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Selective adaptation of internally triggered saccades made to visual targets

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Abstract. We examined whether internally triggered saccades made to a nonjumping target (I-saccades) could be adapted independently from externally triggered saccades induced by a jumping target (E-saccades). Five subjects made I-saccades between two fixed targets, one placed straight ahead and the other one positioned at an eccentricity of 17.5°. The peripheral target was displaced to an eccentricity of 8.75° during the saccadic movements toward this target. Amplitudes of the I-saccades made from the central to the peripheral target before and after adaptation were compared with each other. Saccadic amplitudes after adaptation were between 10% and 42% smaller than those before adaptation. E-saccades induced by a single target which jumped from straight ahead to the same peripheral target position as was used for the I-saccades were also measured before and after the adaptation of I-saccades. Amplitudes of E-saccades before and after adaptation were hardly different from each other except in one subject. The mean decreases in amplitude of the two types of saccades, averaged over all subjects, were 21% for I-saccades and 5% for E-saccades. These results show that I-saccades can be adapted to changed visual conditions while E-saccades remain unadapted. We conclude from this finding that I-saccades and E-saccades are generated by at least partially different neural mechanisms.

Key words: Eye movements – Saccades – Adaptation – Human

Introduction

Saccades are the fast eye movements which bring the projections of interesting, peripheral objects onto the foveae of the two eyes. Recently, based on the results of lesion studies, saccades have been classified in several categories (Tusa et al. 1986). For instance, a distinction has been made between reflexive and intentional saccades. According to the definitions of Tusa et al. (1986), reflexive saccades draw the eyes to novel stimuli which suddenly occur within the environment. Intentional, visually guided saccades are volitional saccades to a predetermined visual target. Saccades made to a target which unexpectedly jumps to new positions as well as saccades made to nonjumping targets are considered to be intentional saccades. Still, there is a distinction between these saccades. Saccades made to a jumping target (E-saccades) are externally triggered by the onset of the target at the new position, whereas saccades made to nonjumping targets (I-saccades) are internally triggered. Different authors have different views about how saccades should be classified. For instance, we could classify E-saccades as reflexive and I-saccades as intentional saccades if we followed the definitions proposed by Pierrot-Deseilligny et al. (1991). Classification of saccades is not just a matter of name-giving but may have neurophysiological relevance, because lesion studies have shown that different mechanisms may be involved in the generation of saccades (for recent reviews see Büttner-Ennever 1988, Wurtz and Goldberg 1989). In the present study we investigate whether classification of I-saccades and E-saccades has also functional significance.

Behavioral studies have shown differences between E-saccades and I-saccades. Collewijn et al. (1988) found that the amplitudes of primary I-saccades were accurate within about 1° for saccades up to 80°. This finding was in contrast with the general belief that primary saccades undershoot their targets by about 10% (Becker and Fuchs 1969; Henson 1978; Pelisson and Prablanc 1988). This belief, however, was based on experiments in which only E-saccades were measured. In a direct comparison Lemij and Collewijn (1990) studied the accuracy of E-saccades and I-saccades and also found that I-saccades were more accurate than E-saccades. Lemij and Collewijn (1990) suggested that the accuracy of saccades depends on the amount of time that the target is presented. This explanation is not very satisfactory because it seems plausible that prolonged presentation

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time may reduce the variability of saccades; however, it is not clear why it should affect the size of systematic errors, i.e., saccadic undershoot. An alternative explanation for the differences between E-saccades and I-saccades is that they are generated by at least partially different mechanisms. In the present paper we test this hypothesis by using the technique of selective adaptation.

The effect of selective adaptation of I-saccades to changed visual conditions on the size of E-saccades may reveal whether E-saccades and I-saccades are generated by the same or different mechanisms. One would expect E-saccades to adapt along with I-saccades if they were generated by the same mechanism, and one would expect no adaptation or only partial adaptation of E-saccades if different mechanisms were involved in their production.

Adaptation of saccades has been studied by making them in changed visual or oculomotor conditions. Reduced strength of an extraocular muscle owing to a paresis (Kommerell et al. 1976; Abel et al. 1978) or to a surgical weakening (Optican and Robinson 1980; Snow et al. 1985), as well as displacement of the visual stimuli due to the wearing of prisms (Allen 1974), the wearing of anisometropic glasses (Erkelens et al. 1989; Lemij 1990), or owing to an electronic arrangement (Deubel et al. 1986), have shown to be effective in inducing adaptation. Typically, in such experiments no attention has been paid to the types of saccades that were made by the subject during the period of adaptation. Only in the experiments of Deubel et al. (1986) was the stimulus such that only E-saccades were induced.

In the present experiments we adapted I-saccades to a target of which the distance was decreased by 50% during the saccades. Great care was taken that E-saccades were not made during the period of adaptation. After this period we tested the effect of adaptation of I-saccades first on E-saccades and subsequently on I-saccades. The effects on I-saccades and E-saccades were clearly different from each other.

Materials and methods

Subjects

Five subjects participated in the experiments. They had visual acuities of 20/20 or better, with (two subjects) or without (three subjects) correction. None of them showed any ocular or oculomotor pathologies. One subject (C.E.) was experienced in oculomotor research. The other subjects were participating in such experiments for the first time. Informed consent was obtained from all subjects before they embarked on the study.

Apparatus

Horizontal movements of the right eye were measured with an induction coil mounted in a scleral annulus in an alternating current (a.c.) magnetic field as first described by Robinson (1963) and modified and refined by Collewijn et al. (1975). The dynamic range of the apparatus was from 0 Hz (d.c.) to frequencies above 100 Hz fulfilling a set criterion (3 dB down or less), noise level less than 10′, and deviation from linearity less than 1% over a range of ±25°. The head position of the subjects was restricted by a chin rest and a head support.

A horizontal array of light-emitting diodes (LEDs) was positioned in front of the subject at a distance of about 50 cm. The LED array was placed about 5° below eye level in the frontal plane. The array consisted of 240 LEDs equidistantly positioned at 0.25 cm from each other.

A microprocessor (Motorola) was used for stimulus generation and data acquisition. Positions of the right eye were digitized on-line at a frequency of 512 Hz with a resolution of 3.5′. The sampling period had a duration of 1.6 s. Between trials the data were transferred to an HP A900 minicomputer system, where they were stored on disk for off-line analysis.

Procedure

The experiments were carried out in a normally lit room which contained many visual cues. A separate set of experiments was carried out in a darkened room to investigate the effect of visual nontarget information on saccadic adaptation. The duration of each experimental session was limited to half an hour.

The sensitivity of the eye movement recorder was adjusted at the start of each experimental session. A calibration target containing ten successive, equally spaced fixation marks was presented. The subject fixated each mark in turn, while the polarity, gain, and offset of the signal for eye position were inspected and adjusted. After these adjustments, voluntary gaze shifts made between the calibration marks were recorded.

Each experimental session consisted of a sequence of 88 trials in which saccades were made under five experimental conditions. In the first two experiments we measured I-saccades and E-saccades under normal viewing conditions. The data from these trials served as a baseline for the adaptation that was measured in the following experiments. I-saccades were adapted to a target which was displaced during the saccades. Subsequently, in two postadaptation experiments E-saccades were measured first followed by I-saccades. Figure 1 shows the results from such an experimental session.

The details of the experiments are as follows:

1. *Baseline: I-saccades.* In a series of 13 trials the subjects made saccades from the central fixation LED to an LED placed at an eccentricity of 17.5° on the right side. The two LEDs were simultaneously visible. The subjects were asked to make the saccades within a period of 2 s after an attention signal (sound pulse 0–500 Hz, 20 ms, 90 dB) was given.

2. *Baseline: E-saccades.* This condition differed from the former one in that the attention signal was not given, only one LED was lit at a time, and the subjects had to respond as quickly as possible to the onset of the target at the peripheral position.

3. *Adaptation: I-saccades.* In a series of 36 trials the subjects made saccades from the central fixation LED to an LED placed at an eccentricity of 17.5° on the right side (target positions identical to the ones in experiment 1). The subjects started by fixating the central LED and were asked to make a saccade within a period of 2 s after an attention signal was given. During the saccade made to the peripheral target this target was displaced from 17.5° to an eccentricity of 8.75° at the same side of the central fixation LED. The target was displaced within 2 ms after the maximum velocity of the saccade had been detected. After the subjects had managed to fixate the peripheral target they were not allowed to refixate the central target. They had to continue in fixating the peripheral target which, after the sampling period of 1.6 s, slowly (2°/s) moved to the central fixation position. Then the subjects maintained their fixation of the central LED while the peripheral target was reset at its initial position. Only after the sound signal was given again were the subjects allowed to make another saccade to the peripheral target. This procedure guaranteed that the number of E-saccades as well as I-saccades, made to readapting stimuli, was reduced to practically zero. At the end of the experi-

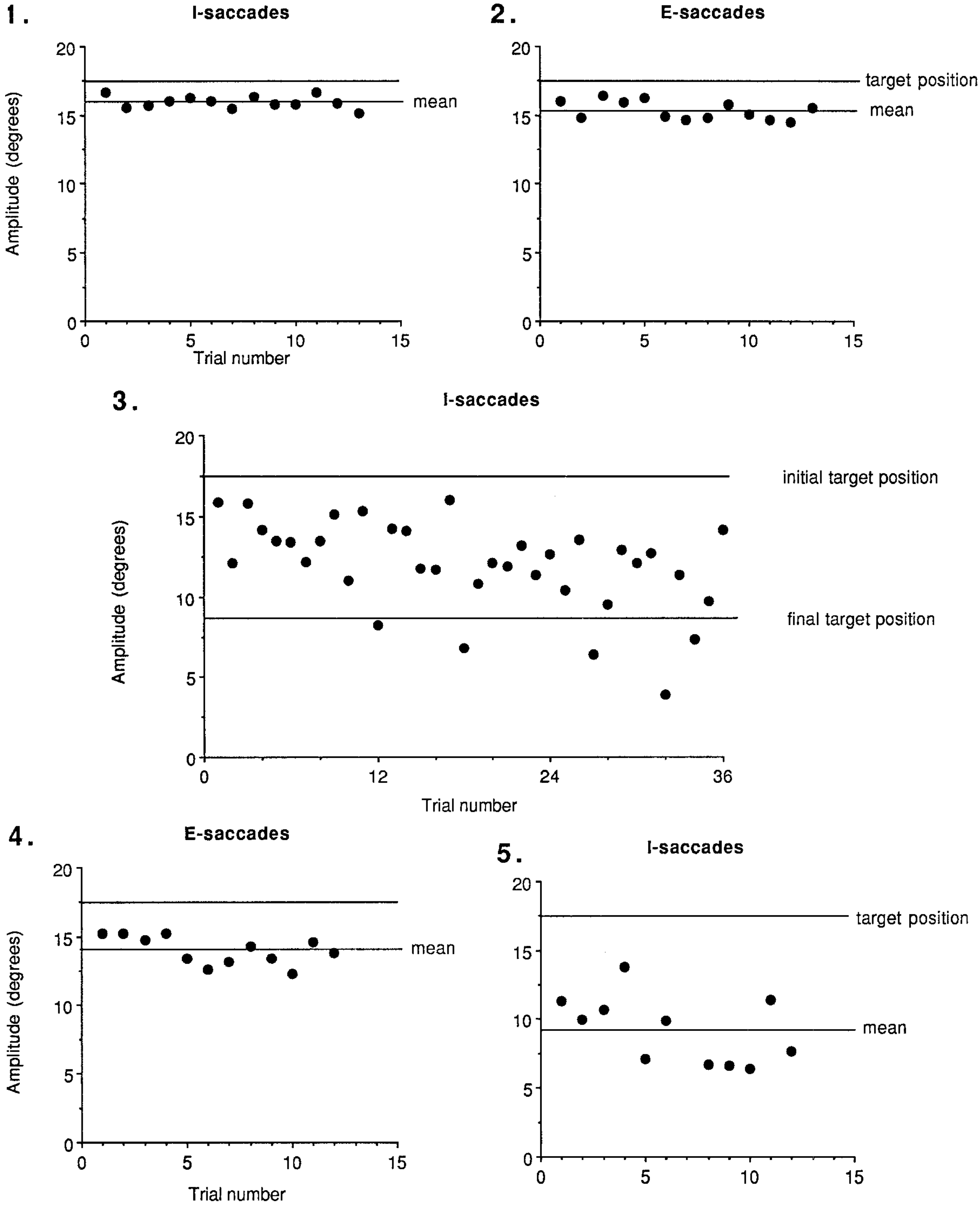

Fig. 1. Amplitudes of primary saccades made by subject C.E. in the different experiments. The *number* in the *upper left corner* of each panel indicates the type of the experiment as described in Materials and methods

ment the subjects were asked to close their eyes until the next experiment started.

4. *Test: E-saccades.* The target was the same as in experiment 2. The subjects started by fixating the central LED. During the saccade made to the peripheral target position, the peripheral target was extinguished within 2 ms after the maximum velocity of the saccade had been detected. The target was off for the remainder of the sampling period of 1.6 s. After this period the target reappeared at the position that was fixated by the subjects at that time. Resetting the target at the fixated position was possible owing to the fact that the eye position was measured on-line. The subjects were asked to wait for the reappearance of the target after they had made a saccade to the peripheral target position. They had to continue in fixating the peripheral target which subsequently moved slowly to the central fixation position. This procedure prevented readaptation of E-saccades to the normal viewing conditions as far as possible. At the end of the experiment the subjects were asked to close their eyes until the start of the next experiment.

5. *Test: I-saccades.* The target was the same as in experiments 1 and 3. The subjects started by fixating the central LED and

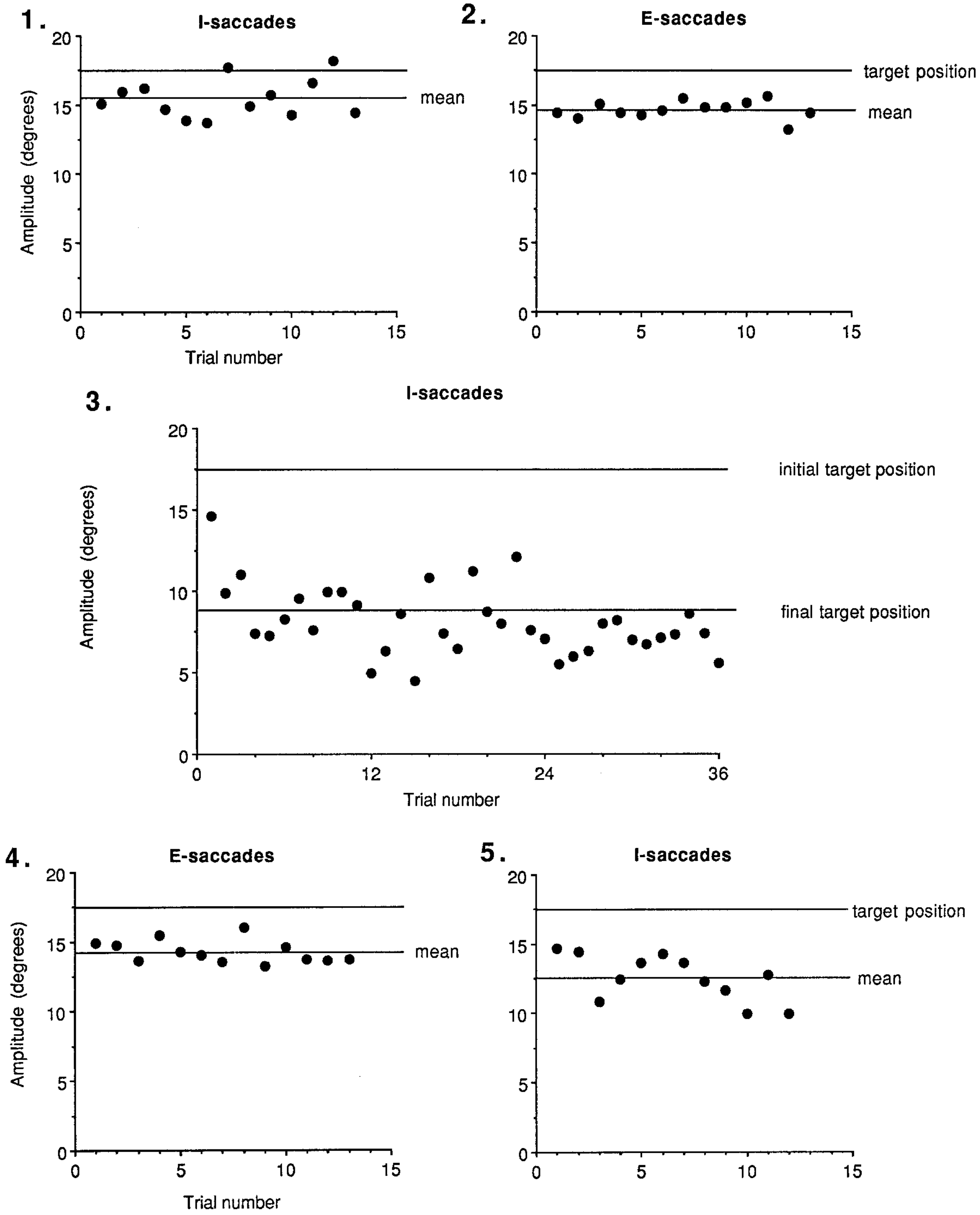

Fig. 2. Amplitudes of primary saccades made by subject G.R. in the different experiments. The *number* in the *upper left corner* of each panel indicates the type of the experiment as described in Materials and methods

were asked to make a saccade within a period of 2 s after an attention signal was given. During the saccade made to the peripheral target position, the peripheral target was extinguished within 2 ms after the maximum velocity of the saccade had been detected. The target was off for the remainder of the sampling period of 1.6 s. After this period the target reappeared at the position that was fixated by the subjects at that time. Again, the subjects were asked to wait for the reappearance of the target after they had made a saccade to the peripheral target position. They fixated the peripheral target which subsequently moved slowly to the central fixation position. The subjects maintained their fixation of the central LED while the peripheral target was reset at its initial position. Only after the sound signal was given again were the subjects allowed to make another saccade to the peripheral target. This procedure was followed to prevent readaptation of I-saccades to the normal viewing conditions.

Data analysis

In the off-line analysis, saccade onset as well as saccade offset were detected by a velocity threshold of 15°/s in combination with a required minimum saccade duration of 15 ms. Amplitudes of the saccades were computed from the position signals of the right eye. Mean values and standard deviations were computed of saccades made within each experiment. In order to estimate the amount of adaptation of E-saccades, the means of experiment 4 were compared with those of experiment 2. The amount of adaptation of I-saccades was estimated by comparing the means of experiment 5 with those of experiment 1. The data were analyzed by using *t*-tests and an analysis of variance for the comparison of means.

Results

Adaptation of I-saccades

The light conditions in the room did not have any effect on the amount or speed of adaptation. Since most experiments were executed in a lit room the results presented in this section were obtained from such experiments. I-saccades made during the adaptation trials were initially of the same size as those made in the baseline trials before adaptation (Fig. 1). The primary saccades were followed by a second corrective saccade made in the direction opposite to the direction of the primary saccade. After more saccades to the adapting stimulus had been made, the size of the primary saccades decreased. The speed of the decrease differed somewhat between the subjects. The adaptive process progressed rather irregularly. Figure 1 shows that the size of primary saccades varied strongly in successive trials. After a few trials the primary saccades could even undershoot the adapting target, while in later trials the unadaptive level was almost reached again. In addition to this irregular behavior, a slow overall decrease in the mean amplitude of the saccades was observed. This slow decrease in amplitude represents the adaptational process which was tested after the period of adaptation.

The results of subject G.R. were different from those of the other subjects in that the size of his primary saccades decreased very rapidly (Fig. 2C). The amount of decrease required by the adapting stimulus was already reached after a few trials. The amplitudes of the saccades remained at that level until the end of the adaptation period despite the presence of a large intertrial variability.

The subjects did not notice the displacement of the target during the saccades. However, they noticed that the target position after the saccades differed from the one before they changed their fixation. This was especially clear in experiments in which the room was normally lit and the subjects could relate the position of the target to the position of other objects.

The mean amplitudes of I-saccades before (experiment 1) or after (experiment 5) adaptation are shown in Fig. 3. The mean amplitudes of saccades made before adaptation showed differences between the various subjects and even differences between the two experimental sessions of one subject. There are two reasons for these differences. Firstly, the different subjects made saccades with unequal accuracy. Secondly, the distance between the subject and the stimulus array was not exactly the same in all experimental sessions but could differ by about 2 cm. This difference in distance affected the eccentricity of the peripheral target by about 0.6°. In all subjects the mean amplitudes of saccades after adaptation were significantly ($P < 0.0002$, *t*-test) smaller than those made before adaptation. Generally the variability in saccadic amplitude was increased after adaptation. The acquired amount of adaptation was not enough to meet the requirements imposed by the stimulus. Decreases in amplitude ranged from 10% to 42%, while perfect adaptation would have required a decrease of 50%. Comparison of the results from the two sessions, executed on different days, shows that adaptation did not improve with increasing experience in adaptation. On the other hand it was striking that the amount of adaptation was largest in subject C.E., who had the most experience in oculomotor research.

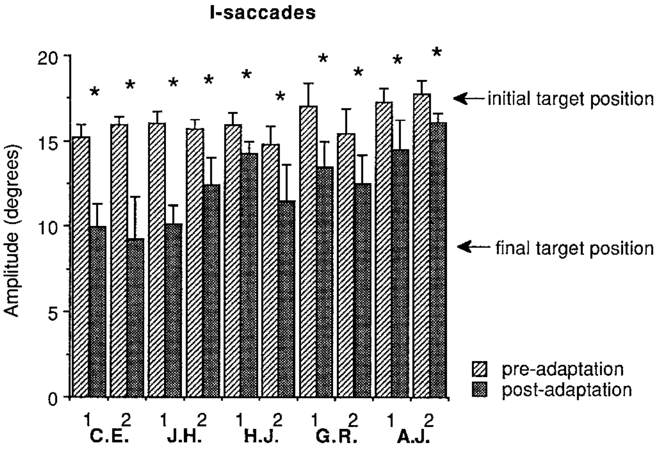

Fig. 3. Mean amplitudes and standard deviations of I-saccades in five subjects. The *numbers below the horizontal axis* indicate the order of the experimental sessions held on different days. The *asterisks* indicate significant differences ($P < 0.0002$) between the pre- and postadaptation results

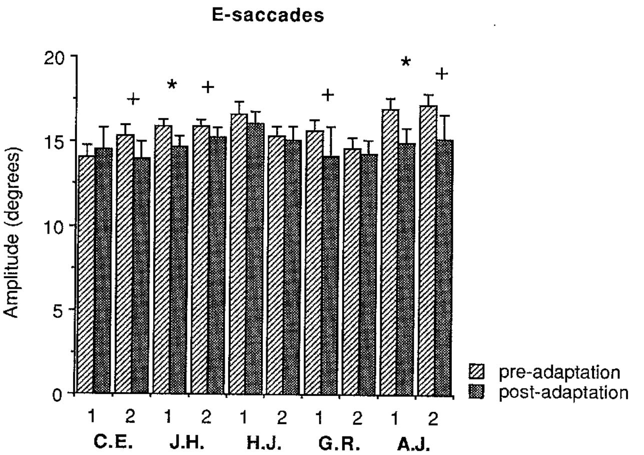

Fig. 4. Mean amplitudes and standard deviations of E-saccades in five subjects. The *numbers below the horizontal axis* indicate the order of the experimental sessions held on different days. The symbols indicate significant differences (*asterisks*, $P < 0.0002$; *crosses*, $P < 0.01$) between the pre- and postadaptation results

The effect of adaptation of I-saccades on E-saccades

The mean amplitudes of E-saccades before (experiment 2) or after (experiment 4) adaptation of I-saccades are shown in Fig. 4. The mean amplitudes of saccades after adaptation were somewhat smaller than those made before adaptation except in one case (subject C.E., session 1) in which the mean amplitude was slightly larger. Only in two cases was the decrease significant when the same confidence level ($P<0.0002$) was used as the one we used previously for saccades made to the fixed targets. In four cases the differences were significant with a lower level of confidence ($P<0.01$), while the differences were not significant ($P>0.05$) in the other four cases. Differences in the mean saccadic amplitude were significant ($P<0.01$) in both experimental sessions in only two subjects.

Difference in adaptation of I-saccades and E-saccades

An analysis of variance was performed to test the difference in achieved amount of adaptation. Two factors, type of saccade and subject, were analyzed as independent variables with achieved amount of adaptation as the dependent variable. The main effects of type of saccade ($F_{1,9}=200.08$, $P<0.001$) and subject ($F_{4,1}=43.75$, $P<0.001$) were highly significant. The reductions in mean amplitudes of I-saccades and E-saccades due to the adaptation of I-saccades are shown in Fig. 5.

This figure shows that the amount of achieved adaptation was much higher for I-saccades than for E-saccades in four subjects, whereas the acquired adaptation was about the same in the fifth subject. Averaging of the data of all five subjects showed that the mean decreases were 21% for I-saccades and 5% for E-saccades. This means that, on average, 42% of the desired amount of adaptation was achieved for I-saccades and 10% for E-saccades.

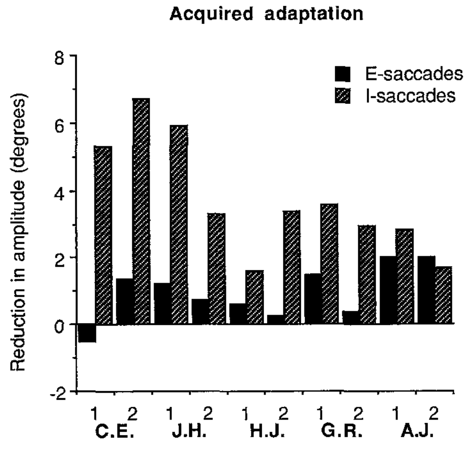

Fig. 5. The acquired amount of adaptation for I- and E-saccades in five subjects. The *numbers below the horizontal axis* indicate the order of the experimental sessions held on different days

Discussion

Adaptation of I-saccades and E-saccades

I-saccades made between fixed targets, and E-saccades induced by a jumping target, which initially were about equally large, became different in size after adaptation of I-saccades. The speed of adaptation found in the present study was faster than was reported in a study of Deubel et al. (1986) in which E-saccades were adapted. There are several differences between the study of Deubel et al. (1986) and the present study which may be the cause of the different results. In the first place, I-saccades may be easier adaptable than E-saccades. Secondly, Deubel et al. (1986) used a combination of adapting and nonadapting stimuli, whereas in the present study saccades to nonadapting stimuli were avoided as far as possible. Thirdly, we used an adapting stimulus which demanded more adaptation.

After the adaptation of I-saccades we found that the acquired adaptation was larger for I-saccades than for E-saccades. This difference was strongly present in four subjects and only weakly in one subject. The clear differences observed in this experiment suggest that different mechanisms may underly the generation of saccades made to fixed and to jumping targets. The order of the test trials was chosen such that if I-saccades and E-saccades were generated by the same process differences just opposite to the ones we found would have been more plausible. For instance, after adaptation of I-saccades we first tested E-saccades, and only after this experiment we tested I-saccades. It seems reasonable to assume that the amount of acquired adaptation was strongest directly after the adaptation period. We, therefore, expected to find a larger effect in E-saccades than in I-saccades. On the contrary, we found just the opposite effect. Adaptation of I-saccades affected E-saccades; however, the amount of adaptation was much smaller.

Other differences between I-saccades and E-saccades

Behavioral studies other than adaptation experiments have indicated the presence of different mechanisms underlying the neural control of I-saccades and E-saccades.

Frens and Erkelens (1991) suggested, on the basis of incorrect movements in combined fixation and pointing tasks, that saccades induced by jumping targets are generated by a mechanism which is exclusively used for saccades, whereas saccades made to guessed or preselected targets are generated by another mechanism, which is also involved in the generation of hand movements. Smit et al. (1987) found that maximum velocity and duration of saccades to jumping targets differed from those made to remembered, and consequently preselected, target positions. They suggested that the differences in the dynamical properties reflected processes in the visuomotor system rather than in the motor system. Furthermore, differences in accuracy have been found between I-saccades and E-saccades. Collewijn et al. (1988) found that the amplitudes of primary I-saccades were accurate within about 1° for saccades up to 80°. Other authors found that primary E-saccades undershot their targets by about 10% (Becker and Fuchs 1969; Henson 1978; Pelisson and Prablanc 1988). In a direct comparison Lemij and Collewijn (1990) found that I-saccades were more accurate than E-saccades. These authors suggested that the accuracy of saccades depends on the amount of time that the target is presented. An alternative explanation for the difference in accuracy may be that I-saccades and E-saccades are generated by at least partially different neural mechanisms.

The interpretation of results from lesion studies

In the past decades anatomical, electrophysiological, and lesion studies have revealed many neural structures and pathways which are involved in the generation of saccades. Many attempts, particularly by using lesion techniques, have been made to find the functional significance of parallel circuits which have been found to exist. Especially the superior colliculus and the frontal eye fields have received considerable attention in lesion experiments. The interpretation of results from lesion experiments has appeared to be difficult and controversial. This has mainly been attributed to shortcomings and drawbacks of the lesion technique (Hepp et al. 1989). Another problem is that different kinds of stimuli and paradigms have been used to test the effects of a particular lesion, mainly because the investigators did not know what to look for. Inspired by the present results we related effects of lesions, reported in the literature, to the used visual stimuli. Wurtz and Goldberg (1972) found that monkeys with collicular lesions made saccades with longer latency and with less accuracy. Butter et al. (1978) reported that such animals had persistent problems in localizing brief flashes of light which were presented in the visual periphery. Comparable difficulties were observed when animals had to make eye movements to such peripheral targets (Kurtz and Butter 1980). Monkeys with collicular lesions were less easily distracted by irrelevant peripheral visual stimuli (Albano et al. 1982). Such monkeys showed a "sensory neglect" of new visual and auditory stimuli (Kurtz and Butter et al. 1980; Schiller et al. 1980; Albano et al. 1982; Keating et al. 1986). Moreover the superior colliculus seemed to be essential for the generation of short-latency, so-called express saccades (Schiller et al. 1987). All these results have in common that lesions in the superior colliculus seem to affect appropriate saccadic responses to new, unpredictable, peripheral stimuli. Lesions in the frontal eye fields seem to affect the generation of saccades to self-selected targets and the suppression of saccades to unwanted stimuli. Hoyt and Daroff (1971) found that patients with lesions in the frontal eye fields had difficulty in looking voluntarily. Guitton et al. (1982) observed that monkeys had difficulty in suppression of saccades to contralateral stimuli. Bruce and Bordon (1986) showed that although normal monkeys could make predictive saccades to regularly appearing targets, monkeys with bilateral frontal eye field lesions could not do so.

Taken together, the effects of collicular and frontal eye field lesions suggest that I-saccades may be generated via the frontal eye field pathways, whereas the collicular pathways seem to be more important in the control of E-saccades. The presence of such a functional organization could be at the basis of several behavioral findings, including the presently found different adaptations of I-saccades and E-saccades.

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