophthalmol Vis Sci [Suppl]* 32:1154
- Albano JE (1996) Adaptive changes in saccadic amplitude: oculo-centric or orbitocentric mapping? *Vision Res* 36:2087–2098
- Becker W (1991) Saccades. In: Carpenter RHS (ed) *Vision and visual dysfunction*, vol. 8. Eye movements. Macmillan, London, pp 95–117
- Biguer B, Prablanc C, Jeannerod M (1984) The contribution of coordinated eye and head movements in hand pointing accuracy. *Exp Brain Res* 55:462–469
- Blouin J, Gauthier GM, Vercher JL (1995) Internal representation of gaze with and without retinal inputs in man. *Neurosci Lett* 183:187–189
- Bridgeman B, Hendry D, Stark L (1975) Failure to detect displacement of the visual world during saccadic eye movements. *Vision Res* 15:719–722
- Bridgeman B, Heijden AHC van der, Velitchkovsky BA (1994) Theory of visual stability across saccadic eye movements. *Behav Brain Sci* 17:247–292
- Carnahan H, Marteniuk RG (1994) Hand, eye, and head coordination while pointing to perturbed targets. *J Mot Behav* 26:135–146
- Chaturvedi V, Van Gisbergen JAM (1997) Specificity of saccadic adaptation in three-dimensional space. *Vision Res* 37:1367–1382
- De Graaf JB, Pélissier D, Parblanc C, Goffart L (1995) Modifications in end positions of arm movements following short-term saccadic adaptation. *Neuroreport* 6:1733–1736
- Deubel H (1987) Adaptivity of saccade and direction in oblique saccades. In: O'Regan JK, Levy-Schoen A (eds) *Eye movements. From physiology to cognition*. Elsevier, Amsterdam, pp 181–190
- Deubel H (1995) Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. *Vision Res* 35:3529–3540
- Deubel H, Wolf W, Hauske G (1986) Adaptive gain-control of saccadic eye-movements. *Hum Neurobiol* 5:245–253
- Donkelaar P van, Fischer C, Lee RG (1994) Adaptive modification of oculomotor pursuit influences manual tracking responses. *Neuroreport* 5:2233–2236
- Erkelens CJ, Hulleman J (1993) Selective adaptation of internally triggered saccades made to visual targets. *Exp Brain Res* 93:157–164
- Fitzgibbon EJ, Goldberg ME, Segraves MA (1985) Short term adaptation in the monkey. In: Keller EJ, Zee DS (eds) *Adaptive processes in the visual and oculomotor systems. Advances in the biosciences*, vol. 57. Pergamon Press, Oxford, pp 329–333
- Frens MA, Opstal AJ van (1994) Transfer of short-term adaptation in human saccadic eye movements. *Exp Brain Res* 100:293–306
- Frens MA, Opstal AJ van (1997) Monkey superior colliculus activity during short-term saccadic adaptation. *Brain Res Bull* 43:473–483
- Fuchs AF, Reiner D, Pung M (1996) Transfer of gain changes from targeting to other types of saccade in monkey: Constraints on possible sites of saccadic gain adaptation. *J Neurophysiol* 76:2522–2535
- Gauthier GM, Robinson DA (1975) Adaptation of the human vestibulo-ocular reflex to magnifying lenses. *Brain Res* 92 (1975) 331–335
- Gentilucci M, Jeannerod M, Tadini B, Decety J (1994) Dissociating visual and kinesthetic coordinates during pointing movements. *Exp Brain Res* 102:359–366
- Goldberg ME, Musil SY, Fitzgibbon EJ, Smith M, Olson CR (1993) The role of the cerebellum in the control of saccadic eye movements. In: Mano N, Hamada I, Delong MR (eds) *Role of the cerebellum and basal ganglia in voluntary movements*. Elsevier, Amsterdam, pp 203–211

- Hansen RM, Skavenski AA (1977) Accuracy of eye position information for motor control. *Vision Res* 17:919–926
- Henson DB (1978) Corrective saccades: effects of altering visual feedback. *Vision Res* 18:63–67
- Inchingolo P, Optican LM, Fitzgibbon EJ, Goldberg ME (1991) Adaptive mechanisms in the monkey saccadic system. In: Schmid R, Zambardi D (eds) *Oculomotor control and cognitive process*. Elsevier, North Holland, pp 147–162
- Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. Clarendon Press, Oxford
- Kommerell G, Olivier D, Theopold H (1976) Adaptive programming of phasic and tonic components in saccadic eye movements. Investigations in patients with abducens palsy. *Invest Ophthalmol Vis Sci* 15:657–660
- Kröll J, Pélisson D, Prablanc C (1996) On the short term adaptation of eye saccades and its transfer to head movements. *Exp Brain Res* 111:477–482
- Mack A, Fendrich R, Pleune J (1978) Adaptation to an altered relation between retinal image displacements and saccadic eye movements. *Vision Res* 18:1321–1327
- Mather JA, Fisk JD (1985) Orienting to targets by looking and pointing: parallels and interactions in ocular and manual performance. *Q J Exp Psychol* 37A:315–338
- McLaughlin SC (1967) Parametric adjustment in saccadic eye movements. *Percept Psychophys* 2:359–362
- McLaughlin SC, Kelly MJ, Anderson RE, Wenz T (1968) Localisation of peripheral target during parametric adjustment of saccadic eye movements. *Percept Psychophys* 4:45–48
- Melis BJM, Gisbergen JAM van (1996) Short term adaptation of electrically induced saccades in monkey superior colliculus. *J Neurophysiol* 76:1744–1758
- Miller JM, Anstis T, Templeton WB (1981) Saccadic plasticity: parametric adaptive control by retinal feedback. *J Exp Psychol* 7:356–366
- Optican LM, Robinson DA (1980) Cerebellar-dependent adaptive control of primate saccadic system. *J Neurophysiol* 44:1058–1076
- Pélisson D, Prablanc C (1988) Kinematics of centrifugal and centripetal saccadic eye movements in man. *Vision Res* 28:87–94
- Pélisson D, Prablanc C, Goodale MA, Jeannerod M (1986) Visual control of reaching movements without vision of the limb. II. Evidence for a fast unconscious process correcting the trajectory of the hand to the final position of a target step. *Exp Brain Res* 62:303–311
- Prablanc C, Echallier JF, Komilis E, Jeannerod M (1979) Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationship when varying the amount of visual information. *Biol Cybern* 35:113–124
- Prablanc C, Bailly G, Pélisson D (1986) Etude des mouvements oculaires chez l'homme par la technique électro-oculographique. *Bull Soc Ophthalmol France* 12:1447–1452
- Rosetti Y, Stelmach G, Desmurget M, Prablanc C, Jeannerod M (1994) The effect of viewing the static hand prior to movement onset on pointing kinematics and variability. *Exp Brain Res* 101:323–330
- Semmlow JL, Gauthier GM, Vercher JL (1989) Mechanisms of short-term saccadic adaptation. *J Exp Psychol Human Percept Perform* 15:249–258
- Snow R, Hore J, Vilis T (1985) Adaptation of saccadic and vestibulo-ocular systems after extraocular muscle tenectomy. *Invest Ophthalmol Vis Sci [Suppl]* 26:924–931
- Straube A, Fuchs AF, Usher S, Robinson RF (1997) Characteristics of saccadic gain adaptation in rhesus monkeys. *J Neurophysiol* 77:874–895
- Urquizar C, Pélisson D (1992) A non-contact system for 2-dimensional trajectory recording. *J Neurosci Methods* 43:77–92
- Vercher JL, Magenes G, Prablanc C, Gauthier GM (1994) Eye-hand coordination in pointing at visual targets: spatial and temporal analysis. *Exp Brain Res* 99:507–523
- Weisfeld GE (1972) Parametric adjustment to a shifting target alternating with saccades to a stationary reference point. *Psychonom Sci* 28:72–74
- Werner W (1994) Neurons in the primate superior colliculus are active before and during arm movements to visual targets. *Eur J Neurosci* 5:335–340