

The Role of Fixation and Visual Attention in the Occurrence of Express Saccades in Man

L. Mayfrank, M. Mobashery, H. Kimmig, and B. Fischer

Abteilung Klinische Neurologie und Neurophysiologie, Universität Freiburg, Hansastrasse 9, D-7800 Freiburg, Federal Republic of Germany

Summary. The differential influence of fixation and directed visual attention on reaction times of goal-directed saccades and especially on the occurrence of express saccades was investigated.

In all the experiments the subjects were instructed first to keep their direction of gaze at the center of a translucent screen with or without a central fixation point. When a new stimulus appeared, the subjects had to look at it as soon as possible. In some control experiments the subjects had to direct their gaze to the screen center and simultaneously direct their attention to a peripheral light spot before the target for the saccade appeared.

Many express saccades occurred when either active fixation of a central fixation point or attention directed to a peripheral visual target (regardless of its position) was interrupted 200ms before the target for the saccade appeared.

Express saccades were almost completely abolished in the presence of fixation and/or directed visual attention at the moment in which the saccade target appeared.

We conclude that express saccades occur if visual attention has already been released at the moment when the target for the saccade appears. This disengagement needs some time which adds to the reaction time.

Key words: Attention – Eye movements – Fixation – Express saccades

Introduction

Typical values for saccadic reaction times (SRT) are in the order of 180 to 220ms measured from target appearance. In 1967 Saslow showed that in man the introduction of a temporal gap between the disappearance of the fixation point and the appearance of the target (gap paradigm) decreases the reaction time to about 140ms. If, on the other hand, the fixation point remains visible (overlap paradigm) the reaction time increases to about 220ms.

Using the gap paradigm in the monkey, Fischer and Boch (1983) have reported the existence of a group of saccades with even shorter reaction times (express saccades) in the order of 70ms. Later Fischer and Ramsperger (1984) repeated the experiment of Saslow and showed that human subjects also showed a separate peak in the distribution of their reaction times which corresponds to the express saccades in monkey.

Offprint requests to: L. Mayfrank at the above address

In man express saccades have a reaction time in the order of 100ms. The exact value depends on the physical characteristics of the target (Boch et al. 1984) as well as on the amount of practice subjects or monkeys have had beforehand (Fischer and Ramsperger 1986; Fischer et al. 1984).

Using the gap paradigm in 48 healthy and naive subjects we demonstrated that the phenomenon of express saccades occurs in almost all subjects independent of their age (10 to 87 years). The relative number of express saccades, however, significantly decreased above age 50. The reaction times do not differ significantly from those of younger subjects.

It was assumed in the beginning that the disappearance of the fixation point was necessary to enable the visual-to-oculomotor system to initiate express saccades to the target. This interpretation, however, was rejected by the later observation that monkeys as well as human subjects could eventually also execute express saccades in the overlap paradigm (Boch and Fischer 1986; Fischer and Ramsperger 1986).

We therefore investigated the conditions under which express saccades can be obtained. One hypothesis was that express saccades can only occur if the active process of fixation is already discontinued at the time of the occurrence of the peripheral target, regardless of the existence or nonexistence of a foveal light spot. Alternatively, the direction of visual attention, which usually coincides with the direction of gaze, must be free to move in the visual field when the command to move the eye is given, in order to be able to execute express saccades.

This paper presents the results of several experiments designed to differentiate between these possibilities. We systematically changed the visual conditions and/or the corresponding instructions for the subjects in order to find clearly defined situations in which many express saccades occur, and others in which express saccades cannot be obtained.

The hypothesis that directed visual attention inhibits the saccadic system will be discussed.

Methods

Apparatus. Subjects were placed 67cm in front of a translucent screen. Their heads were stabilized by a chin rest. Visual stimuli were projected onto the screen by light emitting diodes. Horizontal eye movements were recorded by an infrared light technique (Gauthier and Volle 1975) detecting saccades of 0.25° in size. The fixation point appeared straight

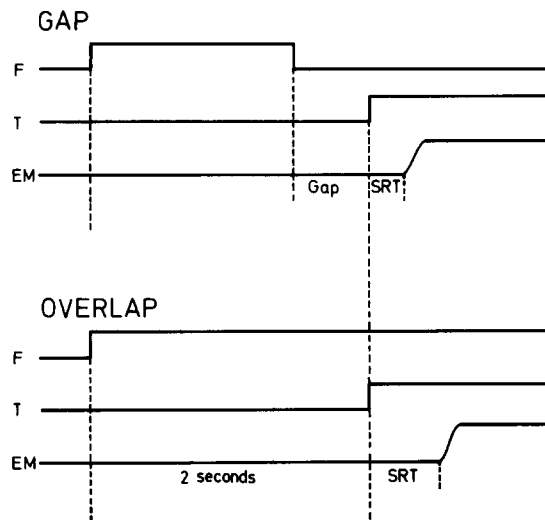


Fig. 1. Temporal aspects of the two experimental paradigms used. *Gap*: the fixation point (*F*) disappears some time (*gap*) before the target (*T*) for the saccade appears. Saccadic reaction times = *SRT*. Eye movement = *EM*. *Overlap*: same as gap paradigm with the only difference that the fixation point remains visible

ahead in all experiments (if there was a fixation point at all) and the target for the saccade was placed at 4° from the center of the screen either in random order to the left or to the right, or to the right only.

Other details of the optical arrangement, data collection and evaluation have been described by Fischer and Ramsperger (1984). To illustrate the distribution of the SRT the number of saccades is plotted versus their reaction times in a bin of 10 ms width, unless stated otherwise.

Data Evaluation. Saccadic reaction times were determined automatically by an electronic threshold detector. Detections of changes in the eye position signal were indicated by brief interruptions of the beam from a storage oscilloscope displaying the eye movements. Artifacts, like blinks and false detections of saccades were eliminated immediately. Distributions of the SRT were obtained on line on a computer terminal screen using a bin width of 10 ms. The number of express saccades in a given distribution was determined by counting the number of saccades with reaction times between 85 ms and the first dip in the distribution, occurring usually around 130–150 ms (see Fig. 5).

Procedure. In all experiments the subjects had first to look at the central fixation point upon its appearance. When the peripheral target occurred they were to make a saccade to it as soon as possible. In each session 100 or 200 saccades were collected.

Two main paradigms were used throughout: (a) gap paradigm: the fixation point appeared and remained on for 2 s and the target occurred (usually 200 ms) after the fixation point had been turned off. (b) Overlap paradigm: the fixation point remained visible while the target appeared. The target always occurred 2 s after fixation point appearance. The time course of the two paradigms is shown in Fig. 1.

In some experiments no foveal fixation point was used: i.e., (I) saccades were made in total darkness to a suddenly occurring target; (II) instead of a fixation point the middle of an incomplete cross was used to define the direction of gaze (and

attention) during the first 2 s of a trial; (III) instead of a central fixation point a peripheral attention target was introduced and subjects were instructed to dissociate their direction of gaze (“Keep it in the middle of the screen”) from their direction of attention (“Pay attention to the peripheral light spot”). More details are described in the appropriate section of the Results.

Subjects. Subjects between age 24 and 42 years were used. Some of them had been well trained to execute express saccades before, others were naive with respect to the experiment (see Results). The number of subjects used in the different experiments is indicated in the appropriate sections of the Results. To eliminate the effects of training, control measurements were always made during the same session.

Results

1. Significance of Fixation

As indicated previously, a small number of express saccades can also be obtained in the overlap paradigm, i.e., in the presence of a central fixation point at the moment of saccade target appearance. This observation could be explained by the assumption that the occurrence of express saccades does not depend on the presence or absence of the fixation point itself, but rather on the visual attention directed to the fixation point. To test this hypothesis, we used five subjects in the overlap paradigm, with the instruction (a) to fixate the central fixation point as attentively as possible, and then (b) just to keep their eyes on it.

The result from one subject is shown in Fig. 2, both for randomized (left) and nonrandomized (right) target position. As a control, and to identify the express saccades, the gap paradigm was also used (top two panels). A comparison shows the drastic decrease in the number of express saccades if one moves from the gap to the overlap paradigm. The lower two distributions show that, in fact, the release of attentive fixation of the fixation point can increase the amount of express saccades, in particular if the target position is not randomized (lower right distribution in Fig. 2). All five subjects showed this kind of result. It should be noted that in all cases, the number of express saccades was largest in the gap paradigm.

If the amount of express saccades had depended on the presence or absence of directed visual attention before saccade target appearance, one would expect, first, only a few express saccades in a task in which the subject attentively fixates the middle of an incomplete cross (see inset Fig. 3C), and, second, an increment in the number of express saccades in a task in which the target appears on the screen in total darkness. The results of these 2 experiments are shown in Fig. 3. Figure 3A,B shows the pooled data of four naive subjects in the gap and overlap paradigm, respectively (the latter with attentive fixation). As expected, there was a distinct subpopulation of express saccades in the gap paradigm, while almost no express saccades were observed in the overlap paradigm. The result of the experiment in which the subjects were instructed to fixate the middle of an incomplete cross attentively (the target appeared in random order at 4° to the right or left) is shown in Fig. 3C: as in the overlap paradigm almost no express saccades were obtained. The same result was obtained if subjects had to look straight ahead in total darkness without any fixation point (Fig. 3D). Comparison of these experiments shows that in the gap paradigm the largest amount of express saccades

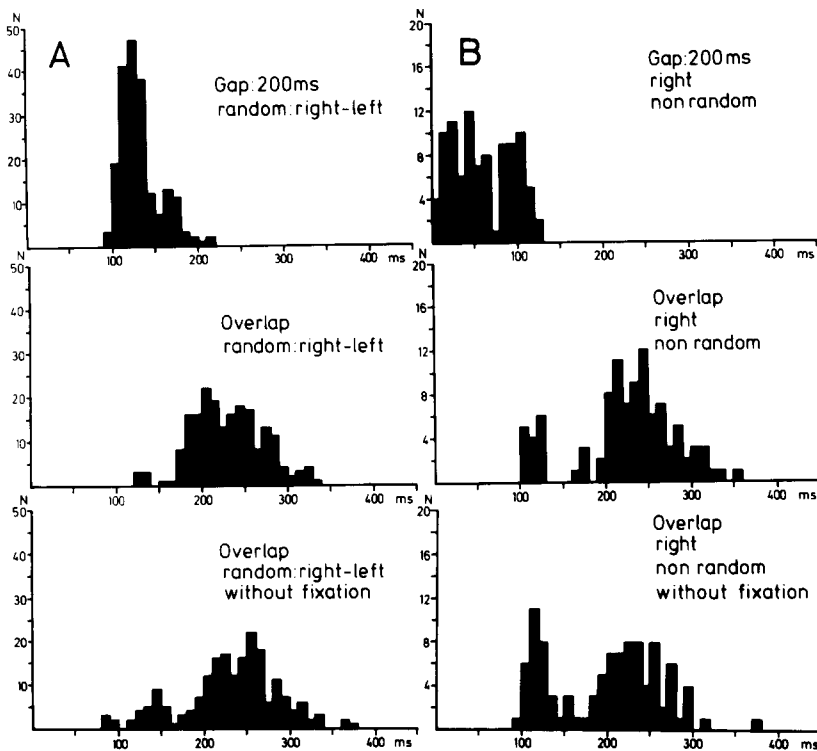


Fig. 2A, B. Distributions of SRT of one subject. Number of saccades (*ordinate*) in a bin (10ms) of reaction time (*abscissa*). Zero at the abscissa corresponds to the time of target appearance. In the top two panels (gap paradigm) the target appeared 200ms after fixation point disappearance. In the other panels (overlap paradigm) the fixation point remained visible while the target appeared. In the two panels in the middle the subject was instructed to fixate the fixation point attentively; in the lower two panels the subject was instructed just to keep the eyes on it. In the diagrams on the left (**A**) the target occurred randomly at 4° to the right or left. In the diagrams on the right (**B**) the target always appeared at 4° to the right. (Note the considerable amount of anticipatory saccades (reaction time below 85ms) at the top right panel)

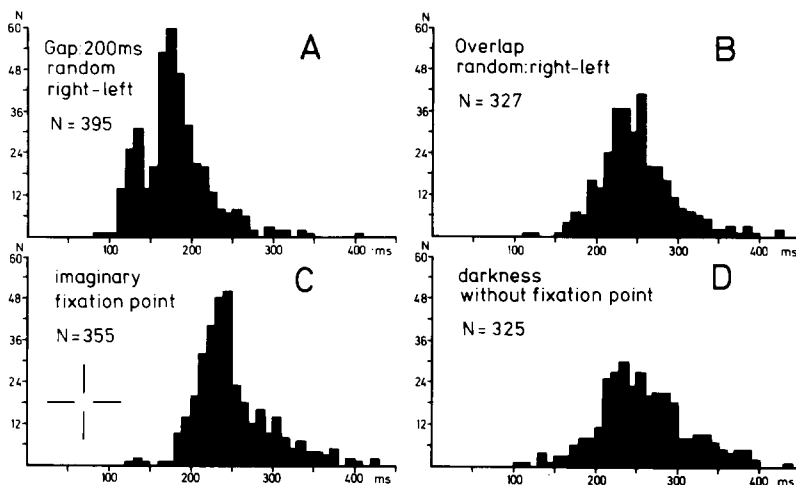


Fig. 3A–D. Same as Fig. 2 but for different conditions. Pooled data of a group of four subjects. **A** Gap paradigm. **B** Overlap paradigm with attentive fixation of the fixation point. In **C** and **D** no fixation point was visible before target appearance. In **C** the subjects were instructed to fixate the middle of an incomplete cross (see insert in **C**) before target appearance. In **D** the subjects had to look straight ahead in total darkness before target appearance. The target position was always randomly varied between 4° to the right or left. Express saccades are seen only in **A** (first peak in the distribution)

was obtained, whereas in the absence of a fixation point (Fig. 3C,D) almost no express saccades were produced. In fact, the distributions of Fig. 3C,D are hardly different from that of Fig. 3B (overlap). Nevertheless, it should be noted that it is not at all impossible to execute express saccades in situations other than the gap situation.

2. Effect of the Luminance of the Fixation Point

To further clarify the role of fixation, the gap paradigm was used and the luminance of the fixation point was systematically changed. The idea is that it is more difficult to fixate a spot which is barely visible.

After 5 min of dark adaptation the luminance threshold of the fixation point was found for each of the three trained subjects used in this experiment. The luminance of the fixation

point was then increased in different steps to 0.1, 0.2, 0.3, 0.4, 0.6, and 0.8 log units above threshold, and in each case 100 SRT were measured.

Figure 4 shows the relation between the luminance of the fixation point and the percentage of express saccades. As expected from Fig. 3D none of the subjects could execute express saccades at threshold. With increasing brightness of the fixation point up to 0.8 log units the maximum number of express saccades was obtained.

Nonrandom conditions were used throughout in these experiments in order to increase the number of express saccades (Fischer and Ramsperger 1984). Anticipatory saccades which are usually identified by their large undershoots (error > 15%) were aborted from the data. In conclusion: neither the physical absence or presence of a fixation point nor the absence or presence of active fixation can account for the occurrence or nonoccurrence of express saccades.

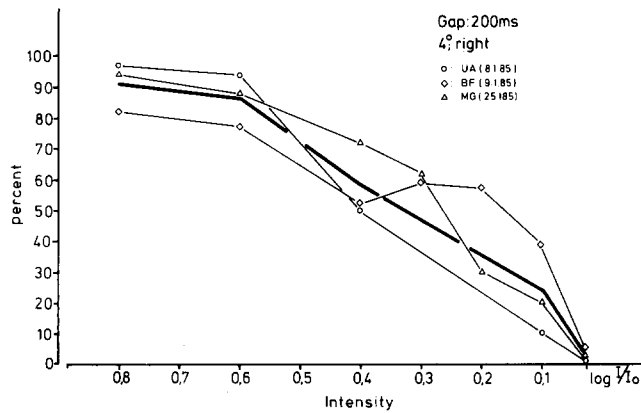


Fig. 4. Amount of express saccades versus intensity of the fixation point. I = absolute intensity; I_0 = intensity at threshold. The heavy line represents the mean values calculated from the three individual data curves

3. Effect of Peripheral Attention

In the experiments described so far, the directions of gaze and attention have been the same or the direction of attention was uncertain. In order to differentiate between the effects of central fixation and peripheral attention we used the gap and the overlap paradigms, with the only modification that the light spot which usually served as the central fixation point was moved 5° up the vertical meridian and served as a target for peripheral attention, while the direction of gaze was kept at about the center of the screen. For comparison the ordinary gap paradigm was also used for each subject. The results are shown in Fig. 5 (target position randomized between right and left, average from five members of the research group).

Most express saccades were obtained in the ordinary gap situation (Fig. 5A). Almost no express saccades occurred in the overlap situation where the subjects paid peripheral attention until the target appeared (Fig. 5C). If the attention target disappeared 200ms before the saccade target appeared (Fig. 5B). For each subject the amount of express saccades was about 20% less in the peripheral attention task. This observation leads to the conclusion that express saccades can be executed if peripheral visual attention is released a short time before saccade target appearance.

In fact, one might argue that the subject has to release, move, and focus visual attention to the new target position before the eye can finally move and that the 'release-move-focus' sequence takes the time included in the reaction time in the overlap but not in the gap paradigm.

To test the differential effect of releasing attention versus focusing attention four members of the research group were run in the same paradigm again with the only difference that the attention target was placed at the position where the saccade target would occur, i.e., at 4° to the right of the center of the screen. In other words the subjects were constantly cued to the saccade target position. The result of this experiment is illustrated in Fig. 6. If the attention target (labeled A) was switched off before the target appeared, many short latency (below 150ms) saccades were obtained (Fig. 6A). If the attention target remained visible, these short latency saccades were largely reduced (Fig. 6B). For control, the usual overlap paradigm was used (Fig. 6C).

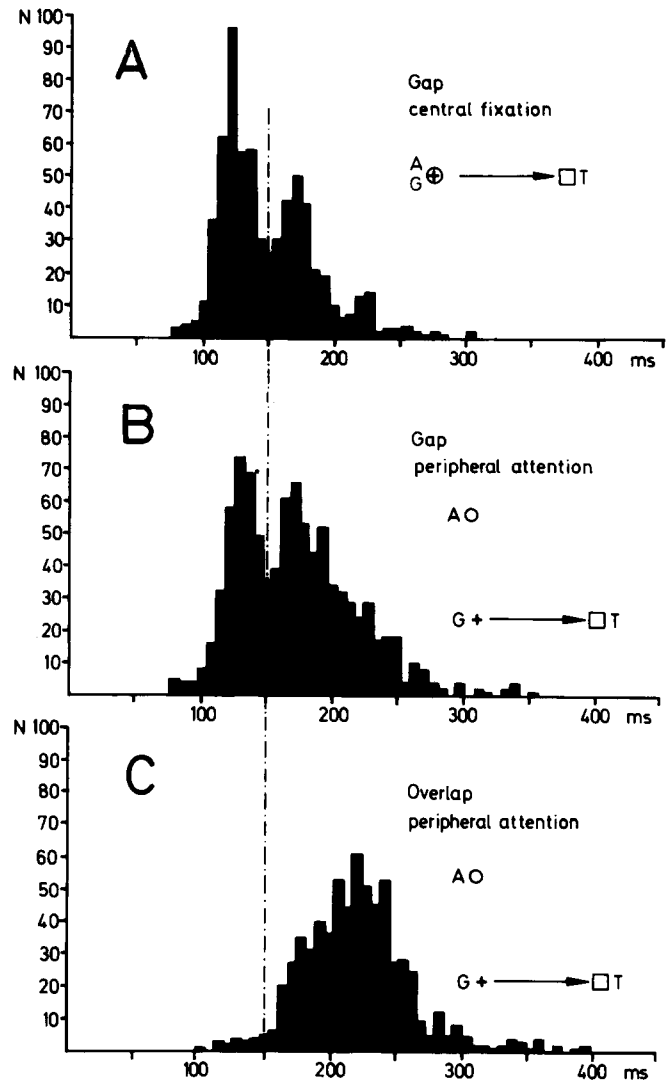


Fig. 5A-C. Distribution of SRT with central (A) and peripheral (B, C) attention (bin width 7ms). Average from five subjects. The circle marks the position of the attention cue; the cross marks the direction of gaze; the square indicates saccade target position which was randomized between right and left

In conclusion from Fig. 6 it becomes clear that even if attention is already focused on the target position, saccadic latencies are long. Attention must be briefly released as a necessary prerequisite for short latency saccades. This still leaves open the question, why no express saccades are made in total darkness, where there is neither a target for fixation nor a target for attention.

To examine this point more clearly, using the ordinary gap paradigm (see Section 1) we systematically increased the duration of the gap.

4. Effect of Gap Duration

As in Section 2, we used the nonrandom condition with the saccade target occurring always at 4° to the right. Four trained subjects were used in the series with different gap durations. In Fig. 7 the percentage of the express saccades is plotted versus the gap duration used. The order of the tests was pseudo-random with respect to the gap duration.

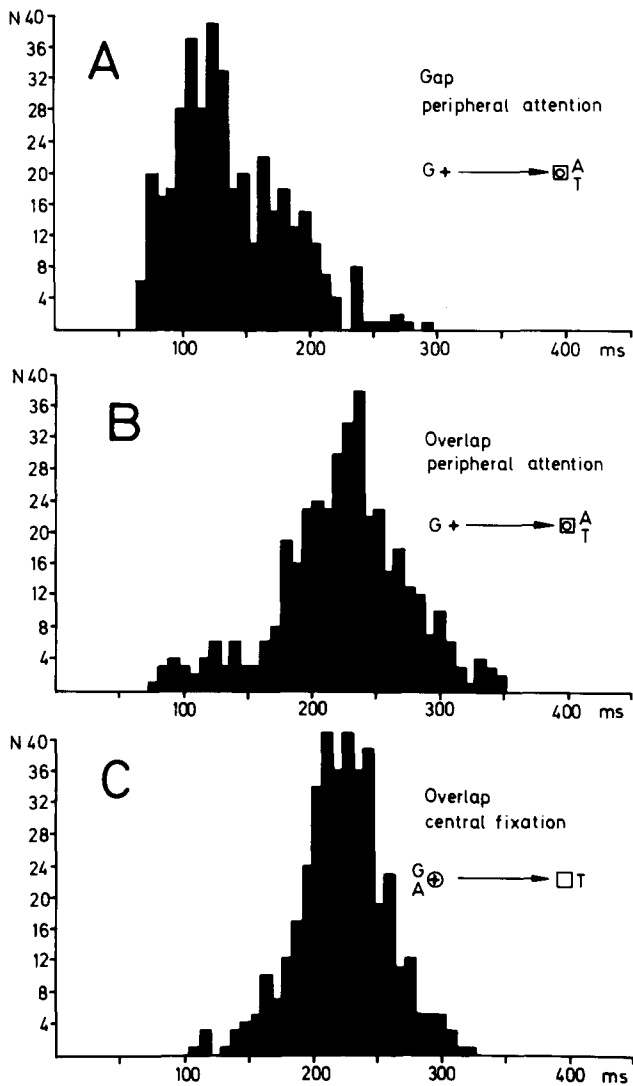


Fig. 6A–C. Distribution of saccadic reaction times as in Fig. 5 (average from four subjects). The target for visual attention was placed at the position of the target for the saccade (A and B). Data in C are obtained in the usual overlap paradigm with attention directed to the center

In the gap = 0 situation in which the target was presented simultaneously with the fixation point offset none of the subjects produced express saccades.

Figure 7 shows a drastic increase in the number of express saccades between gap = 0 and gap = 200 and a slow decrease for longer gap durations. For gap durations longer than 800 ms none of the subjects produced express saccades, in agreement with Fig. 3D.

Discussion

The results of the present study have shown that the physical presence or absence of a fixation point cannot account for the occurrence of express saccades: even in the presence of a foveal fixation point subjects were able to produce express saccades; these were, however, almost completely abolished if that point was attentively fixated. Since active fixation always requires engaged attention, we suggest that directed visual attention prevents the oculomotor system from producing ex-

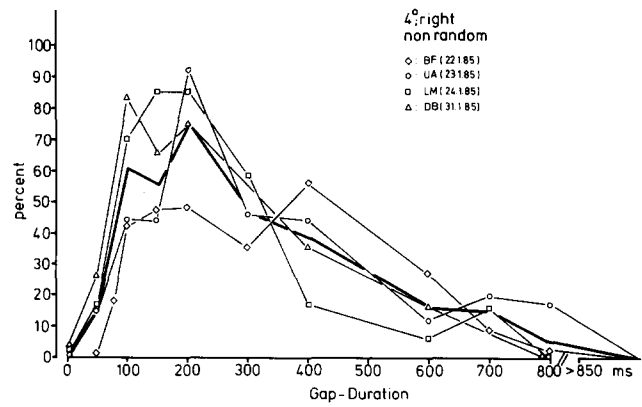


Fig. 7. Amount of express saccades (vertical) versus duration of the gap (horizontal). The heavy line represents the mean of the four individual sets of data

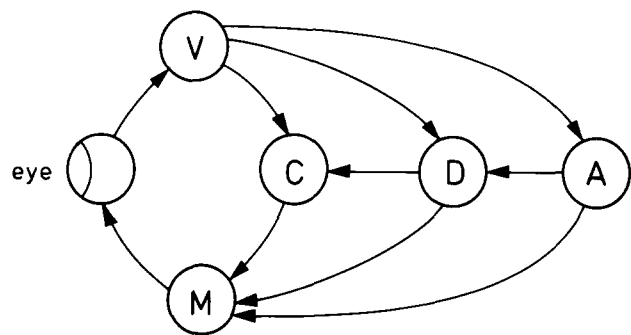


Fig. 8. Schematic diagram showing the main pathways and processes included in the preparation of voluntary goal-directed saccades. V = afferent visual structures including striate and prestriate visual cortex; C = computation of saccadic metrics including the superior colliculus; M = efferent oculomotor centers including the paramedian pontine reticular formation and oculomotor nuclei; D = decision making including the frontal eye fields; A = attention, including visual association cortex and parietal cortex. Arrows represent functional connections. Circles are assumed to operate like logical AND-gates with individual time delays corresponding to a time allowing for each of the intrinsic neural operations. Circles are not necessarily identifiable with single anatomically defined structures

press saccades (overlap paradigm). As a consequence one has to assume that interruption of attention directed to a visible point rather than interruption of fixation itself is responsible for the large number of express saccades in the gap paradigm. This assumption is supported by the other results of this study: (1) even in the absence of a foveal fixated light point almost no express saccades occurred if attention was directed to a definite area of the visual field (in the task where the subjects had to fixate attentively the middle of an incomplete cross before target appearance); (2) almost no express saccades were produced in the absence of a foveal spot if attention was directed to a peripheral “attention target” before stimulus appearance; (3) in the same task the number of express saccades increased considerably if the peripheral “attention target” was turned off a short time (200ms) before stimulus appearance.

In conclusion: if attention is directed to a part of the visual field at target appearance, no express saccades occur; express saccades are produced only if attention is disengaged before target appearance. We propose to include this release of visual attention as a separate process in the preparation of a goal-directed saccade. Figure 8 illustrates how the different proces-

ses – release from attention, A; decision making, D; computation of the metrics, C; afferent and efferent delay times, V and M – that have been discussed elsewhere (Fischer and Ramsperger 1986), are assumed to contribute to the preparation of a saccade. Usually the directions of attention and gaze are the same. As one step in the preparation of a saccade, the process of visual attention (and active fixation) must be interrupted, which takes a time that is included in the reaction time in the overlap paradigm. In the gap paradigm the disappearance of the fixation point initiates the processes V and A (Fig. 8) which are followed by the process D. The corresponding time periods can elapse within the duration of the gap. Therefore extremely short latency saccades occur, because their reaction time includes only processes V, C and M.

To explain the observation that with increasing gap durations above 300ms the amount of express saccades decreases again (Fig. 7) and that in total darkness almost no express saccades occur, two alternative hypotheses are proposed. First, assuming that the disappearance of the fixation point initiates the processes V and A (Fig. 8) which activates the process D, it might be that if the target does not appear within a certain time period (about 300ms) after the initiation of V and A, process D is deactivated which would lead to longer reaction times and to the disappearance of express saccades. Second, it might be that even in darkness the system can stay in the state of released attention only for short periods of time (in the order of 300ms after fixation point disappearance). If no target appears within that time period, attention is locked and must be released again before the next saccade, which therefore has a long reaction time.

Which are the neural mechanisms underlying visual attention? In the monkey's parietal cortex (area 7) cells have been shown to respond to visual stimuli (Robinson et al. 1978; Bushnell et al. 1981; Sakata et al. 1980). Their response is enhanced if the attention of the animal is directed to the stimulus, but the enhancement is independent of the occurrence of a goal-directed movement to the stimulus (e.g., a saccade directed to the stimulus) (Robinson et al. 1978; Bushnell et al. 1981). This behavioral enhancement of visual response of neurons in area 7 is assumed to reflect selective visual attention (Lynch et al. 1977; Robinson et al. 1978; Bushnell et al. 1981). Among the cells in area 7 that respond to visual stimuli, and whose discharge is modulated by visual attention, a subpopulation has been identified which fires tonically while the monkey gazes at a target light ("visual fixation neurons"; Mountcastle et al. 1975; Lynch et al. 1977).

As described above, we suppose that attention directed to a visual stimulus prevents saccades during fixation. Therefore, the oculomotor system cannot produce express saccades to a second visual target in the overlap paradigm. This could be explained assuming that the activity of the parietal "visual fixation neurons" inhibits the saccadic system during fixation and that their activity must be suppressed to enable the oculomotor system to produce a saccade. In fact, Lynch et al. (1977) have shown that 40% of the "fixation cells" in area 7 are suppressed before and during a saccade to a new target. We suppose that this suppression, which reflects interruption and shift of visual attention, takes some time, which leads to long saccadic reaction times in the overlap paradigm. In contrast, in the gap paradigm the inhibiting visual attention is interrupted before the appearance of the new target. The idea that fixation and visual attention is an active process which must be interrupted before a saccade is further supported by

the observations that visual fixation reduces the amplitude of saccades evoked by suprathreshold collicular stimulation and significantly increases the threshold for producing saccades elicited by collicular stimulation (Schiller and Sandell 1983; Sparks and Mays 1983; Goldberg and Bushnell 1981); and also that saccades elicited by electrical stimulation of area 7a are abolished by visual fixation (Shibutani et al. 1984).

There is also direct evidence for the notion that the visual-to-oculomotor system in the absence of saccades can be in two different states. Fischer and Boch (1985) have shown that cells in the visual association cortex (visual complex V4 in the pre-lunate gyrus) are activated in the continuous presence of a receptive field stimulus when the fixation point is suddenly switched off, yet it does not elicit a saccade to the peripheral stimulus. This activation occurs about 180–200ms after fixation point disappearance and is interpreted as a sign of the animal having changed its direction of attention without moving the eye.

The specific aspect of releasing attention as a process separate from moving and refocusing attention has been stressed by Posner et al. (1984). They showed that patients with discrete lesions in the parietal lobe had difficulties in directing their attention to a peripheral target contralateral to the side of the lesion in the presence of a central fixation point or a peripheral (ipsilateral) cue. Their study not only indicates the existence of the suboperation of disengagement, but also presents evidence that this operation needs an intact parietal lobe.

The system that mediates express saccades, therefore, seems to form a visual-to-oculomotor loop which can be inhibited by (cortical) activity reflecting visual attention. Figure 8 suggests further that this loop is also under the control of the process D which in turn is controlled by process A. Evidence that this second control instance is located in the frontal lobe comes from several earlier studies. First of all, the frontal eye fields are intimately related to goal-directed saccades (Bruce and Goldberg 1984). Secondly, it has been shown recently by Guitton et al. (1985), that patients with discrete frontal lobe lesions (following removal of frontal lobe tissue for intractable epilepsy) were unable to suppress saccades to a suddenly-appearing light stimulus. This suggests that the frontal lobes normally suppress inadequate reflexive eye movements towards visual targets. The authors also noticed that the visually-triggered saccades of these patients often had a reaction time of about 100ms, if no fixation point was present at target appearance (express time!) and concluded that a reflex-like loop (via superior colliculus) exists which is usually inhibited by cortical control originating from the frontal lobe.

Acknowledgements. This work was supported by the Deutsche Forschungsgemeinschaft, Sonderforschungsbereich "Hirnforschung und Sinnesphysiologie" (SFB 70, Tp B7).

References

- Boch R, Fischer B (1986) Further observations on the occurrence of express-saccades in the monkey. *Exp Brain Res* (submitted)
- Boch R, Fischer B, Ramsperger E (1984) Express-saccades of the monkey: reaction times versus intensity, size, duration, and eccentricity of their targets. *Exp Brain Res* 55:223–231
- Bruce CJ, Goldberg ME (1984) Physiology of the frontal eye fields. *Trends Neurosci* 7:436–441
- Bushnell MC, Goldberg ME, Robinson DL (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. I. Mod-

- ulation in posterior parietal cortex related to selective visual attention. *J Neurophysiol* 46:755-772
- Fischer B, Boch R (1983) Saccadic eye movements after extremely short reaction times in the monkey. *Brain Res* 260:21-26
- Fischer B, Boch R (1985) Peripheral attention versus central fixation: modulation of the visual activity of prelunate cortical cells of the rhesus monkey. *Brain Res* 345:111-123
- Fischer B, Ramsperger E (1984) Human express-saccades: extremely short reaction times of goal directed eye movements. *Exp Brain Res* 57:191-195
- Fischer B, Ramsperger E (1986) Human express-saccades: effects of daily practice and randomization. *Exp Brain Res* (submitted)
- Fischer B, Boch R, Ramsperger E (1984) Express-saccades of the monkey: effects of daily training on probability of occurrence and reaction time. *Exp Brain Res* 55:232-242
- Gauthier GM, Volle M (1975) Two dimensional eye movement monitor for clinical laboratory recordings. *Electroencephalogr Clin Neurophysiol* 39:285-291
- Goldberg ME, Bushnell MC (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *J Neurophysiol* 46:773-787
- Guitton D, Bachtel HA, Douglas RM (1985) Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. *Exp Brain Res* 58:455-472
- Lynch JC, Mountcastle VB, Talbot WH, Yin TCT (1977) Parietal lobe mechanisms for directed visual attention. *J Neurophysiol* 40:362-389
- Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Agana C (1975) Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J Neurophysiol* 38:871-908
- Posner MI, Walker JA, Friedrich FJ, Rafal RD (1984) Effects of parietal injury on covert orienting of attention. *J Neurosci* 4:1863-1874
- Robinson DL, Goldberg ME, Stanton GB (1978) Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J Neurophysiol* 41:910-932
- Sakata H, Shibutani H, Kawano K (1980) Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey. *J Neurophysiol* 43:1654-1672
- Saslow MG (1967) Effects of components of displacement-step stimuli upon latency of saccadic eye movements. *J Opt Soc Am* 57:1024-1029
- Schiller PH, Sandell JH (1983) Interactions between visually and electrically elicited saccades before and after superior colliculus and frontal eye field ablations in the rhesus monkey. *Exp Brain Res* 49:381-392
- Shibutani H, Sakata H, Hyvaerinen J (1984) Saccade and blinking evoked by microstimulation of the posterior parietal association cortex of the monkey. *Exp Brain Res* 55:1-8
- Sparks DL, Mays LE (1983) Spatial localization of saccade targets. I. Compensation for stimulation-induced perturbations in eye position. *J Neurophysiol* 49:45-63

Received August 9, 1985