Specificity of Saccadic Adaptation in Three-dimensional Space

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The saccadic system is known to exhibit a considerable degree of short-term plasticity. Earlier studies have shown that saccadic adaptation, rather than being a global process affecting all saccades equally, has a certain degree of spatial resolution. Its localized nature has become apparent from studies in the frontal plane which have shown that short-term saccadic adaptation, induced along a given meridian, transfers to only a limited range of neighbouring directions. Considering that most natural gaze shifts also have a depth component, we investigated whether the directional specificity of the saccadic adaptive system can be generalized to three-dimensional (3-D) space.

Binocular eye movements were recorded in seven subjects while they made saccades to visual stimuli in the horizontal plane of regard. Experiments began by recording baseline saccades, all starting from the same fixation point to either a farther target (far saccades) or an equally eccentric nearer target (near saccades). Next, by displacing the target intra-saccadically in opposite directions in alternating far and near trials, we attempted to simultaneously reduce the gain of the far saccades while increasing the gain of the near saccades. These experiments, aimed at eliciting a state of differential gain, were specifically designed to adapt only the saccadic response, since targets were shifted along corresponding iso-vergence circles. To investigate the effect of varying the radial direction difference, similar differential gain adaptation experiments were conducted in the frontal plane for saccades along two different meridians.

Our results show that when the saccadic system is pressured, it is capable of adopting different gains simultaneously for equal-direction saccades to different depth planes. Similarly, opposite gain adaptation can also be achieved in the frontal plane, but only if radial saccade directions are sufficiently separated. The fact that short-term saccadic adaptation can be shown to be directionally specific in two perpendicular planes suggests that the adaptation process is restricted to a limited volume of 3-D oculomotor space. © 1997 Elsevier Science Ltd. All rights reserved.

INTRODUCTION

In this paper we investigate the specificity of saccadic adaptive modifications during rapid refixations in direction and depth. Earlier saccadic plasticity studies have shown that saccadic adaptation has a pronounced directional specificity in the frontal plane. Our experiments explored whether it is possible to extend this concept by giving equal consideration to specificity properties of saccades in the depth dimension. A brief review of the extensive literature on saccade vergence interactions and saccadic plasticity, given below, aims to provide an appropriate context for this study.

Earlier studies on refixations in direction and depth

Traditional thinking on oculomotor system control, motivated by Hering's principle of equal innervation, has envisaged a clear distinction between saccadic and vergence components during natural gaze shifts (see Yarbus, 1967). Refixations were thought to involve a linear addition of a rapid conjugate contribution and a slow disjunctive contribution, but recent evidence indicates that this classical view is oversimplified and that both subsystems are coupled. This is reflected by the fact that the speed of refixation of the binocular fixation point along the depth axis is substantially enhanced in the presence of a simultaneous saccade. These findings have focused attention on the dynamic properties and neural control of these combined responses (Enright, 1984, 1986; Erkelens et al., 1989b; Maxwell & King, 1992; Zee et al., 1992; Oohira, 1993; Collewijn et al., 1995).

In attempts to understand the underlying neural mechanisms, these findings have generally been interpreted in two different ways. One view suggests that the saccadic system is capable of generating unequal saccades in the two eyes and, therefore, cannot be...
regarded as a strictly conjugate system (Erkelens et al., 1989b). Alternatively, it has been proposed that the observed phenomena are the result of a nonlinear interaction, whereby saccades facilitate the vergence system (Enright, 1986; Maxwell & King, 1992; Zee et al., 1992). This latter interpretation seems more compatible with current knowledge regarding the neurophysiological basis of binocular eye movements (for review, see Mays & Gamlin, 1995). In the model of Zee et al. (1992), where this view is adopted, saccadic programming is portrayed as being unaffected by depth information and independent of any required vergence movements. A recent study on saccade–vergence dynamics has, however, provided quantitative evidence that the saccadic system is slowed down when a substantial vergence component is involved in the gaze shift (Collewijn et al., 1995), indicating that interactions between the subsystems are reciprocal. Our present study is relevant for a further understanding of this issue. Adaptation experiments were undertaken to specifically investigate the possibility of whether the saccadic system is capable of having different gains for different refixation directions along the depth axis.

Earlier studies on saccadic plasticity

Owing to disease, injury, growth and ageing, continuous adjustments need to be made by the oculomotor control system to ensure that eye movements remain normometric. Earlier studies of the adaptive capabilities of various oculomotor subsystems, especially those of the saccadic and the vestibulo-ocular reflex (VOR) have firmly established that the primate saccadic system can exhibit a considerable degree of plasticity. Any recurrent retinal error, occurring in the wake of a particular dysmetric saccade, is interpreted by the adaptive mechanism as an internal miscalibration. Short-term saccadic gain adaptation can, therefore, be obtained under laboratory conditions by consistently inducing such a visual error signal. This has been commonly done with the use of an intra-saccadic target shift during visually guided saccades (McLaughlin, 1967; Miller et al., 1981; Wolf et al., 1984; Deubel et al., 1986; Albano & King, 1989; Erkelens & Hulleman, 1993; Frens & Van Opstal, 1994). This systematic target perturbation causes the saccadic system to rapidly adjust its amplitude. Longer-term saccadic gain adaptation can be observed when a motor system deficit occurs in the form of a natural muscular paresis (Komerrell et al., 1976; Abel et al., 1978) or a surgically induced muscle weakness (Optican & Robinson, 1980).

Saccadic adaptation specificity

Earlier studies, using the intra-saccadic shift paradigm, have shown that saccadic adaptation is not a global process affecting all saccade vectors equally. Miller et al. (1981) were the first to show that amplitude adaptation of horizontal saccades in one direction does not transfer to movements in the opposite direction. Later work by Deubel (1987) showed that the directional tuning of saccadic adaptation is in fact limited to an approximately 30 deg wide sector around the adapted direction, where the adaptation effect decreases sharply with increasing angular direction from the adapted direction. These plasticity studies have been largely limited to a two-dimensional subspace: the fronto-parallel plane. Since most natural gaze shifts tend to incorporate a depth component we have investigated to what extent properties of the saccadic adaptive system, derived from studies in the frontal plane, can be generalized to three-dimensional (3-D) space. In this study, we will not consider the amplitude specificity of saccadic adaptation which was shown by Frens & Van Opstal (1994) in a frontal plane study.

While there is a considerable literature on the plasticity of binocular eye movements, most of these studies have employed different techniques and were directed at different questions than our study. By using anisotropic spectacles (Erkelens et al., 1989a; Lemij & Collewijn, 1991a,b, 1992; Oohira et al., 1991) or by presenting aniseikonic dichoptic stimulus patterns (Bush et al., 1994; Van der Steen & Bruno, 1995), the oculomotor system has been brought into a situation requiring disjunctive saccades for fast binocular foveation. A recent study by Albano & Marrero (1995) did use intra-saccadic target displacement, as employed in our paradigms, but was designed to study disconjugate training. None of these studies has, however, specifically considered the question regarding the depth-dependency of short-term saccadic adaptation.

In the present paper we studied the directional specificity of saccadic adaptation in the horizontal plane of regard and in the frontal plane. The latter experiments were primarily used as control studies. We varied saccadic depth direction by presenting equally eccentric real targets, in alternate trials, at two different depths, relative to the same fixation point. After collecting baseline responses we attempted to evoke a state of differential gain adaptation, by means of opposite intra-saccadic target displacements along the corresponding iso-vergence circles. Accordingly, our experiments were designed to adapt only the saccadic response, without requiring a change in the degree of saccadic conjugacy.

METHODS

Eye movement recording

The two-dimensional scleral magnetic induction search coil technique (Robinson, 1963; Collewijn et al., 1975), with the subject placed in the centre of two perpendicular rapidly alternating magnetic fields (horizontal 30 kHz; vertical 50 kHz), was used to record the position of both eyes. For experiments done solely in the fronto-parallel plane (see below), however, only one eye was measured. The coil signals were amplified and demodulated in lock-in amplifiers (PAR 128A) using phase-sensitive detection techniques, low-pass filtered (−3 dB at 200 Hz; 4th order Bessel filter), and sampled at a rate of 500 Hz with a 12-bit resolution. Eye movement
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FIGURE 1. (A) Top view of LED array used for adaptation experiments in horizontal plane of regard (not to scale). LEDs were located at intersection of iso-vergence (2, 5, 10 deg) and iso-version (0, 7.5, 15, 22.5, 30 deg) lines. FIX is fixation LED requiring a vergence angle of 5 deg and a version angle of 10 deg to the right of straight-ahead; T1 and T2 indicate both near targets (vergence angle 20 deg) and far targets (vergence angle 2 deg), respectively, presented during experimental paradigms. T1 always had an eccentricity 15 deg left of straight-ahead. The intrasaccadic target displacement to T2 was always 30% of the required primary saccadic amplitude, and opposite in direction for far and near saccades. T2 has the same target vergence as T1. Arrows depict imaginary eye movements to the far and near targets, together with corrections in response to the intra-saccadic target displacement. (B) Same LED targets in oculomotor space coordinates. Vergence is defined as the angle between the lines of sight of the two eyes. Version angle is defined as the direction of the cyclopean eye. Note that each pair of targets (T1 and T2) had the same target vergence angle. Both far and near T1 targets had the same eccentricity. The eye movement trajectories are the same as in (A).

data were stored on the disk of a SUN-3/140 workstation and analysed off-line.

Subjects
Experiments were carried out with one female and six male volunteers (BW, JG, JVG, KH, HM, SS and VC). Their ages ranged from 22 to 52 yr, and none had any known neurological or oculomotor disorders. Three subjects (JG, HM and VC) wore corrective lenses during the experiment. Two subjects (JVG and VC) were familiar with the purpose of this study while the other five subjects were kept naive. Before application of the coils, the surface of the eye was anaesthetized with two drops of a local anaesthetic (0.4% Novesine). Subjects were seated in a comfortable upright position while their heads were stabilized using a dental impression biteboard. Except during the calibration session, all stimuli were viewed binocularly. Experimental sessions generally lasted up to 50 min. Subjects were instructed not to blink during trials, to fixate targets accurately and quickly, and to refrain from making anticipatory responses.

Calibration and computation of binocular signals
During calibration the subject was instructed to fixate light-emitting diodes (LEDs) of equal intensity, on a fronto-parallel plane, placed at a distance of 125 cm from the subject. The centre LED was aligned with the eye that was being calibrated, while the other eye was kept covered (interocular distance was taken to be 6.5 cm). Subjects were instructed to make visually elicited saccades from the centre LED to one of the peripheral LEDs and to fixate each target for at least 1.5 sec. Nine horizontal and nine vertical LEDs were positioned at different angles from the straight-ahead direction, having a maximum range of ±20 deg. The same procedure was then repeated for the other eye. Both sets of recorded raw data were subjected to a sinusoidal fit procedure to calibrate these signals. By using the best-fit parameters for each eye coil we converted the raw experimental data into calibrated eye position signals. Subsequently, each pair of left and right eye signals, i.e., each binocular point of fixation, was expressed by means of a version angle (direction of the cyclopean eye) and a vergence angle (angle between the lines of sight of the two eyes). The former was computed as the average of both eye positions; the latter was taken to be the difference between left and right horizontal eye positions.

Basic design of the adaptation experiments
A number of different adaptation paradigms, each
was the radial separation between up and down targets. For all angular separations, a 22.5 deg primary saccade was required (from FIX to T1) followed by a 7.5 deg secondary saccade (from T1 to T2). Targets were presented during experimental paradigms. A goal-directed saccade was detected, the primary target position with a target vergence angle of 2 deg. When the stimulus presentation was controlled with a PC, the intra-saccadic target displacement brought the primary target to a nearby target. In the latter type of trial, the primary target was extinguished and a new secondary target appeared (either 10, 50 or 90 deg). It is important to note that each of the respective secondary saccades were detected using a velocity criterion of 7.5 deg/sec to trigger the target displacement. Each adaptation sequence was 30 trials long and was repeated several times.

3. Post-adaptation phase. The final test phase used the same control stimuli as during pre-adaptation and was intended to study readaptation.

Opposite amplitude-adaptation in saccades to different depths in the horizontal plane of regard

After the calibration, a flat board, containing a number of LEDs, was mounted horizontally in front of the subject. LEDs were located along circles of isovergence (ranging from 2 to 10 deg) and along lines of equivergence (ranging from 0 to 30 deg) leftwards and rightwards. The eyes were about 3 cm above the LED array, ensuring that all targets could be seen clearly with both eyes. The fact that the eyes did not lie in exactly the same plane as the LED array merits further mention here since this introduced a slight vertical component in our experimental set-up. Near eccentric targets differed by up to 4.5 deg, in the vertical component of the eye position signal, with the far eccentric targets. Due to this fact, the horizontal plane experiments were also found to have a small radial direction difference (ΔR ≤ 10 deg). As the results from the frontal plane experiments will show, this direction difference is considered too small to account for any of our findings (see Discussion). Note also that, in our experiments, real targets were used ensuring that many depth cues were present (e.g. disparity, accommodation, size, intensity).

Alternating paradigm. This paradigm was used to induce opposite gain adaptation in almost equal radial direction saccades at different depths (ΔD). The stimulus sequence was designed to elicit gain-shortening in diverging saccades and gain-lengthening in converging saccades simultaneously [Fig. 1(A)]. Each trial began with the fixation of a LED with an eccentricity of 10 deg rightwards, of the straight-ahead position, and a target vergence angle of 5 deg, thereby ensuring that all primary saccades had the same offset position. Gain-shortening trials required a saccade (with an amplitude of 25 deg) to a far-off target, 15 deg to the left of the straight-ahead position with a target vergence angle of 2 deg. When the goal-directed saccade was detected, the primary target was extinguished and a new secondary target appeared 7.5 deg leftwards of the straight-ahead with the same target vergence, i.e., along the same iso-vergence circle but at a smaller eccentricity. These gain-shortening trials to a far-away target were alternated with gain-lengthening trials to a nearby target. In the latter type of trial, the primary target was presented at a target vergence of 10 deg, but at the same eccentricity as during the gain-shortening trials (15 deg leftwards). In the gain-lengthening trials, the intra-saccadic target displacement brought the final target position to a larger leftwards eccentricity of 22.5 deg along the same iso-vergence circle. In other words, the primary saccades in both types of trials were, initially, virtually identical, and only the accompanying vergence angle change was opposite (ΔD = 8 deg). It is important to note that each of the respective secondary...
targets required no further change in vergence angle [Fig. 1(B)]. The intra-saccadic target shift amplitude was always 30% of the amplitude of the saccade required towards the initial target. The pre-adaptation phase elicited control responses to both primary (50 trials) and to both secondary targets (20 trials). The post-adaptation phase consisted only of saccadic responses to both primary targets.

**Single paradigm.** This paradigm was used to investigate to what extent a previously induced gain adaptation effect, in saccades to solely one particular depth plane, would show transfer to another non-adapted depth plane. Furthermore, we wanted to see whether this intended singular adaptation effect could be maintained and even increased further when the experiment continued with an alternating paradigm. Thus, gain-adaptation was initially obtained using either only the gain-reduction or only the gain-lengthening paradigm to the same respective targets as shown in Fig. 1(A). When this modification became clearly evident the alternating paradigm was implemented in a similar manner as outlined previously.

**Opposite amplitude-adaptation of saccades in the frontal plane**

In an extension of the Deubel (1987) study, we implemented the alternating paradigm in the fronto-parallel plane for three different sets of angular separations (10, 50, 90 deg) while the vergence angle was kept constant at 2 deg. The radial separation (ΔR) was symmetrical around the left horizontal axis (Fig. 2). The fixation LED was positioned on the horizontal axis (at eye level) and had an eccentricity of 15 deg rightwards from straight-ahead. Both primary saccade targets were located (dependent on the angular separation) along an iso-eccentricity circle of 22.5 deg, taken with respect to the fixation point. During intra-saccadic displacement the target was moved by 7.5 deg (1/3 of the primary saccadic amplitude) along the same meridian. Gain-lengthening was required along the upward-pointing meridian and gain-reduction along the downward-pointing meridian. Eye position recording was monocular (though vision remained binocular). All three phases of this experiment corresponded in length and format with the alternating paradigm done in the horizontal plane of regard.

**Data analysis**

The velocity of the eye movements was calculated by differentiating the position signals in overlapping steps of 5 msec. After filtering with a 33 points, 75 Hz Rabiner.

**FIGURE 3.** Binocular coordinate signals computed for a typical gain-shortening trial to a far target and gain-lengthening trial to a near target i.e., prior to any adaptation effect, in the horizontal plane at an early stage in the adaptation experiment. A positive direction angle denotes a rightward fixation. The horizontal version (A) and horizontal vergence (B) signals of the gain-shortening trial to a far target are shown in the left-hand column. The horizontal version (C) and horizontal vergence (D) signals of the gain-lengthening trial to a near target are depicted on the right. Markers (dotted lines) were used to detect events during each trial. Marker 1 (at 150 msec) indicates the point of fixation. Markers 2 and 3 were used to denote onset and offset of the primary saccade. Marker 4 (at 1250 msec) detected the end fixation point. Note the fast saccadic response and the slower vergence response. The vergence signal was composed of a fast intra-saccadic phase and a slower post-saccadic phase. Although the version and vergence signals generally had similar latencies, the vergence response, in a number of trials, was seen to precede the conjugate response. For the near saccade the vergence signal shifted slowly prior to saccadic onset. Transient divergence effects are noticeable in the vergence signals. Subject BW.
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Digital filter, the resulting velocity signal (30 deg/sec), which was further checked by visual inspection, was used for automatic saccade detection. In the case of the horizontal plane experiments only the horizontal eye position signal was used for saccade detection. For the frontal-plane experiments both horizontal and vertical eye position signals were used to detect saccades, based on their vectorial amplitude. Incorrect trials were excluded from the analysis. This occurred in the case of a wrong fixation at the start of a trial or a predictive response, i.e., having a latency less than 75 msec.

RESULTS

Alternating paradigm in the horizontal plane

Our experiments were designed to investigate the hypothesis that the directional specificity of saccades in the frontal plane might actually be the expression of a more general 3-D property. The results show that frontal-plane sectors could conceivably be perpendicular cross-sections of more extensive adaptation fields in 3-D space. We used the alternating paradigm in the horizontal plane of regard to simultaneously induce saccadic gain-shortening to far targets and saccadic gain-lengthening to near targets.

Figure 3 shows two illustrative trials, from a horizontal plane experiment, that depict the version (conjugate) and vergence (disconjugate) signals that have been calculated from horizontal eye position signals. The gain-shortening trial can be seen in Figs 3(A) and (B) while the gain-lengthening trial is shown in Figs 3(C) and (D). Although our main interest in the analysis concerns the primary saccade, we divided each binocular eye movement response into a number of well-defined stages, as denoted by the vertical lines (numbered 1 through 4). The first characteristic in the eye movement response (150 msec after recording began) was the binocular point of fixation (marker 1). The fixation of the subjects was generally accurate to within 0.5 deg of vergence but in cases where there was considerable discrepancy (>5 deg version; >1 deg vergence) the trial was rejected. The next events included the onset (marker 2) and the offset (marker 3) of the first saccade of the horizontal version signal. We also placed a marker at a time late in the trial (at 1250 msec) to detect the accuracy of final target fixation (marker 4).

It can be seen that a considerable portion of the total vergence response occurs during the first saccade, although the vergence movement typically continued towards its completion long after the first saccade had ended [Figs 3(B) and (D)]. Unlike the fast saccadic responses, the vergence signal is observed to be composed of a fast intra-saccadic and a slow post-saccadic phase. The vergence response is often seen to start somewhat earlier than the conjugate response. Additionally, during the saccades small transients in the vergence signal, known as transient divergence, are often noticeable.

A complementary and, perhaps, more revealing way of
looking at the same response is shown in Fig. 4 where its
binocular coordinates in oculomotor space (horizontal
vergence vs horizontal version) can be seen. The

trajectories of the eye movements, to the far and near
targets in the horizontal plane, correspond to the trials
depicted in Figs 3(A) and (B), and Figs 3(C) and (D),

FIGURE 5. Progress of gain-shortening in far saccades during the alternating adaptation paradigm. The version signal is plotted
in the upper panels and vergence signal in the lower panels. The first five trials of the first adaptation sequence (A, B) and the
first five trials of the last adaptation sequence (C, D) are shown. There were about 75 trials between these two sequences. The
transient divergence peaks are prominent during the correction saccades (B). As the subject becomes adapted and the correction
saccades gradually disappear these effects also became less noticeable (D). Time zero corresponds to the onset of recording
which was 50 msec before fixation LED offset. Subject BW.

FIGURE 6. Progress of the gain-lengthening adaptation during the same experiment as shown in Fig. 5. Note that the version
and vergence axes here are different from those in Fig. 5.
An example of the change in the version and vergence components during the course of the alternating adaptation paradigm is plotted in Fig. 5. The left panels [Figs. 5(A) and (B)] show the first five gain-shortening trials from the first adaptation sequence. The right panels [Figs. 5(C) and (D)] show the first five trials from the final adaptation sequence for the same experiment. Upon visual inspection it is clear that there was a marked change in the primary saccadic amplitude over time but, as might be expected, there appeared to be no consistent change in the vergence component. The same trend was also seen for the gain-lengthening stimulus as shown in a similar plot in Fig. 6. Throughout the paradigm the subject continued to make fast saccades with short latencies.

The time-course of the primary saccadic amplitude, during the alternating paradigm, is shown in Fig. 7, which is subdivided into pre-adaptation, adaptation and post-adaptation phases. The changes in the amplitudes of far and near-directed saccades are depicted by different symbols. The amplitude expected if adaptation had been complete, based on pre-adaptation control saccades to \( T_2 \), is shown by means of two horizontal lines. Not surprisingly, the saccadic amplitudes for both near and far targets were almost identical prior to adaptation. When the adaptation phase began, saccadic gain-reduction and saccadic gain-increase effects manifested themselves gradually. Both sets of gain changes appeared to reach similar degrees of completion although maximum lengthening and reduction was not obtained in the limited period of the experiment. The post-adaptation phase showed distinct readaptation phases for both sets of stimuli. This was noteworthy, since the shortened saccades to the far targets were readapted first separately. During this process the saccadic gain to the near target appeared to virtually retain its adapted state.

Figure 8 shows the degree of opposite gain adaptation, in the far and near saccades, that was obtained in the alternating paradigm for each subject. Despite the idiosyncratic variation in the degrees of completion of adaptation (increase and decrease), it is clear that differential gain adaptation in the horizontal plane was present for each subject. The amplitudes of the saccades during the final adaptation session, in this figure, were compared to the corresponding pre-adaptation controls (TI) and presented as gain changes. Thus, the gain-shortened far saccades have a value less than 1, while the near gain-lengthened saccades have a gain larger than 1. What is interesting to note is the total gain separation that is elicited. Subjects BW (see Fig. 7), JG and JVG have a marked gain-separation, while VC shows this to a lesser degree. Subject KH maintained equal amplitude saccades respectively. The pre-saccadic vergence to the near target is clearly evident.

FIGURE 7. Change in primary saccade amplitude during the alternating adaptation paradigm. The dotted lines demarcate the pre-adaptation test phase, the adaptation phase, and the post-adaptation test phase (from left to right). The dots depict amplitudes of far saccades during gain-shortening and the crosses depict amplitudes of near saccades during gain-lengthening. The horizontal lines at the top and bottom denote the maximum amount of adaptation to be expected (measured during controls). Pre-adaptation amplitudes were observed to be similar. Note that the occurrence of differential gain adaptation (for opposite depth directions) was gradual and clear-cut. Re-adaptation also occurred gradually and was independent for both saccade directions. Subject BW.
DEPTH-DEPENDENCY OF SHORT-TERM SACCADIC ADAPTATION

FIGURE 8. Bar graph showing degree of differential gain adaptation for all subjects during the alternating paradigm in the horizontal plane. The black bars denote the gain of 15 near saccades after the gain-lengthening training, in comparison with the controls (50 pre-adaptation saccades to T1) which were normalized to have unity gains. Similarly, the white bars show the gain changes in far saccades after simultaneous gain-shortening adaptation. Note that the changes were always in the intended direction but that there were considerable inter-subject differences in the size and the degree of symmetry of these effects. Also note that, as previously reported in the literature, gain-increase appeared to be less complete than gain-decrease. Nevertheless, gain separation (the total gain difference between the two sets of differentially adapted saccades) was significant in all subjects (P < 0.05); ns: not significant.

to the near target throughout the experiment (i.e., no significant gain-lengthening) but did show substantial gain-reduction for the far target displacement. Subject SS was the least adapted of all the subjects, but even in this case gain separation (differential adaptation) was significant.

As shown previously in Fig. 3, a large part of the vergence response occurred within the primary saccade. Although our paradigm was designed to adapt only the saccadic component of the response, it seems relevant to investigate to what extent the vergence response, during the saccade, actually did remain stable. Although the vergence during the initial fixation was reproducible from trial to trial, as stated earlier, however, due to presaccadic vergence, the vergence value at saccadic onset (marker 2) was less consistent. We therefore took the change in vergence between initial fixation (marker 1) and saccadic offset (marker 3) as a measure of the vergence response during the primary refixation. It became apparent that there was quite some scatter in the vergence response, especially in the near refixations. The intrasaccadic vergence, to the far targets, diminished slightly over the course of the adaptation phase. Since this effect was similar for control responses to target T2, we judged it to be a direct consequence of the saccade becoming smaller in amplitude rather than an adaptation effect. We observed different effects for near-directed refixations. Both sets of controls showed fluctuations and exhibited approximately the same intrasaccadic vergence responses. As the adaptation sequence began, the vergence fell to a lower value than that observed during the controls and remained at that level during adaptation. This may have been due to the fact that the displaced near target was quite eccentric. These issues, however, should not detract from the main point that the vergence system did not appear to be modified in any way during the differential saccadic gain adaptation.

Single paradigm in the horizontal plane

In the single paradigm in the horizontal plane we used a classical gain adaptation paradigm (either shortening or lengthening) to induce singular adaptation. Once this was achieved to a considerable extent, the alternating paradigm began.

Accordingly, the data representation is divided into a pre-adaptation test phase, a single gain adaptation phase, an alternating phase and a readaptation phase. Figure 9(A) shows a temporal profile of gain-shortening of saccades to the far target. After obtaining fairly extensive gain-reduction, the alternating paradigm was applied. Several phenomena can be noticed. Firstly, far saccades had indeed been shortened, but interestingly, this adaptation did not transfer to near saccades. Secondly, starting the alternating paradigm had the dual effect of
FIGURE 9. (A) The time-course of the primary saccadic amplitude response during the single paradigm. Far saccades are denoted by dots, while near saccades are represented by crosses. Gain reduction in far saccades during singular adaptation was evident. Note, however, how the reduction decreased at the onset of the alternating paradigm. Note, also, the aberrant data point (+) at the beginning of the gain increase stimulus. There was some gain increase in near saccades during the alternating paradigm. Readaptation was gradual. Subject SS. (B) A similar response profile as shown in (A), except that now, initially, only gain-lengthening in near saccades (crosses) was induced. Gain-reduction occurred after onset of the alternating paradigm. Although there was a marked scatter occurring in the near saccade response, differential gain adaptation was evident. Both saccade directions readapted. Note the aberrant saccade amplitude at the onset of the gain shortening stimulus phase. Same subject as in (A).

temporarily reducing the degree of adaptation (gain-shortening) in the far saccades and inducing a limited opposite gain change in the near saccades. Readaptation, tested only for far saccades, was clearly evident. A puzzling response, seen in two out of four subjects tested in this paradigm, was that the first near saccade
TABLE 1. Gain values to show the change in saccadic gain adaptation during the mixed (single and alternating) paradigm, in the horizontal plane

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<td>1.00 ± 0.06</td>
<td>1.00 ± 0.06</td>
<td>0.72 ± 0.07</td>
<td>—</td>
</tr>
</tbody>
</table>

Pre-adaptation control saccades (50 trials) to both far (gain-decrease) and near (gain-increase) targets [see Fig. 9(A) and (B), respectively] were normalized to unity gain and all later changes in saccadic amplitude (15 trials) were compared to these controls. Singular adaptation was elicited either to a far target or to a near target. The gain-increase, to a near target, was less complete than the gain-decrease to a far target. The main point is that there appeared to be no evident transfer of singular gain adaptation to non-adapted saccades, in the opposite depth plane, upon onset of the alternating paradigm.

Table 1 shows the results for different subjects in the single paradigm. As can be seen, it was possible to specifically adapt far saccade gain without major transfer to near saccades and vice versa. Subsequent application of the alternating paradigm ultimately led to further differential gain adaptation. Note, however, that after the single gain adaptation phase in the single paradigm, all subjects lost part of the evoked modification effect at the beginning of the ensuing alternating paradigm. However, there was no apparent transfer of gain adaptation effects to oppositely directed saccades.

Alternating paradigm in the frontal plane

Deubel (1987) proposed the notion of adaptation sectors in the frontal plane. From this hypothesis one would expect that differential gain adaptation should only be possible for an angular separation (ΔR) of targets beyond the proposed sector. Since Deubel suggested that the sector width was in the order of 30 deg, we attempted to test this using the alternating paradigm for smaller and larger ΔR values (10, 50 and 90 deg). The reason for taking such a small radial separation (10 deg) was for the sake of comparison with the horizontal plane experiments. We have already mentioned (see Methods) that a slight vertical component had been introduced into our depth plane experimental set-up, leading to a radial angle up to 10 deg. To rule out any possibility of the differential gain results being caused by this factor we also tested this ΔR value in the alternating paradigm in the frontal plane experiments.

The results supported the expectation that opposite gain adaptation is not possible for relatively small radial separations. From Fig. 10(A) it is clear that differential gain separation did not occur for a ΔR of 10 deg, since it appeared that both the upward and downward saccades underwent gain-shortening to a degree. Similar to the two other subjects involved in this paradigm, this subject failed to exhibit differential gain adaptation to any degree. This is in striking contrast to the horizontal plane results in Fig. 10(B) for the same subject. In this case, along with the ever present ΔR value (≤ 10 deg), there is an added depth separation (ΔD = 8 deg) which enabled the subject to obtain a state of differential gain without difficulty. Since we used real targets, various depth cues, including vergence, were available.

The same paradigm implemented for an angular separation of 50 deg, in the frontal plane, produced results that corresponded to those seen earlier for the horizontal plane (Fig. 11). This indicated that differential gain separation was indeed possible for a larger sector width. We found that differential gain adaptation was even more pronounced for a ΔR of 90 deg. All three subjects tested in the frontal plane showed similar trends and consistent results for all three angular separations involved.

had a similar amplitude to the gain-shortened far saccades. This response may reflect anticipation but this does not explain why its vergence component was, nevertheless, directed correctly (i.e., nearby rather than faraway).

A similar profile is apparent for the same subject in Fig. 9(B), where gain-lengthening was initially induced to a near target. Although the gain-increase to the near targets was maintained when the alternating paradigm started, a great deal more scatter became apparent. Similar to the experiment already shown in Fig. 9(A), opposite gain adaptation (reduction) to the far targets started to take place. Re-adaptation occurred separately for both sets of targets.

It is noteworthy that the same subject, shown above in the single paradigm, had a remarkably poor gain separation in the alternating paradigm. Thus, in this subject, the opposite gain adaptation, starting from an unmodified state, was hardly convincing, but much more obvious when already adapted in one direction (i.e., using the single paradigm). The short-term gain-adaptation effects were more complete for the single paradigm than for the alternating paradigm.

TABLE 1. Gain values to show the change in saccadic gain adaptation during the mixed (single and alternating) paradigm, in the horizontal plane

<table>
<thead>
<tr>
<th>Subj.</th>
<th>Expt.</th>
<th>Initial gains</th>
<th>Final gains</th>
<th>Initial gains</th>
<th>Final gains</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Far</td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
</tr>
<tr>
<td>VC</td>
<td>far (I)</td>
<td>1.00 ± 0.06</td>
<td>1.00 ± 0.07</td>
<td>0.74 ± 0.06</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>near (I)</td>
<td>1.00 ± 0.06</td>
<td>1.00 ± 0.06</td>
<td>—</td>
<td>1.14 ± 0.07</td>
</tr>
<tr>
<td>JG</td>
<td>far (I)</td>
<td>1.00 ± 0.05</td>
<td>1.00 ± 0.06</td>
<td>0.76 ± 0.06</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>near (I)</td>
<td>1.00 ± 0.07</td>
<td>1.00 ± 0.06</td>
<td>—</td>
<td>1.19 ± 0.09</td>
</tr>
<tr>
<td>SS</td>
<td>far (I)</td>
<td>1.00 ± 0.06</td>
<td>1.00 ± 0.06</td>
<td>0.78 ± 0.08</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>near (I)</td>
<td>1.00 ± 0.05</td>
<td>1.00 ± 0.06</td>
<td>—</td>
<td>1.14 ± 0.06</td>
</tr>
<tr>
<td>JVG</td>
<td>far (I)</td>
<td>1.00 ± 0.06</td>
<td>1.00 ± 0.06</td>
<td>0.72 ± 0.07</td>
<td>—</td>
</tr>
</tbody>
</table>

Pre-adaptation control saccades (50 trials) to both far (gain-decrease) and near (gain-increase) targets [see Fig. 9(A) and (B), respectively] were normalized to unity gain and all later changes in saccadic amplitude (15 trials) were compared to these controls. Singular adaptation was elicited either to a far target or to a near target. The gain-increase, to a near target, was less complete than the gain-decrease to a far target. The main point is that there appeared to be no evident transfer of singular gain adaptation to non-adapted saccades, in the opposite depth plane, upon onset of the alternating paradigm.
FIGURE 10. (A) Primary saccade amplitude response for the alternating paradigm in the frontal plane. The angular separation \( \Delta R \) here was 10 deg. Note how both sets of saccades were adapted in the same direction (shortened) even though the experiment was designed to achieve opposite adaptation effects in upward and downward saccades. Thus, for this small angular separation, differential gain adaptation appeared to be impossible. Subject VC. (B) Primary saccadic amplitude response for the alternating paradigm in the horizontal plane, for the same subject as in (A). This experimental set-up has a similar \( \Delta R \) value but has an added depth separation \( \Delta D \). While there is no differential gain adaptation in the frontal plane for this radial separation alone [see (A)], when a large depth component is added opposite gain adaptation is shown to be possible.

DISCUSSION

Directional specificity of saccadic adaptation in the 3-D oculomotor workspace

We undertook this study with the aim of investigating the directional specificity of saccadic adaptation in 3-D space. Our approach was to elicit binocular saccades to equal-eccentricity targets which differed either in the depth direction, or in the radial direction, of the required refixation. It must be noted that the present study was not
Experiments in the horizontal plane. The main question here was whether the existence of adaptation sectors in the frontal plane could be the reflection of a more general 3-D property. Indeed our results suggest, to the best of our knowledge for the first time, that the frontal plane adaptation sectors may form the cross-sections of adaptation fields which occupy a limited volume of 3-D space. Since we had to restrict ourselves to an investigation of only a few saccade pairs in each plane of regard, the shape of these fields remains to be determined by a considerable research effort in 3-D space, in which the limits of independent adaptation are the angular separation in 3-D space, rather than just $\Delta R$, is the determining variable. So, just as the amount of radial separation ($\Delta R$) determines the degree of differential adaptation possible in the frontal plane, we propose that the depth direction separation ($\Delta D$) is the critical variable in the depth dimension. It must also be noted that, since real targets were used in these experiments, subjects had
designed to achieve depth (vergence) adaptation. Rather, the experimental question being posed was whether opposite saccadic gain changes could be achieved in either condition. Intra-saccadic target shifts were specifically designed to create an error signal for the saccadic system so that there was no compelling a priori reason to expect considerable changes in the vergence components of the binocular gaze shifts. Indeed, only small effects were found and these will not concern us further here.

Experiments in the frontal plane. A previous study in the frontal plane has already shown that saccadic adaptation affects neighbouring saccades within a radially directed sector, around the adapted saccade vector, having a width of approximately 30 deg (Deubel, 1987). Our frontal plane control experiments confirm that opposite gain adaptation could be achieved simultaneously if the two saccade directions had a sufficiently large radial direction difference ($\Delta R$). In our experiments a $\Delta R$ separation of 50 deg was sufficient to allow differential adaptation in all three subjects investigated. Also, all subjects showed a greater degree of gain separation as $\Delta R$ was increased from 50 to 90 deg. Our interpretation is that opposite gain adaptation effects may be learned in parallel, without significant mutual interference, as long as the two movement vectors are sufficiently separated. The interference becomes obvious once two vectors in the same depth plane ($\Delta D = 0$) have a small $\Delta R$ value. Deubel (1987) came to the same picture based on somewhat different experiments. However, as seen in the horizontal plane experiments, as soon as a significant $\Delta D$ value is present, the capability for differential gain adaptation resurfaces.

FIGURE 11. A similar plot as in Fig. 10(A) for an angular separation of 50 deg in the frontal plane showing differential adaptation. Subject VC.
access to a variety of depth cues so that vergence was probably not solely responsible for detecting depth direction.

It is clear that the traditional concept of viewing the control of binocular refixations as being due to an independent saccadic system, exclusively concerned with radial corrections, and an independent vergence system, specialized in depth correction, is outdated. In fact our results show that the saccadic system can issue different commands to targets which are aligned for the cyclopean eye, but are located at different depths. Similar ideas have been suggested previously on the basis of studies on disconjugate saccades (Erkelens et al., 1989b). While the proposition that the saccadic system generates unequal saccades in the two eyes cannot be discounted, an alternative explanation of these disconjugate responses has been that a fast vergence contribution combines with a conjugate saccade command. Our experiments, which also yielded disconjugate rapid eye movements, cannot decide this issue but they provide strong evidence that the adaptive modifications in the depth plane experiments must have been saccadic in nature. This interpretation is in line with the fact that our experiments were designed to pressure the saccadic system into boosting or scaling down its response without requiring a change in disconjugacy. Indeed only small effects were observed in the vergence response during saccadic adaptation.

In conclusion, by showing that it is possible to achieve opposite adaptive changes in saccadic gain for different depth directions, the present study provides firm evidence that the metrics of the saccadic response can be depth-dependent. Recently, Collewijn et al. (1995) have shown a similar phenomenon for the dynamic properties of disjunctive saccades.

**Underlying neural mechanisms**

A limited role of high-level processes. A recurrent theme in discussions on short-term saccadic adaptation concerns the extent to which the modification of saccades may reflect a cognitive strategy. In principle, the paradigm employed in our study, involving a regular alternation of gain-shortening and gain-lengthening trials, would allow for this possibility. However, the absence of differential adaptation in frontal plane experiments having a small radial separation appears to argue against this [see Fig. 10(A)]. It seems apparent that if a high-level strategy was being employed, the results observed here would not have been so different. Still, we cannot exclude that some cognitive factor (perhaps anticipation) may account for the peculiar initial responses observed in two of our subjects, when changing from the singular adaptation phase to the alternating phase, during the mixed paradigm [Figs 9(A) and (B)]. It is quite possible that these responses are a sign of context specificity (Deubel, 1995) but, in any case, these effects account for only a small share of the observed changes.

We also found no evidence that experienced subjects had a more complete gain separation and a faster adaptation time-course than naïve subjects. The time-course of saccadic adaptation in our paradigms did not deviate strongly from results obtained in other studies of short-term gain adaptation. An especially fast adaptation would have been indicative of a cognitively controlled response strategy, as opposed to a genuine adaptive modification of oculomotor parameters.

We conclude that lower-level mechanisms were probably predominantly responsible for the generation of the observed gain changes. Bearing this in mind, we now raise several issues concerning the neural basis of our experimental results by discussing a recently proposed model of saccadic adaptation.

**Issues for models of saccadic adaptation.** Electrophysiological studies investigating the neural basis of saccadic adaptation will, of course, have to provide the main evidence, but several interesting suggestions have come from behavioural studies. On the basis of his finding that oblique saccades may be unchanged after adaptation of horizontal saccades, Deubel (1987) came to the conclusion that adaptation must occur at a level above the stage where saccade commands are represented separately for horizontal and vertical components. He further suggested that the metrics of saccades are coded at an earlier stage by using two polar coordinates (eccentricity and radial direction), which can be independently programmed but are not independently adaptable. Collewijn & Collewijn (1992) also suggested that the meridian-specific adaptation of oblique saccades during experiments with anisometropic spectacles, must take place at a stage before the decomposition of motor commands into separate horizontal and vertical components. Finally, Frens & Van Opstal (1994) who proposed the existence of limited saccadic adaptation fields, have suggested that saccadic adaptation occurs in a region that is topographically organized and represents saccades as motor error vectors. Although it is known that saccadic coding, at the midbrain level, can be described using polar coordinates (Wurtz & Albano, 1980; Ottes et al., 1986; Van Gisbergen et al., 1987), which contrasts with more peripheral levels where the saccadic system is thought to be organized using a Cartesian coordinate system, with separate horizontal and vertical components forming the final saccadic vector (King & Fuchs, 1979), these adaptation studies nevertheless allow for other possibilities (see below). An important question is how these suggestions can be reconciled with neurophysiologically oriented models of the saccadic system.

Dean et al. (1994) have recently proposed a scheme which contains specific suggestions about the hierarchical level in the saccadic system where the adaptive changes might occur. This model elaborates on the original Robinson (1975) model for the saccadic pulse generator by introducing the cerebellum as an adaptive controller, in parallel with the original circuit. Recent results by Goldberg et al. (1993), showing that short-term adaptation of saccades is no longer possible after cerebellar lesions, provide evidence that the cerebellum is indeed important. Furthermore, it has long been apparent that the cerebellum is an essential region
required in improving motor performance and regaining saccadic accuracy after muscle injury (Optican & Robinson, 1980).

The most relevant question, in the present context, is to what extent the Dean model can account for the 3-D aspects of saccadic adaptation specificity. Our finding that adaptation specificity also exists in the horizontal plane of regard cannot be explained by this model in its original form. To explain this, the cerebellum would require depth information about the saccadic target or about the impending movement itself and would need to provide depth-selective output commands. Recent neurophysiological evidence has shown that the nucleus reticularis tegmenti pontis (NRTP), a major link of saccadic information between the superior colliculus and the cerebellum, may also be involved in the control of vergence movements (Gamlin & Clarke, 1995). This present study, taken together with the recent neurophysiological data and the Dean model, suggests that it would be very interesting to investigate the 3-D tuning of collicular and cerebellar neurons.

**Functional implications of adaptation specificity**

As we have seen, our finding that adaptation specificity is a 3-D property raises several new questions for further neurophysiological research and modelling. To further examine the broader context of these findings, it is interesting to consider the possible functional significance of bounded adaptation fields. Patients with ocular motor problems often suffer from afflictions which require different localized adjustments for movements in different directions. Consequently, an adaptive system only capable of globally oriented gain modifications seems unsuitable, while directional selectivity would appear to be essential. The other extreme, an adaptive system with a high spatial resolution capable of extremely fine point-by-point tuning, would require many neurons and might be disadvantageous for the speed and generalization of learning (Dean et al., 1994). So, in fact, having 30 deg wide sectors in the frontal plane may be a good compromise for most clinical pathologies where adjustments are typically needed in a wider angular range.

Little can be said about the need for adaptive adjustments of saccadic eye movements in different depth directions. Nevertheless, one can quite well imagine that having a degree of depth specificity may be equally essential for solving saccadic deficiencies. For example, consider a hypothetical case of a patient with paralytic strabismus. This would cause a resetting of the alignment of the eyes, which would be equivalent to starting saccades from a different angle of vergence. Resolving such problems might benefit from an adaptive system with depth specificity. Since little is known about whether these depth-related pathologies are prevalent in the clinic, this question clearly deserves detailed attention in future work.

It is perhaps of interest to compare the directional specificity tuning to the total working range of the two cross-sections of 3-D space that we have studied. For the frontal plane, the 30 deg wide sectors would amount to one-twelfth of the total 360 deg range of radial directions. For the depth domain we only know that 8 deg is an upper limit for most subjects. If this value is taken as a provisional estimate, it would amount to about one-quarter of the total vergence range.

A preliminary report on the vergence-dependent adaptation of the vestibulo-ocular reflex (VOR) has raised some interesting parallels (Clendaniel et al., 1994). These authors have shown that it is possible to train human subjects to have different VOR gains at different levels of tonic vergence, apparently supporting the fact that 3-D specificity in the adaptive mechanism is not limited to the saccadic subsystem. However, this analogy should not be carried too far since our experiments have not explored effects of varying tonic vergence levels.

**CONCLUSION**

Our study has substantiated and extended earlier findings that saccadic adaptation is a local phenomenon by showing its directional specificity in two perpendicular cross-sections of the 3-D oculomotor workspace. Thereby, the results provide firm evidence that the saccadic system can issue different commands for targets at different depths which are aligned for the cyclopean eye. They also suggest the need to extend current models of the saccadic system by incorporating the depth dimension.

**REFERENCES**


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