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Sensory and Motor Aspects of Saccade Control

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Summary. The oculomotor reactions have recently attracted increasing attention for diagnostic purposes. This is in line with the view that the oculomotor system is one of the simpler, machine-like sensorimotor systems. This paper presents two examples to demonstrate that the complexity of sensorimotor processing may be higher than expected from the outcome of experiments under rather restricted stimulus conditions. In the first part it is shown that complex preprocessing including the evaluation of spatial gradients of visual structure is an integral part of the programming of reflex-like saccades. The second part concerns adaptivity of saccadic eye movements. The data demonstrate that saccadic gain control is highly specific to the direction of the saccade. It is suggested that many central deficits may be hidden as a consequence of the effect of specific adaptive mechanisms.

Key words: Saccadic eye movements – Saccadic adaptation – Texture discrimination

Introduction

In the last decade, a large body of work on the neuroanatomical and functional basis of eye movements has been accumulated. As a result, the oculomotor system appears as one of the simpler, machine-like sensorimotor systems. This view is enhanced by the finding that different classes of oculomotor responses are generated in independent, functionally and anatomically well-separated subsystems. Electrophysiological investigations, especially in primates, have led to clear indications of the role of different neural structures in eye movement generation. An important aspect of these findings is that damage of specific neural structures may lead to specific deficits in eye movement control, indicating the location of the central or peripheral desease. Therefore, eye movements are now frequently used in diagnosis.

In fact, damage at various levels of sensorimotor processing has been shown to elicit changes in eye movement behaviour. To give a few examples, lesions of the premotor circuitry of the paramedian pontine reticular formation frequently lead to more or less complete gaze palsy of horizontal rapid and/or slow eye movements, while lesions in the mesencephalon reticular formation seem to selectively affect vertical eye movements (Bender 1980; Henn et al. 1982; Henn and Büttner 1982). Also, slowing of saccadic eye movements is found in supranuclear damage. Superior collicular lesions seem to abolish short-latency saccades (Zihl and von Cramon 1978; Schiller et al. 1987). Frontal eye fields and parietal cortex are supposed to mediate attention-related responses to spatially complex stimuli (Schiller 1985). Thus, unilateral ablation of the frontal eye fields leads to transient neglect of the contralateral field and conjugate deviations of the eye to the side of the lesion (Latto and Cowey 1971). The cerebellum is generally assumed to regulate and improve motor performance, for which the basic program is generated elsewhere. Hence, although saccades can be basically performed in the presence of cerebellar dysfunctions, they are frequently impaired, exhibiting systematic dysmetria (mostly saccadic overshoot) and increased occurrence of square wave jerks (Dichgans 1978). Finally, little is yet known about the specific contributions of striate and extrastriate areas to eye movement generation.

The supranuclear, cerebellar and midbrain diseases mentioned above can be seen as pathological changes in lower-level, motor-related circuitry. Recently, however, there has emerged increasing evidence that the pathophysiology of various psychoses might be

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This article was presented in part at the Symposium on Eye Movements and Psychopathology, Berlin, 23–24 June 1988 linked with abnormalities in eye movements. It has been shown, for instance, that patients suffering from schizophrenia frequently exhibit saccadic dysmetria (Mather and Putchat 1983; Schmid-Burgk et al. 1983), impaired smooth pursuit performance (Shagass et al. 1974; Holzman et al. 1977; Gaebel and Ulrich 1987) and poorer visual search performance (Gaebel et al. 1987). It is unclear, however, whether reduced sensory acquisition of the visual stimulus, attentional deficits or deficits in motor programming may account for these findings.

This paper focuses on two different aspects of saccade control which are deemed important for the interpretation of eye-movement-related syndromes. The first part will emphasize that complex *sensory* preprocessing of visual information forms an essential and often underestimated element of saccadic control. In the second part, the role and properties of adaptive repair mechanisms controlling *motor* performance will be discussed.

Figure – Ground Discrimination in the Programming of Saccades

An increasing amount of work has been concerned with the reaction of the saccadic system to combinations of two or more simultaneously presented, spatially well-separated targets. Findlay (1982) found that in this situation the saccade is directed to a "centre of gravity" of the whole configuration where the "mass" of the individual stimulus is a function of its size. Our group extended this finding and showed that luminance, contrast and spatial frequency are also determinants in the amplitude computation process (Deubel et al. 1984; Deubel and Hauske 1988). Obviously, visual information covering a wide retinal area is integrated in the saccadic response.

The majority of these experiments were performed in the absence of background structure. Our natural environment outside the laboratory, however, is normally characterized by the presence of a many-faceted visual structure. Here, the sensorimotor system should be able to find and follow objects which are distinct from the background with respect to structural features rather than only their global luminance characteristics. This concept requires that borders between different texture areas should form salient features for the oculomotor system. We tested this hypothesis by using stimuli where foreground/background segregation is a necessary prerequisite for saccadic programming.

Experiments were performed which investigated the effect of texture-defined stimuli on saccades in a target-nontarget situation. The experimental set-up is described in detail in Deubel et al. (1988). As an example, for a number of various textures used in the experiments the left part of Fig. 1 gives a sketch of a typical visual stimulus. The scene was composed of line elements of specific contrast and orientation. On appearance of the scene, the subject had to saccade from a fixation cross F to the elongated target structure T, which was in this case defined by elements with an orientation difference of 90° from the background structure. The histogram below is a representative distribution of the saccade landing positions.

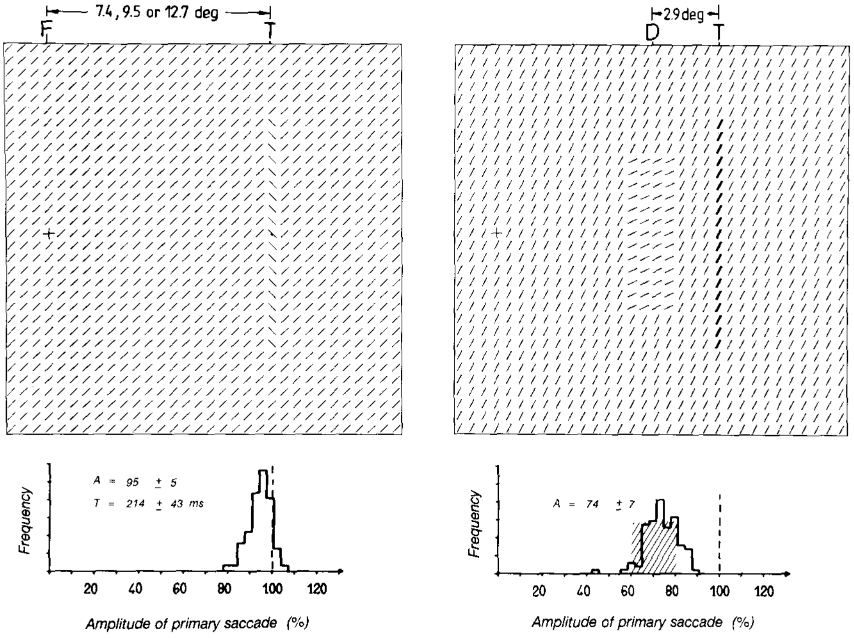

Fig. 1. *Left:* Sketch of a stimulus scene giving sizes and eccentricities in degrees of visual angle. Basic screen luminance was adjusted to 2.9 cd/m^2. The scene is composed of background structure of 5.84 cd/m^2 upon which the fixation cross *F* and the target *T* are superimposed. The target is texture-defined, i.e. constitutes a vertically elongated area of same luminance but different line orientation with respect to the background. Also, the diagram presents the histogram of the amplitudes of the primary saccades, mean saccadic amplitude *A* in percent of target eccentricity and mean saccadic latency *T*. *Right:* The target *T* is luminance-defined (8.76 cd/m^2). Additionally, a texture-defined distractor *D* with an orientation difference of 44° with respect to the background is presented

Our general finding is that subjects have no difficulty in performing this task. This is reflected in the high saccadic accuracy, that is, low standard deviations of amplitudes and in rather short saccadic latencies. The average latency for the five tested subjects was 223 ms, versus 207 ms in experiments without background structure.

The right part of Fig. 1 displays a stimulus scene from another set of experiments. Here, the target T is defined by its higher luminance compared with the background structure. Additionally, a distractor D is simultaneously present consisting of an area of line elements which differ from the background in their orientation. Obviously, in this complex stimulus situation also, the saccade landing position is constituted by some "centre of gravity" of target and distractor, as can be seen by the considerable shift of the distribution towards the distractor. In further experiments not presented here it was found that the amount of distraction is a function of the orientation difference between distractor (foreground) and background (Deubel et al. 1988).

By the introduction of background structure a situation was obtained where the target is not defined by its mere presence, but rather by its structural difference with respect to the background. Obviously, this visually more complex situation does not restrain the oculomotor reaction; the high precision of the saccade is maintained, and latencies are only slightly increased. Suprisingly, spatial averaging in the sense of the "centre of gravity" effect also occurs in the presence of background structure. It turns out that the salience of an object in amplitude computation is a complex function of the visual properties of the scene, and is essentially related to the dissimilarity of stimulus and background. It must be concluded that a considerable amount of sensory processing of visual information is involved in the programming of fast saccades which segregates foreground objects from the background structure. Only then, at a subsequent stage, does spatial averaging occur on the preprocessed information in order to determine saccadic amplitudes. This means that texture gradients form highly important features for the amplitude computation process.

Adaptive Properties in the Control of Eye Movements

Persistent oculomotor malfunction is ostensibly in contradiction to the fact that more and more aspects of oculomotor performance are discovered to be protected by some adaptive mechanism. Clearly, without an adaptive arrangement it would be difficult to conceive how the oculomotor system could maintain proper performance during development, aging, disease, fatigue and so forth. Therefore, specific mechanisms are assumed to detect inappropriate performance by means of highly selective visual cues, and then to re-adjust motor performance adaptively.

Adaptive control of response parameters is of particular value for open-loop reflexes. In fact, it has been demonstrated for the vestibular-ocular reflex (VOR) that the adaptive machinery is able to cope with the extreme demands of reversing prism spectacles by adaptively inverting VOR gain after a few days of (reversed) visual experience (Gonshor and Melvill-Jones 1976). As to saccades, it has been shown recently that saccadic trajectory is under sophisticated adaptive control in which three components of motoneuron innervation (pulse, step and slide) are adjusted independently (Optican and Miles 1985). Also, it is well-known that the accuracy of saccade metrics is adaptively controlled (McLaughlin 1967; Deubel et al. 1986). Most recently, it has been realized that even closed-loop systems like the pursuit system also benefit from gain regulation (Optican et al. 1985). This is not too suprising since, for closed-loop systems also, dynamic performance depends critically on well-adjusted internal parameters.

To what extent adaptive mechanisms are able to repair central damage depends critically on how *specifically* the adaptive controller can respond to detected errors. Recent investigations performed in man and monkey were aimed at analysing the complexity of gain control for saccades with both horizontal and vertical component (cf. Deubel 1987). In these experiments, subjects and trained monkeys had to follow a small target projected on a large screen which was stepped in rapid succession. Eye movements were measured using the scleral search coil technique. A single trial was of the following type (Fig. 2, left). After controlled fixation, the target was rapidly displaced by 6°–12°. The primary saccade triggered an additional small, intrasaccadic target displacement which consistently occurred in the same, or, in another type of session as shown in Fig. 2, in the opposite direction to the first target step. After successful refixation, the next two-step sequence was started. In the adaptation phase, these steps only occurred in predetermined directions. So, for the example to be presented, only horizontal steps eliciting essentially horizontal saccades were offered.

Owing to the intrasaccadic target displacements, the system is initially confronted with a consistent postsaccadic error which has to be eliminated by subsequent correction saccades. It can be observed that after a number of training presentations adaptive changes of saccadic amplitude occur that reduce these artificially induced refixation errors. The right part of

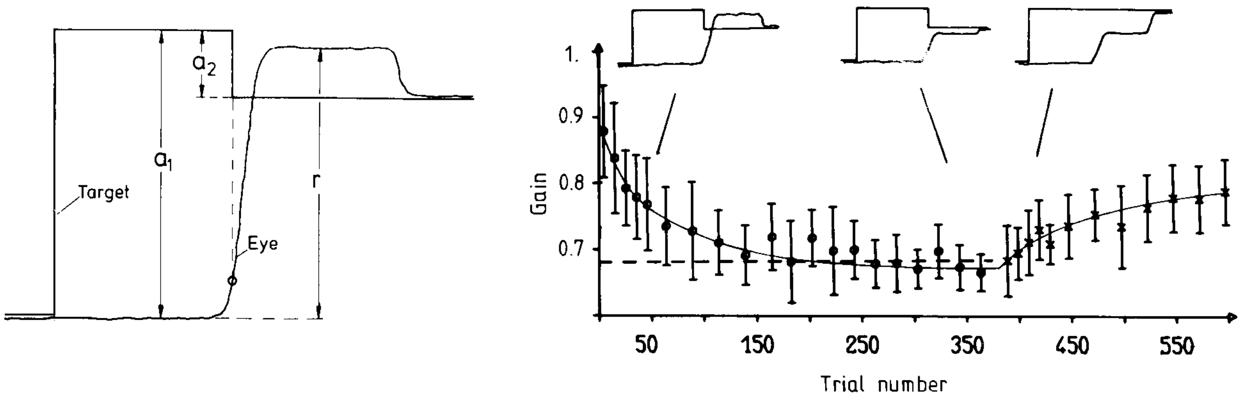

Fig. 2. *Left:* Stimulus movement and examplary oculomotor response. *Right:* Mean gain of saccadic responses as a function of consecutive trial numbers. In this experiment, the size of the intrasaccadic target displacement *a2* was 33% of the initial step *a1* and consistently occurred in the opposite direction of the primary saccade *(dashed line)*. In the period after 375 trials, normal visual feedback (without intrasaccadic target shifts) was provided. Saccadic gain is calculated as $g = r/a1$

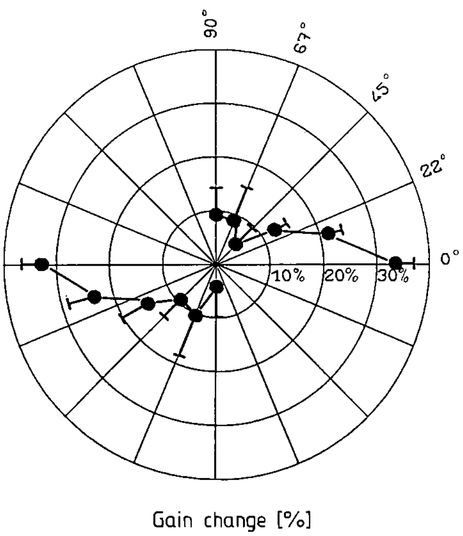

Fig. 3. Precentage reduction of saccadic gain due to adaptation as a function of saccade directions. In the adaptation phase, training was given only for horizontal (left- and rightward) saccades. Radial bars indicate twice the 99.5% significance level of the difference between pre- and post-adaptation means

Fig. 2 displays the adaptive adjustment of saccade gain developing over a number of single trials for human subjects. Obviously, after 150–200 trials, the adaptive mechanism is able to compensate completely for the induced errors, decreasing saccadic gain to less than 0.67. As an interesting property of this kind of adaptive reaction it was observed that gain reduction is quick to occur, whereas gain amplification requires a considerably longer time (Deubel et al. 1986).

After achieving sufficient adaptation for saccades in specific directions during the adaptation phase I investigated how saccades in other directions were affected. Figure 3 provides a polar diagram of the percentage gain reduction induced by adaptation, now determined for saccades in various angular directions. As expected, the largest gain changes occur for saccades in the previously adapted directions, i.e. in this case for horizontal movements. Adjacent directions also show reduced saccadic gain. It can be seen, however, that the effect decreases sharply with angular distance from the adapted direction. As discussed by Deubel (1987), a sharp directional selectivity of gain adjustment exists, which is more specific to the direction than an organization based on independent x- and y-components would predict. This study also showed that these tuning properties are homogeneous for all saccadic directions. Further, it demonstrated that not only saccadic gain, but also saccadic direction is subject to adaptive modification, and exhibits very similar directional tuning.

As a consequence, it seems necessary to assume, at a central level of oculomotor control, the existence of independent adaptive controllers specific for individual movement directions, that is, of a sophisticated system for metrical adjustments.

General Discussion

Several aspects emerge from the experiments described above, which seem of importance for the clinician who employs eye movements for diagnostic purposes. Thus, it was demonstrated that preprocessing of sensory information forms an essential part of saccadic programming. This is reflected by the fact that texture borders are immediately considered in the fast, reflex-like saccadic response. In fact I think a stimulus situation of this kind is closer to the ecological task the oculomotor system is normally confronted with. The finding that saccadic latencies are then only slightly increased suggests that a considerable amount of the latency period observed in a very restricted stimulus situation may be simply idling of a system adjusted to more complex sensory situations. This is consistent with data demonstrating that saccades can in fact be elicited with latencies shorter that 130 ms (Fischer and Ramsperger 1984; Deubel et al. 1982). Also, in order properly to control saccadic parameters in an ecological, richly structured visual environment, a *visual* mechanism has to be postulated which determines motor errors on the basis of highly selective visual cues. As a consequence, it must be assumed that sophisticated early visual processing provides the basis for the control of eye movements. Hence, deficits in *sensory* functions may affect the oculomotor output in a way difficult to predict from current knowledge on sensorimotor processing, and should therefore serve as a continuing hypothesis to explain abnormal motor performance.

Secondly, the data give another demonstration of a flexible mechanism which serves to repair the effects of sensory or motor deficits in order to maintain proper oculomotor performance. At least for the control of saccadic eye movements, this machinery exhibits many degrees of freedom, responding to dysmetria in a strikingly specific manner. Its existence should be kept in mind, since, ironically, one biproduct of adaptive adjustment is to mask oculomotor disorders from the clinician. When a disorder is finally manifest, it could mean either that it has become so large that the adaptive machinery can not cover it up or else that the adaptive controller itself has become involved. This also raises the interesting question of how the brain is able to protect adaptively the repair mechanism itself.

Finally, the effects described above should be considered in the design of experiments. Thus, the results on spatial averaging predict that variable stimulus luminance, high-contrast display borders, additional presence of visual objects and presence of background structure immediately affect oculomotor reactions and should be carefully avoided in the experimental set-up. Also, it seems reasonable to expect that repetitive stimulation with monotonous stimuli will probably encourage some part of the adaptive machinery to respond. Therefore, intensive randomization of stimulus parameters is a necessary precondition for psychophysical testing.

Nevertheless, the oculomotor response provides powerful indices of brain functions. Combined efforts of engineers, physicists and research-oriented clinicians should further refine diagnostics and at the same time arrive at a better understanding of how sensory signals finally lead to a motor response. In this process, the intricate complexity and the amount of mutual interaction of various subsystems in sensorimotor control should never be underestimated. Indeed, eye movements to visually more complex stimuli may prove more sensitive to higher-level deficits.

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