25 Separate Mechanisms for the Adaptive Control of Reactive, Volitional, and Memory-Guided Saccadic Eye Movements

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ABSTRACT Using a paradigm in which the saccade target is consistently displaced during eye movement, adaptive modifications of saccadic magnitude can be easily induced in human subjects. Recently, evidence has accumulated that after such adaptations, the saccades in different situations are not uniformly affected. The present study investigates in detail the mutual transfer of gain adaptation between reactive, volitional, and memory-guided saccades. It is demonstrated that the induced effects are dependent on the mode of saccade elicitation: adaptation of stimulus-triggered, reactive saccades does not transfer to volitional saccades produced when scanning a static display, nor to memory-guided saccades. When saccades are adapted in the scanning situation, induced gain changes show only minor transfer to reactive saccades, but almost complete transfer to memory-guided saccades. Finally, when memory-guided saccades are adapted, induced gain changes transfer neither to reactive saccades nor to scanning saccades. An additional experiment demonstrates that adaptation of express saccades transfers completely to normal reactive saccades, and vice versa. The experimental data are consistent with a model in which three separate mechanisms for the adaptivity of reflexive, volitional, and memory-guided saccades interact in a hierarchical manner.

To inspect their environment, primates make fast and accurate eye movements to bring the target of current interest onto the fovea. These saccades can be described as being "ballistic" movements in that they occur in a pre-programmed, open-loop manner. Even without feedback, saccades are very accurate and reproducible, implying that their *gain*, namely, the ratio of the saccade amplitude to the magnitude of the target step, must be specified precisely before the movement begins. If this system is to function properly over a lifetime, continuous monitoring of saccadic performance and the ability to recalibrate the saccadic response are required.

It is indeed known that the saccadic system can compensate even for very profound dysmetrias that result when the command sent to the extraocular muscles fails to achieve target foveation. For instance, it has been found that patients suffering from abducens nerve palsy manage to adjust saccadic gain within a few days to account for the effect of the disease (Kommerell, Olivier and Theopold 1976; Abel et al. 1978). Optican and Robinson (1980) surgically weakened the medial and lateral recti muscles of one eye in rhesus monkeys. Provided the cerebellum was intact, normal visual experience with the weakened eye then led to a gradual recovery of saccadic accuracy. This adaptive process included not only metrical adjustment of saccade size but

also the gradual compensation of a postsaccadic drift induced by muscle weakness. Thus both saccade metrics and the dynamical properties of the eye movement are under efficient adaptive control.

In the laboratory, the effects of lesions of the peripheral oculomotor system can be mimicked noninvasively by means of consistent, intrasaccadic target shifts while subjects try to acquire the target with a saccade (e.g., McLaughlin 1967; Miller, Anstis and Templeton 1981; Deubel, Wolf, and Hauske 1986; Deubel 1987, 1991). It is interesting to note that, provided the intrasaccadic shifts are not too large, the subjects completely fail to perceive them (Bridgeman, Hendry, and Stark 1975; Deubel, Schneider and Bridgeman 1996). In such a "double-step" adaptation paradigm, subjects have to track steps of a small target; while the eye follows with a saccade, the target is shifted systematically by a small amount, for example into the direction opposite the saccade (see fig. 25.1b). The saccadic system quickly adapts to
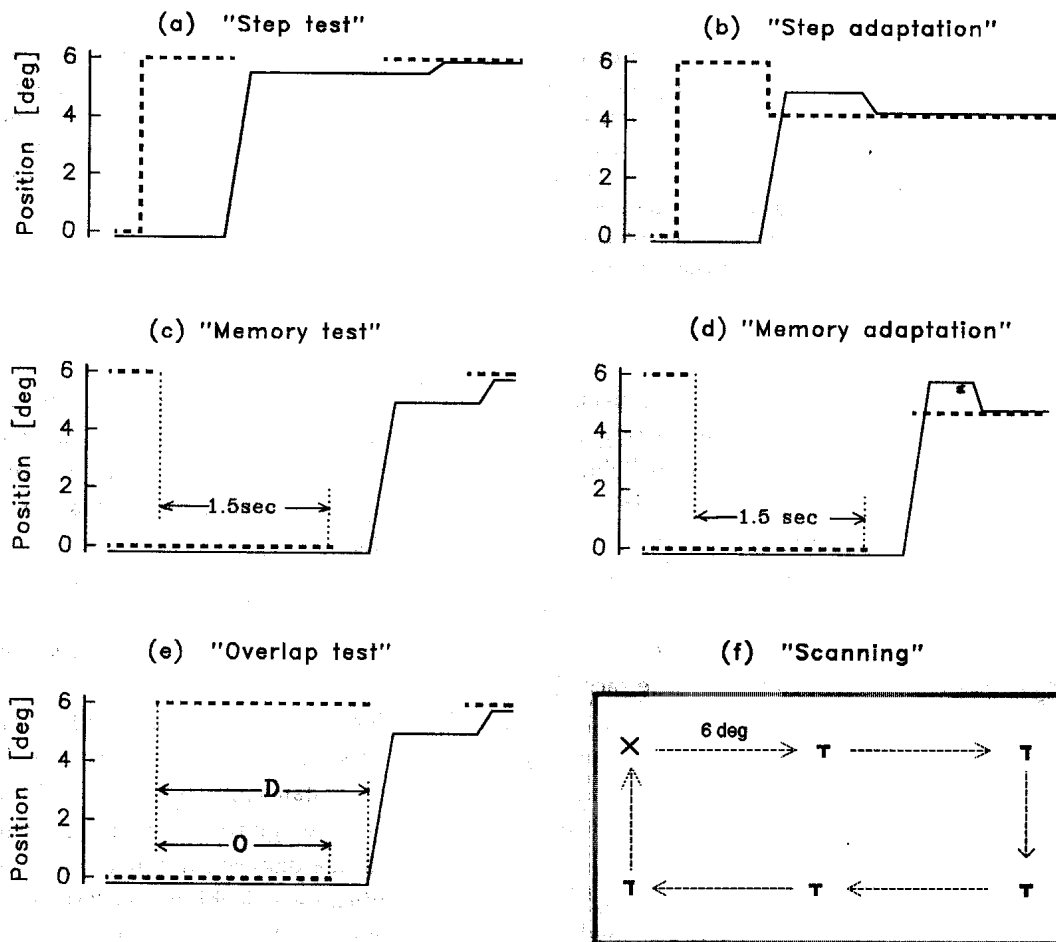
Figure 25.1 Schematic representation of visual stimuli and experimental paradigms. For the graphs a–e, the solid lines represent the eye position as a function of time. The broken lines display the sequence of target jumps and blanking periods.

this situation, by reducing saccadic magnitude to the required value. Typically, the adaptive mechanism can largely compensate for the induced error within 200 training trials. The retinal foveation error forms the essential source of information for the adaptive process: postsaccadic errors are interpreted by the adaptive mechanism as reflecting internal miscalibrations. Moreover, it has been observed that when, after adaptive gain reduction, single steps are provided, recalibration to the normal gain value may take longer than conditioning (Deubel, Wolf, and Hauske 1986; Deubel 1987). The induced effects are so persistent that they sometimes even show up the day after the adaptation session (author's personal observations).

In a considerable number of studies, this double-step adaptation paradigm proved to be very efficient for the investigation of properties of the adaptation mechanisms. For example, by shifting a target vertically during a horizontal saccade, it has been demonstrated that not just saccadic magnitude, but also saccade direction can be easily recalibrated (Mack, Fendrich, and Pleune 1978; Deubel 1987). Saccadic adaptations can be extended to dynamical aspects of the saccadic response: when subjects are treated with systematic, postsaccadic exponential movements of the target, they develop, within a half hour of training, systematic postsaccadic eye drifts that also persist in darkness (Deubel 1991). Both saccade gain adaptation and postsaccadic drift adaptation proved to be highly directionally specific; the effect of adaptation is limited to a narrow (directional) sector around the adapted saccade direction (Deubel 1987, 1993a).

25.1 PARADIGMS, CONDITIONS, AND SPECIFIC METHODS

Almost all of the studies mentioned above have been made with saccades that occur to the onset of a simple stimulus—an isolated target that appears suddenly in the retinal periphery. The reason why researchers use this type of stimulus is obvious: the eye movement target is unambiguously defined, and the response occurs with low spatial and temporal variability, in an automatic, machinelike manner. Indeed, it is safe to say that most studies on saccadic control use this type of stimulus, including the saccade monitoring routinely done for clinical diagnosis. On the other hand, this convenient simplification may entail a dangerous reduction of the ecological validity and generalizability of the findings.

Saccadic Responses

Recently, evidence has accumulated that different central neural structures are involved in the control of different types of saccadic eye movements. The saccadic responses differ depending on how the saccades are elicited, and they exhibit different response latencies. Five types of saccadic responses can be distinguished. First, *reflexive saccades*, which typically exhibit latencies

in the range of 160–200 msec occur in response to the sudden onset of a visual target appearing in isolation in the peripheral part of the retina; these saccades are reflexive in that the subject would have to put some intentional effort into actively suppressing them. Second, so-called *express saccades*, which have latencies of 100 msec and below, occur when the current fixation target disappears 150–200 msec before the onset of the next peripheral target. It has been suggested that they form a population separate from the "normal" reflexive saccades, and that they are produced by a fast neural reflex loop different from the neural mechanisms responsible for other types of saccades (Fischer and Weber 1993). Third, *volitional* or *intentional saccades*, which are internally triggered, occur when subjects intentionally scan a complex visual scene. Fourth, *memory-guided saccades* are directed to a memorized position of a previously visible target in space, or they may predict the locus of reappearance of a moving object that temporarily disappears behind an occluder. Finally, *spontaneous saccades*, which have no spatial goal, occur when thinking with the eyes closed or at rest in darkness. It has been recently suggested that these five types of saccades are controlled by different cortical areas, which could be specialized in the triggering of a specific type of saccade and/or in the calculation of its amplitude and direction (e.g., Pierrot-Deseilligny et al. 1995).

Dissociation and Saccadic Adaptation

The question arises whether these various types of saccades are all protected by a single, unitary adaptive mechanism. This would indeed be predicted by models of adaptive saccade control that place the recalibrations in the brain stem saccade generator common to all types of saccades (e.g., Optican 1982). Such models are, however, difficult to reconcile with the high amount of directional selectivity of saccadic adaptations (Deubel 1993a). Further arguments in favor of higher-level adaptive mechanisms come from recent findings on mutual transfer of adaptation of reflexive and intentional saccades (Erkelens and Hulleman 1993; Deubel 1995a). My own investigations proceeded from a rather occasional observation made when subjects' saccades were adapted by presenting long periods of double-step adaptation stimuli. Because the gain reductions achieved in this paradigm are considerable (up to 40% of the normal saccade gain), large and frequent saccadic corrections should be expected after adaptation sessions when the precise foveation of small targets is required. This is not what my colleagues and I found when we occasionally made subjects scan objects in the normal environment outside the laboratory, measuring eye movements with an electro-oculograph (EOG) (Deubel 1993b). Surprisingly, rough inspection of the eye movement traces showed that the saccadic responses had normal accuracy. This observation seemed to indicate that the induced adaptation effects are limited to the laboratory context in which the conditioning occurred, implying the

existence of context-specific mechanisms and possibly the involvement of higher-level strategies.

This intriguing finding was further elaborated in Deubel (1995a), where adaptive reduction of saccadic gain was induced by means of two basically different paradigms. In the first approach the subjects had to follow a stepwise moving target. During each follow-up saccade, the target was systematically displaced by 25% of the initial step, in the direction opposite the saccade. In the second approach, the subjects scanned a display of six small items. During each scanning saccade, the whole display was displaced by 25%, into the direction opposite the saccade. Although both conditions led to fast and consistent saccadic gain reductions, adaptation with the stepping target (*step adaptation*) did not transfer to the saccades in the scanning situation (*scanning saccades*). Conversely, when saccades were adapted in the scanning situation, induced gain changes did not transfer to saccades following steps of a single target. The results suggested that two separate and, to a large degree, independent mechanisms are involved in the generation of reactive, stimulus-triggered and volitional, internally generated saccades, respectively, and that both types of responses can be selectively adapted.

The work presented here provides a more detailed experimental analysis of this dissociation between different saccade modes. In complement to Deubel 1995a, this study also investigates the saccadic adaptation of memory-guided saccades (*memory adaptation*), and transfer to saccades in an overlap paradigm (*overlap saccades*), and to a paradigm where express saccades were elicited in a gap paradigm (*gap saccades*). The experimental data reveal some surprising asymmetries. Adaptation of step saccades does not transfer to scanning, overlap, and memory saccades. A similar complete dissociation is observed when memory-guided saccades are adapted. Adaptation of scanning saccades, however, transfers to memory-guided saccades. The results are consistent with a model of the cortical control of saccades that assumes different loci of adaptation in hierachical pathways.

25.2 GENERAL METHODS

Subjects

Six subjects aged 21–32 participated in this study, and between 4 and 6 subjects in the individual combinations of adaptation and test conditions. In order to avoid potential cross talk of the various experimental conditions, the sessions for each subject were separated by at least three days. Although all subjects had normal vision and were experienced in a variety of experiments related to oculomotor research, they were naive with respect to the aim of this study. An inquiry after the end of the series of experiments yielded that they had not explicitly noticed the critical features of the experiments, most specifically, the systematic intrasaccadic target displacements.

Experimental Setup

Subjects were seated in a dimly illuminated room. The visual stimuli were presented on a fast 21-inch color monitor (CONRAC 7550 C21) providing a frame frequency of 100 Hz at a spatial resolution of 1,024*768 pixels. Screen size was 40 cm by 30 cm; the viewing distance was 80 cm. The video signals were generated by a freely programmable graphics board (Kontron KONTRAST 8000), controlled by a PC via the TIGA (Texas Instruments graphics adapter) interface. The stimuli appeared on a gray background adjusted to a mean luminance of 2.2 cd/m^2; the luminance of the stimuli was 25 cd/m^2.

Eye movements were recorded with a SRI generation 5.5 dual-Purkinje-image eye tracker (Crane and Steele 1985) providing a spatial resolution of <1 min arc; the analog output signals of the tracker were sampled at 400 Hz. Head movements were restricted by a bite board and a forehead rest. The experiment was completely controlled by a 486 personal computer. The PC also served for the automatic off-line analysis of the eye movement data in which saccadic latencies and saccade start and end positions were determined.

By digital on-line differentiation of the sampled eye position signal, the computer derived a trigger signal indicating saccade onset. The saccade trigger was adjusted at high sensitivity: when instantaneous eye velocity exceeded 30°/sec, saccade-related sensory events such as target displacements were triggered. Early triggering is important because of an eye tracker record delay of up to 20 msec (due to slippage of the lens within the eye; Deubel and Bridgeman 1995) and a screen raster display delay of up to 10 msec. The early triggering ensured that the presaccadic stimulus disappeared before the eye reached maximum velocity.

Calibration and Data Analysis

Sessions started with a calibration procedure in which subjects had to sequentially fixate 10 positions arranged on a circular array of 6° radius. The tracker behaved linearly within 8° around the central fixation. Overall accuracy of the eye tracker for static fixation positions was better than 0.1°. Dynamically, however, the eye tracker records considerable artifactual overshoots of the eye at the end of each saccade, which can be ascribed to the movement of the eye lens relative to the optical axis of the eye (Deubel and Bridgeman 1995). In order to determine the saccadic amplitude, an off-line program for the evaluation of saccade parameters searched the saccade record for the end of the apparent overshoot and then computed eye position as a mean over a 40 msec time window, following the end of overshoot. Saccadic gain was calculated as the ratio of saccadic amplitude to target step size, expressed as a percentage.

Experimental Paradigms

The experiments were aimed at analyzing the amount of mutual transfer of saccadic gain adaptation induced in the traditional double step paradigm, a paradigm in which scanning of a static display was required, in an overlap paradigm, and in a paradigm in which the saccade had to be directed to a memorized target. Accordingly, different types of stimuli and stimulus sequences were used as adaptation and test conditions in various combinations. Figure 25.1 presents a schematic summary of the experimental paradigms applied.

Step test condition In this condition, the gain of saccades elicited by steps of single targets was determined in a paradigm that included a postsaccadic target gap, as shown in figure 25.1a. Subjects had to follow a small cross (size 0.17°) that performed a stepwise displacement about every 2.5 sec. In each such trial, the subject initially fixated the target. After a random delay of 500–1,000 msec, the target was displaced either to the right or to the left; the size of this displacement was 6°, 7°, or 8°. In order to minimize predictability, both displacement size and direction were varied randomly in each experimental block. When the velocity of the primary saccade exceeded 30°/sec, the target was blanked and then reappeared after a gap of 500 msec. The postsaccadic gap was applied for testing actual saccade gain since there is a considerable slowing of recalibration for conditions where no spatial target information is available immediately after the primary saccades (authors unpublished observations). In order to avoid location-specific adaptation effects, the final target position after the sequence was used as the starting position for the next trial.

Step adaptation For the adaptation of stimulus-triggered saccades, a version of the "classical" double-step paradigm was used (figure 25.1b). Again, the subjects had to follow the displacements of the small cross. When the velocity of the primary saccade exceeded 30°/sec, the target was displaced by 30% of the initial step size (i.e., by 1.8°, 2.1°, or 2.4°, respectively), into the opposite direction of the first step. Due to the exogenous target displacement, the saccade normally overshoots the final target position, and a secondary, corrective saccade is typically elicited after about another 160 msec. Again, the final target position after the double-step sequence was used as the starting position for the next trial.

Memory test condition This condition tested the gain of saccades directed to memorized targets (figure 25.1c). For this purpose, the saccade target was presented for 1 sec at its peripheral position, and then disappeared. Subjects were asked to proceed with their saccade to the memorized location only when the actual fixation cross disappeared, which occurred 1.5 sec after peripheral target offset. In order to avoid rapid recalibration of saccadic gain

during testing, the final target reappeared only 500 msec after the primary saccade.

Memory adaptation condition In order to adapt saccades directed to memorized targets, the saccade target was presented for 1 sec at its peripheral position, and then disappeared (figure 25.1d). Again, subjects were allowed to proceed with their saccade to this memorized position only when the actual fixation cross disapeared, which occurred 1.5 sec after peripheral target offset. Triggered by the onset of the saccade, the target reappeared at a position displaced by −30% of the initial target eccentricity.

Overlap test condition This condition was useful in investigating possible effects on saccadic gain of prolonged presence of the peripheral target before the saccade was actually elicited (figure 25.1e). A saccade target appeared 6°, 7°, or 8° to the right or the left of the actual fixation, while the central fixation target remained visible. Subjects were instructed to wait with their saccade to the peripheral target until the offset of the current fixation cross, which occurred a variable overlap time O after the onset of the peripheral target. As a consequence, saccadic latencies D, as measured from the onset of the peripheral target, were accordingly prolonged. As in the step test condition, the saccade target disappeared with the onset of the primary saccade and reappeared only 500 msec later.

Scanning test condition To analyze the metrical properties of saccades in a scanning situation, a display consisting of six items was used, as shown in figures 25.1f. In each trial, the subject was asked to fixate a small cross subtending 0.17° of visual angle presented on the screen. The cross appeared 3° above and 3° to the left, or, in other trials, to the right of the screen center. After a random delay of 800–1,500 msec, five more items appeared, forming a rectangular configuration of 12° by 6°. These items had a horizontal separation of 6° and consisted either of the complete letter "T" or a version of the letter with 3 pixels missing. On appearance of the letters, the subject was given about 4 sec to completely scan the items in order to report, by pressing a button, whether the number of complete "T"s in the display was 2 or 3, finally returning with the eye to the fixation cross. In cases where the cross appeared to the left of the center, the subject was instructed to scan clockwise, and counterclockwise if it appeared in the upper right corner of the rectangle. Because the letters only subtended a visual angle of 0.14°, the task required the precise foveation of each of the items (the size of the items is considerably exaggerated in figure 25.1f). The only trials considered in the off-line data analysis were those in which the subject had produced the correct and complete sequence of saccades that was required, and for which the mean of the magnitudes of the four horizontal saccades was used in further data analysis. The vertical saccades contained in the sequence were not analyzed further.

Scanning adaptation This type of paradigm aimed at the adaptation of saccades that occur during the scanning of the static items and used the same stimulus material as in figure 25.1f. Again, on appearance of the five items, subjects had to scan the items, clockwise or counterclockwise, in an orderly manner. With the onset of each of the large horizontal saccades from one letter to the next, however, all six items on the screen were displaced by 1.5°, into the opposite direction of the saccade. As for the experiments with single targets, subjects only rarely perceived these intrasaccadic stimulus shifts. No stimulus displacements occurred with the vertical saccades.
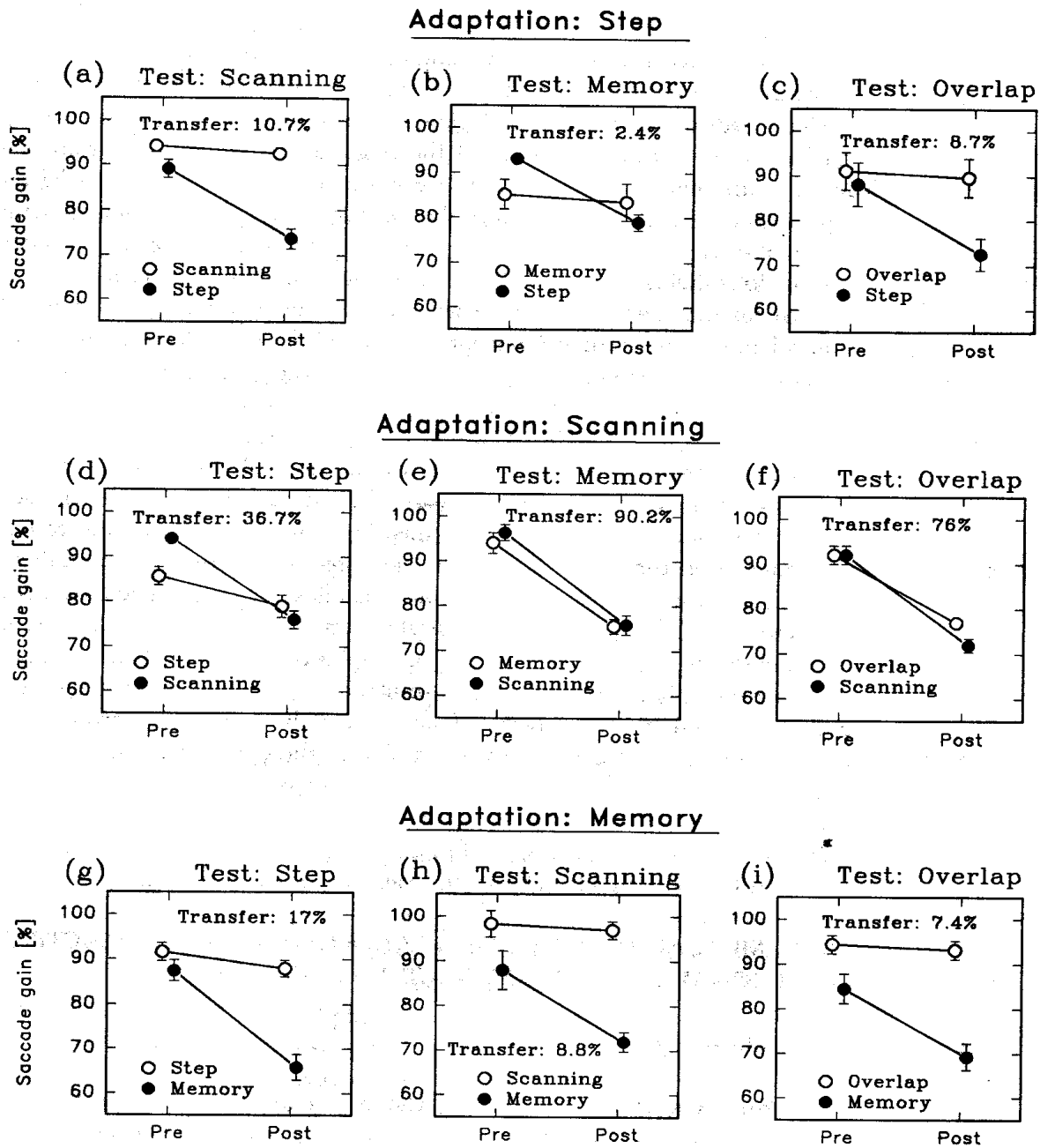
Each session consisted of three separate experimental blocks. In an initial control block, the normal (unadapted) gain of the saccadic responses was obtained. The second (adaptation) block consisted of trials with the adapting stimulation only. In the third block, a phase with adapting stimuli was followed by a postadaptive test phase in which the effect of the previous conditioning on the various saccade types was assessed. The number of trials in the individual experimental blocks was adjusted such that each block took between 10 and 12 minutes. Due to this time limitation, the number of test and adaptation trials was different in the different experimental conditions, with the fewest trials for the conditions including memory-guided saccades. Because most of the adaptation typically occurs during the initial 50–100 adaptation trials, the overall amount of adaptation was nevertheless compara- ble for the different conditions (see results below). The experimental blocks were separated by two breaks of approximately 5 minutes each, during which subjects were allowed to sit back from the eye tracker and relax. In spite of this relatively long time during which subjects could freely perform eye movements in the laboratory, there was no significant recovery from adaptation during the break, confirming the previously described observa- tion that the induced adaptation effects are stable and long-lasting.

25.3 MUTUAL TRANSFER OF ADAPTATION BETWEEN REACTIVE, VOLITIONAL, AND MEMORY-GUIDED SACCADES

Adaptation of Step Saccades

Transfer to scanning saccades The first experiment investigated the amount of transfer of saccadic gain adaptation induced by means of double-target steps on scanning saccades. In the initial control block, a phase of 80 trials with the step test condition (figure 25.1a) was flanked by two phases contain- ing 28 saccades with the scanning test paradigm (figure 25.1f). Subsequently, the subject experienced a total of 560 step adaptation trials (figure 25.1b). The mean saccade amplitude of the 20 last trials of this phase was taken to compute the final postadaptive gain. Finally, the amount of transfer to scanning sac- cades was assessed in another 10 trials of the scanning test condition.

Figure 25.2a presents mean saccadic gain and standard error before and after the adaptation period, given as averages over the six subjects. The solid

Adaptation: Step

(a) Test: Scanning

Transfer: 10.7%
- ○ Scanning
- ● Step

Saccade gain [%]

Pre Post

(b) Test: Memory

Transfer: 2.4%
- ○ Memory
- ● Step

Pre Post

(c) Test: Overlap

Transfer: 8.7%
- ○ Overlap
- ● Step

Pre Post

Adaptation: Scanning

(d) Test: Step

Transfer: 36.7%
- ○ Step
- ● Scanning

Saccade gain [%]

Pre Post

(e) Test: Memory

Transfer: 90.2%
- ○ Memory
- ● Scanning

Pre Post

(f) Test: Overlap

Transfer: 76%
- ○ Overlap
- ● Scanning

Pre Post

Adaptation: Memory

(g) Test: Step

Transfer: 17%
- ○ Step
- ● Memory

Saccade gain [%]

Pre Post

(h) Test: Scanning

Transfer: 8.8%
- ○ Scanning
- ● Memory

Pre Post

(i) Test: Overlap

Transfer: 7.4%
- ○ Overlap
- ● Memory

Pre Post

Figure 25.2 Mean saccadic gain values as percentages pre- and postadaptation. The solid symbols exhibit the gain values for the specific type of saccade under adaptation; the open symbols show saccadic gain for the respective test conditions. The vertical bars represent standard error.

symbols in the plot display the results for the saccades directed to the stepping targets. Saccadic gain for these responses is reduced from the initial value of 89% to 73.7% after adaptation. Statistical analysis reveals that this gain change is significant: $t(5) = 13$, $p < 0.01$. The open circles denote the average gain of the four horizontal saccades elicited in the scanning situation, before and after adaptation. Amazingly, the magnitudes of these saccades are almost unaffected by the intervening adaptation process; saccade gain changes from 94.2% to 92.5%; the final gain is not significantly different from the control condition ($t(5) = 1.3$; $p > 0.05$). The amount of transfer calculated as the ratio of the gain changes for both conditions was 10.7%.

Transfer to memory-guided saccades The second experiment studied the effect of step adaptation on the magnitude of saccades directed to a memorized target. Nominal saccade gain was first assessed in the initial control block which included the presentation of 60 single-step trials (figure 25.1a) and 64 memory test trials (figure 25.1c), presented in a total of four experimental blocks. Subjects then went through a long adaptation phase that included 400 step adaptation trials (figure 25.1b). In the final post-adaptive test block, 64 memory test conditions and 60 step test conditions were applied. Four subjects participated in this experiment.

Figure 25.2b compares mean pre- and postadaptive gain for both conditions. Obviously, saccadic conditioning was successful, reducing mean gain of the step saccades from 93% before adaptation to 78% after adaptation. For the memory-guided saccades, however, gain changes from 85.2% to 83.5%; this change is not statistically significant: $p > 0.05$; amount of transfer is only 2.4%. It can be concluded that step adaptation does not transfer to saccades directed to target positions that have to be memorized for 1.5 sec.

Transfer to overlap saccades Here, the initial control block consisted of phases of 60 step test conditions (figure 25.1a) and 64 overlap test conditions with an overlap duration D of 1.5 sec (see figure 25.1e). Subjects then underwent a long period of conditioning stimuli consisting of 480 step adaptation trials. Finally, the amount of induced adaptation was tested with 60 overlap test saccades. Six subjects participated in this experiment.

Figure 25.2c demonstrates that the adaptation leads to a solid reduction of saccadic gain of the saccades directed to the target steps (solid symbols); gain is reduced from 88.1% to 72.6%; this reduction is highly significant: $t(5) = 8.5$; $p < 0.01$. However, there is no significant transfer to the overlap test condition (open symbols; pre: 91.1%; post: 89.7%, $p > 0.05$); the amount of transfer is only 8.7%.

Adaptation of Scanning Saccades

The previous results demonstrate that when stimulus-triggered saccades are adapted in a double-step paradigm, no transfer of adaptation occurs to

saccades elicited otherwise, such as scanning saccades, saccades directed to a memorized target, and saccades in an overlap paradigm. The question next arises whether it is also possible to adapt scanning saccades without affecting the other three response types.

Transfer to step saccades Here the scanning stimulus (figure 25.1f) was combined with intrasaccadic displacements of the stimulus array. The initial control block of 80 control experiments, consisting of phases of scanning saccades and single-step trials (figure 25.1a and 25.f), was followed by 200 trials in which scanning saccades received conditioning feedback: the whole display was systematically displaced by 25% of the item separation (1.5°) during each horizontal scanning saccade. The shifts occurred into the opposite direction of the saccade. Two test phases, each of 30 single-step test trials (figure 25.1a), were interleaved with these training stimuli. Six subjects participated in this experiment.

Figure 25.2d presents the experimental results as means of the six subjects. Due to the introduction of the conditioning stimulus, the magnitudes of the scanning saccades decreased quickly and consistently in all subjects (pre: 94%; post: 76%; $t(5) = 7.1$; $p < 0.01$). The gain of the step test saccades was also reduced by the ongoing adaptation process (pre: 85.6%; post: 79%; $t(5) = 3.6$; $p < 0.05$), but the mean gain reduction was considerably smaller, leading to an amount of transfer of only 36.7%.

Transfer to memory saccades This experiment was identical to the previous one except that, instead of step saccades, memory-guided saccades (figure 25.1c) were analyzed in the test conditions. Four subjects participated in the experiment.

The data presented in figure 25.2e demonstrate again that the conditioning stimulus leads to a considerable gain reduction (pre: 96.3%; post: 75.8%); the gain difference is significant: $t(3) = 7.3$; $p < 0.01$. However, in contrast to the previous results, this gain modification transfers almost completely (90.2%) to the test condition consisting in the memory-guided saccades: gain change of the memory-guided saccades is also significant: (pre: 94%; post: 75.5%; $t(3) = 5.9$; $p < 0.01$).

Transfer to overlap saccades Here, instead of step saccades, overlap saccades (figure 25.1e) were analyzed in the test conditions; otherwise, the paradigm was identical to the two previous experiments. Again, four subjects participated in the experiment.

The data presented in figure 25.2f show a significant gain reduction for the scanning saccades (pre: 92%; post: 72%; $t(3) = 9.3$; $p < 0.01$). As in the previous result, this gain modification transfers largely (76%) to the overlap saccades: induced gain change of overlap saccades is also significant (pre: 92.2%; post: 77%; $t(3) = 10.4$, $p < 0.01$).

Adaptation of Memory Saccades

The next set of three experiments studied the transfer of memory adaptation, namely, saccades directed to a memorized target position, on step, scanning, and overlap saccades. In the initial control session, a block containing 80 memory test conditions (figure 25.1c) was combined with 60–80 step, scanning, or overlap test trials, respectively. For adaptation, the subjects received a total of 100 conditioning stimuli (figure 25.1d), finally followed by 10 scanning test trials, or 50 step or overlap test trials, respectively. Four subjects participated in each of the experiments.

The data provided in figures 25.2g–25.2i demonstrate that the conditioning leads to significant gain reductions for the memory-guided saccades in all three experiments: $t(3) = 6.6$, $p < 0.05$; $t(3) = 7.2$, $p < 0.01$; and $t(3) = 8.3$, $p < 0.01$, respectively. Thus the adaptation treatment was always effective.

Transfer to step saccades   The data in figure 25.2g show that the gain of the saccades to the single-target steps (open symbols) is reduced only by a small amount; the reduction is nonsignificant (pre: 91.6%; post: 88%; $p > 0.05$). Transfer amounts to only 17% of adapting memory-guided saccades in the same subjects.

Transfer to scanning saccades   The same result can be found when scanning saccades are analyzed (figure 25.2h); amount of transfer is 8.8%, and does not reach statistical significance (pre: 98.3%; post: 96.9%; $p > 0.05$).

Transfer to overlap saccades   Finally, figure 25.2i shows data from the experiment that studied the transfer of memory adaptation to saccades in an overlap paradigm, as shown in figure 25.1e. In this experiment, an overlap duration of $O = 1.5$ sec was used. The data for the overlap saccades (open symbols) reflect only a small transfer of memory adaptation (7.4%) which does not reach statistical significance (pre: 94.3%; post: 93.1%; $p > 0.05$).

Summary

The results from nine transfer experiments demonstrate that saccadic adaptation is not likely to consist in a low-level gain modification that would affect saccades elicited in all contexts in a similar way. Rather, partially asymmetrical dissociations occur, arguing strongly for the existence of separate, largely independent adaptive mechanisms. When reflexive saccades, namely, saccades directed to target onsets, are adapted, this adaptation transfers neither to the intentional, explorative saccades that occur during scanning nor to memory-guided saccades. A similarly clear separation holds for the memory-guided saccades; when they are adapted, there is no significant transfer to the other saccade types. A remarkable asymmetry occurs for the adaptation of volitional saccades occurring when scanning a display. Here, while there is

limited transfer to step saccades, memory-guided saccades are strongly affected by the adaptation. Overlap saccades, finally, are affected by scanning adaptation, but not by step and memory adaptation. This suggests that saccades in an overlap paradigm and the intentional saccades performed during voluntary scanning are controlled by the same adaptive mechanism. In section 25.5, a model will be discussed that can account for these various findings. Before we turn to this discussion, however, two more sets of experiments will be reported.

25.4 TEMPORAL TRANSITION BETWEEN REFLEXIVE AND VOLITIONAL SACCADES

The above results demonstrate that adaptive gain reduction of reactive saccades, namely, saccades that occur in immediate response to the onset of a peripheral target, does not transfer to the saccades with which stationary items are scanned, nor to saccades in an overlap paradigm. A major difference between these two conditions is that, for the scanning and overlap saccades, the oculomotor system has ample time to prepare and program the saccadic parameters on the basis of the complete visual information about all target positions. The elicitation of the saccade is determined, not by the onset of the peripheral target, but by the decision of the subject. For the reactive saccades, on the other hand, processing time is limited to the short saccadic latency period. The temporal transition between both types of responses can be studied in an overlap paradigm (figure 25.1e) in which the overlap interval O is systematically varied; with shorter values of O, the response type should approach that of the reflexive saccades of the step paradigm.

For this purpose, saccadic gain was determined for overlap intervals O varying between 0 sec and 1.5 sec, before adaptation and after a period consisting of 480 step adaptation trials. All six subjects participated in this experiment. Mean saccadic gain was analyzed as a function of the delay D between target onset and saccades onset (figure 25.1e).

The results are given in figure 25.3 presenting the gain of overlap saccades as a function of D. The data points are the means for the six subjects. For the unadapted subjects, the fastest reactions have latencies below 150 msec; these saccades tend to show slightly reduced amplitudes. Otherwise, saccadic gain of the unadapted saccades is largely independent of the delay D, yielding a mean value of 90% ± 1.6% (standard error). This picture changes drastically after step adaptation. Obviously, the amount of gain change induced by the double-step stimuli now depends strongly on the amount of available processing time. Saccades reacting immediately to the target onset (i.e., with latencies below 200 msec) show strongly reduced gain; mean post-adaptive gain for these fastest responses is 73% ± 1.9%. Later saccades, however, are considerably less affected by the previous conditioning; the
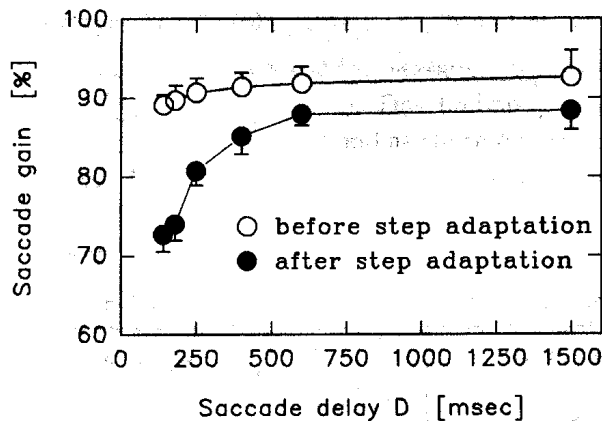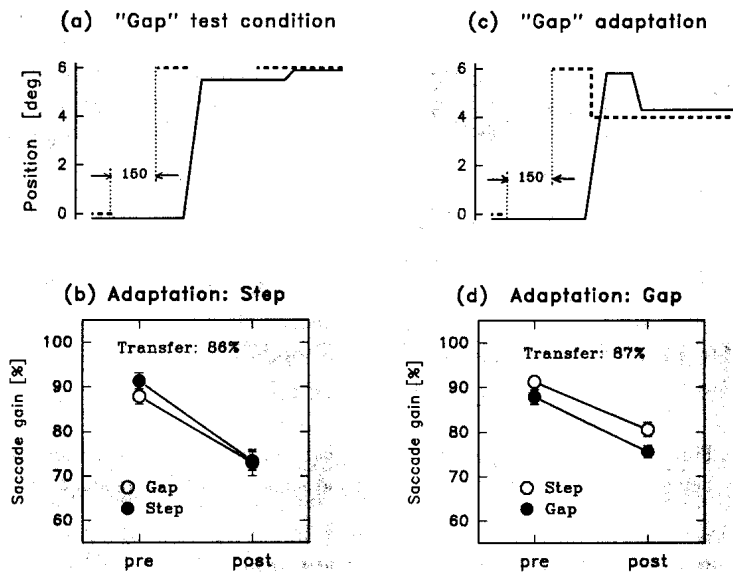
Figure 25.3 Percentage gain of overlap saccades as a function of the temporal delay D between peripheral target presentation and saccade onset, before and after step adaptation.

major transition occurs within the initial 400 msec. This result suggests that saccades directed to an onset target are reflexive saccades only when they occur within 200–400 msec after stimulus appearance; later saccades are controlled by a separate mechanism responsible for the volitional saccades.

25.5 ARE "EXPRESS SACCADES" CONTROLLED BY A SEPARATE ADAPTIVE MECHANISM?

A final set of two experiments studied whether the ultrafast so-called express saccades are governed by an adaptive controller separate from the normal reflexive saccades induced in a step paradigm. It has been demonstrated that saccadic responses with the shortest latencies occur when the current fixation stimulus disappears 150–200 msec before the peripheral target is presented. Frequently, saccadic latencies in this gap condition are 100 msec or even shorter; the multimodality of the latency distributions has led some researchers to suggest that express saccades form a separate class of saccadic responses (e.g., Fischer and Weber 1993). Fischer and collaborators have proposed that the early disappearance of the central fixation would allow attention to disengage from fixation, prerequisite for fast saccadic responses to the onset of peripheral stimuli. More specifically, these authors developed a three-loop model of saccade generation in which these fastest responses are generated by a short-latency loop involving direct pathways to the superior colliculus, while the normal reactive saccades (with latencies of 160–200 msec) involve a second loop through the parietal cortex.

In order to investigate whether a similar dissociation can be found for the adaptive mechanisms governing both response types, two separate experiments were performed. The first experiment studied the transfer of step adaptation to the express saccades occurring in a gap paradigm. Before and after an adaptation period consisting of 520 step adaptation trials (figure

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(a) "Gap" test condition

(c) "Gap" adaptation

(b) Adaptation: Step

(d) Adaptation: Gap

Figure 25.4 *a, c* Sequence of target steps (broken lines) and eye position (solid lines) in the gap experiments. To induce the occurrence of express saccades, the fixation stimulus disappeared already 150 msec before the onset of the saccade target. *b, d* Pre- and postadaptive gain values in the gap test and step test conditions.

25.1b), express saccades were induced in a gap test paradigm in which the fixation target was blanked 150 msec before the onset of the peripheral target (figure 25.4a). Four subjects participated in this experiment.

All subjects produced a large portion of express saccades in the gap test condition; mean saccadic latency was 109 msec, as compared to 165 msec in the normal step paradigm. For the computation of the mean gain of these express saccades, only responses with latencies between 80 msec and 120 msec were considered. This is the range of saccadic latencies considered as typical for the population of express saccades in a target gap condition (e.g., Fischer and Ramsperger 1986). The result is shown in figure 25.4b. As usual, step adaptation leads to a significant saccadic gain reduction (pre: 91.3%; post: 73.9%; $t(3) = 33.9$; $p < 0.01$). This gain change transfers to a large degree (86%) to the express saccades. The gain of these responses is reduced from 88% to 73% after adaptation; this change is significant: $t(3) = 9.0$; $p < 0.01$.

In the second experiment, express saccades were adapted and the transfer to step saccades was tested. For this purpose, a gap adaptation paradigm as shown in figure 25.4c was applied in 520 adaptation trials. In this experiment, however, the conditioning intrasaccadic target displacement only occurred for saccades with latencies between 80 msec and 120 msec. Before and after adaptation, the gain of normal reflexive saccades was assessed by means of the step test paradigm. The same four subjects as in the previous experiment participated.

As can be seen in figure 25.4d, the intrasaccadic target displacement leads to a significant reduction of the conditioned response gain (pre: 87.9%; post: 75.6%; $t(3) = 18.5$; $p < 0.01$). This finding demonstrates that express saccades can be adapted as fast and as efficiently as the other saccade types. The data from the step test condition exhibit a high amount of transfer (87%): induced by the adaptation period, saccadic gain changes from 91.3% to 80.6% ($t(3) = 8$; $p < 0.01$). In summary, there is mutual transfer of gain adaptation between normal reflexive and express saccades; seemingly, both types of saccades are governed by the same adaptive mechanism.

25.6 GENERAL DISCUSSION

This study is the first to demonstrate that adaptation of saccades following steps of a single target, adaptation of saccades during scanning, and adaptation of memory-guided saccades lead to gain changes that are specific for the type of saccadic elicitation. Adaptation with the stepping target transfers neither to the saccades in the scanning situation nor to delayed saccades in an overlap paradigm, nor to memory-guided saccades. Conversely, when memory-guided saccades are adapted, saccades to target steps and scanning saccades remain completely unaffected. Finally, with adaptation of scanning saccades, induced gain changes transfer to overlap and memory-guided saccades, but only weakly to saccades following steps of single target. All this strongly indicates that the amplitudes of saccadic responses (for saccades in a certain direction) are determined, not just by a single gain parameter, but by at least three separate and largely independent mechanisms.

An interesting aspect of the paradigm here developed is that it may serve as an empirical means for categorizing different types of saccadic responses. Obviously, delayed saccades can be identified as belonging to the category of volitional saccades; express saccades, to the category of normal reactive saccades. Anticipatory saccades to predictive target locations should belong to the category of memory-guided saccades; accordingly, they are found to be affected by scanning adaptation, but not by double-step adaptation (Deubel 1994). Also, it should be expected that antisaccades (Hallett 1978) should show the properties of volitional responses.

What are the features that distinguish the different groups of saccade modes? One of the characteristics of the former experiments with double-step adaptation was that subjects' eye movements were completely guided by the stimulus: all these saccades were "reactive" saccades in that they were triggered by an external event and that the location of where the eye had to go was determined by the location of the single stimulus in the visual field. Most of our everyday saccades are not determined by external events, however; we intentionally decide where to move the eyes next and when to trigger a saccade, and the information about target position can come from visual input and from spatial memory. The scanning paradigm thus aimed at mimicking a situation where the saccades are not determined by the onset of

a single target in an otherwise empty field, but where the subject intentionally selects a target from several alternatives, has ample time to prepare the sequence of eye movements, and performs a self-paced timing of the scanning eye movements. These saccades are called "volitional" here in order to emphasize their intentional and voluntary character. The results from this investigation show that the reactive and the volitional types of saccadic responses can be selectively adapted, suggesting the existence of separate adaptive mechanisms for the metrical control of these saccades.

The finding that, when internally guided saccades are adapted, this conditioning transfers only to a small degree to stimulus-elicited saccades confirms recent findings by Erkelens and Hulleman (1993), whose data suggest that internally triggered saccades can be selectively adapted, leaving stimulus-triggered eye movements largely unaffected. However, for the adaptation of internally guided saccades these authors used very large (50% of initial step) backward displacements of a target the subjects were certainly aware of. Also, target positions were not varied during a session. Accordingly, oculomotor learning took place within a few saccades, arguing for a cognitive-strategic mechanism of saccade size change. Fuchs, Reiner, and Pong (1996), in analyzing the transfer of step adaptation to overlap saccades in macaque monkeys confirmed the present findings of complete dissociation in their human subjects, although their nonhuman subjects behaved differently, showing a considerable amount of transfer of step adaptation to the volitional saccades. This striking difference between human and nonhuman primates seems to indicate that different adaptation mechanisms are employed in humans and in monkeys in otherwise similar situations. This is also consistent with the difference in the time courses of saccadic gain adaptations. Humans can adapt within 50–150 saccades, while monkeys require more than 500 trials to achieve comparable adaptation effects (Deubel 1987).

Other behavioral studies also hint at a dissociation of endogenously and exogenously controlled saccades in humans. Lemij and Collewijn (1990) found that saccades to stationary targets are more accurate than saccades to jumping targets. Collewijn, Erkelens, and Steinman (1988) demonstrated that the amplitudes of volitional saccades do not show the 10% undershooting that is normally seen in saccades to suddenly appearing targets. Finally, saccades directed to memorized targets exhibit slightly lower maximum velocities than target-driven saccades (Smit, van Gisbergen, and Cools 1987).

The question arises whether other aspects of saccadic eye movements under adaptive control would also show a similar dissociation between reactive and volitional response modes. Deubel (1991, 1993a) found this indeed to be the case for the adaptation of postsaccadic eye drift. Postsaccadic drift was induced by systematic exponential target movements at the end of each saccade. The results demonstrated that the amount of induced postsaccadic eye drift is dependent on the method of testing. According to later findings (Deubel in preparation), transfer of adaptation is significantly smaller to scanning saccades and to spontaneous saccades in the dark than to reactive

saccades. It should be mentioned that experimental indications for context-specific adaptive mechanisms are not limited to the saccadic system. Evidence is accumulating for context-specific gain switching even in the vestibulo-ocular reflex (Tan, Shelhamer, and Zee 1992; Shelhamer, Robinson, and Tan 1992).

A surprising result from the present study is that memory-guided saccades are controlled by yet another separate mechanism. While Deubel 1995a,b assumed that memory-guided saccades behave as volitional saccades to visible targets, the experiments with the memory adaptation condition demonstrate that this is not the case: memory-guided saccades can be adjusted quite independently from the other types of saccades. This confirms a report by Fujita, Amagai, and Minakawa (1995) that adaptation of memory-guided saccades does not transfer to overlap saccades.

The data shown here are another demonstration of the amazing adaptability of certain aspects of the saccadic response to the requirements of the environment. Some of the adaptations reported in the literature are extremely fast, even when the system is confronted with the additional demand for disconjugate changes (Eggert, Kapoula, and Bucci 1994; van der Steen and Bruno 1995). In considering the general validity of ultrafast adaptations as truly adaptive processes, it is important to recognize that these changes could reflect the switching to a specific strategy rather than the plastic modification of peripheral oculomotor processing. Deubel 1995b demonstrated that visual stimulus features (such as color and form of the target, presence or absence of background structure) cannot be used by the saccadic system to switch between different sets of response parameters, suggesting that there is no specificity of saccadic gain control with respect to visual aspects of the target. The finding that visual target features per se cannot serve for selecting specific response modes seems to argue against the hypohesis that ultrafast adaptations represent the cognitively controlled selection of response strategies.

Further indications for a basic dissociation between reflexive and volitional actions come from other areas of motor control. Bizzi, Kalil, and Morasso (1972) reported that the neuromuscular activity underlying active eye-head coordination displays distinct characteristics depending on whether these were stimulus-triggered movements or the result of prediction. Frens and Erkelens (1991) find different interactions of hand and eye movements depending on whether the target was actually visible or the movements were anticipatory. Bridgeman et al. (1979) and Paillard (1987) propose, on the basis of a variety of experiments, a distinction between two separate mappings of spatial relationships that might independently contribute to the nervous organization of spatial behavior. The first refers to a sensorimotor mode which is uniquely spatial, generally unconscious, and motor-oriented. The second, "representational" mode of processing spatial information refers to a system with a more symbolic, conscious content, forming the basis of perception. Finally, the proposed dissociation may also be related to the field

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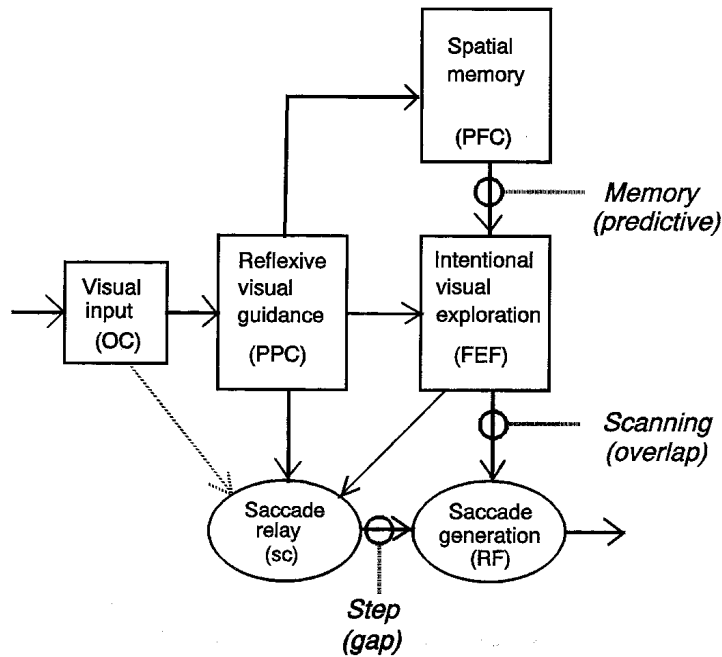
Figure 25.5 Tentative model for the contribution of cortical and subcortical pathways in the generation of reflexive, volitional, and memory-guided saccades. The circles denote the proposed locations where adaptive modifications for the specific saccade types take place. Abbreviations: OC = occipital cortex; PPC = posterior parietal cortex; FEF = frontal eye fields; PFC = prefrontal cortex; SC = superior colliculus; RF = brain stem reticular formation.

of visual attention. A number of workers (e.g., Jonides 1981; Nakayama and Mackeben 1989) report that exogenous shifts of visual attention elicited by cues such as the abrupt onset of a peripheral stimulus and endogenous, volitional shifts of visual attention exhibit basically different properties.

The findings of this study have implications for the understanding of the neural control of saccadic eye movements, confirming recent assumptions that reflexive, stimulus-guided saccades, intentionally elicited saccades, and memory-guided saccades are controlled by different cortical neural mechanisms (e.g., Pierrot-Deseilligny et al. 1995). A tentative diagram for the information flow in the various cortical and subcortical pathways is given in figure 25.5. Visual information from the retina is mainly entering the cortical areas in the visual areas of the occipital cortex (OC), from which it is provided to the posterior parietal cortex (PPC). However, there also exist more direct projections from the retina and the OC onto the main saccade relay structure, the subcortical superior colliculus (SC). It is tempting to speculate that the neural substrate mediating the ultrafast express saccades might be this rather direct retinocollicular pathway, possibly including the primary cortex. "Normal" reflexive saccades are assumed to be controlled by the PPC, more specifically, by the lateral intraparietal area (LIP, also termed parietal eye field), which is a first major cortical structure from where saccades

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are elicited. The LIP projects to the SC, but not directly to the brain stem reticular formation (RF). Typically, lesions affecting the PPC result in marked latency increases for reflexive, visually guided saccades (e.g., Pierrot-Deseilligny et al. 1991). The PPC also projects to the frontal eye fields located around the lateral part of the precentral sulcus. In the monkey, the frontal eye field (FEF) projects to the deep layers of the SC and also directly to the premotor reticular formation of the brain stem, that is, the saccade generator. In patients with FEF lesions, the triggering of intentional saccades is impaired, and they produce less volitional saccadic activity in picture scanning. Interestingly, also memory-guided saccades and predictive saccades are frequently affected (for a summary, see Pierrot-Deseilligny et al. 1995). Finally saccades to memorized targets require the retention of the target position in a spatial working memory, which is probably provided by the dorsolateral prefrontal cortex (PFC) (Funahashi, Bruce, and Goldman-Rakic 1990, 1993). The PFC receives afferent visual information mainly from the PPC and projects to the FEF. In patients with PFC lesions, the accuracy of memory-guided saccades is impaired, and predictive saccades are less frequent. Moreover, the PFC is believed to control the inhibition of unwanted reflexive visual guided saccades via inhibitory projections to the SC (Pierrot-Deseilligny et al. 1995).

The resulting flow diagram given in figure 25.5 makes obvious that the various experimental results from this study can be elegantly described by assuming that the adaptive modification of the various response types occur at three different locations in the neural pathways. First, it is assumed that step adaptation and express adaptation both affect the fast, short-latency collicular pathways; accordingly, adaptation may occur downstream the SC. Because intentional saccades and memory-guided saccades are generated mainly through the direct projection from the FEF to the RF, these saccade types are not affected. Adaptation of memory-guided saccades may occur at the output of the PFC and will not affect other saccade types. Finally, adaptation of intentionally guided saccades is assumed to modify the strength of the projection from the FEF to the RF. Accordingly, the effect of adaptation will spread completely to memory-guided saccades and, to a smaller degree, to (slower) saccades occurring to the onset of peripheral targets.

Converging evidence for the proposed model comes from a study of short-term adaptation of electrically induced saccades in monkey SC by Melis and van Gisbergen (1996), who elicited saccades by electrical stimulation in the deep layers of the SC and found that these could be adapted by systematically presenting a visual target at a small distance from the expected endpoint, immediately after saccade onset. This suggests the existence of an adaptive corrector *downstream* from the SC. Moreover, this adaptation showed incomplete transfer to normal visually guided saccades, which the authors attribute to cortical input from the frontal eye fields to the brain stem saccade generator.

The present study raises new questions about the role of the cerebellum in the selective adaptation of the various saccadic response types. It is well established that cerebellar structures, especially the cerebellar midline vermis and the fastigial nuclei, are essential for the adaptive maintenance of saccadic accuracy (e.g., Ritchie 1976; Optican and Robinson 1980; Dean, Mayhew, and Langdon 1992). From the experimental findings presented above, the question arises whether these cerebellar mechanisms are responsible for maintaining proper functioning of all three of the postulated pathways. To evaluate possible differences of cerebellar involvement in the different types of saccadic responses, the above experimental paradigms have recently been applied to patients suffering from cerebellar diseases. Preliminary results from these studies indeed suggest that cerebellar lesions may specifically affect only one response type, namely, the reflexive saccades. My colleagues and I studied a patient suffering from a bilateral lesion of the fastigial nucleus caused by a large cystic tumor extending into the medial cerebellum (Straube et al. 1995). Six days after surgery, the accuracy of both reflexive saccades to stepping targets and volitional saccades was examined in paradigms identical to the ones described here. For saccades in response to the stepping targets, the patient's responses showed the prominent saccadic overshoots that clinically characterize disease of the midline cerebellum. For saccades in the scanning situation, however, no such signs were observable. In other words, while the patient's reflexive saccades were clearly hypermetric, the internally guided saccadic responses were perfectly normal. This indicates that the cerebellum—possibly, the cerebellar fastigial nucleus—is involved in the generation of externally triggered saccades toward a jumping target but not in the generation of scanning saccades toward a stationary target.

In general, the data presented in this chapter suggest that it may be rewarding to apply the adaptation paradigm developed here to patients with lesions in the parietal or frontal cortex. Evidence that specific lesions abolish the capability for adaptive responses of the respective saccade types would strongly suggest that the plastic modification of saccades occurs in brain areas that are also (mainly) responsible for their generation.

Another, more practical implication follows for the clinical diagnosis. The analysis of saccadic performance is now an important element of the clinical screening of patients with certain neurological deseases. In the clinical routine, this is frequently done by letting patients follow a small jumping target with their eyes, or by asking them to perform saccades between two stationary targets. The present findings call attention to the fact that the oculomotor response to these two stimulus types can potentially be very different. As a consequence, we need to develop new, more complex paradigms that test oculomotor responses separately for all the diffferent saccade types. Finally, training protocols in rehabilitation should consider that motor learning may be surprisingly context-specific, limiting the effect of learning to situations similar to those in which the training occurred.

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