

Express saccades and visual attention

B. Fischer and H. Weber

Department of Neurophysiology, University of Freiburg, D - 78 Freiburg, Germany

Electronic mail: franz.aiple@sun1.ruf.uni-freiburg.dpb.de

Abstract: One of the most intriguing and controversial observations in oculomotor research in recent years is the phenomenon of express saccades in monkeys and man. These are saccades with such short reaction times (100 msec in man, 70 msec in monkeys) that some experts on eye movements still regard them as artifacts or as anticipatory reactions that do not need any further explanation. On the other hand, some research groups consider them not only authentic but also a valuable means of investigating the mechanisms of saccade generation, the coordination of vision and eye movements, and the mechanisms of visual attention.

This target article puts together pieces of experimental evidence in oculomotor and related research – with special emphasis on the express saccade – to enhance our present understanding of the coordination of vision, visual attention, and the eye movements subserving visual perception and cognition.

We hypothesize that an optomotor reflex is responsible for the occurrence of express saccades, one that is controlled by higher brain functions involved in disengaged visual attention and decision making. We propose a neural network as the basis for more elaborate mathematical models or computer simulations of the optomotor system in primates.

Keywords: attention; cortex; dyslexia; express saccade; eye movements; fixation; oculomotor system; reaction time; saccade; vision

1. Introduction

Visual perception and cognition, movements of the retinal image, and eye movements are so closely related that one wonders how one can be studied without taking into account the others. The facts are straightforward:

1. During natural viewing conditions a normal adult subject makes 3–5 saccades in a second separated by periods of 200–300 msec during which the eyes do not make large or fast movements. These periods are usually called “fixations”: This terminology is avoided here because – as will become clear below – periods of no eye movements are not necessarily periods of active and attentive fixation but can just as well be periods where the eyes simply do not move.

2. If the retinal image as a whole is prevented from moving (by successful voluntary attempts not to move the eyes or by technical means), vision rapidly becomes blurred and the perception of the retinal image eventually fades away completely within 10 seconds.

3. The highly inhomogeneous structure of the primate retina, with an extremely high density of receptor and ganglion cells in the center, a specialized fovea, and a rapid decline of the cell densities toward the periphery makes it almost impossible to have a homogeneous and simultaneous percept of the total visual field without somehow moving the fovea to different positions and acquiring and integrating information from these successive “looks.” The existence of a fovea requires both eye movements and periods of fixation, that is, the active suppression of saccadic eye movements.

4. As a result of a complicated interaction between afferent, central, and efferent neural processes we perceive a complete and stable visual field, which can serve as a frame within which we see motion and within which we move ourselves or parts of our body.

This target article analyzes the coordination of visual processing as well as the generation and suppression of saccadic eye movements. Based upon experimental data rather than upon theoretical assumptions, visual attention emerges as an important mechanism that governs both visual perception and saccadic eye movements.

We first consider the result of a simple experiment in which express saccades are found. Express saccades are defined by their extremely short reaction times (70 msec in monkey, 100 msec in man), which often form a separate peak in the reaction time distribution. The reaction times of fast regular saccades are usually about 50 msec longer and often form a second peak in the distribution. Slow regular saccades have still longer reaction times of 200 msec or more. The experimental demonstration of express saccades is controversial because some authors report failing to elicit express saccades. Wenban-Smith and Findlay (1991) observed visually guided saccades with latencies of 100 msec but could not verify these as part of a bimodal distribution. Reuter-Lorenz et al. (1991) also found unimodal distributions, except for one subject who clearly showed a separate express peak. Kalesnykas and Hallett (1987) believe in express saccades but claim that visually guided saccades have latencies above 120 msec, whereas we maintain that under appropriate conditions the express saccades can have latencies even below 100 msec.

msec, in agreement with the findings of Jüttner and Wolf (1992).

Even when the existence of express saccades is accepted, there is the question of why such short-latency saccades occur. Is it an effect of warning or alerting which decreases reaction time (Ross & Ross 1980) or does anticipation produce an artificial peak in the distribution (Kowler 1990)? Premotor priming and sensory facilitation could also explain the latency reduction. In this article we argue that the attentional system controls the saccade system in such a way that express saccades occur in a certain state of disengaged attention, allowing other preparatory steps (e.g., decision making) to take place before target stimulus onset. This hypothesis is laid out in the form of a three-loop model.

In the first part of this article (sects. 3 and 4) a hypothesis will be developed mainly on the basis of work on human subjects. The second part (sect. 5) of the article analyzes data from corresponding experiments in monkeys to provide a neurophysiological and anatomical basis for the hypothesis. Both human and monkey data suggest that the attentional system controls vision and eye movements and that it has a dual functional structure which is under different amounts of voluntary control depending on the amount of practice the subjects have and on the state of maturation of the brain (sect. 7). Further supporting data from dyslexic subjects (sect. 8) and patients with neurological problems will be considered at the end (sect. 9).

It is up to future theoretical work to find a mathematical formulation for the hypothesis. Logical AND-gates with certain time constraints have been already used (Rogal & Fischer 1986) to model the data from experiments on eye-hand coordination in man (Fischer & Rogal 1986) as well as monkey (Rogal et al. 1985). This basic approach is used to simulate reaction time distributions and show how the model can work quantitatively.

2. Basic observations

Because any rapid shift of gaze by means of a saccadic eye movement (head and body movements, and hence the vestibular ocular reflex, are therefore not considered here) is preceded by a time of no eye movements (micro-saccades and slow drifts are not considered here either) one can manipulate the visual conditions prior to a saccade to get an idea of what goes on when the eye does not move; that is, when it is supposed to "see." The most straightforward manipulation is to remove the stimulus the eye is "looking at," that is, the fixation point, before the next saccade is generated. Such a situation can then be compared with one in which the fixation point remains visible. To determine whether the visuo-oculomotor system is actually in two different states at the time of occurrence of a new visual stimulus in these two situations, the subject can be required to make a saccade to the new target, with the reaction time used as an index. These two experimental conditions – the gap and the overlap paradigm – have been used in many of the reaction time studies.

2.1. Methods

Some of the data presented here have not been published elsewhere, therefore the experimental details are de-

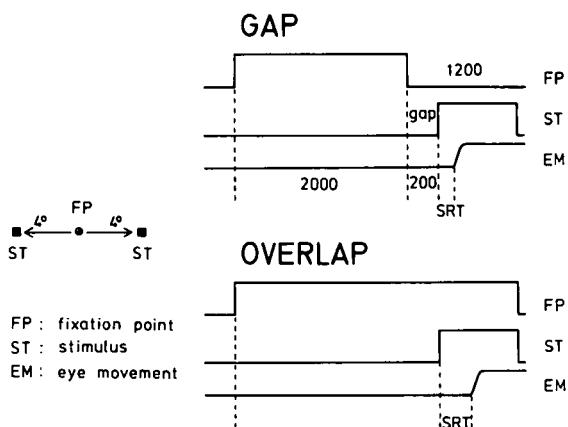


Figure 1. Spatial (left) and temporal (right) arrangements for a typical gap (upper) and overlap (lower) paradigm used in studies in man. Unless stated otherwise, the target stimuli were always presented randomly 4 deg to the left and right of the fixation point.

scribed below. The temporal and spatial arrangements are illustrated in Figure 1: During gap trials the fixation point was turned off before the target appeared; during overlap trials it remained on. The visual targets were computer-generated white squares (0.2×0.2 deg) presented in random order 4 deg to the right or left from the small (0.1×0.1 deg), red central fixation point on a green background at a distance of 57 cm from the subjects' eyes. The luminance of all stimuli was well above perceptual threshold. Target onset was synchronized with the frame impulse (frame rate 83 Hz) and, since the stimuli always appeared at the same horizontal level, the physical delay between the desired onset and the real onset of the stimuli was in the order of microseconds. Reaction times were determined offline by an analysis program which detects saccades by a velocity (30 deg/sec) and a duration (15 msec) threshold criterion. The result of the automatic evaluation of a trial was presented on the computer monitor. In case of artifacts or false detections the experimenter could either abort the trial or reanalyse it "manually" under visual control using the cursor. The data were stored and analysed further using a commercial graphics and statistics program (NCSS). The reaction time data are presented mostly in the form of a histogram using a bin width of 10 msec. Data from different subjects were pooled only if they all showed similar results. Statistical evaluation of the data is given in case it is necessary to support the interpretation of the results. Mean values are given in certain cases only, because most of the reaction time data are poorly characterized by a single mean value. Rather, the distributions and scatter plots are presented; in many cases these are self-explanatory with respect to the conclusions drawn here. To characterize multimodal distributions quantitatively we used a 3-Gaussian curve fitting procedure described in detail by Fischer and Weber (1990) and Weber et al. (1991). Further methodological details are given in the appropriate sections where the data are presented.

2.2. The gap effect and the express saccade

Saslow was the first to use gap and overlap trials with human subjects. He reported that under gap conditions saccadic reaction times are considerably shorter (ca. 140

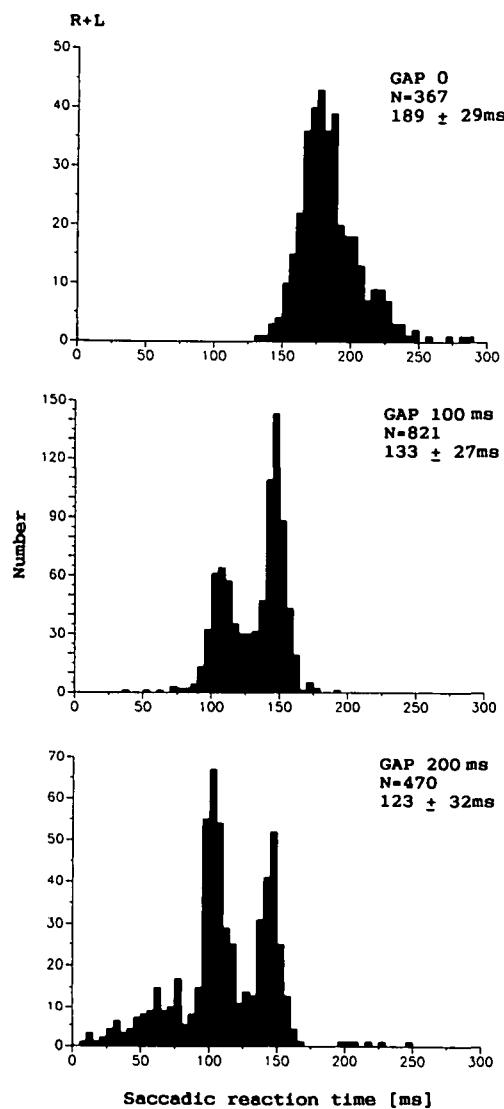


Figure 2. Effect of gap duration on the distributions of saccadic reaction times in man. The reaction times for right (R) and left (L) directed saccades are accumulated. Gap durations, numbers (N) of saccades, mean values, and standard deviations are given in each panel. Anticipatory saccades with latencies below 80 msec are excluded from the calculations.

msec) than under overlap conditions (ca. 200 msec; Saslow 1967b). This phenomenon is now called the gap effect. (As we will see below, the gap effect and express saccades are not the same phenomenon.)

When the experiment was repeated by Fischer and Ramsperger (1984), it was found that the distribution of saccadic reaction times was bimodal or even trimodal in gap trials: A first peak occurred around 100 msec and a second at about 170 msec; so the mean value was indeed on the order of 140 msec (Fischer & Ramsperger 1984). The middle and bottom panels of Figure 2 show such a distribution. Saccades contributing to the first peak are called express saccades; the others are fast regular saccades. The development of the express peak with increasing gap durations from zero to 200 msec is shown by Figure 2. The top distribution was obtained using the classical condition, that is, the fixation point was turned off at the same time the stimulus was turned on. Introducing a gap of 100 msec drastically changed the distribution.

It now consists of two peaks, one at about 100 msec and another at about 150 msec. Note that all reaction times became shorter: The mean value of 189 msec obtained with a gap of zero is reduced to 133 msec with a gap of 100 msec. The introduction of the gap has not only a latency-reducing effect but it also turns the distribution into a bimodal one. We will discuss this double effect further in section 10. Further increasing the gap duration to 200 msec increased the first peak and decreased the second peak. In addition, reaction times were between zero and 85 msec. We will see below that the latter are due to reactions of the subject to the offset of the fixation point or in anticipation of the target. The data presented in Figure 2 stem from a single subject who had considerable practice in oculomotor investigations.

After training the subjects in the gap experiment for many days it was found that the first peak increased and the second decreased or eventually disappeared altogether (Fischer & Ramsperger 1986), thus resulting in a unimodal distribution consisting almost exclusively of express saccades. Some other research groups (Reuter-Lorenz et al. 1991; Wenban-Smith & Findlay 1991) claimed to have difficulties in replicating the presence of double peaked distributions in the gap paradigm. However, looking at the data of Reuter-Lorenz et al. one finds that some of the distributions are indeed bimodal. For example, in their Figure 6 subject REP exhibits clearly separated peaks of express and fast regular saccades in the two gap conditions. Wenban-Smith and Findlay (1991) even question the existence of a separate population of express saccades. Only three subjects were tested in their study, however, one of them producing a single peak of express saccades while the others showed "some suggestion of bimodality." To clarify this critical point by looking at the interindividual variability in the data of many subjects, we have recently measured the saccadic reaction times of 20 naive adult subjects (Fischer et al. 1993). Analysing the data statistically with the help of a curve-fitting procedure it was found that in the gap paradigm the vast majority (17 subjects) produced reaction times in the express range and, in addition, 12 of them showed clearly separated peaks of express and fast regular saccades as indicated by a bimodality factor. Only three subjects did not produce any express saccades. Thus, a bimodal distribution of express and fast regular saccades is quite frequently observed, but its presence is not a prerequisite for the existence of an express saccade population. These data also show that express saccades can be obtained in naive subjects without any previous training.

The distribution of reaction times from overlap trials exhibits a rather broad peak with values scattered around 200 msec. These saccades are called slow regular saccades. An example of this general result is given in Figure 3B. In A the distributions for gap trials are shown from the same subject and from the same experimental session. This subject was highly trained and produced a single peak around 100 msec consisting almost exclusively of express saccades (Fig. 3A); a few saccades below 85 msec may be anticipatory and very few fast regular saccades can be seen at about 160 msec.

By contrast, saccadic reaction times are all longer than 150 msec during overlap trials (Fig. 3B). Thus, keeping the fixation point visible changed the distribution of saccadic reaction times completely and the question

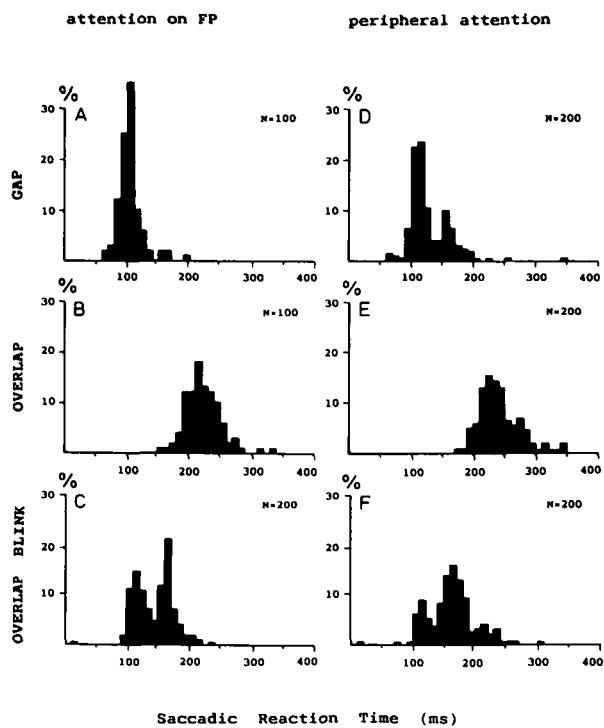


Figure 3. Effect of central (left part) and peripheral (right part) attention on the distribution of saccadic reaction times in gap (A and D), overlap (B and E), and overlap with blink trials (C and F). Data from a single subject with target location randomized between right and left (further description in the text).

arises: Why? Obviously, the difference between gap and overlap trials is not only that in one case the fixation point is absent (gap) while in the other it is present (overlap) at the time the target occurs but also that there is an event (the offset of the fixation point) that precedes the saccade in gap but not in overlap trials. This event (one may argue) elicits a saccade which anticipates the occurrence of the target.

Before we discuss other processes that may give rise to the large difference in reaction times, we will first consider the many pieces of experimental evidence indicating why express saccades cannot be anticipatory or predictive in nature but rather are to be considered as visually guided saccades. (The rest of Fig. 3 will be treated later.)

3. Express saccades: Anticipatory or visually guided?

Express saccades were first identified by Fischer and Boch (1983) in the monkey and subsequently by Fischer and Ramsperger (1984) in man. In both studies, in which gap trials were used, several control experiments were conducted to eliminate anticipation or prediction as an explanation of the occurrence of express saccades. Here we list the arguments (in no particular historical or logical order).

1. On trials where, unexpectedly, no target appeared after the gap (catch trials), neither human subjects (Jüttner & Wolf 1992) nor monkeys (Fischer & Boch 1983)

make saccades at the corresponding time of 300 msec or 270 msec after fixation point offset, respectively.

2. Express saccades can be obtained in overlap trials both in human subjects (Mayfrank et al. 1986) and in monkeys (Boch & Fischer 1986). This takes some practice or training for monkeys and normal adults, but children and youngsters (aged 8 to 17 years) and in particular certain dyslexic children make express saccades in the overlap condition spontaneously and without any practice (Fischer & Weber 1990).

3. If the gap duration is randomly varied between 200 and 220 msec the narrow express peak is displaced by 20 msec (as measured from fixation point offset) in the 220 msec gap trials as compared with the 200 msec gap trials (Fischer & Ramsperger 1984). If the gap duration is randomly varied between 100 and 200 msec or between 200 and 300 msec so that the onset time of the target is unpredictable, express saccades are still obtained. Examples of the corresponding distributions are shown in Figure 9.

4. The exact reaction times of the express saccades depend critically on the luminance contrast, size, and eccentricity of the target stimulus (Boch et al. 1984). This fact alone contradicts the notion of anticipation. It is not the luminance contrast itself that determines the reaction time, however, because isoluminant colour contrast target stimuli elicit express saccades of about the same latency (Weber et al. 1991).

5. The number of express saccades depends on the relative luminance of the fixation point (Mayfrank et al. 1986).

6. The size of the express peak in the monkey can be increased by daily practice. The practice effect, however, occurs only for saccades of the same size and direction as have been used during the training session, not for other saccades (Fischer et al. 1984).

7. There are subjects who produce many express saccades to one side but not the other. Figure 6 presents the data of such a subject.

8. The number of express saccades is decreased rather than increased if the subject directs his attention to the target position (see below).

9. Anticipatory saccades are obtained and identified by their reaction times below 85 msec (in humans) in gap trials with constant (nonrandomized) target position. These saccades disappear almost completely when the target position is randomized, while express saccades are still present. This is true regardless of whether only the direction or both the direction and the location are randomized (Weber et al. 1992). Anticipatory saccades have a somewhat smaller velocity as compared with the main sequence (Bronstein & Kennard 1987), whereas express saccades have normal velocities (Fischer & Weber 1992).

10. If the target position is randomized between right and left, saccades are sometimes made in the wrong direction. These saccades have latencies below 90 msec and are anticipatory by definition. This can be seen from Figure 4, where we plot the reaction time distribution for saccades that are correct and incorrect in direction. These data have been accumulated from a single subject using the methods described above. The minimum reaction time of a visually guided saccade is therefore in the order of 100 msec, which comes very close to the number estimated by other authors (Kalesnykas & Hallett 1987;

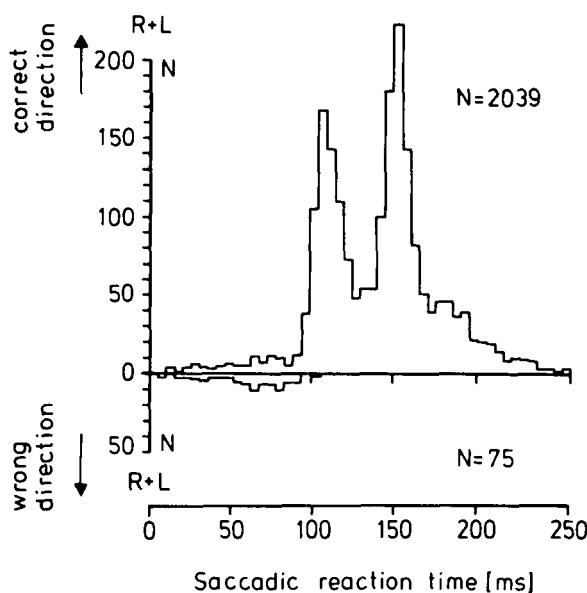


Figure 4. The distribution of saccadic reaction times of 2,114 saccades (randomly to the right or left) from a single subject. The reaction times of the 75 direction errors the subject made involuntarily are depicted below.

Wenban-Smith & Findlay 1991). The direction errors as well as amplitude errors of these anticipatory saccades can be corrected (after extremely short intervals down to zero!) at express saccade latencies (Fischer 1986).

11. In an "anti"-saccade task, express saccades are absent, but anticipatory saccades occur (see Fig. 5). The details of the "anti"-saccade experiment are described elsewhere (Fischer & Weber 1992).

12. Patients with frontal lobe lesions are unable to anticipate but they make a large number of express saccades (Braun et al. 1992; Guitton et al. 1985).

On the basis of these arguments it is evident that the notion of the express saccades being anticipatory or predictive in nature must be wrong. It will become clear, however, that anticipatory and express saccades may both be preceded by certain common preparatory processes. The difference is that express saccades are visually guided (i.e., they need the onset of a visual stimulus as a trigger and a target) but anticipatory saccades are not. In addition, anticipatory responses require the presence of the frontal lobe but express saccades do not (Braun et al. 1992).

Several studies of saccade dynamics have shown that saccades elicited in the absence of a visual stimulus and, in particular, predictive or anticipatory saccades, have slower velocities than visually guided saccades (for a review see Becker 1989). Consequently, there have been attempts to make use of this velocity difference as a criterion to distinguish between anticipatory and visually guided saccades. The reaction time of this velocity transition indicates that it occurs surprisingly early, that is, between 30 and 70 msec (Smit & van Gisbergen 1989). Nevertheless, these authors concluded that visually guided saccades in man cannot have reaction times below 120 msec, thereby confirming the claim of Kalesnykas and Hallett (1987). The data of Smit and van Gisbergen (1989), however, as well as the existence of express saccades with latencies even below 100 msec (given optimal physical

and psychological conditions) obviously show that the minimum latency of a visually guided saccade is on the order 100 msec.

4. The express saccade: An optomotor reflex

So far we have argued that the express saccade is visually guided, that is, it occurs in response to the onset of a visual stimulus. Now we will argue that the express saccade occurs only in response to the onset of a visual stimulus, which is not only the temporal trigger but also the spatial target for the eye movement.

Let us consider a situation that is physically identical with the normal gap task (in which express saccades can be obtained easily and frequently), but the instruction is changed: The subjects are asked to make a saccade in the direction opposite to the side where the stimulus occurs. In this so-called antitask the visual information is no longer in register with the motor information necessary to guide the eye to the desired position. The distribution of reaction times obtained in the normal and the antitask is shown in Figure 5. The top distribution shows the usual bimodality with a clear express peak at 100 msec. The second panel shows the reaction times of those saccades that the subject made involuntarily to the target rather than to the opposite side (these are "direction errors" in the sense of the antitask). It is interesting to note that this distribution shows a clear express peak as well. The bottom panel shows the reaction times of the antisaccades: An express peak is clearly missing. This experiment shows the impossibility of generating express saccades to a position where no target appears. This point can be made even stronger by a slight change in the experiment. The subject is instructed to make saccades always in the same direction, whereas the stimuli occur randomly on the right or left side. Yet in this situation express saccades are obtained only on trials that happen to be normal ones even though on antitrials the subjects know in advance the time, direction, and size of the saccade they are supposed to make (Fischer & Weber 1992).

The conclusion from this experiment is that the express saccade needs the onset of the stimulus at the position to which the saccade will be directed. The express saccade appears as a reflex-like optomotor reaction that brings the fovea to the stimulus or close to it. We will see below that this reflex is usually inhibited and we will consider the different circumstances under which the reflex is disinhibited. For example, in neurological patients, in some dyslexics, and in normal adults after practice or when given certain instructions, express saccades occur much more frequently than in normal naive adults. It must nevertheless be borne in mind that there are naive normal adult subjects who make express saccades in the gap task and even in the overlap task (Fischer et al. 1993). The notion that express saccades occur only after training is wrong.

4.1. Gain control of express saccades

For regular saccades (above 2 deg in size) the gain, that is, the ratio between the size of the saccade and the eccentricity of the target, is one or slightly less for larger

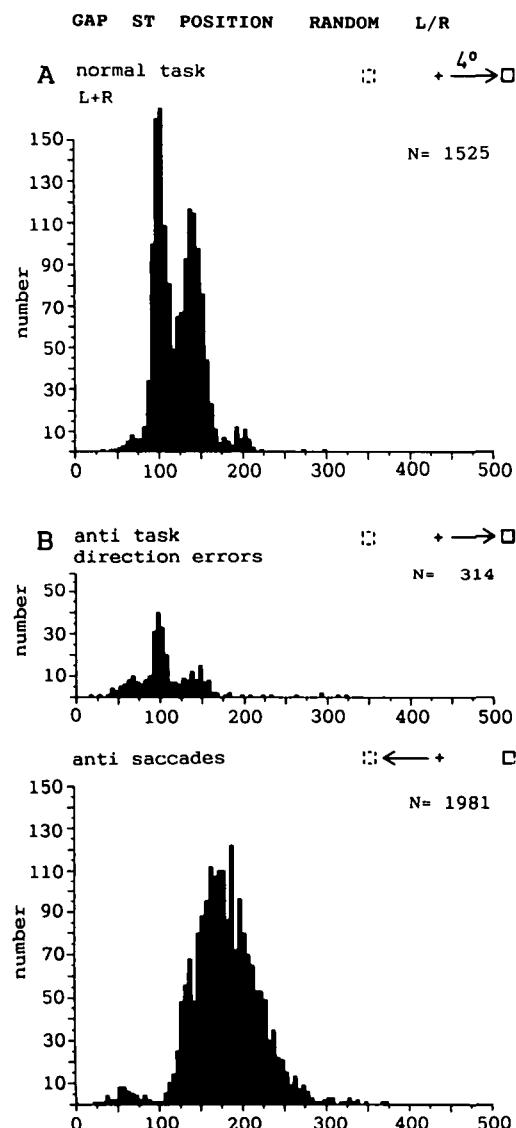


Figure 5. Distributions of saccadic reaction times in a normal gap task (upper) and an antigap task (lower). Note the absence of an express peak in the lower graph. The middle panel shows the reaction times of the saccades the subjects made involuntarily to the target rather than in the opposite direction as required in the antitask. Note the presence of an express peak. The data are taken from Fischer and Weber (1992).

saccades, which quite often undershoot the targets (Becker 1972; Henson 1978). The mean value of the gain of express saccades appears to be smaller than that of regular saccades. Figure 6 shows a scatter plot of saccadic amplitude versus reaction time. The data are obtained with random target position for a single subject as described above. One clearly sees the anticipations (only to the right side for this subject) characterised by a large scatter of their amplitudes. The express saccades, in particular those to the left side, have smaller amplitudes than the regular saccades. According to our unpublished observation (3 subjects, 4,361 saccades), the express gain (target at 4 deg) is 0.91 whereas that of the regular saccades is 0.99. These numbers may depend on the eccentricity of the target because for very small saccades (below 1 or 2 deg) the proportion of express saccades has been found to decrease (see below) and all saccades begin

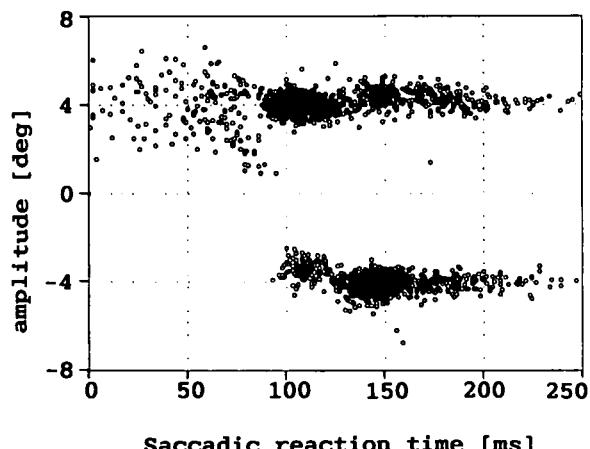


Figure 6. Scatter plot of saccadic reaction time versus saccade size for right (positive) and left (negative) directed saccades of a subject who produced an asymmetric pattern of reaction times. The data points below 80 msec are from anticipatory saccades to the right as well as from direction errors (i.e., saccades to the right when the target occurred at the left). Note the complete absence of anticipations toward the left side. The graph also shows the difference in amplitude between express and regular saccades.

to show a tendency to overshoot the targets so that their gain becomes larger than one (Weber et al. 1992).

Under certain circumstances the saccadic gain is changed, however, and the question arises whether or not the express saccades undergo similar gain changes. Because the express saccade obviously uses a rather short pathway (see below), one might expect its gain to be fixed and not modifiable by the experimental conditions. Instead, the experimental results are quite different:

1. The global effect, first described for regular human saccades (Findlay 1982), exists also for express saccades in man. This means that an express saccade elicited by the simultaneous onset of two stimuli at different but neighbouring positions lands somewhere in the middle rather than at one of the two targets (Weber et al. 1993).

2. Similarly, express saccades in the monkey are subjected to an adaptive gain change, already described for regular saccades in the monkey (Albano & King 1989; Fitzgibbon et al. 1985) and in man (Albano & King 1989; Deubel et al. 1986; Miller et al. 1981). If the first target for the saccade is replaced by a second target at the beginning of the saccade to the first target then – after some practice time – the saccade to the first target becomes larger or smaller, that is, the gain increases or decreases, depending on whether the second target occurs farther away or closer than the first target (Latanov et al., unpublished observation).

3. Finally, we observed that human but not monkey express saccades show a considerable range effect, as described for human regular saccades (Kapoula 1985; Kapoula & Robinson 1986). This means that the size of the express saccades to a target at a given position depends on whether the target at that position is presented in random order together with single targets at other positions or in the same position all the time (Weber et al. 1993). Other intertrial effects will be considered in section 6.3.

These gain changes must occur in the striate cortex or beyond, because electrical stimulation of the superior

colliculus of already adapted monkeys results in saccades of the unadapted size (Fitzgibbon et al. 1985). If one assumes that prestriate cortical areas do not contribute to the determination of the amplitude of a saccade then it must be concluded that the direct or indirect messages from striate cortex to the oculomotor centers can be modified.

5. The express way – anatomy and physiology

Investigation of the anatomical connections from the retina to the oculomotor centers in the brain stem reveals several possible pathways (for review see Fischer & Boch 1990): (1) The shortest connection originates from the large retinal ganglion cells that send their axons directly to the superior colliculus (Perry & Cowey 1984), which in turn projects to the brain stem (Harting et al. 1980). (2) Another pathway includes the lateral geniculate body and the striate cortex, from which layer V cells send their axons to the superior colliculus (Tootell et al. 1988). (3) A still longer pathway runs through the visual cortex to the frontal eye fields (Barbas & Mesulam 1980) and from there either directly to the brain stem (Glickstein et al. 1985) or indirectly through the superior colliculus (Künzle et al. 1976) to the brain stem or even more indirectly through the caudatum and the substantia nigra pars reticulata to the superior colliculus (Astruc 1971).

Possibility (3) must be excluded because express saccades – unlike regular saccades – survive lesions of the frontal eye fields but not lesions of the superior colliculus (Schiller et al. 1987). Possibility (1) must likewise be excluded because express saccades cannot be obtained without the striate cortex (Boch 1989). Higher cortical areas – such as the prelunate cortex (V4) or the parietal cortex (A7) – can be involved only indirectly, because the latencies of the visual responses of the cells in these cortical areas are in the same range or even longer than the express saccade reaction times (Tanaka et al. 1986) and/or because their malfunction increases the number of express saccades, as has been shown, for example, by chemical lesions in area V4 (Weber & Fischer 1990b). Another intriguing result came from an experiment in which a monkey was trained to make saccades to a small white stimulus appearing at a particular location in the visual field. In parallel with the training the stimulus preferences of single cortical cells in V4 with receptive fields including the “trained” location were modulated. After several weeks of recording the majority of these cells responded optimally to the “training” stimulus whereas cells with receptive fields elsewhere showed no changes of their stimulus preference. This effect paralleled a spatially selective increase in the proportion of express saccades toward the “trained” stimulus (Weber & Fischer 1990a). Both long-term effects may be regarded as a stimulus-selective “sensory priming,” which also favours the execution of a very fast response toward an object of special importance in the life of the animal and may therefore be of behavioural significance.

The indirect control of the parietal cortex over the generation of saccades becomes evident from the fact that electrically elicited eye movements are abolished when the monkey actively fixates a foveal stimulus during the stimulation (Shibutani et al. 1984). A very similar observa-

tion has been made in the frontal eye fields (Goldberg et al. 1986). The frontal eye fields nevertheless contribute considerably to the control of saccades, not only directly to the generation of regular saccades, but also indirectly by sending foveal signals for maintaining or releasing fixation (Latto & Coway 1971).

Finally, we consider the temporal aspect: Retinal ganglion cells have latencies of their visual responses in the order of 20 msec or more. Another 10 msec are needed for transmission up to the striate cortex. Electrical stimulation in the superior colliculus elicits saccades after about 20 msec from the stimulus. Given a saccadic reaction time of 70 msec there are only 20 msec left for central computational time, which is needed to evaluate the correct direction and amplitude of the express saccade.

In conclusion, lesion experiments and considerations of transmission times suggest that the express way includes the lateral geniculate body, the striate cortex, the superior colliculus, and the brain stem. Control over this pathway may be taken – directly or indirectly – by the frontal eye fields or the parietal cortex. The nature of this control mechanism should become clear from experiments in which one attempts to suppress the occurrence of express saccades.

6. Suppression of express saccades

Because neither the physical conditions nor anticipation and prediction can account for the occurrence of express saccades, the difference of saccadic reaction times (SRT) in gap and overlap trials calls for another explanation. One possibility is to study the conditions – besides the overlap paradigm – under which express saccades are suppressed in subjects who can make them in the gap task.

6.1. Engagement of visual attention

In this section we will discuss the idea that the disappearance of the fixation point in gap trials facilitates the disengagement of visual attention leading to a state in which saccades can be generated after shorter reaction times, whereas during overlap trials visual attention is engaged and saccades are inhibited. The time it takes for visual attention to disengage adds to the reaction time and accounts for the long latencies in overlap trials as compared with the short latencies in gap trials, where the disengagement (*and perhaps other preparatory processes*) can take place during the gap.

The first attempt to test the hypothesis was to very briefly (15 msec) extinguish (blink) the fixation point 200 msec before the target occurred. Except for the extinction (blink), this situation is physically identical with overlap trials. The idea is that the blink can be used as a physical event to initiate the process of disengagement. The result of this experiment is shown in Figure 3C. One clearly sees a peak of express saccades and many fast regular saccades. The introduction of the blink (a physical change) has changed the unimodal distribution of slow regular saccades (Fig. 3B) into a bimodal distribution. Figure 3A shows the result of the usual gap task with a single express peak.

The second attempt to test the hypothesis was to ask the subject always to direct (engage) his attention to one

of the two possible positions of the peripheral target during gap trials. Figure 3D shows the result (same subject). The peak at 100 msec (express saccades) is clearly reduced and a second peak (fast regular saccades) appears. The change in instruction (a mental change) has changed the unimodal distribution of express saccades (Fig. 3A) into a bimodal distribution. Important to note here is that visual attention directed to the target position increased the number of fast regular saccades rather than reducing it. In other words: Engaged visual attention produced a "cost" of time in some trials and no "benefit" in others.

If the blink facilitated the disengagement leading to express saccades in overlap trials and if the instruction to direct attention facilitated the engagement in gap trials leading to a reduction of the number of express saccades then the instruction to direct attention to the target position instead of the fixation point should leave saccadic reaction times unchanged in overlap trials because attention is engaged in both situations. The result of this test, shown in Figure 3E, when compared with the result in Fig. 3B confirms the above prediction.

If, finally, the instruction to pay attention to the target position is given in overlap trials with a blink, the number of express saccades should be reduced (Fig. 3F) as compared with the case where attention is directed to the fixation point (Fig. 3C) because the blink has a lower chance of initiating the disengagement. The equivalence of the fixation point and a peripheral stimulus as attention targets for the occurrence of express saccades has been explicitly shown by Braun and Breitmeyer (1988).

In conclusion, visual attention acts on the preparation of visually guided saccades in a way suggesting that directed (engaged) visual attention increases the overall reaction time whereas disengaged attention reduces it. The change in reaction time, however, is not a shift of a (unimodal) distribution but rather a modulation of the size of (at least) three distinct peaks in the distribution. In particular, engaged visual attention tends to eliminate the express peak as well as the peak of fast regular saccades. In light of the reflex hypothesis one can say that engaged attention inhibits the saccade system and especially the reflex. Attentive fixation in this context appears as just a special state of engaged attention in which attention is directed to a foveal stimulus thereby inhibiting the saccade system.

The idea of the attentional system acting in three different steps – disengage, move, engage – as derived here from eye movement data alone was first proposed by Posner (1984), who studied manual reaction times of patients with parietal lobe lesions. Posner's concept is that a "benefit" in reaction time is obtained when attention is engaged at the position where the stimulus is going to be presented and a "cost" when the stimulus appears somewhere else. We have found that the subjects can maintain the state of disengaged attention for some time in the order of some hundred milliseconds and that the most dramatic changes in reaction time are observed when the target stimulus is presented during the time of disengaged attention (Mayfrank et al. 1986). Recently, Mackeben and Nakayama (1993) found that in normal human subjects shifts of visual attention as measured by a vernier detection task are speeded considerably by the introduction of a temporal gap between fixation mark offset and

cue onset. They concluded that their results support directly the three-step concept of attention, especially that of the disengagement. There of course exists a large body of work on attention in the psychology literature, but here we have considered only those aspects that are closely related to the saccade system.

Other authors have also used the gap task and found express saccades in only some of their subjects (Reuter-Lorenz et al. 1991). Their methods were not identical to the simple task we used, however, because they randomly inserted catch trials and always used a warning tone even in overlap trials. These authors nevertheless obtained a gap effect. Its size was unusually small, however, in the order of 30 msec, which we attribute to a latency decrease resulting from the introduction of the tone (see also sect. 6.1.1 of this article). Moreover, they found no gap effect at all with antisaccades, which is in clear contrast to our results (Fischer & Weber 1992); neither did they find a decrease of manual latencies, which is also at variance with earlier studies in man (Fischer & Rogal 1986; Ross & Ross 1981) and in monkeys (Rogal et al. 1985). Despite this difference in the experimental results, Reuter-Lorenz et al. attributed the gap effect to a facilitation of premotor programming in the superior colliculus. This idea is not necessarily in contrast with the concept of attentional disengagement, because they leave open what the physiological/psychological meaning of "facilitation" is, from whence the corresponding signal arises, and along which pathways it arrives at the superior colliculus. For example, one could regard the facilitation as a neural sign of attention becoming disengaged.

Further investigations of the gap phenomenon come from Ross and Ross (1980; 1981). These investigators obtained a considerable gap effect (about 75 msec with gap durations of 100 and 300 msec) with saccadic (Ross & Ross 1980) as well as manual choice reaction times (Ross & Ross 1981). Unfortunately, all reaction times below 130 msec were excluded from their analysis, so that eventually occurring express saccades would have been eliminated. These authors consider the extinction of the fixation stimulus prior to target onset a warning event, which is assumed to exert a facilitating effect on the latency of saccadic or manual responses to a peripheral target. The resulting reduction of latencies is assumed to reflect a "general preparatory or alerting process that affects the preparatory steps related to the programming of the saccade to the target stimulus that follows." Although this claim is not at variance with our concept of saccade preparation, we regret to see that the Ross and Ross papers lack any discussion about the neurophysiological nature of such facilitatory processes.

A general shortcoming of the facilitation concept, proposed also by Reulen (1984), is that it cannot explain the occurrence of more than one mode in the latency distribution; neither can it account for the occurrence of express saccades in overlap trials, where there is no external stimulus triggering the facilitation process. We will take up these points again in section 10.

6.1.1. Nonvisual stimuli. If the offset of the fixation point initiates the disengagement of visual attention, thus triggering one process in the preparation of the next saccade, it should be possible to disengage one's attention also on the command of a nonvisual stimulus. Kimmig (1986) has

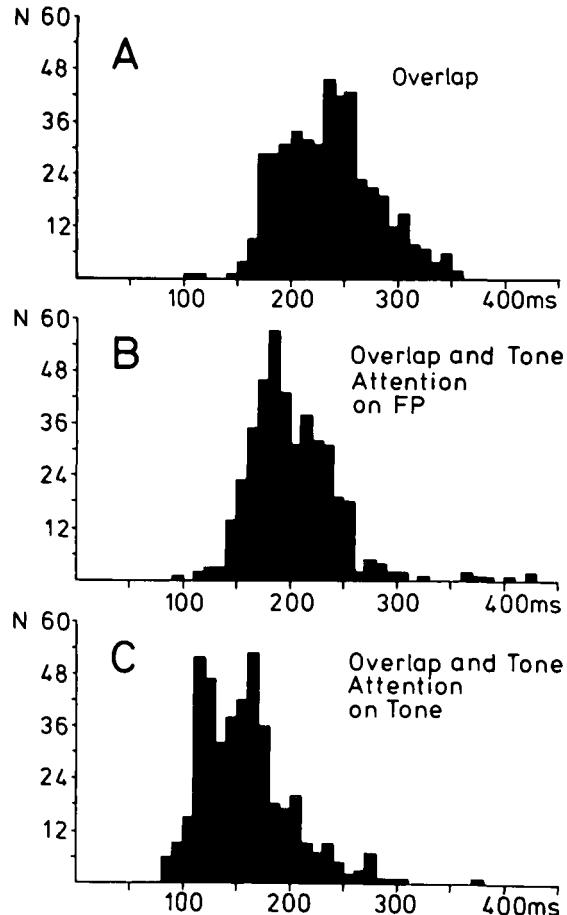


Figure 7. Saccadic reaction times obtained in the overlap task (A) and with an additional tone (B and C). In B the subject attended to the fixation point ignoring the tone; in C the subject attended the tone ignoring the fixation point. Note that the distribution turns into a bimodal one when the tone is attended.

used a short acoustic signal preceding target onset by 200 msec in the overlap task. Whether express saccades were obtained or not depended on whether the subject paid attention to the tone or to the fixation point. Figure 7 shows this effect. In A the result of the control experiment with overlap trials is shown. In B and C the physical conditions were the same, but the subject was told to pay attention to the fixation point (B), whereas in C the tone had to be attended. As a result, an express peak was absent in B but present in C. The distribution in B nevertheless differs from that in A: The tone, even when not attended, reduced the reaction times. What exactly the tone does for the preparation of the saccade in this case is not clear. It is evident, however, that whatever it is, it cannot be prevented voluntarily. Note also that the tone does not by itself trigger an express saccade – this is done by the onset of the target. Rather, the tone provides a signal that can be used to disengage attention, which will in turn enable express saccades to occur in response to the target. The same of course applies to the offset of the fixation point or any other external (sensory) or internal event that gives rise to a disengagement of attention.

Ross and Ross (1981) also found a considerable reduction of saccadic latencies with the onset or offset of an auditory signal 100 or 300 msec prior to the onset of the saccade target, comparable to their gap effect obtained

with visual events (even though these authors considered only saccades with latencies above 130 msec). They emphasize the generality of what they call the facilitating effect of a nonspecific warning event preceding target onset. We, however, feel that saying the tone is used by the subject as a warning signal is not an explanation but rather another verbal description of the latency-decreasing effect of the tone. Reuter-Lorenz et al. (1991) used an overlap condition with a warning tone occurring either 200 or 300 msec before target onset, which resulted in latency distributions with mean values of about 180 msec (mostly fast regular saccades). This is very fast when compared with other studies, where mean values in the order of 200 to 250 msec are reported (Kalesnykas & Hallett 1987; Mayfrank et al. 1986; Saslow 1967b; and others), and is likely to result from the introduction of the tone. This assumption might explain the small latency differences (gap effect) between gap and overlap distributions in that study, because a kind of gap effect is already present with the overlap-tone condition.

All these data nevertheless show that the signal for the disengagement may be generated through different sensory systems, the visual system (e.g., the offset of the fixation point) being only one possibility. The fact that express saccades can be obtained during overlap trials without any physical event preceding target onset (see sect. 7) also shows that the disengagement signal can be generated internally.

6.2. Small saccades

Figure 8 shows a scatter plot of saccadic reaction times versus saccade size for a single human subject in a gap experiment with the targets appearing randomly at different positions between 0.5 and 10 deg from the fixation point. The horizontal band at 100 msec represents the express saccades. Saccades above 5 deg are almost exclusively of the express type. Between 2 and 4 deg one clearly sees regular saccades in addition to the express saccades. Below 2 deg express saccades are virtually absent and below 1 deg the regular saccades have increasingly long latencies (Weber et al. 1992). An increase of saccadic latency for small saccades (below 0.5 deg) has been reported earlier (Wyman & Steinman 1973b) but these authors did not distinguish between different groups of saccades according to their latencies.

The experiment with small saccades was repeated in a monkey. The animal was trained in a fixation and a saccade gap task and produced a reasonable number of express saccades to a target positioned at 4 deg in the left visual field. If the target eccentricity was decreased stepwise below 1 deg express saccades disappeared but regular ones were still present in quite the same way as in man.

This experiment shows that the fovea is surrounded by a region into which one can make saccades but these cannot be of the express type. Even extensive training of the subjects (man and monkey) did not lead to small express saccades. Thus it looks as though an express way exists only for larger saccades. Alternatively, the offset of the fixation point and the following disengagement could disinhibit only that part of the saccade system, that generates saccades larger than 1 or 2 deg.

It was also found that anticipatory saccades were largely reduced in number as compared to the case in which the

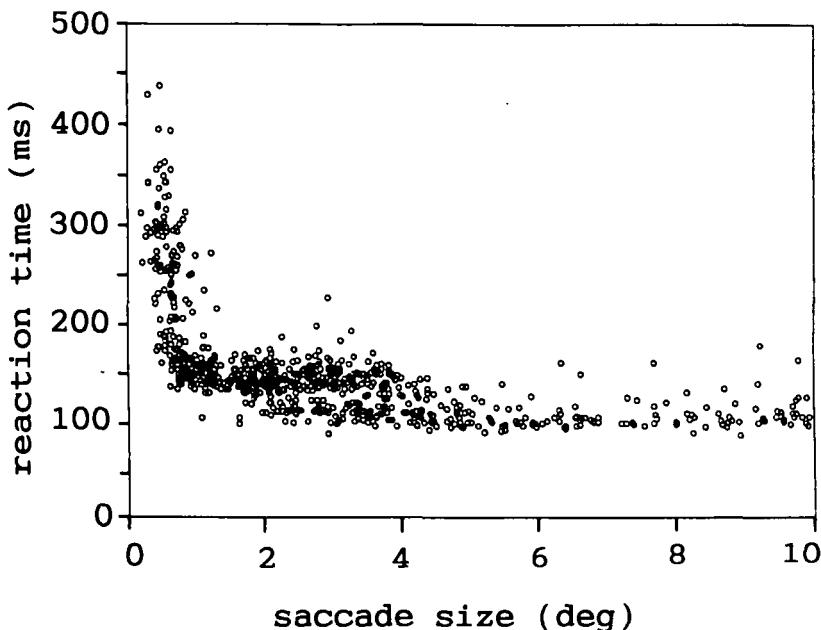


Figure 8. Scatter plot of saccade size versus reaction time. Express saccades can be seen between 2 and 10 deg. Fast regular saccades occur between 0.5 and 4 deg. Below 0.5 deg reaction times increase drastically. The data are taken from Weber et al. (1992).

target always appeared at larger distances, say 4 deg to the right. This observation shows that anticipatory and express saccades have something in common: They both need the disengagement of visual attention as one condition for their occurrence. The express saccade, however, in contrast to the anticipatory saccade, needs the physical onset of the target at a sufficiently large distance from the fovea.

The reduction of the number of anticipations for small eccentricities raises another question. Is it possible to make small saccades – voluntarily or involuntarily – in the absence of a target? The answer comes from an experiment in which the target again appeared always in the same position at 1 deg but on some trials – unpredictably for the subject – no target appeared (catch trials). The task was always to make a saccade to the 1 deg position. The result was that on both types of trials many saccades were triggered by the offset of the fixation point and express saccades were absent. The important observation was that the size of the saccades obtained on the catch trials was clearly greater than 1 deg and clearly larger than the size of the saccades obtained on the target trials. This observation confirms a previous report (Haddad & Steinman 1973) that subjects could make voluntary saccades as small as the miniature saccades during fixation only if the targets were visible. This explains the reduction of the number of small anticipations because the anticipations must be regarded as saccades that are initiated before the information of the target position was properly received.

In a further experiment we applied the overlap paradigm with small (1 deg) and larger (4 deg) saccades. Comparison of SRTs in gap and overlap conditions with the same target eccentricities revealed that a clear gap effect was also present for the small saccades: Although slow regular saccades were obtained mostly with the overlap condition, the gap favours the occurrence of fast

regular saccades. It can therefore be concluded that the signal of a disengagement of attention (facilitated by fixation point offset) is provided for small saccades as well. We assume that the "express way" does not exist or is interrupted for saccades in the close vicinity of the fovea. This probably implies that the intratectal anatomical connections from the superficial to the deep layers of the superior colliculus (Moschovakis et al. 1988; Paige & Sargent 1991) spare the center of the visual field representation. In any case, the earlier notion of an oculomotor dead zone (Rashbass 1961) seems to be invalid for regular saccades (Wyman & Steinman 1973a) but valid for express saccades.

6.3. Intertrial effects

We have seen in section 4.1 that the gains of saccades can be modulated by the context in which they are being made. We now consider the possibility that the probability of an express saccade on a given trial may also depend on what happens on other trials.

Jüttner and Wolf (1992) did the following experiment: They randomly mixed target trials with catch trials (trials in which no target occurred) in an otherwise normal gap condition. The result was that the higher the proportion of catch trials in a block the lower the proportion of express saccades. In particular, they found that the probability for an express saccade was most strongly reduced on the trials following a catch trial. The authors believe that this effect has to do with the process of the decision to make or not make a saccade because, as a rule, on catch trials no saccades were made by the subjects and consequently the decision to make a saccade was not made (Jüttner & Wolf 1992).

We modified this experiment by randomly mixing long gap trials (instead of catch trials, which can be considered

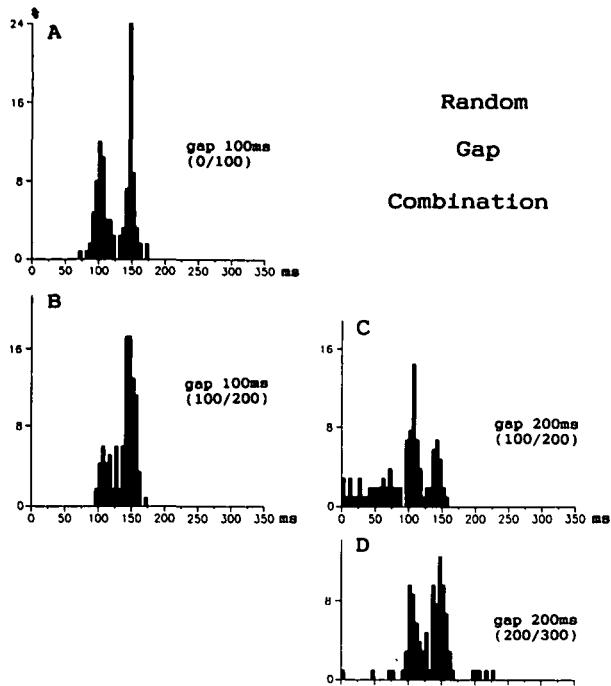


Figure 9. Saccadic reaction times from trials with randomly mixed gap durations in different combinations. Part A depicts the data from gap 100 msec trials when mixed with gap zero trials. Part B shows the results from 100 msec trials when mixed with gap 200 msec trials. Part C: same but for gap 200 msec trials when mixed with gap 100 msec trials. Part D: data from gap 200 msec trials mixed with gap 300 msec trials.

as trials with an infinitely long gap) with short gap trials. Under these conditions the subject makes a saccade on every trial. Figure 9 illustrates the result: In A and B the gap duration was 100 msec, but in A the gap 100 trials were randomly mixed with gap 0 trials, whereas in B they were mixed with gap 200 trials. Similarly, in C and D the gap duration was 200 msec, but in C the gap 200 trials were mixed with gap 100 trials (same experimental session as in B), and in D they were mixed with gap 300 trials. Clearly, the physical conditions of a given trial alone do not determine what kind of saccade is going to occur. The last experiment shows that it is not just a question of the decision to make no saccade on one trial and to make one on the next trial.

The results of this section show that there are internal states of readiness that determine whether or not express saccades are generated. The effect of intermingling catch trials or long gap trials seems to be that in order not to make mistakes subjects do not use the offset of the fixation point as frequently to start the disengagement but rather wait more often until the target appears before starting any preparatory processes for the next saccade. One can say that the subjects maintain fixation until the target appears.

7. Effects of practice and age on saccadic reaction times

First, we recall that the data discussed so far are obtained from highly trained subjects. Naive and normal subjects above age 20 may produce everything between zero and

50% express saccades during gap trials and usually no express saccades during overlap trials. Practice using gap trials increases the number of express saccades both in monkey (Fischer et al. 1984) and in man (Fischer & Ramsperger 1986).

The important point here is that with practice express saccades can also be obtained from adult subjects in overlap trials, that is, when there is no physical event preceding the onset of the target. This has again been shown for monkey (Boch & Fischer 1986) as well as for human subjects (Fischer 1987).

The fact that instructions concerning the direction of visual attention change quite drastically the sizes of the different peaks in the SRT distribution offers an explanation of what is changed by practice: the ability to disengage one's attention without the help of the onset of the new target. The disengagement is relatively easy and largely facilitated in gap trials but relatively difficult in overlap trials. The disengagement is a state in which one cannot stay for long periods of time because with increasing gap durations the number of express saccades reaches a maximum around values of 200–300 msec and then decreases continuously to zero with longer gap durations up to 800 msec (Mayfrank et al. 1986). The disengagement therefore seems to be a state which is reached more or less automatically before any saccade during the natural inspection of a large visual field. To reach this state voluntarily at a given time and to hold it over a certain time interval may indeed need practice for a normal and naive adult observer but it may be the "normal" state for children or subjects with certain problems leaving them in a state of almost permanent disengagement (see sects. 8 and 9).

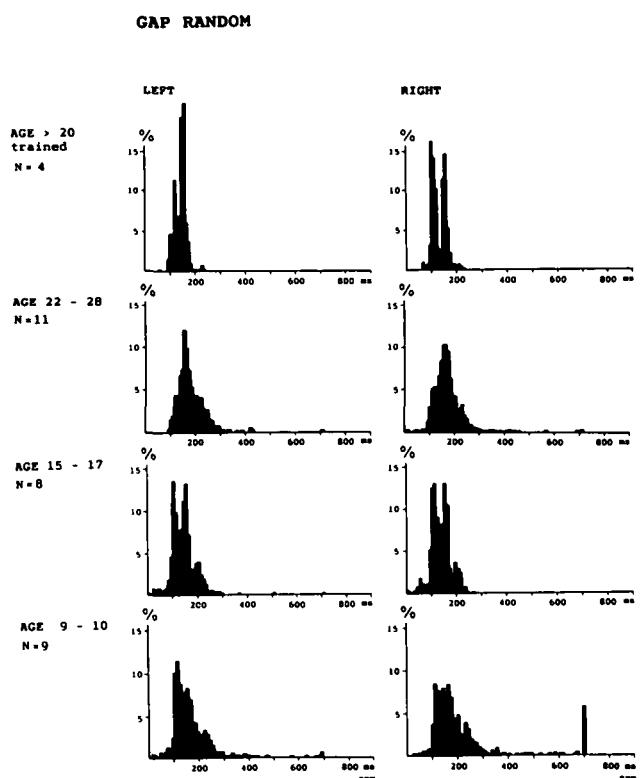


Figure 10. Effect of age on the distribution of saccadic reaction time. Note the strong asymmetry between right- and left-directed saccades for the adult group (upper panel). In all cases the target was randomly presented to the right or left.

The small number of express saccades during gap trials and their virtual absence during overlap trials in normal adults changes abruptly if one looks at younger subjects. Whereas there are only minor differences between age 50 and age 25, the number of express saccades in the gap task is much higher for youngsters of age 15–16 and children of age 8–10. Figure 10 shows the distribution of naive subjects in three different age groups (22–28, 15–17, and 9–10 years). The figure not only shows that even at age 16 the control of eye movements is not fully developed, but also that the number of express saccades is highest in early life (it is still an open question what happens at preschool age).

In conclusion, maturation beyond age 16–18 years decreases the chances of producing express saccades but through practice an adult subject may regain this ability. It looks as though with increasingly difficult tasks in life – such as learning to read – more control over the saccadic systems is necessary. This control is provided at least in part by the attentional system and has the consequence that reflex-like optomotor reactions, that is, express saccades, are rarely seen in the gap trials and almost completely absent in overlap trials.

8. Dyslexia and saccades

We now consider the possibility that a child does not develop attentional control over the saccade system, either because the attentional system is not properly developed or because the control action is not properly passed onto the saccade system. In either case one expects unusual patterns of saccadic eye movements and changes of saccadic reaction times in noncognitive tasks and of course during reading and during any other task requiring proper coordination of vision and eye movements.

Such reports were published by Pavlidis (1981; 1985), who claimed that dyslexic children often overshoot the targets when they are asked to scan them by saccadic eye movements. The result – according to Pavlidis – was an increased number of regressions in the eye movement records (Pavlidis 1981; 1985). Olson – in his attempt to replicate the results of Pavlidis (1981) – failed completely and concluded that dyslexic children have normal eye movements (Olson et al. 1983).

On the basis of the express saccade and its possible relationship to visual attention we looked at saccadic latencies of dyslexic children using gap and overlap trials (Fischer & Weber 1990). We found that dyslexics clearly differ from controls in their latency distribution. In particular, we found a group of dyslexics (group II) who produce almost exclusively express saccades regardless of whether gap or overlap conditions were used (Fischer & Weber 1990). This most interesting observation was later supported and extended by Biscaldi and Fischer (1992), who found another 4 children among 12 other dyslexics who showed this striking pattern of saccadic latency distribution. Figure 11 shows the distributions of saccadic reaction times of control children and of two groups of dyslexic children all tested in the overlap paradigm. First, one sees that children make more short-latency saccades but also more long-latency ones. They seem to be unable to set properly the time they make the eye movement. There is clearly a preponderance of express saccades in

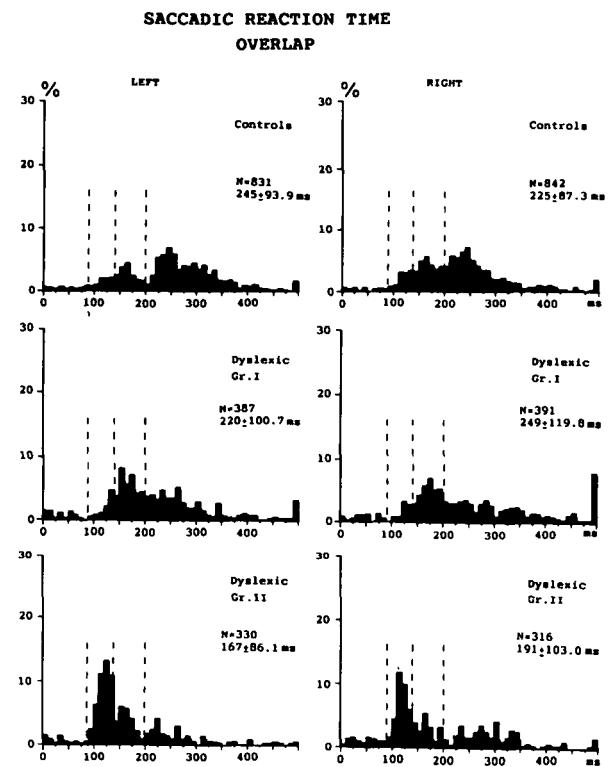


Figure 11. Saccadic reaction times of normal readers and two groups of **dyslexic readers** obtained in overlap trials. Note the big population of express saccades in the group II dyslexics. The saccade target was presented randomly at 4 deg to the right or left of the fixation point.

the group II dyslexics that differentiates them not only from adults but also from age-matched controls and other dyslexics.

Biscaldi and Fischer (1992) also used the light test of Pavlidis. In their data the number of regressions was normal for all the dyslexics – in disagreement with Pavlidis – but other parameters of sequences of the saccades, for example their number and size, were abnormal. In disagreement with Olson, it is concluded that the eye movement patterns, in particular, the reaction times, of many if not all dyslexics at age 9 to 11 years are different from those of normal readers. The analysis of the eye movements in noncognitive tasks may even be used as a diagnostic tool to distinguish dyslexics from normals or from children with other problems that might have contributed to their deficit in reading.

The main conclusion of this section is that understanding the role of attention in controlling the saccadic system gives insight into why reading is impaired when this control mechanism does not work properly. The problem for such subjects is twofold: On the one hand, they have difficulties in their attentional system; on the other hand, and as a consequence of the attentional problem, they have difficulties in producing proper saccades at proper times. More specifically, excessively short latencies and in particular express saccades under overlap conditions are obtained if the subject fails to engage attention consistently. These subjects are ready to move their eyes whenever a new target appears. One can even say that their attention is very likely to be distracted. The opposite happens with subjects who cannot consistently disengage their attention. They stay in the engaged state with the

consequence of prolonged reaction times. Finally, one could even consider the possibility that a subject has difficulties in switching from one state into the other: Once engaged they cannot disengage in time; once disengaged they cannot engage in time. In this case one predicts bimodal distributions with a "too early" peak and a "too late" peak as compared with control subjects. These aspects of dyslexia and of the concept of engaged/disengaged attention are rather speculative at the moment and need more theoretical and experimental evaluation.

The attentional problem may not necessarily show up in a neuropsychological test because it may be that although subjects have difficulties in switching to the engaged state, once there they can perform perfectly well in any task which requires engaged visual attention but no saccades.

It would be very interesting to study the development of the saccadic and the attentional system from birth to see at what time express saccades and slow regular saccades can be obtained. Infants below 2 months of age can certainly make target-directed saccades but their latencies are broadly scattered and rather long and their amplitudes are much too small (Aslin & Salapatek 1975). These saccades may be the result of still immature reflex (the use of which is necessary for the development of the saccade system), which only later will be controlled by cortical structures.

9. Clinical observations

In this section we consider data from neurological patients contributing to our present understanding of saccade generation and visual attention. A basic observation was reported by Guitton and his group: Patients with unilateral lesions of the frontal lobe were unable to suppress saccades to a suddenly appearing visual stimulus at one side when they were asked to make saccades to the opposite side (antisaccade task). When another stimulus occurred a few hundred milliseconds later they made saccades toward this new target after reaction times of about 100 msec, that is, they made express saccades (Guitton et al. 1985). The inability to suppress initial glances at potentially distracting stimuli after frontal lobe lesions was also reported earlier (Milner 1982). One could argue that inhibitory action through the frontal eye fields onto the saccade-generating system was no longer effective, thus allowing for express saccades. This does indeed seem to be the case whenever frontal patients are tested in a gap condition. In the overlap condition, however, the saccadic reaction times are in the normal range. The suppressive effect of the presence of a fixation point on the occurrence of express saccades is intact in these patients (Braun et al. 1992), indicating that the occurrence of express saccades with frontal lesions is highly dependent on the state of fixation. The source of the inhibition may be the parietal cortex, because electrically elicited saccades are abolished in monkeys who are actively fixating a foveal target (Shibutani et al. 1984). Braun et al. (1992) found that with lesions of the dorsolateral parietal cortex express saccades were significantly reduced, but this effect was the result of a general large scatter of the latency distributions of these patients. Parietal lesions thus appear to cause a destruction of stimulus-triggered saccadic timing affecting the whole

spectrum of saccadic reaction times rather than any special latency population.

The mechanisms of visual attention have long been associated with the parietal cortex. For instance, from Posner et al. (1984) we know that patients with lesions in the parietal cortex are unable to use a foveal cue to direct their attention to the periphery. It was concluded that visual attention must be disengaged from wherever it had been engaged before it can be moved to another part of the visual field. Our present notion of the mechanisms of visual attention as derived from eye movement data alone very much support this idea. Further evidence in favour of the "disengage-move-engage" hypothesis comes from measurements of visual attention without eye movements (Mackeben et al., personal communication). They used vernier acuity measurements in the parafoveal region and introduced a gap between fixation-point offset and the onset of a spatial cue that indicated where the vernier target would be presented. Performance was best with gap durations of 100–300 msec. The authors conclude that subjects can accelerate their "attentional deployment" if they are given enough time to disengage their attention by means of fixation-point removal before cue presentation.

10. Theoretical considerations

As a possible basis for mathematical models or computer simulations, Figure 12 depicts schematically the most important anatomical projections that connect the retina with the eye movement generating structures (EM) in the region of the brain stem.

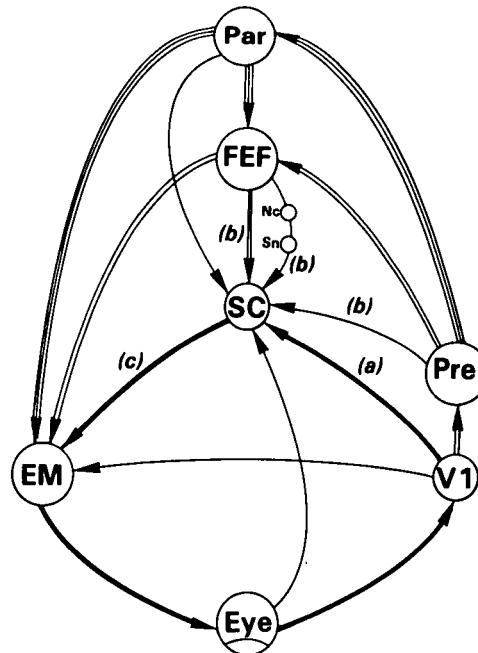


Figure 12. Schematic drawing of the anatomical projections connecting the retina of the eye with the efferent eye movement generating structures (EM) in the region of the brain stem. Three loops can be seen, as indicated by the single, double, and triple heavy lines. V1 = striate visual cortex (the lateral geniculate nucleus is omitted), Pre = prestriate visual cortex including areas V2 and V5 and area MST, Par = parietal cortex, FEF = frontal eye field, SC = superior colliculus, Nc = nucleus caudatus, Sn = substantia nigra pars reticulata. Figure taken from Weber et al. (1992).

The pathway mediating the express saccades is drawn in single heavy lines. This pathway is obviously not always functionally available, because otherwise any sudden appearance of a visual stimulus would lead to a saccadic eye movement, which would immediately create an impossibly chaotic situation. (The direct projection from the retina to the superior colliculus and from striate cortex to the brain stem alone [thin lines] cannot mediate saccadic eye movements because without striate cortex or without the superior colliculus express saccades are abolished. The significance of these connections therefore remains unclear in this context.) It is assumed that a cortical control mechanism, presumably through the frontal eye fields, acts on this first, most primitive reflex loop to prevent the generation of reflex-like saccades. It is only when this inhibitory action is stopped that a saccade can be initiated directly through this pathway by the onset of a stimulus. Such a saccade occurs as an express saccade. The disinhibition may be direct or indirect through the nucleus caudatus and the substantia nigra pars reticulata (Hikosaka & Wurtz 1983a). Similarly, the second loop is only available if another inhibitory action, presumably through the parietal cortex, is taken away. This control – we propose on the basis of the data described above – is taken by visual attention being engaged or disengaged. In the disengaged state the inhibitory action is stopped and saccades are permitted; in the engaged state the generation of saccades is inhibited either directly by the projection from the parietal cortex to the superior colliculus or indirectly through the frontal eye fields. The inhibition of saccades may also or in addition occur at the brain stem level. For example, the continuous firing of the pause or omni-pause cells may drive this inhibitory mechanism.

The neurophysiological aspects of saccade generation are summarized by Fischer and Boch (1990), where the different types of presaccadic modulation of neural activity in the superior colliculus, the frontal eye fields, the

parietal cortex, and the visual association cortex are described. It is essential to notice that in each of these structures different aspects of the saccade are important: the voluntary aspect in the frontal eye fields (Bruce & Goldberg 1984; Pierrot-Deseilligny et al. 1991a), the attentional aspect in the parietal cortex (Mountcastle et al. 1987; Robinson et al. 1978), and in the visual cortex (Haeney & Schiller 1988), the saccade as a pending motor action in the superior colliculus (Goldberg & Wurtz 1972).

In this target article we have concentrated on the significance of visual attention for the generation of saccades. Little has been said about the decision process preceding each single saccade. However, a complete discussion of saccade generation must include this aspect. Without it one would not understand the existence of the three different modes in the distribution of saccadic reaction times. The model outlined and described below will therefore take into account decision making and computation of the metrics of the saccade as well as the processes of visual attention.

10.1. A computer-simulated model

The three-loop model proposed by Fischer (1987) is outlined at the top of Figure 13. Besides the afferent visual inputs ("vis," the signals from the fixation point and from the stimulus) and the efferent output to the oculomotor nuclei ("mot"), the model includes three central states denoted by "att" (for attention), "dec" (for decision to make a saccade), and "com" (for computation of saccade size and direction). A central state, as indicated in the middle, has three input lines (a = afferent, r = random, and c = central) and one output line. By r we denote a random process which is governed by other brain functions that may act on the optomotor system, for example, general alertness or effects of the instruction for the subject. The output line becomes active according to the

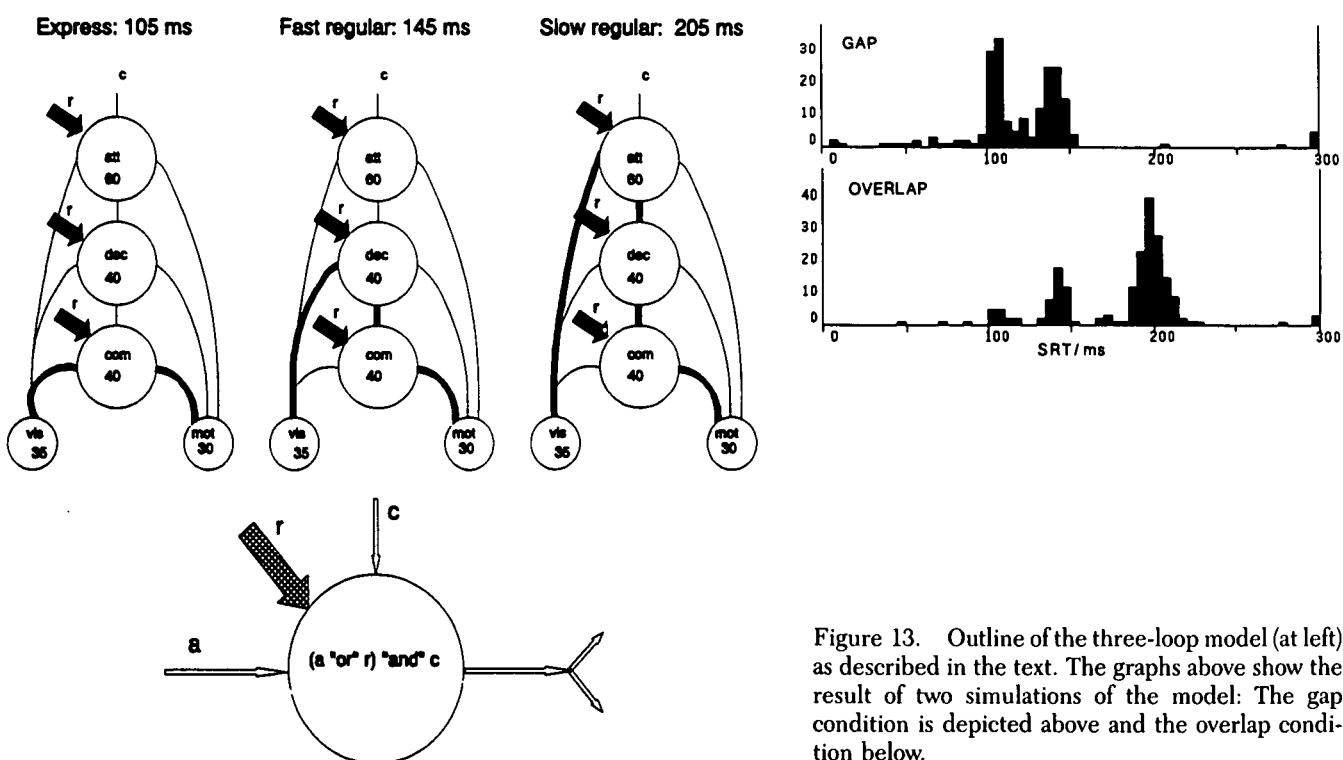


Figure 13. Outline of the three-loop model (at left) as described in the text. The graphs above show the result of two simulations of the model: The gap condition is depicted above and the overlap condition below.

logical rule that c and at least one of the other input lines (a or r) are active. Once this condition is fulfilled the output becomes active after a transition time varying randomly (mean T and standard deviation s). T and s are model parameters set for each of the three central states, for the afferent, and for the efferent process. In principle, each of these processes has the same effect as the facilitation generator proposed by Reulen (1984). However, instead of using it only for the time after fixation point offset, we use this principle for all states.

The model also includes the possibility of any state's becoming inactive at random with a given probability. Before the final output line of the model can become active all three input lines to the motor state "mot" must still be active. This is realized by the links between "att" and "mot" and between "dec" and "mot" together with a threefold AND operation at the mot-level.

The heavy lines in the three (otherwise identical) graphs on top of the figure show the model pathways for the three types of saccades according to their latencies. The histograms at the bottom of Figure 13 display the result of a computer simulation of 200 gap trials and 200 overlap trials. One sees the three peaks clearly in the overlap case and the two peaks in the gap case. Note that anticipations occur in gap trials much more often than in overlap trials. The model also produces a few cases, representing so-called misses, with rather long reaction times (above 300 msec). The effect of the gap – in the light of the model – is to initiate "att," that is, the disengagement of attention, which then after a delay can also initiate "dec." If after another delay "dec" also initiates "com," an anticipatory saccade is the result. If the target occurs and leads to the initiation of "com" an express saccade is the result. If "att" has not initiated "dec" the occurrence of the target will do this and the result is a fast regular saccade. Slow regular saccades are obtained very rarely in the gap condition as the chances of a deactivation of "att" within the gap are rather small. The opposite is true in the overlap condition: During attentive fixation, "att" usually remains inactive until the target occurs. This then leads to a preponderance of slow regular saccades. For the simulation shown in the figure we have deliberately set the parameters so as to produce a few express saccades in the overlap condition. A smaller chance of random switches of "att" and "dec" would have decreased or even completely eliminated the express and fast regular peak leaving the monomodal distribution as one usually obtains in the overlap task (see, e.g., in Fig. 3B).

10.2. Other theoretical concepts

There exists a large body of work concerned with models of the saccade system. A good review is given by Becker (1989). Most of this work, however, is devoted to an understanding of how brain stem structures determine the size and direction of a saccade from what is called the "retinal error" signal. This process would be included in process "com" of the present model and its details are not considered here. The present approach is concerned with the total loop from the retina to the brain stem including the influences from higher brain functions. To explain the effect of the gap on the saccadic reaction times Reulen (1984) has proposed a facilitation model. This model explains the latency-reducing effect of introducing a gap

but it has several disadvantages: First, one does not know what is meant by "facilitation" in terms of a physiological or psychological process; second, it cannot explain the occurrence of short-latency saccades in overlap trials as they are observed in children and in specially trained adults; third, the model fails to produce bimodal distributions. The last point is very important in considering the double effect of the gap condition. In accordance with the experimental findings, the three-loop model produces a reduction of the duration of the latencies and the appearance of a bimodality or even a trimodality. The latency distributions become unimodal when the gap durations are too short and yet the latencies are reduced as compared to the no-gap or overlap case. None of the models we are aware of can produce this basic feature of the saccade system. The latency reduction and bimodality are both inherent features of the model and do not need two different explanations.

Since the gap task is most favourable for generating express saccades and since in a condition where the gap duration as well as the target position is kept constant, the offset of the fixation point may be considered a cue that can be used by the subject to activate what has been called "premotor priming" (for review see Oakley & Eason 1990). This concept, however, has difficulty in explaining express saccades during overlap trials, where there is no cue preceding the target onset. Another difficulty arises from the fact that express saccades can be obtained with unpredictable gap durations or target positions: How could the priming process possibly facilitate a target-directed movement when the size and direction of the movement are not yet known? In addition, we have shown that express saccades have smaller amplitudes and they undershoot the target more often and by a larger amount, compared with regular saccades (Fischer et al. 1993; see also Fig. 6). This observation would imply that the premotor priming makes the movement more inaccurate rather than leading to an improvement. Finally, the priming concept predicts shorter latency for valid as compared to neutral or invalid cues. Saccadic latencies, even though shorter for valid than for invalid cues, are shortest in the gap task with no spatial cues (Biscaldi et al. 1989). This means that, if anything, the knowledge of the future target location increases the reaction time rather than decreasing it. The disengagement-engagement concept offers an explanation of this experimental finding by assuming that the cue – valid or not – may catch one's attention, thereby leading to an increase in latency.

We wish to emphasize that the model has a rather simple structure consisting essentially of three identical central elements. Yet it produces rather complex sets of data which very closely resemble what one sees in real life experiments on saccadic reaction times. It remains open for future mathematical work to elaborate the model and to embed it into other brain functions such as visual perception, visual-vestibular interaction, and locomotion.

ACKNOWLEDGMENTS

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Express saccade programming produces visually triggered saccades

J. E. Albano

Center for Visual Science, University of Rochester, Rochester, NY 14627
Electronic mail: jea@cvs.rochester.edu

The three-loop model presented by Fischer & Weber (F&W) conceptualizes the sequence leading to the visually guided saccade as ordered, serial processes interposed between the afferent signal and the efferent pathway. Before a visually guided saccade can occur the processes of attention, decision, and computation must be activated, respectively. Each process is activated by either an afferent or a random input (representing cognitive influences) and the activation of the previous central state. Thus, all three processes must be "held high" in order for the motor output to occur. The model predicts that distinguishable peaks will occur in the latency frequency distribution when components of the saccadic program are prepared in advance of the saccade target onset. Express saccade programming (ESP) accordingly occurs when only a computation time is required; the attention and decision process is activated in advance by the stimulus offset in the gap condition. The basic premise of F&W's model is that these processes are necessarily serial, of fixed duration, and unitary. If we allow that the saccadic program is composed of parallel interacting modules and of variable duration, however, then the model encounters difficulties. This commentary will consider some of these difficulties and look beyond the "gap effect" literature to suggest some modifications.

Double-step experiments support the view that at least some steps leading to the initiation of visually guided saccades are parallel and variable in duration (Becker 1989). When a second saccade target is presented within one saccadic reaction time, the output of the system reflects the location of both targets as a function of time. To explain their data, Becker (1989) and colleagues proposed that retinal error and decision processing occur in parallel; the retinal error processing is ended when the decision stage reaches completion. We can deduce that the retinal error stage does not simply precede the decision stage since saccade metrics varies with latency. We can deduce that the components of the program are interacting because a change in the target direction can produce complete cancellation of the saccade. The Fischer model does not concern itself with saccadic metrics but the discussion asserts that the "C" input to attention includes the retinal error processing. Determination of the retinal error signal therefore precedes the attention and decision stages and should not be influenced by double-step stimuli or by multiple targets that appear in the field (global visual processing). So the first point is that there is evidence that the retinal error stage and the decision stage occur in parallel; when the decision interval is extended, saccade metrics suggest that there is a time-averaged sampling of the retinal error. A model of ESP should be consistent with these observations.

The second point is that the timing of saccadic processes may be affected by interactions between and additivity of the effects of the particular experimental conditions. For example, using experimental conditions that otherwise produced saccadic latencies in the slow regular range (200–250 msec), Reulen (1984) found that a 200 msec gap reduced the average by 40–60 msec

(to latencies of 180–200 msec). This is the true "gap effect," because the target locations and timings were randomized and "catch" trials were interspersed. "Catch" trials contain a gap, but no target (i.e., the fixation point disappears and then reappears); thus there is no precuing to initiate saccade preparation. The combination of direction randomization and variability in timings and directions means that saccades could not be efficiently preprogrammed and held in readiness until a trigger appears. Combining target location predictability and timings means that some benefit is gained by holding a selected movement in readiness and awaiting a trigger to move. If the trigger is in the wrong direction then the previous saccade is cancelled and the latest sampled retinal error is selected and triggered. The cost of this preparation is one decision cancellation time and one decision making time. The benefit, when combined with the additional savings of fixation disengagement is the production of triggered saccades or ESP. The result of this strategy is visually triggered saccades with more than one latency peak, the earliest representing the triggered saccades, and the second peak after one decision cancellation and activation.

In this alternative view, ESP is the saccadic program that results when fixation disengagement is combined with limited target directions, timings, and locations. This scheme differs from a simple sequential model because the interactions between parts of the program result in a change in the sequence of events, that is, a cancellation of a preprogrammed saccade and triggering to the continuously sampled retinal error. It is consistent with the parallel processing model of Becker (1989) and with the observations of Fischer and colleagues that early saccades have normal metrics and dynamics. As F&W point out, practiced subjects with exposure to target parameters can produce ESP even in overlap conditions. This must mean that subjects learn to preprogram the saccade and disengage the fixation mechanism through cognitive influences. It also provides an explanation for the occasional bimodality of latency distributions; subjects who do not consistently preprogram their saccade and await the trigger have a broad distribution of saccades that include normally programmed saccades. The bimodality of latencies in the ESP paradigm parallels the bimodality of latencies in the pulse overshoot double-step experiments, where a cancellation of saccade direction is thought to occur between saccades directed to the first target and saccades that bypass the first target location and land in the opposite direction (see Becker & Jurgens 1979, Fig. 5). Physiological evidence also supports the notion of the triggered visual saccade. Some movement-related cells of the substantia nigra and superior colliculus begin their discharge before the saccade target appears, when the animal awaits a trigger to move his eyes to a remembered target location (Hikosaka & Wurtz 1983b).

Gap effects on saccadic latency in infants and children

Janette Atkinson and Bruce Hood

Visual Development Unit, Department of Experimental Psychology,
University of Cambridge, Cambridge CB2 1QA, England
Electronic mail: bmh11@phx.cam.ac.uk

This target article provides wide coverage of many aspects of express saccades and a plausible model of the neural programmes integrating attention and saccadic generation.

A main concern of Fischer & Weber (F&W) is to validate the phenomenon of express saccades and reject the notion that they are anticipatory or a product of training. Infants are one group of subjects in which training factors are unlikely to play a major role in determining behaviour. Hood and Atkinson (in press) have examined the gap effect in 1.5-, 3-, and 6-month-olds and adults. From these data, there was no evidence in any age group of a multimodal distribution nor did any group (or individual)

produce responses within the express saccade range. However, there are a number of differences between our study and the optimal paradigm for express saccades. First, the stimulus characteristics were substantially different, with our subjects responding to larger (16 by 32 deg) targets at greater eccentricities (23 deg). In addition, saccadic latencies were measured in terms of video frames (giving a resolution of 40 msec). Most important, variation in latency distribution between subjects was quite large and when data were pooled, a normal distribution emerged. Individual profiles of latency distribution were not possible, as the average number of trials per infant subject was small. Nevertheless, a comparison of saccadic latencies between a no gap condition and a 240 msec gap condition revealed a gap effect of 89 msec ($p < 0.05$) for 1.5-month-olds, 83 msec ($p < 0.01$) for 3-month-olds and 174 msec ($p < 0.01$) for 6-month-olds. The gap effect for adults was 66 msec ($p < 0.01$) for saccadic latencies and 62 msec ($p < 0.001$) for manual responses. Given that the four different conditions were interleaved and the position of the target was varied randomly from trial to trial, this study is able to confirm the existence of a gap effect in infants which is unlikely to be attributable to either training or anticipation.

These infant studies, together with those on both dyslexic and normal children described by F&W, raise the question of how valid comparisons may be made across widely separated age groups. First, the fact that children spontaneously make more very short latency saccades than untrained adults could be used either for or against the argument that these fast saccades are truly express saccades. If the increased percentage of fast saccades in children were accompanied by increased errors compared to adults this would imply that children are operating with a different speed-accuracy trade-off, with many of their fast saccades being anticipatory rather than express. If, however, children and untrained adults did not differ in error rates, or latency range for these saccadic errors, we can agree with F&W's analysis that children show a genuinely increased incidence of express saccades. This would support the argument that children and some dyslexics (similar to some frontal patients) can easily achieve a state of disengagement.

It is not clear why an asymmetry in the distribution in the right and left field (seen in some adults and not children) is taken as evidence against anticipation. In fact, side biases might be expected as a property of anticipatory responses, especially if fixation was slightly eccentric.

The validity of F&W's subgrouping procedure for dyslexic subjects depends on the calculation of the peak of the multiple Gaussians that have been fitted to the individual subjects' data. From this analysis, different profiles have been derived from different dyslexic subgroups without the same detailed analysis being applied to controls. Presumably, similar differences between subtypes were not found in the controls (for instance, between different-aged children). If this is so, then such data would be strong support for the proposal that dyslexic subgroups show abnormal profiles rather than age-delayed profiles. Further data analysis on the control groups would answer this question. It would also be interesting to analyze longitudinal data on dyslexics to see whether they change from one subgroup to another with age or whether these saccadic distributions are the "signature" of different types of dyslexics. It might be, for example, that most dyslexics start with a very variable range of latencies, including increased anticipatory eye movements and inadequate fixations (they spend most time in a disengaged state no matter what the target duration) and that they progress to increased periods of engagement and fixation, but still experience difficulty in switching regularly from engaged to disengaged states. Some evidence that the differences between dyslexics and normals is in the dyslexics' increased anticipatory eye movements and reduced fixation has already been found in poor readers as compared to good readers in a study by Cohen and Ross (1977). Some dyslexics might of course put a lot more

effort into fixating and engagement than their controls, thereby producing an increased percentage of long saccadic latencies in both gap and overlap conditions (as seen in some of the teenage dyslexics). We should perhaps not assume that the rapid saccades made after training in adults are quite the same as the rapid saccades made extensively by young dyslexics. Perhaps with further experiments in which motivational state is manipulated we may be able to tease apart short-latency saccades of different origins. Some might result from a conscious effort to disengage rapidly from the fixation target and others from unconscious spontaneous disengagement of attention.

Finally, one problem with the neurophysiological basis of express saccades is the role of the cortico-tectal pathway described by F&W. The evidence suggests that this pathway is exclusively driven by magnocellular input (Schiller et al. 1979), which is usually described as insensitive to isoluminant colour stimuli, yet F&W claim that these are stimuli that can elicit express saccades.

Visual attention is visual, too

Talis Bachmann

Rector's Office, Tallinn Pedagogical University, Tallinn EE0100, Estonia
Electronic mail: tbach@tpedi.ioc.ee

The target article is a well-systematized general account of express saccades from the behavioristic perspective on attention. There is no doubt that (1) express saccades in the reaction time (RT) range of 100 msec can be reliably obtained as a separate RT distribution; (2) these saccades are visually guided sensorimotor events; (3) crucial conditions for obtaining this express population include the introduction of a gap or blink into the exposure regime of the fixation point. The concept of attentional disengagement therefore stands as a cornerstone of Fischer & Weber's (F&W's) conceptualization. The authors will no doubt continue the excellent studies; the following questions seek some clarification of their views.

(1) Do you agree that in order to be sure about the effective disengagement of attention from the fixation as a result of blinking or offset we need some additional sensory/psychophysical experimental controls? On logical grounds, without specific empirical checks, blinking or offset of fixation could instead be cues for some additional attentional engagement or global facilitation. Thus, some sensory probes (e.g., light increments to be detected, vernier stimuli to be evaluated, probe digits recognized, etc.) at various spatiotemporal intervals in the context of visual displays used in the express saccade paradigm would help to test the spatial direction of sensory attention in space-time after the putative disengagement. Effective disengagement would predict relative loss of sensitivity at fixation. A specific prediction would be that the sensitivity to target-related probes with express saccades at a particular postgap, presaccadic interval T should be higher than with fast regular saccades. In other words, if we postulate some sensory-attentional event, we also need some relevant sensory-attentional experimental control of the reality of this event.

(2) Do you agree that "express saccade . . . as a reflex-like optomotor reaction that brings the fovea to the stimulus" (sect. 4, para. 3) within 100 msec is too fast to allow more or less complete build-up of a covert spatial-attention focus at the target locus before a saccade?

Our analysis of a random sample of some pertinent studies – Buchtel & Butter 1988; Chastain 1992 (with sensitivity measures); Eriksen & St. James 1986; Eriksen & Webb 1989; Heijden et al. 1988; Lyon 1990; Mondor & Bryden 1992 (with RT as a dependent measure); Murphy & Eriksen 1987; Nakayama & Makeben 1989; Shulman et al. 1979; Tsal 1983; Warner et al. 1990 – has revealed that cue-to-target stimulus

onset synchronies (SOAs) sufficient for asymptotic performance fall within the interval of 100–350 msec for various targets at eccentricities from 1 deg–12 deg; average asymptotic SOA epochs equal 180 msec and 140 msec for RT-measures and sensitivity-measures, respectively. If we now add motor preparation and execution times we clearly arrive at the region of fast or slow regular saccades. Asymptotic SOA values of visual masking, for example 150–250 msec (cf. Bachmann 1993) also point to the doubtfulness of sufficient target image buildup with express regime.

Express saccades may operate according to an “exploratory” strategy: (i) detect, (ii) fixate, (iii) analyse – instead of an “analytic” strategy: (i) detect, (ii) analyse, (iii) fixate. From the adaptive standpoint maintaining former fixation while (pre)processing signals from the periphery should have its benefits. What if bimodality (peaks of RTs at 100 and 140 msec) represents a spontaneous distribution between these two natural oculomotor strategies? In one part of the response population (express saccades at 100 msec) we may be dealing with trials indicative of the “exploratory” response mode, free of covert attentional focus formation; in another part (slower RTs) with the “analytic” mode, which requires the presaccadic formation of a covert attentional focus at the locus of the target. In the target article one can find several hints supportive of this view: (i) the gain for express saccades is smaller and more “imprecise” than for regular ones (0.91 vs. 0.99); (ii) saccades with small amplitudes (i.e., those within the established attentional focus) lack an express population; (iii) attention, if directed to the target, minimizes express saccades; (iv) dyslexia, viewed as a probable covert attentional failure, is predictive of express saccades.

(3) Do you agree that sensorimotor reactions can be speeded up through an increase in stimulus contrast (Klein et al. 1992). If so, then blinking or offsets of the fixation point could be considered sensory events capable of increasing subjective contrasts in the subsequent target stimuli, thus speeding up reactions to targets, given that in a corresponding subpopulation of trials the direction of spatial shift of the induced contrast enhancement matches the actual direction of the target.

We have been able to demonstrate that the subjective contrast or the subjective speed of the moment of perceptual actualization of a critical visual stimulus can be increased by exposure to an inducing preliminary transient in close spatiotemporal proximity to this stimulus (Bachmann 1988; 1992). Stroboscopic motion and metacontrast substantiate the possibility of spatiotemporal anisotropies in such effects. (By the way, the preponderance of rightward express saccades represents another hint of some spatial bias in this kind of hypothetical facilitation.) Direct psychophysical controls (e.g., via some auditory or visual reference events) to trace the time course of the emergence of subjective visual experience of targets in express versus regular saccadic regimes would in any case be informative. It is noteworthy that the time courses of the gap effects (150–300 msec; cf. target article; Wenban-Smith & Findlay 1991) with rise-and-fall envelopes coincide surprisingly well with the time course of the above-mentioned enhancing role of subjective contrast (selection efficiency) as a function of the SOA between the inducer (precue) and the target (Bachmann 1988; Nakayama & Makeben 1989).

(4) Do you agree that the difficulties some investigators have had in finding bimodality in the RT distribution in the express range (Klein et al. 1992; Wenban-Smith & Findlay 1991) may require even stronger experimental controls to demonstrate the absence of artifacts or experimenter-induced biases? Some potential sources of artifacts may include (i) saccadic suppression as a phenomenon which defines the split of RT distribution into two or more populations (fewer RTs at about 120 msec as a region wherein spontaneous avoidance of detrimental saccadic suppression effects takes place) and (ii) laterality artifacts (see Figs. 6 and 10 of the target article; cf. RVF advantage at short cue-to-target SOAs in Mondor & Bryden 1992 and the absence of

express range in Klein et al. (1992). In other words, in some studies subjects tend to saccade to the right according to reading-related habits, which yields a clear express population of RTs. When this direction occasionally fails or is intermixed with leftward preferences, a slower RT population will also be generated.

To summarize: In order to put the phenomenon of express saccades into a more cognitively defined attentional perspective we perhaps need to widen our context to consider more sensory-perceptual and subjective-experience-related (though psychophysically testable) variables.

The spatial dimension in visual attention and saccades

Victor I. Belopolsky

Institute of Psychology, Russian Academy of Science, 129366 Moscow, Russia
Electronic mail: vbelop@ipras.msk.su

The saccadic reaction time (SRT) paradigm seems to be an indirect source of some misconceptions in eye movement control studies. The sudden appearance of a visual stimulus during a fixation task is very convenient for measurement, but it presents a rather artificial situation. In investigating the express saccade phenomenon, Fischer and his colleagues have made a successful attempt to overcome the contentions that SRT reflects the duration of a programming stage in the saccadic system. In their target article Fischer & Weber (F&W) give an impressive summary of their set of related publications. In their discussion they have avoided using the terms “fixation” and “saccade latency.” Trimodality of the SRT distribution, although not obtained in one experimental session, is treated in the target article as consisting of two preparatory stages preceding the generation of a saccade. In my commentary I would like to take a step out of the paradigm’s constraints and raise some questions about the role of attentional dynamics in controlling the timing and metrics of eye movements.

F&W have explicitly restricted the validity of their three-loop model to when the saccade occurs “in response to the onset of a visual stimulus, which is not only the temporal trigger but also the spatial target for the eye movement.” The explanatory range of their model accordingly covers only the inhibition and disinhibition of the optomotor reflex: “Directed (engaged) visual attention increases the overall reaction time whereas disengaged attention reduces it.” Thus, anticipatory, wrongly directed and antisaccades are omitted from the analysis, although it is assumed that these and visually guided saccades may be preceded by certain common preparatory processes. Even more significant is the lack of an explanation of everyday regular saccades generated by one of numerous potential stimuli in the visual field; in fact, the definition of retinal error signal is included in the C (central) process of the present model (i.e., it is shifted out of the attentional mechanism).

On the other hand, there is the well-known fact that subjects can voluntarily prevent the saccadic response to onset of a peripheral visual stimulus. This and other “instruction effects” have likewise not received operational explanation and are included in the R (random) process of the model.

Let us now try to look more closely at the engagement-disengagement states of attention as presented in the target article. These terms are borrowed from Posner’s description of the covert attention cycle (Posner et al. 1984), but omitting its important “move” step. In general, the description of engagement-disengagement in the target article gives not even a hint about the spatial dimension of the attentional states. Biscaldi et al. (1989) and Mayfrank et al. (1986), however, have shown that any spatial cue located in valid, invalid, or neutral

(central) positions leads to an engagement state and thereby increases SRT. In turn, a disengagement state, which develops more or less spontaneously in the gap task or after another warning signal or during training sessions, promotes shorter SRT (see Posner et al. 1986 for a contrary point of view).

The weakness of the two-state attention concept can be illustrated by the results of a simple experiment (Belopolsky 1989a). Subjects were instructed to allocate their attention between two points of light separated vertically by 1, 3, 5, or 10 degrees of arc. The duration of this "fixation" was 40 sec. As expected, the proper sizes of an attentional field affected the recorded eye movements differently. The measurements showed that the larger the interstimulus space, the greater the accompanying amplitudes of vertical deviations of the eyes, velocities of smooth eye movements, and intersaccadic intervals. Only the last parameter gradually increased, on average, from 380–420 msec (1 deg) to 1,500–1,900 msec (10 deg) with different subjects. A similar microsaccadic frequency effect was reported by Steinman et al. (1967), who manipulated the directness of the fixation task through instructions. This reveals a possible cause for the gap-overlap effects: The expansion of the attentional field reduces the probability of microsaccades during the gap period, but in case of steady focused attention it is expected to rise. Thus, one can expect shorter SRTs in the first but not in the second case, taking into consideration the typical intersaccadic interval distribution (e.g., Ford et al. 1959).

The idea of attention as a spatial phenomenon is the backbone of the adjustable-beam spotlight or zoom lens model of visual attention (Erikson & James 1986; LaBerge & Brown 1986). There have been attempts to assess, to a first approximation, the time cost for spatial scaling of attention (Belopolsky 1988; 1989b; Cave & Kosslyn 1989; Egeth 1977). A consideration of the spatiotemporal aspects of attentional dynamics can accordingly throw more light on the mechanism of voluntary saccadic control. Specifically, I think it could be helpful in analyzing how instructions (e.g., to make or refrain from making a saccade, to perform an antisaccade, and so on) affect oculomotor behavior (see Belopolsky 1985).

Henderson (1991) summarizes three hypotheses about the relationship between visual-spatial attention and the metrics of saccadic eye movements. These are (1) independence of the attended location and the position of fovea; (2) permanent centration of the attention around the fovea; and (3) transient coincidence of foveal and attentional areas, which are interrupted by reallocations of attention and recovered by the saccades. As can be understood in context of the target article, F&W are closer to the first hypothesis. Both the first and the second hypotheses, however, address the different momentary states of a whole perceptual cycle and require a complementary central, or extraretinal, signal to explain the metrics of saccades (see Becker 1989). On the other hand, the third hypothesis is free of such prerequisites. The SRT paradigm is unlikely to be effective for direct testing of the hypotheses; a more sophisticated technique is needed to do so. For example, in several studies (Barabanshchikov et al. 1981/1982; McConkie & Rayner 1986; Morrison 1984) visual feedback has been manipulated to obtain data consistent with the third hypothesis.

The express saccade: Autobahn or short circuit of the brain?

R. Martyn Bracewell

Magdalen College, Oxford OX1 4AU, England
Electronic mail: bracewel@vax.oxford.ac.uk

In their target article, Fischer & Weber (F&W) review the behavioural work on the express saccade. They posit that these saccades are of such short latency because their control signals

pass along an express way (Autobahn?) that short circuits some of the usual cortical way stations controlling saccades. In this commentary I shall consider the role of one of these cortical stations – the posterior parietal cortex – in the control of attention and saccades. I shall also suggest that we widen our perspective to consider nonvisual control of attention.

Posterior parietal cortex. Fischer (1987) has argued that the attention/saccade system exists in two states, engaged and disengaged. Only in the latter state may express saccades be produced. In the target article, F&W note the similarity of this position to that of Posner, who has argued that the reorienting of (overt and covert) attention may be decomposed into three mechanisms: (1) disengagement from the current locus of attention, (2) shifting to, and (3) engagement at the new locale for attention (see, e.g., Posner et al. 1984). The results of experiments on patients suggest that the neural substrate for the disengagement operation may be in the posterior parietal cortex (Posner et al. 1984). Further support for this suggestion may be adduced from the recent clinical studies of Pierrot-Deseilligny et al. (1991b), who investigated the effects of various cortical lesions on the latencies of saccades in a gap paradigm. Only patients with parietal lesions showed an increased latency of visually triggered saccades; patients with prefrontal, frontal eye field, and supplementary eye field lesions had latencies not significantly different from controls. If parietal lesions were indeed to disrupt the "disengage" operation, one might expect an increased latency of saccades. In support of this notion, Braun et al. (1992) found that express saccades were decreased following parietal lesions. Also, Lynch and McLaren (1989) reported an increase in saccadic latency in monkeys with lesions in the inferior parietal plus adjacent prestriate cortex.

Auditory control of attention. In F&W's account of express saccades, visual attention plays a central role. They argue that "the express saccade occurs only in response to the onset of a visual stimulus" and they go on to suggest that the "express way" (Autobahn?) runs from the retina to the lateral geniculate nucleus to striate cortex to superior colliculus (SC) and thence to the brainstem. Here I should like to suggest that we consider the role of other modalities, and entertain the possibility of express saccades to auditory targets.

Why might modalities other than vision be involved? First, it is clear that attention is not limited to vision. Indeed, it is an attractive hypothesis that we have a single supramodal representation of extracorporeal space upon which our attentional system operates (e.g., Luria 1966). Auerbach and Sperling (1974) provided strong evidence that there is a common frame of reference for auditory and visual localisation. Auditory and visual spatial deficits do co-occur after neurological damage in man (reviewed in de Renzi 1982). In particular, auditory hemi-inattention is often reported (when tested for) in association with visual neglect (e.g., Battersby et al. 1956; Butter et al. 1989; Dehen & Cambier 1980; Schott et al. 1966; Wortis & Pfeffer 1948).

In a variant of the celebrated task used by Posner et al. (1984), Farah et al. (1989) have shown that patients with parietal lesions have difficulty in disengaging their attention from ipsilesional locations, whether cued by auditory or visual stimuli. These data provide evidence that parietal attentional mechanisms – discussed above and in the target article – operate on a supramodal (at least auditory and visual) spatial representation.

Second, in section 6.1.1 F&W discuss some of the evidence that the presentation of appropriately timed auditory stimuli can reduce saccadic reaction times to visual targets. Other investigators using different paradigms have reached similar conclusions (e.g., Engelken & Stevens 1989; Konrad et al. 1989). The experiments of Kimmig (1986) suggest that auditory cues can "disengage" attention.

Can auditory targets also evoke express saccades? This might be expected if there is a unitary attentional system. On the other hand, perhaps vision is indeed a "privileged" modality – for eye movements, at least. Is there any evidence for either position?

In most studies, saccades to auditory targets have been found to have a longer latency than those to comparable visual targets (Lueck et al. 1990; Zahn et al. 1978; Zambarbieri et al. 1982), but this does not always appear to be the case, particularly for more eccentric targets (Engelken & Stevens 1989; Zahn et al. 1979). In none of these studies were express saccades reported – or sought, one surmises – to auditory (or indeed visual) targets. It remains to be seen whether or not express saccades can be made to nonvisual targets.

The occurrence of express saccades to auditory targets would perhaps force us to construct further express routes. Such a route would presumably involve the auditory brainstem and SC. Schiller et al. (1980) have demonstrated that the SC is essential for the production of express saccades. More traditionally, the SC has been considered a centre for orientation to stimuli of various modalities, and neurones that respond to auditory targets have been reported in the optic tecta of a number of species (e.g., Knudsen 1982; Stein & Meredith 1990). Jay and Sparks (1987) recorded single units in the intermediate layers of the monkey SC, and found a majority of premotor units – including so-called visual-motor cells – to be active before saccades to visual or auditory targets. Such units might mediate our putative express saccades to auditory targets.

reappearing stimulus to reengage attention or to null the decision was noticeably stronger when the reappearing stimulus was the fixated, centrally attended one rather than the peripherally attended one. This result indicates that the center of the visual field has a privileged status and hence that fixation somehow adds to the effects of attention. It could do so in one of several likely ways. First, fixation *per se* could add to the inhibitory effect on fast-regular and express saccades. Although this alternative does not square with the primacy on attention or with the three-loop model proposed by F&W, it is testable by having subjects attend to a peripheral stimulus while passively fixating a central one. Extinguishing the passively fixated stimulus should not produce many express saccades, whereas extinguishing the peripherally attended stimulus should (Braun & Breitmeyer 1988). Second, it is possible that the center of the visual field is more salient attentionally, because attention is directed and engaged there most of the time. Hence stimuli (re)appearing in the visual field would (re)activate the engagement of attention more effectively at the center of the field than peripherally. A third and related possibility is that (re)appearing stimuli are more effective visually in the center as compared to the periphery of the visual field because of the cortical magnification factor. Hence central stimuli would be more effective than peripheral ones in (re)engaging attention or nulling the decision to move the eyes.

Express saccades: Attention, fixation or both?

Bruno G. Breitmeyer

*Department of Psychology, University of Houston, Houston, TX 77204-5341
Electronic mail: psycm9@uhupvm1.bitnet*

Fischer & Weber (F&W) present a strong, well-documented case for the existence of three distinct types of saccades: express saccades, fast-regular saccades, and slow-regular saccades. Moreover, their functional model of the processes contributing to and controlling the generation of each of these saccades – tied credibly as it is to existing psychophysical and neural models of spatial attention and orienting (Posner & Petersen 1990) – has extensive implications for current developments in cognitive neuroscience. F&W give primacy to the role of attention over that of fixation. I suggest that although attention plays a critical role in the timing and control of saccades, the role of fixation is not to be minimized.

In a recent study, Braun and Breitmeyer (1990) looked at how, in a gap paradigm, the reappearance of a centrally fixated and attended stimulus or a peripherally attended stimulus near the time of saccade-target onset affects saccadic reaction times (SRTs) and the relative frequency of the three types of saccades. Without the reappearance of the centrally or peripherally attended stimulus the SRTs were, as expected, short and dominated by express saccades. When the central/peripheral attention stimuli reappeared at or near the time of target onset, SRTs increased. This increase was accompanied, as expected, by a decrease in the frequency of express saccades and by approximately equal increases in the frequencies of fast-regular and slow-regular saccades. According to the three-loop model illustrated in F&W's Figure 13, the increase in the frequency of fast-regular saccades indicated that on a significant number of trials only the decision process needs to be reactivated by the decision-nulling reappearance of the fixation/attention stimuli, whereas the equal increase in the frequency of slow-regular saccades indicates that on about the same number of trials not only the decision process but also the attention-disengagement process is reactivated. Such results are to be expected, because the model indicates that the visual signal generated by the reappearance of the fixated or attended stimuli has parallel access to the attention and decision stages.

However, what was further found was that the tendency of a

A speed/accuracy tradeoff in saccadic latency

E. Leslie Cameron and Peter Lennie

*Center for Visual Science, University of Rochester, Rochester, NY 14627
Electronic mail: leslie@cvs.rochester.edu*

Fischer & Weber (F&W) review results they believe imply a distinctive neural pathway that gives rise to a separate population of fast saccades. The principal evidence is the existence of bimodal distributions of saccadic latency (e.g., Fischer & Boch 1983). However, these are not always readily seen – indeed we have found no evidence for bimodality in our experiments with human subjects (and neither have Reuter-Lorenz et al. [1989] and Wenban-Smith & Findlay [1991]). We have observed very fast saccades (approximately 110 msec mean), but we see no bimodality in the distribution of latencies.

What conditions encourage the production of fast saccades? There are two important ones. The first is one in which there is a single target location. It should be noted that many of the published results come from experiments using a single target location (e.g., Fischer & Boch 1983). A single target location may not be the best stimulus to measure the latency of visually guided saccades because it is likely to encourage anticipatory saccades which may not be readily identified (see below). Increasing the number of targets to two (randomly presented left or right) results in an increase in mean latency of about 15 msec (Fischer & Ramsperger 1986). The second condition is one in which there is a gap between fixation offset and target onset. This will also tend to encourage anticipatory saccades. For these reasons, we think saccadic latencies could profitably be treated as a choice reaction time problem where the tradeoff between speed and accuracy is examined systematically.

Error rates have typically been ignored in work on express saccades. Trials in which a saccade is initiated in the wrong direction or has a latency below a value (e.g., 80 msec) believed to be too short to be visually triggered are discarded from the analysis. In our own studies we have found that saccadic latency is inversely related to error rate and that, as is true of reaction time in general, even correct directional saccades are faster when errors are tolerated.

In an experiment with catch trials (Cameron & Lennie 1991)

Table 1 (Cameron & Lennie). Mean saccadic reaction times and error rates (in parentheses) in gap and no gap conditions with and without catch trials

	Gap	No gap
No catch trials	106 (36%)	150 (1.6%)
25% catch trials	136 (4%)	172 (<1%)

we demonstrated that decreasing their number (from 25% to zero) resulted in a corresponding increase in the number of errors (direction or amplitude of saccades) and a corresponding decrease in mean saccadic latency. We observed this result for both gap and no gap conditions. Table 1 shows mean saccadic latencies of correctly directed saccades for one subject in this experiment. Error rates are in parentheses.

In fact the entire distribution of correctly directed saccades shifted to shorter latencies. Results of this kind lead us to view the "gap effect" as a choice reaction time problem, where error rates affect the overall distribution of saccadic latencies. It is interesting to note that in a study that discussed error rates for normal and dyslexic children's saccadic responses in the gap paradigm, Fischer and Weber (1990) found that faster saccades were produced at the expense of producing more errors. Dyslexic children produce a greater number of fast saccades and they also make a larger number of errors.

We think it is premature to conclude that a special mechanism is responsible for a distinct population of fast saccades in humans.

Is attention engaged or disengaged in saccade programming?

Daniel Cavegn

Laboratory of Experimental Psychology, University of Leuven, B-3000
Leuven, Belgium
Electronic mail: daniel%psl%psy@cc3.kuleuven.ac.be

Fischer & Weber's (F&W's) three-loop model rests on a crucial assumption: Express saccades and regular saccades are preceded by identical preparatory steps. These steps have to be completed in strict serial order before a visually guided saccade can be executed. The assumption of an identical preparation process underlies what I call the disengagement hypothesis, according to which attention disengagement is necessary in programming express saccades and regular saccades. F&W cite the evidence for attention disengagement before express saccades. They cite no evidence that attention is disengaged before regular saccades elicited by a peripheral target or before saccades that serve to scan the visual environment.

Does the disengagement hypothesis hold for all types of saccades, as implied by the three-loop model? To answer this question, it is necessary to present it in more detail. There are at least four propositions that constitute F&W's *disengagement hypothesis*: (1) Attention disengagement initiates saccade preparation; (2) attention engagement inhibits further steps in saccade preparation and inhibits saccade execution; (3) the locus of attention engagement in the visual field is irrelevant for the computation of saccade metrics; and (4), the degree to which attention is focused plays no role in saccade programming.

In contrast to F&W's disengagement hypothesis, let us propose the *engagement hypothesis*: (1) Shifts of attention initiate saccade programming without necessarily resulting in saccade execution; (2) peripheral attention engagement does not inhibit further steps in saccade preparation and does not inhibit saccade

execution; (3) the locus of peripheral attention engagement is relevant in saccade programming because attention serves to select saccade targets; and (4) focused attention at fixation inhibits saccades. Presaccadic attention shifts have been postulated in reading research (see McConkie 1979; Morrison 1984) and in research on object and scene perception (see Henderson 1992a; Henderson et al. 1989). Posner (1980) and Remington (1980) have shown that attention shifts precede a saccade when both are elicited by a peripheral target (see also Crawford & Muller 1992). When saccades were initiated by a central movement signal, Klein (1980) and Remington (1980) found no evidence for presaccadic attention shifts. However, positive evidence was reported by Shepherd et al. (1986): Making a voluntary saccade to a peripheral location facilitated simple manual reactions to targets at the same location; attention allocation to a peripheral location decreased saccade latency (these effects were replicated by Cavegn, unpublished data). In all the studies cited, saccadic reaction times were well above 200 msec. In conclusion, the current evidence in experimental psychology favors the hypothesis that attention is engaged before (at least) slow regular saccades.

Does the disengagement hypothesis or the engagement hypothesis account for express saccades? Let us assume that F&W's explanation of express saccades in terms of an optomotor reflex is correct: Express saccades are fast because a visual stimulus can directly specify the movement parameters and trigger saccade execution. Let us further assume that express saccades are not possible if another process has control over parameter specification and saccade execution. F&W are right to look at visual attention for such a control process. According to the engagement hypothesis, peripheral attention engagement serves to specify saccade parameters and saccade execution is inhibited if attention is still focused at fixation. According to the disengagement hypothesis, saccade preparation and execution are inhibited as long as attention is engaged somewhere in the visual field.

It has been shown repeatedly that abrupt target onsets at a peripheral location draw attention to that location (see, e.g., Posner 1980; Yantis & Jonides 1984). There is currently debate as to whether abrupt onsets result in automatic attention shifts or whether subjects have some control by endogenously allocating and focusing attention (Theeuwes 1991; Yantis & Jonides 1990). F&W defend the disengagement hypothesis by assuming that attention engagement is too late to influence saccade preparation and execution. Express saccades have latencies of 100–130 msec. Subtracting the transmission time from the oculomotor centers to the eye muscles, which amounts to 30 msec (value according to F&W), still leaves 70–100 msec to engage attention. Even if this time is not sufficient, F&W should spell out precisely the dynamics of attention relative to saccade programming and execution: When can attention be (re)engaged without inhibiting oculomotor processes? When does attention engagement at the new location occur relative to saccade execution?

A further point of discussion concerns the locus of attention in the visual field. F&W refer to Mayfrank et al. (1986) and to Braun and Breitmeyer (1988) for evidence that the initiation of express saccades is not influenced by the locus of attention relative to the next fixation position. Subjects were required to fixate centrally (for 2 sec) while attending to a peripheral location. This location either did or did not coincide with the location of target appearance. The occurrence of express saccades only depended on the duration of the gap between the disappearance of the attended stimulus and target onset and not on the locus of peripheral attention. This finding seems to contradict the engagement hypothesis for express saccades (and for fast regular saccades). There is an alternative explanation, however, based on a type of control process different from that of attention engagement. We are able to suppress saccades while attending to different parts of the visual field. F&W maintain that the suppression of saccades depends on attention engage-

ment and that attention disengagement triggers the decision to make a saccade. If that is true, attention shifts during a fixation are difficult to explain because they require attention disengagement at the old location before it can be engaged at a new location. The ability to shift attention repeatedly within a fixation is best explained by assuming that we have voluntary control over saccade execution. This voluntary control is linked to the decision process postulated by F&W and not to attention engagement. In the studies of Mayfrank et al. (1986) and Braun and Breitmeyer (1988), the disappearance of the attended point acts as a signal to release voluntary suppression of saccades and the target stimulus can then trigger the optomotor reflex. Since the target stimulus directly specified the movement parameters, there is no effect of prior attention allocation. Although the previous discussion may question the disengagement hypothesis, further experiments that strictly manipulate visual attention are needed to decide between the engagement and disengagement hypothesis for express saccades.

In summary, F&W's disengagement hypothesis has been challenged by proposing an alternative, the engagement hypothesis. In the case of slow, regular saccades, the current evidence favors the engagement hypothesis, whereas it remains possible that the disengagement hypothesis accounts better for the phenomenon of express saccades. In any case, the three-loop model needs to be revised to account for the role of attention engagement in programming visually guided saccades.

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Attentional engagement, disengagement and preparatory intervals

T. J. Crawford

Academic Unit of Neuroscience, Charing Cross and Westminster Medical School, London W6 8RF, England

Fischer & Weber (F&W) are to be congratulated on a rigorous edifice of empirical data which they have attempted to embed in a coherent theoretical framework. This target article represents an excellent constellation of a series of studies conducted over several years. There are, however, important doubts concerning the possibility that express saccades may not constitute visually guided eye movements, but rather a form of anticipatory behaviour. Although the authors allay many of these fears, a double dissociation study in which express and anticipatory (or predictive) saccades are investigated in a single study is now long overdue.

A central thesis of F&W's paper concerns a neurobiological process linking the release of visual attention and the phenomenon of express saccades. In one gap experiment the proportion of express saccades was clearly reduced when visual attention was engaged at a peripheral location compared to a condition where attention was allocated to the fixation point. Given that express saccades can be manipulated by voluntary attention as they have shown, the phenomenon is open to the whims of voluntary manipulation by experienced and motivated subjects. This point appears to have been acknowledged by the authors (sect. 1, para. 5) where they state that visual attention is "under different amounts of voluntary control depending on the amount of practice the subjects have," but it is not clear from studies on express saccades whether the implications have been fully appreciated. Unfortunately we ourselves have not succeeded in distinguishing bimodal peaks in the gap paradigm, and thus in agreement with Wenban-Smith and Findlay (1991) have not found a clear distinction between anticipatory and express

saccades. Factors such as these may explain, to some extent, the problems experienced by other laboratories in replicating the express saccade distribution.

The results of a key experiment are summarised in Figure 3 and discussed in section 6.1 of the target article. It is of some concern that only data from a single subject are shown and that no indication of statistical analyses of the conclusions on ambiguous data are included. Concerning the role of attention, F&W predicted that when attention is directed peripherally (sect. 6.1, para. 5) "the number of express saccades should be reduced (Fig. 3F) as compared with the case where attention is directed to the fixation point (Fig. 3C)." This seems an unnecessarily weak prediction. If the authors are right that a disengagement of attention from the centre is a prerequisite for express saccades, the correct prediction should surely be that express saccades are largely *abolished* because, in the case of peripherally allocated attention, the condition required for express saccades would be absent: Express saccades are not abolished, however, as shown in Figure 3F. Moreover, it is doubtful whether Figures 3C and 3F are qualitatively different as the authors assume.

F&W hold the view that the disengagement process is the primary or sole attentional parameter necessary for the facilitation of saccadic reaction times (sect. 6.1, para. 6): "Visual attention increases the overall reaction time whereas disengaged attention reduces it . . . engaged visual attention tends to eliminate the express peak as well as the peak of fast regular saccades." Current views on the interaction of visual attention and saccadic eye movements take a somewhat different approach.

Covert shifts of attention precede saccadic eye movements (by ~200 msec) whether saccades are elicited by peripheral cues or central cues (Shepherd et al. 1986). Klein (1980) demonstrated that voluntary shifts of attention and saccadic eye movement can be decoupled. Shepherd et al., however, showed that saccadic eye movements are always preceded by shifts of spatial attention in the cued hemifield. Recently, Crawford and Muller (1992) have shown that when attention is engaged at a forthcoming target location by a spatial precue, saccadic latencies are reduced to targets appearing at the same eccentricity, particularly to targets which follow shortly (i.e., 100 msec) after the attentional cue. Thus, not only does attentional *engagement* reduce saccadic latencies but it does so only when spatial attention and target are topographically aligned. We account for the benefits of spatial attention as follows. In agreement with F&W we believe the saccadic eye movement is preceded by disengagement of visual attention from fixation. Attention is then realigned toward the target and then subsequently engaged in a spatially specific manner. Spatial cueing confers benefit on both saccadic and manual reaction times by setting these processes in motion prior to the onset of the target. Hence both attentional disengagement and the spatially specific attentional engagement processes appear to facilitate saccadic latencies. One worrying observation is that we do not detect express saccadic distribution peaks under these spatial cueing conditions.

Attentional cueing facilitates saccade latencies by approximately 20 msec; however, the effects of increasing the stimulus onset interval from 100 to 500 msec are at least twice as large as that for spatial cueing. This suggests that the attentional disengagement from the central fixation point exerts a statistically reliable but small reduction in saccade latencies in comparison to a far more substantial decrease in saccade latencies resulting from extended saccadic preparatory intervals (Crawford & Muller 1992). At the present time we therefore need double dissociation studies on the interaction of express saccades, anticipatory saccades, attention mechanisms, and preparatory intervals, which should yield a substantial advance in our understanding of the processes underlying the control of saccadic eye movements.

There is no expressway to a comprehensive theory of the coordination of vision, eye movements and visual attention

H. Deubel^a and W. X. Schneider^b

^aMax-Planck-Institute for Psychological Research and ^bDepartment of Experimental Psychology, Ludwig Maximilians University, D-8000 Munich 40, Germany

Electronic mail: deubel@mpipf-muenchen.mpg.dpb.de

Since its invention in 1967, the gap paradigm has become an elegant tool for shortening saccadic reactions. It sprang to full life, however, only after 1983, when a series of papers on "express saccades" (ESs) was published by Fischer and coworkers. The considerable disbelief of other workers in the field was mainly due to the fact that a number of laboratories have simply failed to find the combination of 100 msec latencies and multimodal latency distributions that characterize ESs. Why this occurs is still unclear; and, unfortunately, Fischer & Weber (F&W) do not really answer this important question.

1. Saccadic programming. The most exciting property of ESs is certainly that, in humans, a saccade can be elicited within 100 msec or even less. It should be emphasized here that empirical work exists suggesting that the spatial properties of the saccade can be evaluated at a still shorter time scale. Experimenters using secondary target steps occurring shortly before a saccade have demonstrated that visual information about target position affects the amplitudes of saccades that occur as early as 70 msec after the target displacement (Becker & Jürgens 1979; Deubel et al. 1984). This leads us to an important point we feel is missing, namely, the attempt to insert the ES findings in prominent models of saccade control. It is important to note that many of these models (e.g., Becker & Jürgens 1979) include a temporal integration of the retinal error signal as an essential element. Because of the long time constant of this processing stage, these models are not able to generate spatially precise saccades with latencies in the express range. We would like to mention that one of us (Deubel et al. 1984) has proposed a spatiotemporal model of saccade control that is able to produce spatially correct responses within less than 100 msec.

The above findings suggest that saccades with latencies of 70–90 msec are already target-guided in the sense that they may include information about spatial target position. We indeed found indication for this prediction in a recent series of experiments where we investigated the occurrence of "express corrective saccades." Subjects had to refixate targets that disappeared with the onset of the primary saccade and reappeared after a gap, at the same or a slightly displaced position (Fig. 1a). Figure 1b demonstrates that the individual amplitudes of the corrective saccades for the cases with (I) and without (II) second target displacement separate as early as 60 msec after target reappearance, leading to a gradual transition to the final target location. Moreover, confirming former work (Deubel et al. 1982), the latency histograms given in Figure 1c for the gap condition (I) and the control condition (III) demonstrate that gap introduction leads to reduced latencies for the saccadic corrections, producing a prominent peak of saccades in the express range. In the model put forward by Fischer and collaborators express saccades occur because target offset allows the system to forestall the process of attentional disengagement. Applied to corrective saccades, this concept would require that after the saccade has landed and before the computation of the corrective saccade attention must pass sequentially through the states of engagement and disengagement. This would predict long latencies for saccadic corrections and would not be very plausible functionally.

2. Attention. Attentional processes represent an intensively investigated topic (for overviews, see Allport 1989; van der Heijden 1992). Despite the diversity of models, a core definition exists which is shared by most researchers in this area: Visual attention is conceptualized as a brain operation producing a

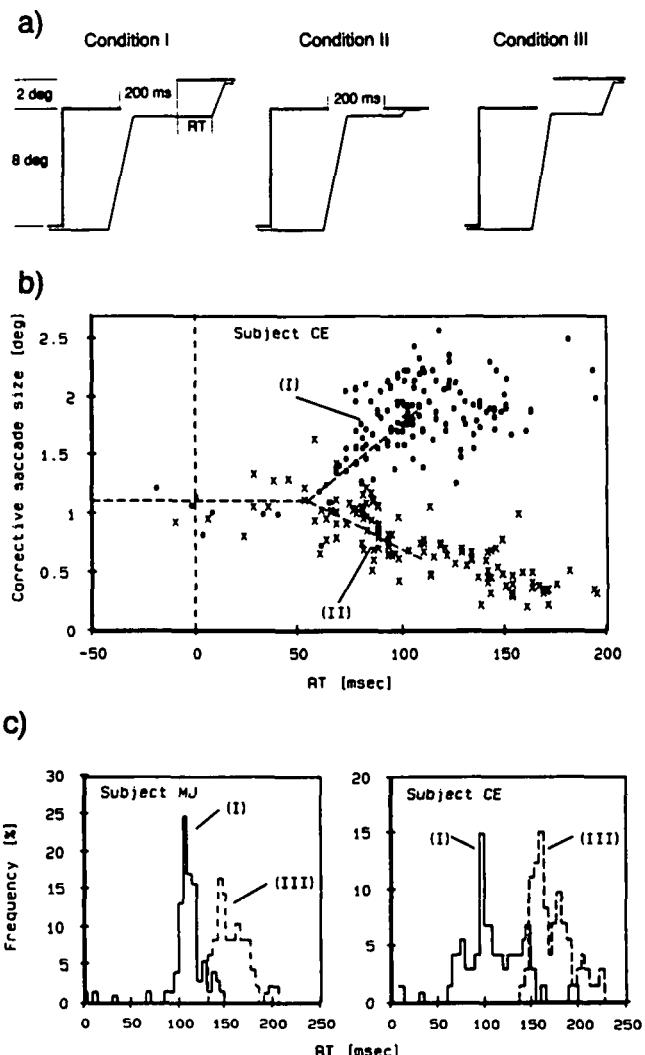


Figure 1 (Deubel & Schneider). (a) Experimental paradigm. Target and eye positions for the three experimental conditions that occurred randomly in a session. The target was a bright spot on a fast video display (frame rate 150 Hz). Eye movements were measured with the Generation-V dual Purkinje-image eyetracker. The primary saccade triggered the target offset. Condition I: The target reappeared after a 200 msec gap and with a displacement of 2 deg into the direction of the first step. Condition II: 200 msec gap, no target displacement. Condition III: The target reappeared at the displaced position within 10 msec after the end of the primary saccade. (b) Amplitude vs. reaction time of corrective saccades to target onset in conditions (I) and (II). (c) Reaction time distributions in condition (I) and (III) for two subjects.

localized priority in information processing – an attentional "window" or "spotlight" that locally improves the speed and reduces the threshold for processing events. According to F&W, the gap condition leads to a state where the attentional window is not engaged at a specific location. Unfortunately, F&W do not provide direct empirical evidence for this central claim, for example, by determining perceptual performance at the locus of fixation. Recently, Mackeben and Nakayama (1993) measured performance in a vernier-acuity task where a peripheral cue indicated the location of the target among the distractor elements. A gap paradigm led to higher efficiency in the attentional manipulation. However, since performance was not determined at the *fixation point*, their data did not elucidate the disengagement hypothesis – the hypothesis that attention

must be disengaged prior to ES has not yet been empirically substantiated.

It is interesting to note that Mackeben and Nakayama have a conception of the role of attention different from that of Fischer and coworkers, assuming that during the preparation of a saccade the disengagement of attention from the fixation point is followed by an *engagement* of attention at the target location – before the saccade can be initiated. For F&W (see also Fischer 1987), by contrast, *disengagement* is the last attentional state before a saccade can be made. This leaves open the role of engagement of attention at the future fixation location which is perceived by many workers as an obligatory step before goal-directed saccades.

3. Coordination of vision and eye movements. Another somewhat neglected point in the understanding of ESs concerns whether or not they have ecological validity outside the extremely visually reduced laboratory situations. Normally, the observer is confronted not with one target standing in isolation, but with a highly complex visual structure, requiring elaborate visual processing to select the next saccade target. Recently, we (Deubel & Frank 1991) studied an experimental situation in which saccadic eye movement had to be directed to targets embedded in a prominent background structure. Target and distractor differed in their textual properties rather than in their global luminance characteristics. We applied a modified gap paradigm in which the visual scene did not appear until 200 msec after the offset of a central fixation point. The fastest visually guided saccadic reactions had latencies of 165 msec or more, which compared with minimum reaction times of 120 msec in the reference situation without background structure. So, ESs disappear with the presence of complex structure in the visual field.

In conclusion, the work summarized in the target article is important and has already inspired considerable empirical effort. However, some of the claims put forward by Fischer & Weber seem premature; particularly those concerning attention do not seem to be warranted by extant empirical data. We suggest that for now ESs should be seen, less emphatically, as one of a number of possibilities of investigating fast sensorimotor processing and they should be integrated with current research on attention and saccadic programming.

Does the attention need to be visual?

John M. Findlay

Department of Psychology, University of Durham, Durham DH1 3LE,
England

Electronic mail: jmf1@durham.ac.uk

In the ten years since their first report of express saccades, the Freiburg group have carried out an impressive programme of research and this seems a very opportune moment to assess its diverse implications. The work is clearly of considerable significance. The topic of saccadic eye movement programming holds the real prospect that we may be able to trace a scientific progression from oculomotor physiology to voluntary activity.

Most (although not all) of the facts concerning express saccades are well established and uncontroversial. When tested in the gap paradigm for target-elicited saccades, subjects invariably show reduced saccade latencies, producing mean latencies well below 150 msec and sometimes as low as 100 msec. It has long been a source of puzzlement why the visual/oculomotor system should need, for a simple orienting movement, the 200 msec or even 250 msec planning time that appears in many textbooks. It is clear that these short-latency saccades are not anticipatory ones, although conditions that favour their occurrence also increase the proportion of anticipatory saccades that occur. There remains a difficulty, of which Fischer & Weber (F&W) are aware, concerning whether express saccades form a

qualitatively distinct category. The strongest evidence for such a dichotomy comes from the many reported cases, from several laboratories, of bimodal distributions of saccade latencies. Other workers, however, have looked carefully for such bimodal distributions, without success.

F&W favour an explanation of the results in terms of "disengagement of visual attention." This term is appealing but on close examination it seems to lack explanatory power. At an operational level, the only available measure for attentional disengagement seems to be the speeding of saccadic or motor programming. There is a body of work in experimental psychology concerned with visual attention but no satisfactory overall theoretical framework has emerged. Indeed, some theorists are looking to oculomotor programming as a possible basis (Rizzolatti et al. 1987; Umiltà et al. 1991) and relevant discoveries in oculomotor neurophysiology (e.g., Munoz & Wurtz 1992) are still emerging.

A critical question concerns what, if anything, is specifically visual about the speed-up produced by the gap paradigm. The following pieces of evidence all support the alternative view that the speed-up is the result of a modulation of a general state of alertness. (1) The gap speed-up is found whether or not the target position or direction can be predicted in advance. (2) The speed-up produced by the gap shows no statistical interaction with other factors affecting saccade latency (Findlay, unpublished results; Honda & Findlay 1992). (3) Saccade latencies (and also fixation durations during scanning) may be modified by a wide range of nonvisual factors (e.g., cognitive load – see Findlay 1992). A substantial situation-specific speedup as a result of practice is also found (Findlay & Crawford 1983). (4) Jüttner and Wolf (1992) have clearly demonstrated that non-visual factors (expectancy) can influence the occurrence of express saccades.

Based on this approach, one might suggest that generation of a saccade requires the co-occurrence of two signals. The first is a general "ready" signal, the second a spatial signal, which will, for target-elicited saccades, be carried in some retinotopic map by the activation arising from the target onset. Models of this sort in which the "when" and "where" decisions are made separately have already been postulated (Becker 1989; Becker & Jürgens 1979; Findlay 1983; 1987) and can account for a variety of results in saccade programming. There is good evidence from the work on brain potentials preceding manual responses that both a specific and a nonspecific, readiness signal is involved (Donchin & Coles 1991; Kornhuber 1974).

This suggestion is not far removed from that of F&W, but by transferring emphasis from pathways to processes, it may open the possibility of a more integrative account. The bimodal distributions would then indicate, not saccades produced by separate pathways, but two points in time at which the hypothesized readiness signal had a peak. The existence of nonspecific short-term anticipatory processes is well established, although the possibility of temporal modulation of such processes is unexplored. Such an account might permit the incorporation of practice effects and also explain why some individuals do not show any differentiation between normal and express saccades (Wenban-Smith & Findlay 1991). It is notable that, although bimodal distributions have been obtained from unpractised subjects, the most strikingly bimodal ones come from very well-practised individuals.

Two observations concerning express saccades could be damaging for this alternative "nonspecific" position. First, the speeding produced by the gap might be a separate process from that which produces express saccades. Such a possibility was suggested in some early accounts (the transition from "slow regular" to "fast regular" of Fischer & Boch 1983). This distinction does not receive much emphasis in the target article. A second apparent problem concerns the absence of express antisaccades. This is used in the target article to argue that express saccades require an explicit visual onset at the target

position. Logical though this argument is, I believe an alternative must be considered. When two targets are presented bilaterally, saccade latencies are longer than when one target alone is presented (Lévy-Schoen 1969). We have recently shown that this effect occurs even when the subject is instructed in advance in which direction to move the eyes (Findlay et al., in preparation). In this situation, the conditions laid down in the target article – visual onset and appropriate readiness – can co-occur, but saccade latencies are prolonged. A third precondition appears necessary, namely, the *absence* of visual onset elsewhere in the visual field other than at the position that is the goal for the saccadic movement.

On the functional significance of express saccades

Martin H. Fischer^a and Keith Rayner^b

Department of Psychology, University of Massachusetts, Amherst, MA 01003

Electronic mail: ^afischer@titan.ucc.umass.edu; ^brayner@psych.umass.edu

Fischer & Weber (F&W) acknowledge the controversy regarding express saccades: Some investigators have had difficulty obtaining evidence for the phenomenon. However, we are not so much concerned with the controversy as we are with the functional significance of express saccades.

According to F&W, attention and the programming of saccadic eye movements are highly related. They suggest a cycle of attentional engagement followed by disengagement, with disengagement triggering saccades. They also argue that express saccades are not anticipatory movements but are visually guided. Typically, express saccades occur when a foveal target is turned off before the onset of a peripheral target (the gap paradigm); they do not occur when the foveal stimulus remains on (the overlap paradigm) because the foveal stimulus continues to engage attention. However, F&W claim that express saccades can be obtained in the overlap paradigm through practice.

F&W's theory is based on the absence of attentional effects on the distribution of saccadic latencies: The distributions from the overlap conditions presented in Figure 3 are similar despite an attentional manipulation (central vs. peripheral engagement). Instead of supporting a disengagement hypothesis, this casts doubt on F&W's approach of inferring attentional processes from a single dependent measure while controlling for allocation merely by instruction. Even if the instructional manipulation is successful, the presumed difference between the two gap conditions (Fig. 3A and 3D) could simply reflect invalid preparation on half the trials for peripheral orienting rather than engagement costs. It is noteworthy that Klein et al. (1992) have reported that attentional allocation (as inferred from reduced manual detection latency) does not facilitate saccades; they presented evidence against the disengagement hypothesis.

Measurement of simultaneous eye and hand movements provides further reason to doubt the proposed theoretical account. The reduced latencies for both eye and hand in the gap condition are interpreted as evidence for a common disengagement benefit (Biscaldi et al. 1989). This benefit is not always reflected in the latencies of both effectors, however: The correlation between eye and hand latencies increases in response to central offsets (Frens & Erkelens 1991) but decreases in response to peripheral onsets (Fischer & Rogal 1986).

Further elaborating the attentional account (e.g., visual capture) would not aid in understanding the functional relationship of attentional mechanisms to overt response patterns. From studies requiring single responses of either the hand or the eye we know that the time course of attentional facilitation is slower for the hand than for the eye (Shepherd et al. 1986; Crawford & Mueller 1992). This seems functional in light of longer manual

than saccadic latencies and suggests that saccadic programming overrules manual preparation with respect to attention allocation. We recently found a different pattern in reading-like situations, however. Subjects scanned lines of pseudo-text made of "words" of x's. We examined attentional allocation by measuring manual responses to an asterisk appearing slightly above the line. The asymmetry of the perceptual span toward the direction of the forthcoming saccade is thought to reflect attention allocation (see Rayner & Pollatsek 1989). This implies that manual latencies should be facilitated if the asterisk appears within this span. The probe appeared briefly, with eccentricity varied relative to the fixation location. Manual latencies did not reflect span asymmetry and the manual response triggered by the probe onset increased the current fixation duration by about 20%. Hence, measurement of attention might even interfere with allocation processes.

Reading research provides a further reason for our reluctance. Like F&W's model of express saccades, Morrison's (1984) model of eye movement control in reading relies heavily on a relationship between attention and saccade programming. According to Morrison's model, at the outset of a fixation, attention is directed to the fixated word (word *n*). When lexical access for that word is sufficiently complete, attention shifts to the next word to the right (word *n* + 1), with the saccade following in a time-locked fashion. This model accounts for short fixations (between 50–100 msec) that occasionally appear during reading by appealing to work by Becker and Juergens (1979). Basically, Morrison's argument was that there are occasions in which word *n* + 1 is identified before a saccade is made to that word. If the saccade program for word *n* + 1 is so far along that it cannot be canceled, a saccade to word *n* + 2 is programmed in parallel with the ongoing program for word *n* + 1. The result is a very short (50–100 msec) fixation on word *n* + 1 followed by a saccade to word *n* + 2.

Are the short fixations that occur in reading express saccades? We doubt it. Although F&W have not suggested that express saccades occur in reading, others might be tempted to do so. However, if express saccades can be induced via practice in the overlap paradigm, as argued by F&W, then surely they should be quite frequent in reading, because readers only need about 50–75 msec to abstract the visual information from the text (Ishida & Ikeda 1989; Rayner et al. 1981). Given the latter point, if express saccades are visually guided and induced via practice, why aren't short fixations more prevalent in reading? The fact that they are not argues against the notion that express saccades are functional in reading; Morrison's model provides a better account of short fixations in reading than arguments based on express saccades.

F&W address the issue of functional significance to some extent by examining express saccades in dyslexic readers. Wisely, they note that it is only a subgroup of dyslexics that show a pattern different from that of their more skilled counterparts. Many attempts have been made to explain dyslexia as arising from some type of oculomotor abnormality. The evidence (see Rayner 1985, for a review), however, overwhelmingly indicates that only a small percentage of dyslexic readers have erratic eye movement patterns outside of a reading situation and that their erratic eye movement patterns during reading are due to comprehension difficulties. Thus, although we agree with Fischer & Weber that only a subgroup of dyslexics have eye movement abnormalities, we fail to see logical or empirical arguments for the functional significance of express saccades in complex situations.

Frontal eye fields: Inhibition through competition

Steven D. Forman,^a Jonathan D. Cohen^b
and Mark H. Johnson^c

^{a,b}Department of Psychiatry, University of Pittsburgh School of Medicine, Pittsburgh, PA 15213 and ^{b,c}Department of Psychology, Carnegie Mellon University, Pittsburgh, PA 15213

Electronic mail: ^asf22@andrew.cmu.edu; ^bjc5e@andrew.cmu.edu;
^cmjk@andrew.cmu.edu

Fischer & Weber (F&W) suggest the frontal eye fields (FEF) as a center through which attentional engagement inhibits the production of express saccades. In this view, a primary function of FEF is inhibition of the express pathway mediated through the superior colliculus (SC). In this commentary we will emphasize instead the role of FEF as a control structure for saccadic eye movements parallel to and in competition with the express pathway. In this view, FEF mediates more sophisticated control of eye movements than SC (e.g., memory-guided saccades, or planned sequences of eye movements) and inhibitory effects arise as a consequence of the competition between FEF and SC, rather than as a primary function of FEF. A corollary of this view is that there is no need to postulate a discrete disengagement mechanism to account for the behavioral data in the gap paradigm. F&W's emphasis on the inhibitory function of FEF leads to their hypothesis that this inhibition must be released to allow the production of express saccades and that this release relies on the action of a discrete attentional disengage mechanism. In contrast, our view of parallel, competing systems does not require a discrete disengager. Inhibitory and disengagement-like effects arise from the dynamic interactions between competing systems (see Cohen et al., in preparation). Below, we discuss developmental, neurophysiological, and computational considerations that support our view of FEF function.

One source of evidence F&W cite to support inhibition of the express pathway as a primary function of the FEF comes from developmental studies indicating that the frequency of express saccades decreases with age (presumably as a consequence of increasingly mature cortical systems). Johnson (in press) reports preliminary data from human infants that are consistent with this observation, indicating that the frequency of express saccades may decrease between 6 weeks and 6 months of age, under certain testing conditions. Although these findings suggest that cortical circuits have an inhibitory influence on express saccades, other experiments with infants have revealed a variety of improvements in saccadic control following the onset of frontal eye field functioning, such as the ability to learn regular sequences of saccades (see Johnson 1990 for review). Thus, developmental data appear to support the involvement of FEF in both the inhibition of express saccades and the control of more sophisticated saccadic movements.

Other evidence suggests multiple roles for FEF. For example, behavioral evidence from patients with frontal lesions (Guitton et al. 1985) supports a role for FEF in suppressing reflexive saccades. Electrical stimulation of the FEF, however, (Robinson & Fuchs 1969) results in production rather than suppression of saccades. Moreover, the nature of the anatomical projections from the FEF both directly to the SC and indirectly through the caudate and substantia nigra appears to support excitatory or, at least, disinhibitory roles (for reviews, see Chevalier & Deniau 1990; Guitton 1991). Finally, electrical stimulation delivered to either SC or FEF produces similar results: Hybridization between visually triggered saccades and electrically stimulated ones is observed (Schiller & Sandell 1983). Thus, it appears that both SC and FEF contribute to the formation of saccades and that the role of FEF is not restricted to inhibition of the express pathway.

As noted above, the hypothesis that FEF serves primarily an inhibitory role leads to the postulation of a disengagement mechanism responsible for overcoming this inhibition when an

express saccade must be made. F&W present behavioral findings consistent with this view. When subjects are given a cue (e.g., the offset of a fixation point, or a nontarget stimulus), they are faster to respond to the target than when no cue occurs. Since the cue is not physically related to the target, it is assumed that the cue facilitates responding (and increases the number of express saccades) by activating the disengage mechanism, releasing the express pathway from FEF inhibition. There is an alternative interpretation of these findings, however, one that is consistent with our view of FEF and SC as separate, competing systems for saccadic control: It is possible that the cue produces a transient increase in the subject's level of arousal, accompanied by a change in catecholaminergic tone. Servan-Schreiber et al. (1990) have used computer simulation models to show that one effect of catecholamines may be the modulation of response properties of processing units in neural networks. Preliminary results suggest that when a response is determined by more than one processing pathway, an increase in modulatory tone can favor direct (e.g., subcortical) over indirect (e.g., cortical) pathways. We are currently extending this work to investigate whether these effects result in multimodal distributions of responses like those reported by F&W in the target article.

Our hypothesis can also be tested empirically by measuring established correlates of arousal such as galvanic skin response during SRT experiments in gap and overlap paradigms. We would predict negative correlations between measures of arousal and saccadic response latency and a positive correlation between arousal and the number of express saccades. Positive results would support our alternative interpretation of the findings reported by the authors, which (a) does not assign inhibition as a primary role for the FEF and (b) does not postulate a specific disengagement mechanism.

Complexity and modes as factors underlying saccadic latencies

P. E. Hallett

Departments of Physiology, Zoology, Ophthalmology, and Institute of Biomedical Engineering, University of Toronto, Toronto, Ontario, Canada M5S 1A8

Electronic mail: peter@biovision.med.toronto.edu

Complexity: Hence the value of the longer view of saccadic latency. Express saccades are most usefully regarded as complex high-level behaviours with an *effective latency* (= "set-up time" + conventionally measured latency) that is at least comparable to the classic interval of 200 or more msec between tracking saccades. Set-up time for express saccades is explicit in the computational model of the Freiburg group (Fig. 13 of Fischer & Weber [F&W]) because the activation of the minimal latency path "vis/com/mot" requires the activation of higher brain structures prior to the target displacement. Given repeated warnings that eye movements are ultimately subject to cognitive constraints (Hallett 1986; Steinman 1986; Steinman et al. 1990), it is high time to take a longer view of reaction times.

The choice of weak randomization of stimulus conditions by the Freiburg group was daring because others had already established the importance of expectations and strategies in temporally well-separated "single-shot" trials (e.g., Findlay 1980; Kowler & Steinman 1981). It was subsequently shown that saccadic latencies are altered when the number of target positions is increased or catch trials are introduced or the foreperiod is manipulated (Hanes et al. 1992; Jüttner & Wolf 1992; Kalesnykas & Hallett 1987). By contrast, the sequences of tracking saccades seen in the classical open-loop servo studies were at intervals nearer 200–270 rather than 105 or 70 msec in both man and monkey (Fuchs 1967; Robinson 1964; Young & Stark 1963)

even though the open-loop condition involves no extra randomization (in the sense that the target is locked to the eye). Nor were express saccades seen in an extension of the servo paradigm that randomized the appearance and direction of the target (large low contrast targets, Perron & Hallett 1991). As the consensus has always been that the eye is not under voluntary control in open-loop tracking (at least not initially in man, Hallett 1986), the necessary conclusion is that *automatic* tracking latencies are longer than conventionally measured express latencies (200–270 msec > 105 msec). The discrepancy is the relative advantage due to expectation, practice, and set-up under the conditions of the express saccade paradigm.¹

One direct estimate of the set-up time for express saccades is provided by the optimal value of the gap in the gap task (150–200 msec; F&W's Fig. 2; Kalesnykas & Hallett 1987). A second approximate estimate comes from an experiment with B. D. Adams in which the instructions "normal foveating task" or "anti task" were given as foveal visual cues at variable times in advance of the target displacement (Fig. 10.85 of Hallett 1986). An "advance" of less than 250 msec severely inflates latency; several hundred msec are required if the conventionally measured latency is not to be inflated at all. This approach overestimates set-up time because a control experiment using the same cues but only one instruction also required an appreciable advance (suggesting possible fixational or attentional "engagement" by the cues; F&W, sect. 10.2). However, either estimate supports appreciable set-up time. The effective latency of express saccades is therefore at least comparable to the intersaccadic interval of 200–270 msec in the classical open-loop experiments of Young and Stark (1963) and later workers (e.g., 200 msec set-up + 105 msec measured latency = 305 msec effective latency > 200–270 msec tracking latency).

Modes: The virtues of a finer look at latency. Perhaps the contribution of the Freiburg group that I most appreciate has been their repeatedly demonstrating the existence of distinct latency modes for saccades, for example, premature, anticipatory, express, fast regular, late, and so on, in their monkeys and many of their human subjects (Fischer & Ramsperger 1984; 1986; Weber & Fischer 1992). The corresponding concept of *varieties of saccadic planning* actually emerged from several laboratories prior to Fischer and Boch (1983), but it is considerably strengthened by repeated large samples in the Freiburg studies. Varieties of saccadic planning with cancellation and modification of saccades on a time scale of about 120 msec or even less are indicated by many studies: gap and overlap tasks (Saslow 1967a), two-step tracking (Becker & Jurgens 1979; Findlay & Harris 1984; Taumer et al. 1972), anti saccades (Hallett & Adams 1980), secondary or correction saccades (Becker 1976; Hallett 1978; Prablanc et al. 1978; Shebilske 1976), and predictive tracking (Smit & Van Gisbergen 1989). In a review of this topic I normalized and replotted latencies from 10 two-step tracking studies in the literature and found evidence for varieties of saccadic planning (Fig. 10.97 of Hallett 1986). Also discussed were two essentially visual modes in the latencies of secondary saccades to moderate amplitude target displacements (4–15 deg), with a possible division at about 150 (range 130–170) msec from the end of the primary saccade in about half of 11 subjects in this laboratory. Considerably prior to this, Becker (1972) had identified visual and nonvisual secondary saccadic modes for large target displacements. More recently, Kalesnykas and Hallett (1989) examined instructions, combined with different patterns of fixation point and target lightings, that should a priori lead to systematic increases in mean latency for the different conditions (because of increasing dependence on voluntary actions rather than stimulus initiated ones). Experimentally, the mean latencies progressed in steps of roughly 35–45 msec from one condition to the next. Finally, the Freiburg computational model shows latency modes with separations of 40 or 60 msec (F&W's Fig. 13).

The notion that various latency modes can arise from different

combinations of a set of neural processes or pathways would seem to be well worth pursuing (Fig. 13 of Fischer & Weber; Hallett 1986; Hallett & Adams 1980). Apart from several statistical issues, a potential difficulty for comparisons across different studies is the possible need to make allowances for the effects of expectation and strategy on the measured modes. In addition, one commonly neglected process or subprocess is the waiting time for sufficient photons (Barnes & Hallett 1992; Doma & Hallett 1988; 1989). Because this waiting time has varied between about 1–180 msec in our different conditions, it is important that it be controlled (Boch et al. 1984; Weber et al. 1991) or normalized so that theorists can usefully compare latencies across different lightings, adaptations, pupil sizes, or tasks.

NOTE

1. The discrepancy should be reduced if human or primate subjects are inhibiting and delaying tracking in the open-loop case. However, the only grounds for this speculation (the tendency for latencies to often be somewhat less than 200 msec when practised subjects saccade to targets in single moderately randomized trials) is also a situation where expectation, set-up, and practice must help.

Visual attention and saccadic eye movements in complex visual tasks

John M. Henderson

*Eye Movement Laboratory, Department of Psychology, Michigan State University, East Lansing, MI 48824
Electronic mail: johnh@msu.edu*

Fischer & Weber (F&W) provide an interesting summary of the evidence concerning the phenomenon of express saccades and propose a model of saccadic eye movement programming in which attentional disengagement is a prerequisite for saccadic programming. The question I want to address here is whether visual attention is normally disengaged from all visual stimuli prior to a saccadic eye movement during complex, real-world visual tasks such as scene viewing and reading. There is in fact a large body of evidence suggesting that prior to a saccadic eye movement in complex tasks, visual attention is disengaged from the foveal stimulus and *reengaged* at the extrafoveal stimulus that is the target for the saccade prior to that saccade (Henderson 1992b).

Most of the evidence concerning the allocation of visual attention during complex visual tasks derives from the "eye-contingent display change technique" (McConkie & Rayner 1975), in which the visual stimulus presented to the viewer is changed as a function of eye position. Initial experiments using this technique involved the use of the moving window paradigm in reading: Subjects read text in which a window or region of normal text was surrounded by regions of uninformative visual information. As the reader moved through the text, the window moved along with the eyes. Results from these studies indicate that visual information is acquired from an asymmetric region around the current point of fixation. This is shown by the finding that reading rates (and comprehension) are identical when the reader is given an asymmetric window with 4 character spaces to the left and 15 character spaces to the right of the current fixation point and when the entire line is visible (McConkie & Rayner 1975, 1976; Rayner et al. 1980; Underwood & McConkie 1985). These findings are not simply due to left-hemisphere (right hemifield) language dominance: Pollatsek et al. (1981) showed that when English-Hebrew bilinguals were reading English, they acquired information asymmetrically to the right, but when these same subjects read Hebrew, which is read from right to left, they acquired more information from the left side of the fixation point. Similarly, Inhoff et al. (1989) showed that when native readers of English were asked to read from right to left text that was presented in several backward formats (e.g.,

words facing forward but ordered right-to-left; letters within words and words ordered right-to-left), their perceptual spans were found to be asymmetric to the left, in the direction that the text was being read.

These results are not specific to reading: Henderson et al. (1989) had viewers engage in an object identification task. The viewers examined displays composed of four line drawings of objects positioned at the corners of an imaginary square. To determine which object or objects were being attended on each fixation, a two-dimensional variation of the moving window paradigm was used. The main finding was that parafoveal information concerning object identity was acquired only from the object currently fixated and the object about to be fixated next. Even though eye movements were changing direction after each object was fixated, the object about to be fixated next was the only one in addition to the object currently fixated that was processed during a given eye fixation. This indicates that attention is allocated dynamically during each fixation to the location to be fixated next. Together, these results strongly suggest that the allocation of visual attention to the location about to be fixated next prior to a saccadic eye movement is a general aspect of complex visual-cognitive functioning.

There is also evidence suggesting that prior to a saccade, attention *must* be allocated to the target location of that saccade. Shepherd et al. (1986) had subjects press a button whenever they detected a simple light flash. At the same time, they were to execute an eye movement to a predetermined target location. In one condition, the light flash was most likely to appear at the same location as the target for the saccade. In another condition, the light flash was most likely to appear at a location that was different from the location toward which they were to execute the eye movement. Shepherd et al. found that subjects could strategically direct attention to the more likely location *unless* the eye movement was imminent. When an eye movement was imminent, however, subjects could only direct attention to the location that was the target of the saccade. Thus, these results indicate that before an eye movement, attention must be allocated to the location about to be fixated.

Finally, there is evidence that prior to a saccade, attention is disengaged from the fovea and reengaged at the specific target location of the impending saccade. Henderson (1992b) had subjects participate in a transsaccadic word identification task. The subject began each trial fixating a central cross presented on a computer monitor. Two preview letter strings were then presented, one just to the right of the subject's point of fixation and the other several degrees to the right. In the *move* condition, the subject was asked to execute an eye movement to the location of the letter string furthest to the right as soon as the letter strings appeared. The eye-contingent display change technique was used so that during the saccade the two letter strings could be replaced by a single target word positioned at the location of the letter string toward which the eyes were moving. Because the change was accomplished during the saccade, the subjects never saw the change itself. The task was to name the target word aloud as quickly as possible once the eyes had landed. Naming latency was taken as a measure of word identification time.

The results indicated that when the subject was maintaining fixation on the central cross (no-move condition), preview of the target word at the far location provided no preview benefit. In contrast, when the subject was about to execute an eye movement (move condition), a preview of the target word at that far location led to significant preview benefit. These data indicate that attention precedes an eye movement to the location toward which the eyes are about to move. In contrast, the amount of preview benefit derived from the near location when the eyes were moving to the far location was *less* than the amount derived when the eyes remained stationary. The finding that the preview benefit at the near location was reduced in the move

compared with the no-move condition suggests that attention moves away from the fixation point prior to the saccade.

Taken together, the above results, along with similar findings (see Henderson 1992b for a review), strongly suggest that during complex visual tasks involving multiple eye fixations, visual attention is disengaged from the foveal stimulus and reengaged on the extrafoveal target of an upcoming saccade prior to that saccade. These results are difficult to reconcile with the view that attention must be in a disengaged state in order to permit (disinhibit) a saccade, as proposed by Fischer & Weber.

Visual attention may not control the occurrence of express saccades

Albrecht Werner Inhoff

*Department of Psychology, State University of New York at Binghamton,
Binghamton, NY 13902
Electronic mail: inhoff@bingvmb.bitnet*

Is there a distinct population of express saccades, as argued by Fischer & Weber (F&W)? The experimental data are persuasive. Furthermore, express saccades appear to fit into a comprehensive model of saccade control that considers evidence from several sources. These include behavioral data from different species, neuroanatomical findings, data from cognitive-attention studies, and results of mathematical modelling. Although I am intrigued by the scope of this work, I am hesitant to endorse the use of attention as the central explanatory construct.

Several findings suggest that a relatively abstract cognitive process such as attention is implicated in the occurrence/absence of express saccades. For example, express saccades disappear when the subject is *instructed* to "attend" to the periphery, irrespective of whether overlap or gap tasks are used. Auditorily provided information can trigger express saccades to visually presented lateral targets, suggesting the use of abstract-amodal control processes. Furthermore, neuroanatomical as well as behavioral studies (e.g., Klein 1980; Posner 1980) reveal a functional relationship between saccade programming and visuo-spatial attention.

Other aspects of the described data argue against the use of attention, however. First, express saccades do not occur when the eyes are moved across less than 2 degrees of visual angle in the gap and overlap tasks. Disengagement of attention, as it is expected to occur in a standard gap task, should be unaffected by the eccentricity of the *subsequently* presented target.

Second, none of the studies provides an independent measure of attention; and at least one consideration suggests that disengagement of attention per se may not account for the gap effect. According to F&W, the disengagement of attention should require approximately 40 to 50 msec, roughly corresponding to the difference between the modal values of express (110 msec) and fast regular (150 msec) saccades. It is unclear, however, whether a short gap duration of approximately 40 msec will yield express saccades. A distinct distribution of express saccades emerges when gaps of 100 msec or more are used. The distinct express mode is also evident at considerably longer gap intervals of up to 500 msec. In these conditions, considerable time elapses between the disengagement of attention and the occurrence of the peripheral target. What occurs in this interval? Does the system enter an attentional void state? Do express saccades occur when the system has entered the attentional void state? Can the system remain for a considerable time within an attentional void state, knowing that a visual target is to be presented?

Since no independent measure of attention is provided, the attention hypothesis could be turned on its head and still

plausibly account for a large set of the findings. Specifically, offset of the fixation marker in the gap task may provide a cue that permits the focusing of attention, hence the gap effect. Likewise, a blinking of the fixated stimulus or a tone in another modality prior to the occurrence of the peripheral target may support the focusing of attention, again yielding express saccades (it appears quite plausible that a blinking stimulus will engage, rather than disengage, attention). Express saccades may emerge with practice, possibly because practice improves the focusing of attention. Furthermore, asking subjects to attend to the periphery may inhibit express saccades because it prevents subjects from focusing attention at fixation. Of course, this reversed attention hypothesis could account neither for the lack of express saccades when saccades of 2 degrees of visual angle or less are to be executed nor for effects of saccade latency on saccade size, described below.

Third, the attention hypothesis predicts that the specification of movement parameters such as movement direction and movement size should be identical for express saccades and regular saccades as the longer latency of regular saccades is due solely to attention disengagement demands. Yet effects of saccade latency (or prior fixation durations) on saccade size exist. We compared effects of task demands on the size of saccades following (short) fixations of less than 150 msec and (long) fixations of 150 msec or more (Inhoff et al. 1992). In general, the eyes were moved to a less optimal viewing location after short fixations.

Fourth, we completed an experiment that was suggested by B. Fischer during a recent conference (Inhoff et al., submitted). In the study, subjects "read" homogeneous strings of letters by moving their eyes along strings of homogeneous letters, for example, zzz zzzzzz zzzzz zzzzzzz zzz. The task should have imposed few, if any, visual or linguistic processing demands. Consequently, a distinct distribution of express saccades was expected to occur. Yet the resulting distribution was strictly unimodal, with no tendency toward an express peak.

Subanalyses of the z-text study suggested that subjects generally moved their eyes off the center of z-strings to the center of parafoveally available z-strings. Saccade planning thus took the spatial composition of a complex visual display into consideration. When this occurs, execution of express saccades may be inhibited.

To my knowledge, all demonstrations of express saccades have used relatively simple fixation and target stimuli, generally consisting of bright squares, bright dots, bright asterisks, and so on. Furthermore, the subject is required to execute a single movement (i.e., the following fixation location has no impact on further task performance and a "loose" accuracy criterion can be adopted). Express saccades may thus occur when the oculomotor system has learned to respond to peripheral luminance changes without taking spatial configurations into account.

ing their model more explicit. In this commentary we focus on the connection between the saccadic control system as discussed in the target article and the control system for covert attention as recently proposed by Jackson and Houghton (1992).

F&W suggest that suppression of the primitive reflex loop responsible for express saccades is mediated by the frontal eye fields (FEF) and they imply that this may be carried out either directly via the FEF → superior colliculus (SC) projection or indirectly via the nigrotectal projection. This assumption implies that these two forms of FEF control over SC are computationally equivalent. We believe that this is unlikely to be the case. The direct FEF → SC pathway is probably glutamatergic and excitatory. Thus it cannot act to inhibit the SC unless one also postulates that this projection synapses onto inhibitory interneurons. We would like to make the following points with regard to the computational role of the basal ganglia:

(1) The basal ganglia receive inputs from the entire neocortex, including prefrontal, parietal, and occipital cortex. FEF and parietal projections terminate in a series of alternating columns, maintaining the topographical integrity of spatial information originating within these two areas and perhaps allowing for the synthesis of spatial information originating within anterior and posterior areas of the cortex (Mesulam 1990). Thus, the nigrotectal projection to the SC may be modulated by the overall pattern of activity throughout the cortex, which may have important implications for the type of information that can be conveyed to the SC by the nigrotectal projection.

(2) It is largely assumed that the basal ganglia projection to the SC does not communicate the oculomotor command signal, as direct stimulation of the stratum is not sufficient to elicit eye movements (Goldman-Rakic & Selemon 1990). Instead, it is likely that saccadic parameters are communicated via direct corticocollicular projections, including that linking the FEF and SC. In contrast to the FEF, the basal ganglia may not map any of the specific parameters of the saccade. Evidence in favor of this suggestion has recently been provided for limb movements. Mink and Thatch (1991a; 1991b) demonstrated that pallidal neurons did not appear to initiate or control any of the movement parameters associated with several different kinds of limb movement. If not, then what do they code? We have recently suggested that the basal ganglia system facilitates the disengagement and reengagement of processing resources between different attentional sets across a variety of domains (Jackson & Houghton 1992). Within the context of the oculomotor system, the basal ganglia may function to enable or suppress the command signal originating elsewhere, according to the nature of the task as reflected in the overall pattern of cortical activity.

(3) Cortical input to the striatum results in the suppression of activity in the substantia nigra (SNr) and to disinhibition of the SC. As Hikosaka (1991) has recently pointed out, (dis)inhibition forms a computationally powerful and efficient means of selection. Moreover, the phasic and tonic natures of the direct and indirect FEF pathways may also have significantly different computational consequences. Although the phasic excitatory signal conveyed by the direct projection is limited to simply increasing the activity of its SC targets, the tonically active (60 Hz) nigrotectal projection may convey more information. In the absence of cortical input, the striatum is quiescent and the SC is tonically inhibited (Chevalier & Deniau 1987). In response to cortical input, the SNr is inhibited, which results in SC disinhibition. In contrast, increased activity in the subthalamic nucleus (STN), which projects via an excitatory link to the SNr, may increase SNr activation and thus further suppress SC activity. Recent evidence has suggested that STN activity is associated with fixating a visual target and, by implication, the suppression of saccades (Hikosaka 1991). The control processes outlined above appear to us to be computationally sufficient to explain the inhibitory effect of engaged attention on express saccades so well illustrated in the target article. We would

The significance of the basal ganglia in suppressing hyper-reflexive orienting

Stephen Jackson and Marek Lees

*Center for Cognitive Neuroscience of Attention, Institute of Cognitive & Decision Sciences, University of Oregon, Eugene, OR 97403
Electronic mail: pss042@bangor.ac.uk*

Fischer & Weber (F&W) mount an impressive array of empirical evidence in support of their contention that the attention system modulates activity within the saccadic system and that express saccades only occur when visuospatial attention is disengaged. Although we feel that the views expressed in the target article have important implications for the modelling of saccadic and attentional control, we are disappointed by the authors' apparent reluctance to make the neurophysiological details underly-

suggest that these control processes are computationally isomorphic to those required for the control of spatial attention itself, in which a number of recent studies have implicated the basal ganglia.

Posner and Peterson (1990) distinguish between a posterior attention network which controls spatial orienting and an anterior attention network which is related to the volitional control of attention, particularly awareness of target stimuli. Posner and Peterson do not explicitly include the basal ganglia within either their anterior or posterior attentional networks but there are several reasons to suppose that these structures are critical to the operation of both networks. Damage to the posterior attentional network is typically associated with increased attentional costs in reaction time for responses to stimuli appearing at unattended locations (Posner et al. 1984). Recent evidence suggests that damage to the anterior attentional network may have the opposite effect and may result in hyper-reflexive orienting, that is, decreased attentional costs, as a result of reduced levels of inhibition for unattended locations (see below).

We feel that the phenomena of express saccades may reflect but one aspect of a more general phenomenon of hyper-reflexive orienting associated with the disengagement of attention. Recent studies of covert orienting in patients with basal ganglia dysfunction (i.e., Parkinson's disease) reveal that attentional costs which normally follow an invalid spatial precue may be eliminated or substantially reduced in this group (Kingstone et al. 1992; Wright et al. 1990). Several other studies support the suggestion that frontostriatal pathways through the basal ganglia may function to actively suppress distracting stimuli. First, healthy adult volunteers injected with D-roperidol, a dopamine antagonist, also show paradoxically reduced attentional costs to stimuli that appear at unattended locations (Clark et al. 1989). Second, having subjects carry out an attentionally demanding secondary task (i.e., shadowing a prose passage) also eliminates costs in a covert orienting task (Posner et al. 1989). Finally, a recent PET study revealed significant levels of activation in the basal ganglia during a selective attention task, that is, a task requiring the suppression of distractors, but not during a divided attention task (Corbetta et al. 1991).

In conclusion, we support F&W's contention that the attention system modulates saccadic activity and that express saccades occur when visuospatial attention is disengaged. We further suggest that the data presented in the target article are broadly consistent with recent evidence of hyper-reflexive orienting, which may be associated with impairments of the anterior attentional network, and which we have previously interpreted as consistent with a failure to suppress unattended spatial locations or stimuli (Jackson & Houghton 1992).

Express saccade – really a specific type of saccade?

Martin Jüttner^{a,b} and Werner Wolf^b

^aInstitut für Medizinische Psychologie der Universität München, D-8000 Munich 2, Germany and ^bInstitut für Mathematik und Datenverarbeitung, Universität der Bundeswehr München, D-8014 Neubiberg, Germany
Electronic mail: martin@groucho.imp.med.uni-muenchen.de

"What is a normal saccade?" is the first sentence and question of an excellent review on saccades by Becker (1991) that includes express saccades in this category, although with some critical comments. Express saccades have matured from a controversial phenomenon to a specific type of saccade attributed to a specific internal state of the oculomotor system. Recently, Fendrich et al. (1991) have published data which – on closer inspection – may even indicate that express saccades are not specific to visual stimuli only but also occur with proper acoustical stimulation. Of course, not all question marks attached to the issue of express saccades can yet be removed by the neurophysiological and

psychophysical research efforts described comprehensively in the target article by Fischer & Weber (F&W). But the large number of references cited as submitted and in press indicates that a lot of work is actually going on in this field and further insights can be expected.

An open point of discussion concerns how well express saccades are characterized by a well-defined region of latency values, that is, whether their latencies build up a peak in a histogram representation, and this is again related to the problem of how to distinguish express saccades from anticipatory saccadic eye movements on the one hand and from regular saccades on the other. Although F&W have already extensively considered the problem of anticipation in their paper (which is reasonable in the light of the literature mainly focusing on this issue, e.g., Kowler 1990), we think the dichotomy between express and so-called fast regular saccades, which can often be observed in experiments under the gap condition, is of at least equal importance for an understanding of the underlying process of saccade initiation. We have studied this problem in a modified experiment of the gap type, where regular target trials were mixed with catch trials, that is, trials with no saccade targets (Jüttner & Wolf 1992). The resulting latency histogram (Fig. 1, left side) was split up according to trial history, that is, into a distribution from trials with a preceding target trial and another distribution from those with a preceding catch trial (Fig. 1, right side). This decomposition reveals a strong effect of stimulus sequence: The probability of express saccades clearly diminishes in trials that followed catch trials compared with those following target trials, whereas the probability of fast regular saccades behaves inversely. We would like to comment upon two aspects of this result, the first concerning the (practical) problem of the evaluation of multimodal latency distributions, the second the problem of an adequate theoretical concept for the process of saccade initiation.

First, whether express saccades really form a distinct class of saccades has frequently been related to the question of whether multimodalities in latency histograms are significant. Formal statistical variation of two or three distinct peaks in the saccadic latency spectrum, however, which is reported by some in the scientific community, often proves problematic because of the variability of the underlying neural processes. The influence of both physiological and psychological factors leads to nonstationary system behaviour over the long period required to collect the number of responses necessary to establish statistical significance for distinct classes (see McLachlan & Basford 1987 for a comprehensive discussion of this problem). F&W's approach describing the multimodal distribution by three Gaussians fitted to the data is a useful assessment but no final solution to this

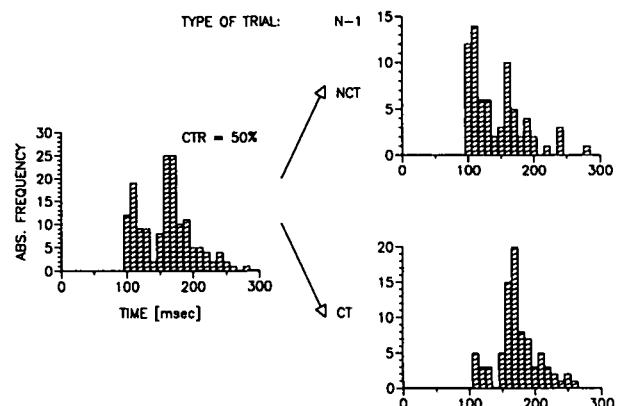


Figure 1 (Jüttner & Wolf). Decomposition of the latency distribution of a subject in a gap experiment (50% catch trial rate) into distributions resulting from trials with a preceding target (noncatch) trial (NCT) and with a preceding catch trial (CT), respectively.

problem. Here, the method of sequence analysis illustrated in Figure 1 may provide another way to demonstrate that a given latency histogram is actually the result of a superposition of different distributions. Such an analysis, which can be extended to even more than one trial backwards in the stimulus sequence history (Jüttner & Wolf, in preparation), can help to decompose original multimodal distributions into basic unimodal histograms that are easier to interpret.

Second, the finding of such a sequence determined behaviour (or, as F&W call it, an intertrial effect) has implications which go beyond the scope of a purely statistical description. It must instead be considered with respect to our notion of the process of saccade initiation. The neuroanatomically motivated three-loop model proposed by F&W summarizes the basic facts concerning express saccades and describes the formation of different modes in the saccadic latency histogram. It is undoubtedly worthwhile to relate the abundance of neurological structures and interconnections involved in the generation of saccades to a scheme of corresponding processes but abstractions of a model have some shortcomings. One of these concerns the explanation of intertrial effects as the catch trial effect discussed above and demonstrated in Figure 1. F&W suppose that because of the introduction of catch trials, subjects tend to adopt a strategy where attention is not going to be released upon the offset of the fixation point but rather this disengagement is delayed until the target actually appears – in order to prevent predictive saccades (i.e., occasionally wrong responses in the case of catch trials). As a consequence of the structure of F&W's three-loop model, however, a target-triggered disengagement of attention inevitably leads to a slow regular saccade, because the attention loop triggers all subsequent processes of decision making and computation of the saccade metrics. This is in contrast to the response pattern actually observed, where it is not the number of the slow but that of the fast regular saccades that increases.

According to F&W's model, fast regular and express saccades are temporally separated by a delay caused by the decision stage. Within this framework, it is plausible to attribute the intertrial effects described above to the structure of the underlying decision process. Here a problem arises about the sorts of mechanisms actually covered by the term "decision" in this context. Does this term simply mean "to initiate a saccade immediately" (regardless of whether or not there is a target in the periphery)? Obviously not, because the result would be an anticipated response. However, express saccades are, as F&W have pointed out, visually guided voluntary eye movements. Hence, the decision process cannot be regarded as unconditioned. Rather, it depends on the actual presentation of a saccade target, that is, "initiate a saccade if a target appears." This requires a further stage in the decision process however: the decision to select a stimulus presented in the periphery as a target for the saccade. This second stage reflecting the process of target selection is obviously triggered by the stimulus onset. If we now assume that this second stage can sometimes be skipped (in the case of express saccades) and sometimes not (in the case of fast regular saccades), we arrive at the notion of a decision process that does not require a fixed period of time but can be modulated between a short-term and a long-term operation mode. In the gap paradigm, the short-term (quasi reflex-like) mode leads to express saccades and the long-term (more reflective) mode leads to fast regular saccades.

It is interesting to note that the switching between these two modes of operation is almost purely sequence determined and can be described by a stochastic process (Jüttner & Wolf, in preparation). Furthermore, the short-term mode, which by definition skips the stage of target selection, seems to work nearly exclusively under very poor, artificially reduced stimulus conditions (e.g., with a homogenous screen and LEDs as targets), whereas with more complex structures (e.g., texture defined targets) express saccades are no longer observed (see,

e.g., Deubel & Frank 1991). This also indicates that the three-loop model of attentional, decisional and computational processes is only a first approximation to reality and that under natural viewing conditions the question of what actually makes a stimulus in the visual field a target for a saccade is no longer trivial. The problem of figure-background segregation probably then makes it necessary to consider far more complex interactions and to extend the model accordingly.

Why do visual offsets reduce saccadic latencies?

Raymond M. Klein^a and Alan F. Kingstone^b

^aPsychology Department, Dalhousie University, Halifax, Nova Scotia, Canada B3H-HJ1 and ^bCenter for Neuroscience, University of California at Davis, Davis, CA 95616

Electronic mail: ^aklein@ac.dal.ca; ^bafkingstone@ucdavis.edu

1. What are express saccades? "When human subjects are asked to execute saccades from a fixation point to a peripheral target, if the fixation point is turned off some time (200 ms) before the target is turned on, the distribution of the saccadic reaction times is bimodal. The first peak occurs at about 100 ms and represents the population of express saccades" (Fischer & Ramsperger 1986, p. 569). Early claims like this one led many investigators to assume that bimodal saccadic latency distributions, with an early mode around 100 msec, are ubiquitous in the gap paradigm and might be used as an "express saccade diagnostic." When others attempted to obtain this result, bimodality was sometimes observed, but in a number of studies it was the exception rather than the rule (e.g., Kalesnykas & Hallett 1987: 1 out of 4 subjects showed bimodality; Kingstone & Klein, in press a: 1 out of 5; Reuter-Lorenz et al. 1991: 1 out of 13; Wenban-Smith & Findlay 1991: 1 out of 3). Although bimodality, when it occurs, might appear to facilitate the classification of a saccade as "express," an early mode of a clearly bimodal distribution is not diagnostic. First, it is possible to obtain bimodality with both peaks outside the express range. Second, it is possible to obtain a unimodal distribution in which all the saccades are in the express range.

Because bimodality cannot be consistently relied upon to classify saccades as express, perhaps we might rely on an absolute latency criterion (as implied by Fischer & Weber [F&W] in their target article). This diagnostic is also inadequate, however, as the following example illustrates. The reduction in saccadic latency occasioned by the prior removal of the fixation stimulus (the "gap effect") is the same for bright and dim targets (Kingstone & Klein, in press a; Klein et al. 1992; Reuter-Lorenz et al. 1991). This indicates that whatever mechanism is facilitating saccades in the gap condition when a target stimulus is bright is also facilitating saccades in the gap condition when a target stimulus is dim – and by an equal amount. However, when saccadic RTs to dim targets are not in the express range then these eye movements would not be classified by the absolute latency criterion as "express saccades." It is illogical that saccadic responses whose latencies have been reduced by equivalent amounts through the prior removal of fixation should be classified differently merely because the sensory processing in one case is retarded by a lower target intensity.

Since neither bimodality nor absolute latency can be reliably used to determine whether a particular saccade is "express," we encourage investigators to focus their attention on those factors that modulate the gap effect (also see Kowler, 1990, for a different analysis that supports this recommendation).

2. The gap effect and covert visual attention? F&W (see also Fischer & Breitmeyer 1987) claim that the saccade system is inhibited when covert attention is engaged and that the disengagement of attention is a prerequisite for saccade initiation. It

follows from this proposal that a reduction in saccadic latency will accompany the prior removal of attended, but not unattended, stimuli (whether or not the removed stimuli are at fixation). In studies that appear to support this proposal (Braun & Breitmeyer 1988; Mayfrank et al. 1986) covert attention was manipulated by instruction but no objective measures were provided to confirm the locus of attention. Moreover, in some cases the experiments were methodologically flawed by the use of unvarying target onset time or position without the inclusion of catch trials.

To determine whether the gap effect could be attributed to the predisengagement of attention rather than removal of fixation per se, we conducted three experiments in which precues and cost-benefit analysis (cf. Posner 1980) allowed us to determine objectively whether and where covert attention was engaged (Kingstone & Klein, in press b; Klein et al. 1992). Saccadic RT was reduced when any stimulus in the visual field was extinguished 200 msec before saccadic target onset. The gap effect was always larger following fixation offsets than peripheral offsets, but it was unaffected by whether an extinguished peripheral stimulus was attended or unattended. These results, which were observed with both endogenous and exogenous covert orienting, show that covert visual attention plays no role in the gap effect.

3. Components of the gap effect. There is good behavioral evidence that two independent components combine to produce the gap effect (see Kingstone & Klein, in press b; Reuter-Lorenz et al. 1991; Ross & Ross 1980; 1981). One component is a *motor preparation* effect that can operate on *any* response modality and is critically dependent on the foreperiod between a warning signal and a subsequent target (in our experiments this effect varies from 0 to 60 msec, depending on the subject's level of alertness and the response information conveyed by offsets). The other component is a *fixation offset* effect that operates specifically to reduce saccadic latencies by freeing the oculomotor system from fixation (in our experiments this effect is stable at about 35 msec) and is probably mediated by the rostral pole of the superior colliculus (Muñoz & Wurtz 1992). Although this might be viewed as a disengagement operation, in contrast to the Fischer and Weber proposal, it would be the *overt* (saccadic) not *covert* (attentional) orienting system whose predisengagement reduces saccadic latencies in the gap paradigm.

Express attentional shifts

Ken Nakayama^a and Manfred Mackeben^b

^aVision Sciences Laboratory, Department of Psychology, Harvard University, Cambridge, MA 02138 and ^bThe Smith Kettlewell Eye Research Institute, San Francisco, CA 94115

Electronic mail: ^aken@isr.harvard.edu; ^bmm@skivs.ski.org

Fischer & Weber's (F&W's) target article brings together new and old information linking express saccades to visual attention, strongly supporting Fischer's (1987) attentional disengagement hypothesis. Not only do the authors provide extensive documentation of the existence of express saccades, they also indicate that the rapid deployment of attention to the peripheral target site is responsible for them. Their main argument is that the gap paradigm allows attentional disengagement, a faster engagement of attention elsewhere, and, in turn, express saccades.

F&W's arguments rely on just one general class of data, however: the characteristics of short-latency saccades under various conditions. In none of the studies mentioned has attention been assessed except as it might influence eye movements. No independent measure of attention has been made.

In a recent paper, we confirmed Fischer's hypothesis by using pattern recognition rather than eye movements as an indicator

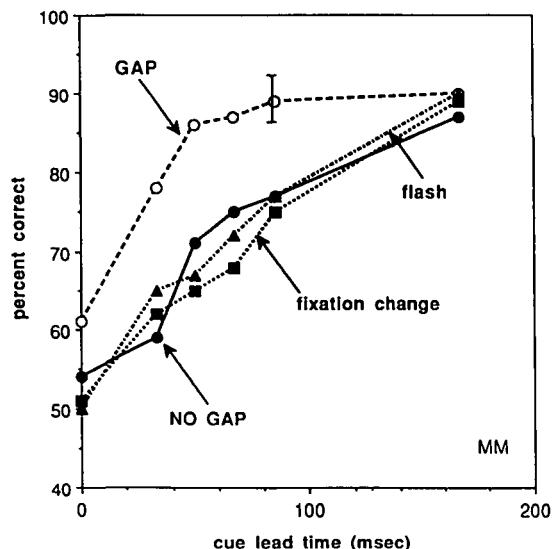


Figure 1 (Nakayama & Mackeben). Time course of attentional shifts to a peripherally positioned vernier acuity target. Percent correct plotted as a function of cue lead time for four different conditions (see text). Eighteen stimulus elements (17 distractors plus 1 target) were arranged in a circle having a 5 deg radius. A fixation cross was positioned in the center of this array. The stimulus was presented for a fixed duration in all trials and subsequently masked by a patterned field (from Mackeben & Nakayama 1993, with permission).

of attention (Mackeben & Nakayama 1993). Using a cued vernier acuity task, the observer was presented with a circular array of distracting elements in which a single vernier acuity target was embedded. The upcoming target location was precued for varying time intervals (cue lead time) by a small circular cue. Under normal circumstances in which the central fixation point simply remains on during the whole sequence of trials, functions relating cue lead time to performance have been obtained (Nakayama & Mackeben 1989). Labeled "no gap" in Figure 1, we assume that this rising curve is an indicator of attention, progressively deployed to the eccentric retinal site.

To provide a direct test of Fischer's attentional disengagement hypothesis, we examined the deployment of attention in the "gap" paradigm. Thus, 200 msec prior to the presentation of the cue, the fixation point vanished and remained off for the duration of the stimulus presentation. Because the fixation point has recently been extinguished, Fischer's hypothesis predicts that attention is now disengaged and thus more available to be deployed elsewhere. In this case the rising curve should rise even more quickly. If we focus on the curve labeled "gap" in Figure 1, it should be clear that this prediction is fulfilled.

To deal with the possible criticism that the onset of the gap might have provided the observer with a nonspecific "warning" or "ready" signal just prior to the trial, thus facilitating performance, we ran two additional control conditions. In the "fixation change" condition we changed the shape of the fixation at just the same time the fixation would have disappeared in the gap condition. In the "flash" condition we presented a brief diffuse flash at this same time. In neither case was performance enhanced (see Fig. 1).

Having used the gap paradigm to establish the existence of express attentional shifts, we sought additional evidence that it is related to express saccades. Fischer and colleagues observed that a 200 msec gap interval leads to the greatest number of express saccades (Mayfrank et al. 1986). If Fischer's hypothesis regarding express saccades is correct, then the gap intervals best suited to elicit express saccades should be the same to elicit rapid attentional shifts. To explore this issue, we conducted a

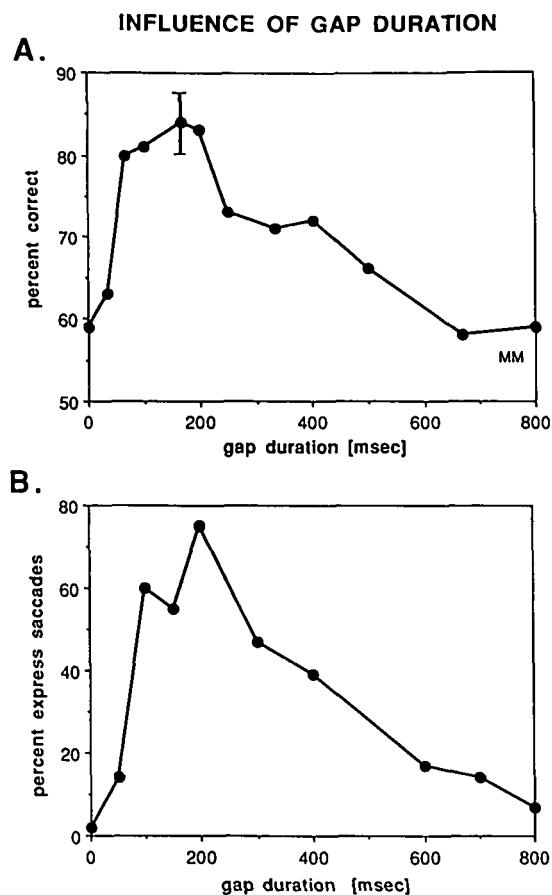


Figure 2 (Nakayama & Mackeben). Influence of gap duration. A: Performance plotted as a function of gap duration in a cued vernier acuity task. Cue lead time is fixed at 33 msec (data from Mackeben & Nakayama 1993, with permission). B: Data obtained by Mayfrank et al. (1986) showing the average percentage of express saccades for four human observers as a function of gap duration.

new experiment, fixing cue lead time at 33 msec, and varying gap duration. Figure 2A shows vernier acuity performance as a function of gap interval. Note that there is the predicted best interval of approximately 200 msec. For comparison, we have summarized data from Mayfrank et al. (1986), in which the percentage of express saccades is plotted versus gap interval (see Fig. 2B). The shape of the two functions is remarkably similar. In each case, there is a rapid rise followed by a slow fall, each function peaking at 200 msec.

These results provide independent evidence to support the F&W explanation of express saccades. Not only do they show that attention is deployed more rapidly in the gap paradigm, as predicted, they also show that express attentional shifts and express saccades occur over the same range of gap durations. As such, our results add to the growing evidence that focal attention is important for the initiation of saccadic eye movements.

Warning signals, response specificity and the gap effect: Implications for a nonattentional account

Patricia A. Reuter-Lorenz^a and Howard C. Hughes^b

^aDepartment of Psychology, University of Michigan, Ann Arbor, MI 48104
and ^bDepartment of Psychology, Dartmouth College, Hanover, NH 03755
Electronic mail: ^aparl@psych.lsa.umich.edu; ^bhch@dartmouth.edu

Fischer & Weber (F&W) assert that the gap effect and express saccades are different phenomena. According to their view,

fixation point offsets lead to the disengagement of visual attention that facilitates all saccadic responses (anticipatory, prosaccades, and antisaccades), as well as manual responses. They propose that express saccades reflect an optomotor reflex that is enabled by disengaged visual attention. Since only prosaccades can be generated via this reflex pathway, only prosaccades can be of the express type. Thus, response specificity is found for express saccades but not for the gap effect, because the latter is due to disengaged attention. We disagree with this account for at least three reasons: (1) We question the reliability of Fischer's method for identifying and thus measuring the occurrence of express saccades; (2) when the proper experimental controls are utilized, the gap effect itself is response specific; and (3) the notion of disengaged visual attention is inconsistent with this response specificity and with a number of other experimental results. We address each of these points in turn.

In two previous articles (Fendrich et al. 1991; Reuter-Lorenz et al. 1991), only two subjects (out of 21) demonstrated bimodal latency distributions. However, we consistently find a "gap effect" (faster mean saccadic RTs in the gap relative to the overlap condition) and many subjects generated saccades in the 100–120 msec range. Were these express saccades or not? Did our subjects fail to generate enough "fast regular" saccades to create a separate mode? Fischer's own unimodal distributions (e.g., Fig. 3) are apparently to be interpreted as pure express saccade distributions when the mode is around 100 msec. The exact latency cannot be the sole criterion, however, because latencies depend on target size and luminance (Boch et al. 1984; Reuter-Lorenz et al. 1991). F&W acknowledge that neither an absolute latency criterion (sect. 2.2) nor bimodal distributions (sect. 3) can be used to identify express saccades. How should express saccades be identified, then? Without specific diagnostics, the investigation of express saccades can be capricious and, at best, unreliable. In Fischer's own hands, only 60% of naive subjects generate express saccades. We are left to wonder why a "reflexive," presumably hard-wired, response should be so elusive. Although we question the reliability of quantifying express saccades, we agree that the gap paradigm can elicit visually guided saccades with latencies of 100 msec. It is our view that facilitative influences on saccadic control can be investigated more profitably and reliably through an analysis of the gap effect rather than by restricting analyses to the occurrence of "express saccades" as defined by F&W.

Fischer and colleagues view this approach as unacceptable because they find the gap effect and express saccades to be dissociable phenomena. They report a gap effect for both pros and antisaccades, whereas only prosaccades can be "express." However, our own earlier investigation revealed a gap effect for prosaccades only (Reuter-Lorenz et al. 1991). F&W suggest that our failure to find a gap effect for antisaccades and choice manual RTs resulted from including a warning tone in both gap and overlap conditions (sect. 6.1). It is a fundamental fact of human performance, however, that warning signals decrease RTs (e.g., Keele 1986), producing generalized alerting effects that are independent of response mode, stimulus intensity, modality, and so on. If one simply compares gap and overlap trials, subjects undoubtedly receive differential warning effects that favor faster responding on gap trials. Clearly, the interesting feature of the gap effect is *not* its role as a warning signal, but rather its possible role in modulating oculomotor processes. It is for this reason that Reuter-Lorenz et al. (1991) and Fendrich et al. (1991) used warning tones in their analyses of the gap paradigm. Our results undoubtedly differ from those of Fischer and colleagues because of these procedural differences. By controlling general warning effects, the effects that are unique to fixation offsets can be revealed.

We believe that F&W's finding of a gap effect for antisaccades is flawed by their failure to control for generalized alerting effects. Since in section 6.1 F&W dismiss our results in favor of their own, they apparently believe that omitting a warning

signal is a virtue rather than a flaw. We have recently found that without an acoustic warning signal, antisaccade latencies are reduced by fixation point offsets (Reuter-Lorenz et al. 1993). However, with a warning signal, the gap has little effect. This is not so for prosaccades: The latency difference between gap and overlap trials increases without a warning signal, but even with a warning signal the gap effect is robust. The implication is clear: For antisaccades, fixation point offsets do little more than alert the subject to the imminent occurrence of the target. When another stimulus event serves this function there is no further benefit from fixation point offsets. For prosaccades, fixation offsets reduce response latencies even when the alerting function has been controlled.

This basic methodological issue bears on a crucial theoretical point. When generalized warning is controlled, the gap effect is *response specific*. Evidence for response specificity is simply incompatible with the view that the gap effect is due to *attentional disengagement*. Posner's three-stage model accounts for precuing effects that are not response specific. Moreover, according to Fischer, the gap effect arises from the fact that the disengagement process, having occurred prior to target onset, does not contribute to response time (sect. 6.1; Fischer & Breitmeyer 1987). If this is the basis for the gap effect then antisaccade latencies should also benefit from fixation point offsets. They do not. Furthermore, if attention enhances sensory processing, as Posner and others propose (Hawkins et al. 1988; Mangun et al. 1992), then a larger gap effect is expected for dim than for bright targets if the gap effect is attentional (Hughes 1984). We found that gap effect size is independent of target luminance (Reuter-Lorenz et al. 1991). Finally, at least some explicit tests of the attentional hypothesis have failed to find that engaged attention inhibits the gap effect (Kingstone & Klein 1990).

On the basis of our results indicating that the gap effect is specific for prosaccades and independent of target luminance and stimulus modality, we suggested that fixation offsets facilitate collicular-based premotor processes that mediate the foveation of eccentric targets (Fendrich et al. 1991; Reuter-Lorenz et al. 1991). Invoking attentional explanations adds little to our understanding and may obscure important differences between the mechanisms underlying short-latency saccades and other oculomotor effects which more strongly compel attention-based accounts (e.g., Reuter-Lorenz & Fendrich 1992). Since attentional processes are themselves the center of a great deal of controversy, it seems at least premature to use one poorly understood phenomenon to "explain" another. We believe that when general alerting effects have been controlled the gap effect can be more parsimoniously and correctly understood as the release of a reflexive oculomotor response that is normally inhibited by voluntary fixation.

Attentional engagement and the pulvinar

David Lee Robinson^a and Robert J. Cowie^b

^aSection on Visual Behavior, Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, MD 20892 and ^bDepartment of Anatomy, College of Medicine, Howard University, Washington, DC 20059
Electronic mail: dlr@lsr.nei.nih.gov

In the target article, Fischer & Weber (F&W) present an overview of the work on express saccades and hypothesize that it is the timing of attentional shifts that is a critical feature in the occurrence of this type of eye movement. They present experimental data supporting roles for the superior colliculus, frontal eye fields, striate cortex, and prelunate cortex in the mediation of this type of behavior. There have been studies on monkeys and humans, however, which have demonstrated that the pulvinar participates in visual spatial attention (Petersen et al. 1985;

1987; Rafal & Posner 1987; Robinson & Petersen 1992). In addition, a hypothesis has been proposed suggesting that it is the pulvinar that performs the engagement function for which F&W are searching (Rafal & Posner 1987). Our commentary will first focus on the pulvinar's relation to spatial attention and then we will discuss how it might participate in the engagement of attention.

The first data suggesting a relation of the primate pulvinar to attention were the demonstrations of its visual properties and the behavioral effects of lesions (Bender 1982; Chalupa et al. 1976; Gattass et al. 1979; Mathers & Rapisardi 1973; Petersen et al. 1985). Subsequently, we described a subdivision within the pulvinar, area Pdm, which shows properties similar to those of the parietal cortex, one of the principal attentional regions (Bushnell et al. 1981; Petersen et al. 1985; Robinson et al. 1978). Cells of Pdm respond to visual stimuli presented during periods of fixation and this activity can be enhanced when a monkey actively uses such stimuli. This enhancement is demonstrable when a stimulus is the target for a saccadic eye movement and also when the animal uses its peripheral attention to discriminate changes in the stimulus. Such enhancement is not due to changes in levels of alertness because the effect is spatially selective. That is, modulation is present when the animal attends to a stimulus within the visual receptive field of the pulvinar cell, but it is not present when the animal attends elsewhere. In addition to these visual neurons, there are also cells in Pdm that discharge during and after saccadic eye movements. Since the visual scene changes with each eye movement, such eye movement-related activity might signal the need to initiate a new attentional scan in order to evaluate the current visual environment.

If these electrophysiological observations support an attentional relation for this part of the brain then changing the functioning of Pdm should alter attentional performance. We trained monkeys on a cued-reaction time task which provides a simple means of covertly shifting the animals' attention (Posner 1980). While they performed this task, we micro-injected GABA-related drugs into Pdm (Petersen et al. 1987). When we injected muscimol, a GABA-agonist, the animal performed the task as if it were having difficulty shifting attention to the contralateral visual field. Conversely, when we injected bicuculline, a GABA-antagonist, the monkeys performed as if they were facilitated in shifting their attention to the contralateral visual field. These observations, combined with the physiological properties described above, strongly support a role for the pulvinar in visual spatial attention.

Studies of patients with thalamic lesions tested with the same cued-reaction time task also support an attentional function for the pulvinar (Rafal & Posner 1987). These studies demonstrated that such subjects are deficient in performing this task, and in ways different from other patients with parietal cortex or mid-brain lesions. The patients with thalamic lesions were slow in responding to all targets in the visual field contralateral to their lesions. This was true whether targets were validly or invalidly cued. However, they revealed only a transient slowing of responses to invalidly cued targets, which suggests that they remain able to disengage attention, a defect for patients with parietal damage. Because these patients show the normal speeding of reaction times with increasing cue-target temporal intervals, they appear to have no defect in moving their attention, as subjects with midbrain lesions do. Finally, their overall slowness in saccading to all targets in the contralateral visual field suggests that their difficulties lie in engaging attention once it has been disengaged and moved to the new location. Thus Rafal and Posner (1987) have hypothesized that the pulvinar functions to engage attention at new loci.

The electrophysiological studies, pharmacological manipulations, and testing of patients with thalamic lesions strongly support a relationship between the pulvinar and visual spatial attention. How might these data fit with F&W's attentional

hypothesis for express saccades? It appears that the most consistent trigger leading to express saccades is the early termination of the fixation point. If the pulvinar functions to engage attention after it has moved, its operation must be inhibited as an initial step for an express saccade. The termination or blink of the fixation point may serve to inhibit the pulvinar's engagement processes and thereby start the chain of events leading to an express saccadic eye movement. Given this framework, it would be informative to study the functional and topographical relations of the foveal representations in the pulvinar and parietal cortex to determine how they connect with brainstem oculomotor centers and what their functional relation is to the occurrence of express saccades (Cowie & Holstege 1992; Munoz & Wurtz 1992).

In attempting to integrate the pulvinar with express saccades, there is one point that is unclear from the experiments in the target article. The question, which is addressed by the studies depicted by Figure 3 but not resolved convincingly, concerns the extent and direction of the disengagement that will lead to express saccades. Is it enough for attention to be removed from the fixation point? Must attention be disengaged from everything and committed to nothing? If attention is not at the fixation point but is actually engaged at a point in the periphery, will this lead to express saccades to that point? Until the essence of these questions is clarified, it will be difficult to establish clearly the exact contributions of various neural centers.

how are they modulated by the whole context of the experiment?

Jüttner and Wolf (1992) demonstrated the influence of catch trials on the distribution of saccadic latencies between express and regular saccades: This is a step toward clarifying these questions, as is the experiment of randomly mixing long with short gap trials (F&W, sect. 6.3). However, F&W's interpretation of their results is obscure. They conclude that "there are internal states of readiness that determine whether or not express saccades are generated." Do these states belong to decisional or attentional processes? Also, F&W's suggestion that "the subjects maintain fixation until the target appears" is not consistent with their three-loop model because this predicts slow regular saccades.

The role of the parietal and frontal contributions in F&W's model is unclear. Inhibitory functions of the frontal lobes and facilitatory functions of the parietal lobes upon saccade triggering are well established (Pierrot-Deseilligny et al. 1991b). Physiologically, the model is supported also by positron emission tomography (PET) scan (Fox et al. 1985) and evoked potential studies (Brooks-Eidelberg & Adler 1992; Kurtzberg & Vaughan 1982). Our conjecture is that, through a kind of slow potential cortical negativity control (Birbaumer 1992), one might achieve the kind of "internal state" F&W mention but do not develop explicitly. We would expect that the liberation of the low-level reflex arc may with practice allow long-term potentiation (LTP) in the superior colliculus (SC) (Okada & Miyamoto 1989; Roberts et al. 1991).

In short, F&W's model encompasses all the pertinent neuronal structures, with the possible exception of the consequences of parietal lesions in humans (Braun et al. 1992). But what if the information flows controlling saccade triggering in the brain were really parallel and distributed (van Essen et al. 1992)? If processing were really *parallel*, the parietal lobes and the frontal eye fields (FEFs) should work concomitantly (Funahashi et al. 1989; 1991; Goldman-Rakic 1988; 1992). If processing were really *distributed* the parietal lobes should be involved in "decision-making" (Goldberg et al. 1990). Lateral intraparietal neurons are not only involved in coordinate system transformations required for visual-motor integration in saccade programming (Andersen & Gnadt 1989), but also code information about the intended movement (Duhamel et al. 1992). Conversely, FEF neurons are involved in direct retinal to motor coordinate system transformations and thus also contribute to the maintenance of the spatial accuracy of saccades (Goldberg & Bruce 1990).

SC functions, together with striate cortical functions, may be essential for express saccades, but the role of the FEFs and the inferior parietal lobe (LIP) in saccade triggering must be interchangeable to a certain degree. No doubt LIP and FEF are connected in series as F&W propose. Anatomical and physiological studies, however, suggest that two other loops, one involving FEF and the other involving LIP, may work in parallel to trigger visually elicited saccades. Only if this were the case could we think of incorporating the notion of express saccades as a genuine oculomotor phenomenon. Moreover, we could try to improve the model, adding the notion of discrete temporal processing as a necessary prerequisite to understanding how all these different structures are nested together.

3. Oscillations, elementary Integration units and saccades. Synchronized oscillations in the visual cortex (Eckhorn et al. 1988; Gray & Singer 1989; Gray et al. 1989) may provide a possible basis for object binding. Considerable data (Frost & Pöppel 1976; Haase et al. 1992) suggest there might be a connection between neuronal oscillations and the execution of saccades.

Each sensorimotor performance is characterized by a specific pattern of spatially distributed activities in neuronal assemblies. This indicates that neuronal integration mechanisms are required to create a unique and focused experience. The basis for

Parallel distributed processing and integration by oscillations

Eva Ruhnau and Vitor G. Haase

Institut für Medizinische Psychologie, Ludwig-Maximilians Universität, 8000 Munich 2, Germany

Electronic mail: ruhnau@psychologie.medizin.uni-muenchen.dbp.de

1. Attention and attention again. "Most theories of information processing regard attention as a homogeneous component of the processing system (homogeneity assumption) that is basically different from the other, 'structural' components (duality assumption)" (Neumann 1992). We share Neumann's conclusion that "these assumptions are unwarranted." The alternative view postulates not one but several components of attention and it modified the strict separation of automatic versus attentional processes (i.e., the duality assumption). We think that confirmation or refutation of homogeneity and duality provides a useful classification scheme to deal with "attention" more precisely.

Behavioral inhibition, in Fischer & Weber's (F&W's) article the suppression of saccadic eye movements to render periods of fixation possible, is certainly only one prominent component of attention, thus providing an argument against the homogeneity assumption. However, F&W are unclear on the duality assumption. At first they seem to support it. The disengagement of attention allows the release of the optomotor reflex, revealing a clearcut separation between an attentional and an automatic process. However, this would be obvious only if there were only two populations of saccades: the express saccades and the slow regular saccades. But what about the fast regular ones? Their explanation through the "decision loop" of the three-loop model seems to us most critical.

2. The fuzziness of the decision loop. F&W distinguish between attention and decision. However, the postulated independence (parallel operation) and dependence (serial operation) between the two processes may be inadequate. Novel stimuli can automatically draw attention without intention (Johnston et al. 1990). Contrarily, "any voluntary initiated saccade needs a decision as to whether or not it should be executed" (Fischer 1987). What types of interference between involuntary and decision processes occur under experimental conditions? And

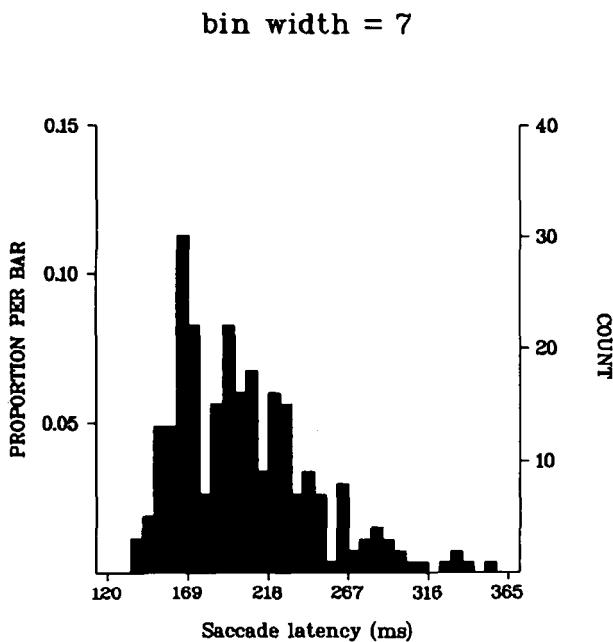


Figure 1 (Ruhnau & Haase). Example of periodic multimodal distribution in visually elicited saccadic reaction times with the overlap paradigm. Modes are estimated as being around 163.75, 198.66, and 220.99 msec respectively. $N = 266$, median = 198 msec, Subject 4, 15th session. Eccentricities used were 7° and 21°, randomly distributed to the left or right, with ISIs (interstimulus intervals) between 1,500 and 4,000 msec.

binding could be provided by neuronal oscillations that define elementary integration units (EIUs) (Ruhnau & Pöppel 1991). EIUs or zones of cotemporality are characterized by the fact that temporal relations between events cannot be defined. The generating oscillations of such temporal windows should be entrained by a stimulus, that is, they should be stimulus-triggered.

We recently obtained evidence for a periodic multimodal distribution in visually elicited saccadic reaction times with the

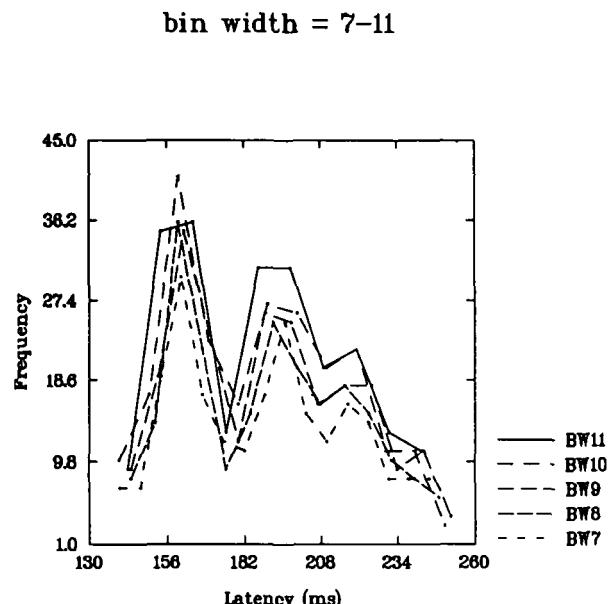


Figure 2 (Ruhnau & Haase). Periodic multimodal distributions of saccadic reaction times are not contingent upon the bin widths used to construct the histogram. Peaks remain constant regardless of the different bin widths. (Data are the same as in Fig. 1.)

overlap paradigm (see Figs. 1 and 2). The postulated underlying oscillatory processes could also influence reaction time distributions under the gap paradigm. They suggest another way to understand the reduction of saccadic latencies with training (F&W, sect. 2.2). Choice reaction times to visual or auditory stimuli improved markedly, but discontinuously (Pöppel et al. 1990). This may be due to a shift between temporal windows (with a period length of 30–40 msec) confining reactions to the earlier of two such windows.

The occurrence of fast regular saccades can be similarly explained. In this case, however, it is the later of two temporal windows that accounts for the fast regular saccades. If, after disengagement of attention, the SC is not yet disinhibited when stimulus occurrence triggers the corresponding coherent oscillation (Pöppel et al. 1991), the neuronal mass activity during the following 30–40 msec may not be enough to exceed a threshold value to elicit the first loop. Because of the assumption of stimulus-triggered, not stimulus-induced, oscillations this is a temporally segmented process, not a temporally smeared one.

Especially because of this potential alternative explanation for some of the experimental findings of F&W we would like to add a criticism of the computer-simulated model. The simulation is persuasive but, in our opinion, of no real explanatory value concerning the critical points. One should never forget that computer simulations of certain models are like mathematical proofs: They can confirm the correctness of logical conclusions, but never the assumptions on which the models are based.

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Saccade latency in context: Regulation of gaze behavior by supplementary eye field

Jeffrey D. Schall and Doug P. Hanes

*Department of Psychology, Vanderbilt University, Nashville, TN 37240
Electronic mail: schalljd@vuctrax.bitnet*

Fischer & Weber (F&W) demonstrate that saccade latency reduces as the time and location of the target become more predictable. The conditions yielding the shortest latency saccades are exactly those in which the distinction between anticipatory and visually guided saccades blurs (Figs. 2 and 6).

These findings replicate numerous investigations of the effects of foreperiod on response time (Niemi & Näätänen 1981). Response time is reduced if prior warning is given, and the degree of reduction is proportional to the reliability and salience of the warning event. The improvement in performance is commonly conceived as a result of covert preparation of the movement before execution.

We argue that latency in a gap task can be understood in terms of preparatory processes. Constant 200 msec gap durations are commonly used (e.g., Fischer & Boch 1983). To control for the obvious predictability, gap durations are selected randomly from a specific range (e.g., Schiller et al. 1987; Wenban-Smith & Findlay 1991); a 20 msec variation is hardly sufficient, however (Fischer & Ramsperger 1984). Using delays from 0–300 msec, saccade latency declines and the incidence of express saccades increases (Schiller et al. 1987; Wenban-Smith & Findlay 1991).

We measured latency in a rhesus monkey performing a modified gap task. Unlike other studies, the fixation spot changed color rather than disappearing. A green fixation spot signaled go trials (80%); red signaled no-go, with the monkey rewarded for maintaining fixation after target presentation. No-go trials were included to prevent anticipatory saccades. The target could appear at one of 4 positions (10° ecc). In one condition, gap durations were sampled with equal likelihood from 0–300 msec. Our findings (Fig. 1) replicated Wenban-Smith and Findlay (1991) with no bimodal latency distributions

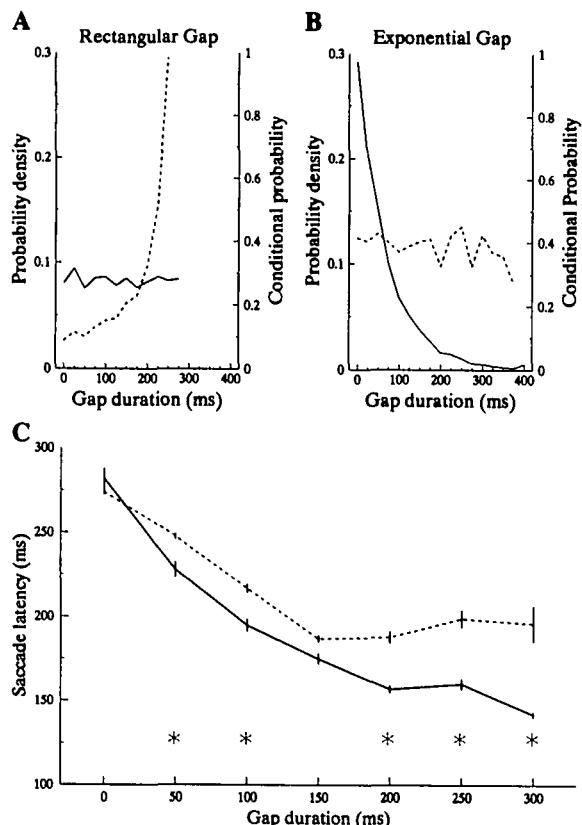


Figure 1 (Schall & Hanes). Saccadic performance with aging and nonaging gap durations. Gap delay was varied in two ways. A: Probability density (solid line) and conditional probability (dashed line) for gap delays sampled from a rectangular distribution ranging from 0–300 msec. With a constant probability density the conditional probability is initially low and increases for longer gaps. B: Probability density and conditional probability for gap delays sampled from a nonaging, exponential distribution. Note the constant conditional probability. C: Saccade latency as a function of aging (solid line) and nonaging (dashed line) gap delays. Vertical bars represent 1 standard error of the mean (SEM). Asterisks indicate delays at which the latency following nonaging gaps was significantly longer than the latency following aging gaps (t test, $p < 0.01$).

following any gap delay even though mean latency declined significantly (linear regression $df = 550$, $t = 13.4$, $p < 0.001$). The higher latency of these express saccades is explained by the use of four target positions, no-go trials, and the continued presence of the fixation spot.

This latency reduction following longer delays can be explained in terms of the conditional probability of target presentation at different times. Because the probability of each gap is constant and limited if the target has not appeared following a given time, then the probability of its appearing in the next interval increases. Thus, the passage of time itself conveys information that can lead to enhanced readiness to initiate the movement.

This temporal predictability can be controlled by using gap delays with constant conditional probability. Such a "nonaging" distribution of foreperiods has an exponentially declining probability of successively longer times (Fig. 1). Manual response times become unchanged with nonaging foreperiods (e.g., Baumeyer & Joubert 1969). Using nonaging gap delays we found less latency variation. In the first 150 msec latency declined for both aging and nonaging conditions. Whereas latency in the remaining 150 msec for the aging condition continued to decline

significantly ($df = 299$, $t = -2.6$, $p < 0.01$), latency in the nonaging condition did not. Furthermore, express saccade latencies following nonaging gaps were longer than those following the uniformly sampled gaps ($df = 302$, $t = -6.3$, $p < 0.01$).

The temporal pattern that influences latency cannot be identified on a single trial; it must be sensed in the context of many trials. This fact, in combination with the extremely short latency of express saccades, suggests that the state from which an express saccade can be generated must be achieved *before the trial begins*. F&W review the evidence for inhibitory control over the SC from the substantia nigra, controlled via the caudate nucleus from the cortex. They illustrate caudate afferents from FEF but the oculomotor caudate also receives afferents from the supplementary eye field (SEF) rostral to the supplementary motor area (SMA; Parthasarathy et al. 1992).

Neurons in SEF discharge before voluntary saccades (Schall 1991a; Schlag & Schlag-Rey 1987) and saccades are evoked by intracortical microstimulation of SEF (Schall 1991b; Schlag & Schlag-Rey 1987). SEF projects to superior colliculus and the brainstem saccade generator (Huerta & Kaas 1990; Shook et al. 1990).

Many studies have indicated that SMA is involved in planning and regulating movement (Goldberg 1985). Lesions of SEF in humans specifically impair the generation of sequences of remembered saccades (Gaymard et al. 1990). Moreover, SMA neurons discharge specifically for movement sequences (Mushiake et al. 1991). Recordings in FEF and SEF also indicate that whereas neurons in FEF are linked to visual stimuli and saccade metrics, cells in SEF are modulated more according to movement intention (Schall 1991a; 1991b). We believe a useful hypothesis is that SEF is responsible for organizing saccadic behavior in the context of current task contingencies. Thus, when conditions merit, SEF, in concert with FEF, allows the superior colliculus to generate express saccades.

What neural pathways mediate express saccades?

Marc A. Sommer,^a Peter H. Schiller^b
and Robert M. McPeek^c

Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139

Electronic mail: ^aalco@athena.mit.edu; ^bschiller@wccf.mit.edu; and ^crmm@isr.harvard.edu

In the target article, Fischer & Weber (F&W) present a timely and useful review of recent work on the so-called express saccades. Their work was the first to demonstrate the curious bimodal nature of visually elicited saccadic eye movement latencies, the early distribution of which forms the "express" mode. Fischer and his collaborators have carried out a series of fine experiments illustrating the conditions under which such saccadic latencies do and do not occur. They and others have convincingly demonstrated that the effects are not artifactual and that the express saccades are indeed visually triggered.

We would like to address the question of what neural pathways contribute to the generation of the express saccades and how the facts gathered so far in this regard fit with the neural model proposed by F&W. In earlier work we have shown that at least two major parallel pathways are involved in the generation of visually guided saccadic eye movements, one of which reaches the brainstem oculomotor centers via the superior colliculus and the other through the frontal eye fields. At least two lines of evidence support this idea: (1) Electrical stimulation of the superior colliculus, the frontal eye fields, and occipital cortex all elicit saccadic eye movements; following superior collicular lesions saccades can still be produced by stimulation of the frontal eye fields but not of the visual cortex (Schiller 1977).

(2) Only relatively minor deficits arise in the generation of visually guided saccadic eye movements following either frontal eye field or superior collicular lesions; however, when both are ablated, monkeys can no longer generate visually guided saccadic eye movements (Schiller et al. 1980). Having made these observations, we went on to determine how express saccades are affected by such lesions (Schiller et al. 1987). We found that ablation of the frontal eye fields alone left the bimodal distribution of saccadic latencies unaffected. On the other hand, as described in the target article, superior collicular lesions eliminated express saccades, leaving only a unimodal distribution of long saccadic latencies. In fact, both express and fast regular saccades, as defined by F&W, were eliminated.

We went on to study the role of other visual pathways in the generation of saccadic eye movements (Schiller et al. 1990). For example, it was thought that the fast-conducting parasol (M-pathway) system might account for the "express" distribution, with the slower conducting midget (P-pathway) system mediating the longer latency modes. Lesions that separately disrupted either of these pathways, however, left the bimodal short-latency distribution intact. In contrast, when both of these pathways were blocked, as noted by F&W in their target article, animals became virtually blind and could not make any visually guided eye movements into the scotoma, suggesting that the direct retinotectal pathway cannot be involved in the generation of either phase of the bimodal distribution of saccadic latencies.

We also tested the role of the hypothesized two major streams emanating from the striate cortex to the inferotemporal cortex via V4 and to the parietal cortex via area MIT by selectively disrupting these pathways (Schiller et al. 1990). Neither V4 nor MT lesions produced significant changes in the bimodal latency distribution; even paired lesions of V4 and MT failed to alter the distributions.

This body of evidence suggests that the superior colliculus is the prime conduit for the generation of express saccades. It seems likely that a generally unimodal oculomotor signal reaches this structure via cortex and that it is at, or downstream from, the superior colliculus that the bimodality is introduced.

These observations, taken together, are at odds with the model proposed by F&W according to which express saccades are mediated by a striate cortex-to-superior colliculus path but slower saccades are mediated by other cortical routes that bypass the superior colliculus (Fig. 12 of target article), with bimodality generated by varying attentional states. We would like to propose an alternative mode that relies on one additional important finding about the superior colliculus: Many neurons in the intermediate and deeper layers of this structure produce a dual, temporally separate discharge, firing first to a visual target and then prior to observed saccades. Neurons downstream from these "visuomotor" cells, possibly including the superior colliculus's own saccade-related burst neurons, could theoretically use either signal to initiate a saccade command (as noted by Sparks 1989). We therefore propose that these visuomotor cells of the superior colliculus naturally introduce bimodality through their temporally separate "visual" and "motor" bursts. The neurons that receive this bimodal signal would be responsible for the selection of which discharge to use as the saccadic trigger. This decision would probably be influenced by the cortex via inhibitory innervation (e.g., through the substantia nigra pars reticulata). In simple detection tasks the visuomotor cells' "visual" response could be utilized, generating express saccades, whereas during more complex tasks this first discharge would be ignored in favor of the later burst and express saccades would not appear. Thus, we suggest that bimodality of those neural signals causal to short-latency saccades is neither generated at the cortical level nor is this bimodality's genesis influenced by attentional or other "cognitive" states. Rather, such states are probably only involved in the *selection* of one of a pair of discharges that are already available, being naturally produced by visuomotor cells of the superior colliculus as a

general response to visual stimuli. This model, and recent psychophysical evidence in support of it, will be presented in more detail elsewhere (Sommer, submitted).

Where do the three central issues stand?

Wa James Tam

Communications Research Centre, 3701 Carling Avenue, Ottawa, Ontario, Canada K2H 8S2

Electronic mail: james@dgbt.doc.ca

Fischer & Weber (F&W) assume that attention controls eye movements. In their model of oculomotor control, disengagement of attention plays an important role, which is manifested in the occurrence of express saccades in the gap paradigm. Here, I will draw attention to three important issues concerning the model: (a) whether express saccades exist, (b) whether express saccades are anticipatory, rather than visually guided, and (c) whether attentional disengagement plays a dominant role in determining saccadic latencies. I will comment briefly on each.

Latency distributions: One peak, or more? Using the gap paradigm, Fischer and his colleagues have repeatedly shown bimodal distributions for saccadic latencies, with peaks centered at about 100 msec (express saccades) and 150 msec. They use the bimodal character of the latency distributions to argue that express saccades exist as a separate population of saccades.

Wenban-Smith and Findlay (1991), however, failed to find bimodality in the latency distributions of their subjects. This discrepancy between studies suggests a caveat. When the studies in question are examined, it appears that the discrepancy may have resulted from individual differences (few subjects were used) and from differences in experimental designs (random vs. fixed gap periods and/or random vs. fixed target locations). Based on this comparison, it appears that bimodality in the latency distributions depends not only on a gap period but also on individual subjects and stimulus conditions. Consistent with this analysis, F&W themselves admit that some subjects do not demonstrate clearly separated peaks. In a recent study, it was found that 8 out of 20 (40%) naive subjects did not show bimodality (Fischer et al. 1993). Furthermore, Findlay (1981), Fischer and Ramsperger (1986), Jüttner and Wolf (1992), and others have shown that saccadic latencies can be greatly affected by stimulus uncertainty. In particular, Jüttner and Wolf demonstrated that the peak for express saccades is diminished or eliminated if the proportion of catch trials (trials in which the saccadic target does not appear) is increased. Keeping this caveat in mind, the weight of the evidence suggests that there may indeed be a separate population of extremely fast saccades, centered around 100 msec.

Are express saccades visually guided? The second issue is more controversial. Although F&W have assembled evidence supporting the argument that express saccades are not anticipatory but visually guided, the evidence is equivocal. For example, they present evidence that latencies of express saccades depend on target luminance, target size, and retinal eccentricity. However, this evidence need not mean that express saccades are "visually guided." Instead, it is possible that increasing the luminance, contrast, or size of the saccadic target promotes early detection of target onset and thus facilitates the elicitation of a saccade. Independent of this, however, the direction and extent of the saccade could still have been anticipated and preprogrammed, especially if the target were presented at a fixed location or at a fixed retinal eccentricity.

Furthermore, and consistent with the foregoing analysis, some of the evidence that has been presented suggests that express saccades may be anticipatory. For example, it has been shown that the number of express saccades diminishes as the proportion of catch trials is increased (Jüttner & Wolf 1992).

Thus, it is possible that when it is feasible to anticipate the target (i.e., when few or no catch trials exist), subjects make anticipatory express saccades, but that when it is not feasible to anticipate (i.e., when the proportion of catch trials is increased), subjects refrain from anticipating the target.

Considered together, the evidence in favour of express saccades being guided visually is not compelling. In particular, more research is required to examine why the occurrence of express saccades depends on stimulus uncertainty.

Is the gap effect due to attentional disengagement? Critical findings from our laboratory have forced us to reexamine the role of attention in the control of eye movements. Specifically, attentional disengagement cannot adequately explain some of our experimental results (Tam & Stelmach, *in press*). Our experiments consist of a typical overlap-gap paradigm, with the exception that subjects are required to direct their attention to an eccentric stimulus while fixating a stimulus at the centre of the display (dissociation paradigm; see Mayfrank et al. 1986). Then a target is presented to the left or right of fixation and subjects are asked to saccade to the target as quickly as possible. In these experiments, we find a larger gap effect (shorter saccadic latencies) when the unattended-foveated stimulus is turned off than when the attended-eccentric stimulus is extinguished. Under the attentional disengagement hypothesis, the opposite result would have been expected; that is, saccadic latencies should be shorter when the attended-eccentric stimulus is extinguished than when the unattended-foveated stimulus is extinguished. In addition, our experiments show that the offset of the foveated stimulus always results in shorter latencies than the offset of the eccentric stimulus, regardless of the direction of attention. This indicates that extinguishing the fixation point plays an important role in generating the gap effect and suggests that the gap effect (and, possibly, express saccades) is generated when the ocular system is disengaged and made ready to move, not when attention is disengaged.

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Toward an alternative scheme for the generation of express saccades

J. A. M. Van Gisbergen and A. W. H. Minken

Laboratory of Medical Physics and Biophysics, 6525 EZ Nijmegen, The Netherlands

Electronic mail: admin@mbfys.kun.nl

Fischer & Weber (F&W) have shown how the systematic study of what at first seemed just a curiosity has yielded a useful benchmark of the saccadic system that can tell us a lot about how it is organized. One of the reasons F&W's review is very useful is its impressive analytic survey of experimental data supporting the claim that express saccades are really visually guided movements rather than anticipatory reactions. Our commentary will accept the conclusion that express saccades are visually guided and will focus mainly on the problem of how the processes underlying them can be modeled in a way that is in line with what we know about the neurophysiology of the system.

Need for an alternative model. According to the F&W model of the saccadic system (Fig. 13), there are three major signals (att, dec, and com) which must be prepared before a saccade can be generated. The processes responsible for generating these signals are embodied in three hierarchically arranged loops which exert their influence by affecting the lower-order loops. An important question to be discussed in this commentary

concerns the possibility that a parallel arrangement might actually fit the data in the literature better.

As the target article makes clear, there are good reasons to assume that the release of attention is an important mechanism in the explanation of saccade latency distributions. A significant role in this process has been assigned to the parietal cortex (third loop). For reasons that have not become completely clear, the attentional process in the model affects the colliculus indirectly in a serial arrangement through the dec mechanism in the second loop. Based on recent neurophysiological evidence, we would like to consider an alternative arrangement. Munoz and Wurtz (1992) have shown in the monkey that the colliculus contains two functionally distinct populations of neurons which modulate their activity in relation to eye movements. It had been established a long time ago that the caudal colliculus contains saccade-related burst cells. Munoz and Wurtz have now found fixation-related neurons in the rostral zone. These cells fire tonically when the animal is actively fixating a visual stimulus and pause during a saccadic eye movement. It is interesting to note that suppression of the activity of these cells by local injection of muscimol reduces the ability to maintain fixation and facilitates the generation of express saccades.

Thus, there is now direct evidence that the attention-related signal impinges directly upon the colliculus, a situation that is not accounted for in the F&W model, where the colliculus only provides the com signal. One can therefore envisage a revised scheme where the third loop, lumping together the attention-related signal processing in both parietal cortex and the collicular fixation zone, is connected directly to the com box in the colliculus. Such a revised scheme would have two parallel loops overlaying the fast loop through the colliculus: one system affecting fixation, the other the specification of movement. Lesioning the frontal eye fields in such a system removes the tonic inhibition but leaves the att system intact and thereby still allows the generation of express saccades that have been observed in this condition (Schiller et al. 1987).

F&W have proposed a close link between the three latency groups distinguished in the experimental data and the three-loop concept. However, their idea that the second peak in the latency histograms may be due to the loop responsible for the dec signal is not supported in the literature. Schiller et al. (1987) have reported that the latency histogram in monkeys with a frontal eye field lesion may show both an express peak and a later peak. The latter finding argues against a role of the frontal eye fields in the generation of these saccades. One explanation which might be considered is that the collicular visual signal elicited by the target stimulus is often not a sustained burst of action potentials but consists of a short burst, followed by a pause and a later resumption of firing at a lower rate (see, e.g., Ottes et al. 1987). So, the dip between the first and second latency peak may reflect the pause in the collicular visual signal.

Target selection. It would be interesting to know whether it is still possible to activate the very fast pathway when the visual scene requires target selection. This also raises the question of how the present model deals with target selection. F&W mention that express saccades are still possible when two peripheral stimuli are presented simultaneously at different but neighbouring positions and they report that this situation gives rise to the global effect (averaging). Earlier work by Ottes and coworkers, using a similar paradigm, has led to some interesting observations on the interrelations between temporal and spatial properties of the saccadic response. As long as the two stimuli are not too far apart, latency remains comparable with what is found in single target trials and the global effect is observed. As stimulus spacing increases, latency is definitely prolonged and the response becomes bistable: The eye goes to one or the other stimulus (Ottes et al. 1984). Similar observations were made using a double stimulus paradigm requiring target-nontarget choice (Ottes et al. 1985). The latter study showed that a modest separation of the target/nontarget pair gave rise to the global

effect in short-latency responses but not in long-latency saccades. Extrapolating from these results, one can predict that widely spaced double stimuli will produce neither the global effect nor express saccades. One wonders whether the dec mechanism in the model could be somewhat more broadly defined so that it incorporates target selection. Since the nigrocollicular connection is topographically organized, this seems a reasonable possibility. It is conceivable that the preparation of such a signal (lifting the veto for one stimulus but not the other) takes longer, thereby prolonging saccadic latency.

Prediction as an explanation for the occurrence of express saccades

Françoise Vitu

Laboratoire de Psychologie Expérimentale, CNRS, EPHÉ, EHESS,
Université René Descartes, 75006 Paris, France
Electronic mail: upecvit@frors31.bitnet

The attention-disengagement theory of Fischer & Weber (F&W) is based on the hypothesis that express saccades differ from anticipatory saccades as well as from "predictive regular saccades" (some of whose parameters can be defined in advance). This commentary will present evidence against this hypothesis by showing that the occurrence of express saccades depends on the predictability of several characteristics of the target that the eyes must saccade to, and independent of attention-(dis)engagement.

Prediction of target appearance. Several studies show that express saccades occur only when the moment of target appearance is predictable or can be estimated by subjects. For example, Jüttner and Wolf (1991) have shown that the probability of observing express saccades depends on the number of catch trials mixed with normal gap trials. This suggests that in normal gap conditions subjects predict when their saccade must be executed and that they abandon this strategy when a peripheral target to which to saccade appears only in a few trials. Similarly, Fischer and Ramsperger (1984) have shown that the saccade latencies obtained for a gap duration of 200 msec are much shorter when the 200 msec gap trials are mixed with 100 msec gap trials than when they are mixed with 300 msec gap trials. This suggests that subjects estimate the moment when the target appears, this estimation corresponding to the mean of the various possible gap durations in the session. However, it is probably easier to estimate the moment of target appearance when the gap duration varies in a session within small ranges (as in Fischer and collaborators' studies where the gap duration range never exceeds 100 msec) than when it varies within large ranges (as in the study by Wenban-Smith and Findlay (1991) where the gap duration is randomly varied between 0 and 300 msec by 20 msec steps in the same block of trials. Thus, unlike Fischer and collaborators, Wenban-Smith and Findlay (1991) fail to obtain express saccades.

Reuter-Lorenz et al. (1991) also fail to find express saccades in a gap condition. In their experiment, however, gap and overlap trials are run in the same session, whereas in Fischer and collaborators' studies, gap and overlap conditions appear to have been systematically run separately (although this is not clear, because their experimental design was never precisely described). If this was the case, it is easier to predict the target appearance on Fischer and collaborators' gap trials than in the study of Reuter-Lorenz et al. (1991), where target appearance is not systematically preceded by fixation point disappearance (because gap and overlap trials are mixed). Thus, unlike Fischer and collaborators, Reuter-Lorenz et al. (1991) fail to find express saccades.

Prediction of target eccentricity and/or target position. Express saccades occur not only when the moment of target appearance is predictable, but also when the position of the

target relative to the fixation point (right or left) or the target eccentricity is predictable or can be estimated. When the fixation point disappears, the system is alerted that the target will appear after a certain delay. *If the target eccentricity and its position are predictable*, the system can start computing the saccade and be ready to send the command when the delay has passed. *If only the target eccentricity is predictable*, the preparation time is longer, because the system has to wait for the target to appear before adding the direction parameter to the already computed saccade. Fischer and Ramsperger (1984; 1986) therefore observe more express saccades in gap conditions when the target appears systematically at 4 degrees to the right than when it appears randomly at 4 degrees to the right or left.

After several trials, the task is probably sufficiently automated to allow the system to guess the direction of the saccade to execute before target appearance, or even to adopt a systematic strategy such as preparing a movement to the right every three trials. This may be why express saccades mainly emerge after training. The fact that subjects produce many express saccades to one side but not to the other side (cf. F&W's Fig. 6) is also compatible with this hypothesis. If subjects adopt the strategy of going to the right most of the time, rightward saccades will have a shorter latency than leftward saccades since in the latter case the system must change the computed direction. For the same reason, the proportion of directional errors in an antitask condition is preponderantly rightward (Fischer & Weber 1992).

If the target eccentricity is unpredictable, subjects might try to guess it in order to shorten their saccade latencies. The existence of a range effect in the case of express saccades supports this hypothesis: When the target appears at variable eccentricities, the eyes tend to saccade toward the middle of the range of possible eccentricities whatever the target eccentricity, which means that the system does not wait for target appearance to compute the saccade size. Fischer and Ramsperger (1986) reported that saccade latencies are the same when a target systematically appears at 4 degrees and when it appears randomly at 4 and 8 degrees. However, since the authors did not require subjects to make accurate saccades, the uncertainty of target eccentricity need not have changed saccade latency or the proportion of express saccades. In the random 4–8 degree condition, saccades were probably not accurate and the eyes probably landed at the middle-range position (6 deg).

The existence of a global effect for express saccades is not very surprising because this effect depends on saccade latency: The longer the time spent programming the saccade toward a given target, the smaller the influence of other peripheral targets on saccade size computation and the more accurate the saccade (Coëffé & O'Regan 1987). Thus, the global effect is even more likely to occur in the case of express saccades, whose latency is short, than in the case of regular saccades. This highlights the fact that express saccades are not meant to be accurate and that subjects do all they can to generate a short saccadic reaction time.

Last, the fact that children, and particularly dyslexic children, make express saccades spontaneously in gap and overlap conditions does not necessarily show, as F&W claim, that express saccades are not anticipations. It might in fact show just the opposite. Children and dyslexics might make more anticipated movements and/or inaccurate movements than other subjects. Besides, as shown by Fischer and Weber (1990), dyslexic children's saccades are much less accurate than normal children's. As Becker (1989) pointed out, it is unfortunate that express saccade accuracy was not analysed more systematically in the different gap and overlap situations used by Fischer and collaborators.

Express saccades: A separable population?

M. G. Wenban-Smith

Wolfson College, University of Oxford, Oxford OX2 6UD, England

Fischer & Weber (F&W) state that "a bimodal distribution of express and fast regular saccades . . . is not a prerequisite for the existence of an express saccade population." This is correct in so far as one can conclusively demonstrate for a particular subject that such bimodality does in fact exist. On the basis of such a demonstration one can determine latency criteria by which express (E) and fast regular (FR) saccades can subsequently be defined even if bimodality is no longer shown.

In the absence of training, the distribution of saccade latencies for a subject should be as in Figure 1, being determined by the length of gap/overlap, and the relative proportion of E:FR saccades. The distribution should be separable into three populations. The difference between the two longer latency populations is due to the greater number of relatively long overlap trials leading to regular (R) saccades and of relatively long gap trials leading to FR saccades, compared with the small number of trials with intermediate gap lengths. The difference between the two shorter latency populations is not due to the differences in gap time per se, but to differences in the mechanism of saccade control occurring in a single gap condition. Before one can accept this description of saccade latency distributions, however, it is necessary to eliminate the possibility that the "E" population is simply a practice-improved FR population. For this reason it is not sufficient to rely initially on only very low latency saccadic reaction times (SRTs) as evidence for E saccades.

This possibility is shown diagrammatically in Figure 2i. SRTs are reduced with practice so that the improved FR population (FR') is within the range of the proposed E population. The results of intermediate gap trials should also show an orderly reduction in saccadic latencies.

This differs from the prediction of an express population, in which the results of intermediate gap trials should show an orderly reduction in latencies until they reach FR' latencies and thereafter there should either be evidence of a bimodal distribution in latencies between FR' and E saccades (2ii) or a discontinuity between the intermediate condition SRTs and the express SRTs (2iii).

These three possibilities should be distinguishable by considering separately the distribution of SRTs for each gap condition, as the gap length changes. In the first case (2i) there is no reason to expect any change in standard deviations of SRT for a particular gap condition as the gap is increased. In the second case (2ii) one expects an increase in standard deviations as the area of divergence between FR' and E saccades is reached. Finally, in the third case (2iii), one would expect a "blip" of high standard deviation at the point of the discontinuity. Wenban-

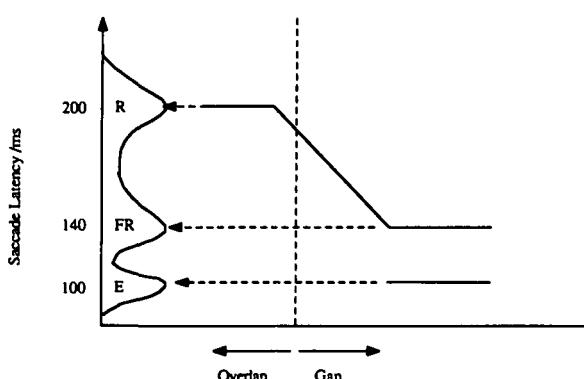


Figure 1 (Wenban-Smith). The proposed distribution of saccade latencies into regular (R), fast regular (FR), and express (E) populations, depending on overlap or gap length.

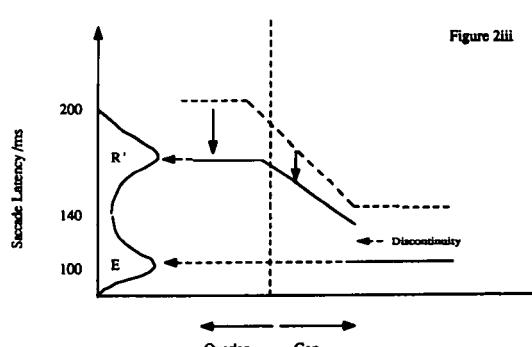
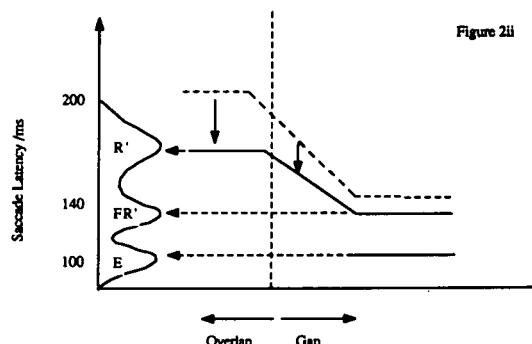
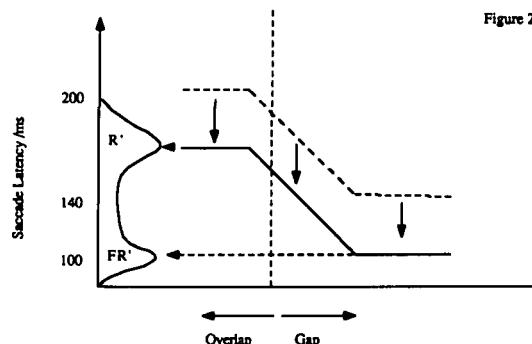


Figure 2 (Wenban-Smith). The possible effects of practice on saccade latency populations: (i) a general reduction in saccade latencies across all conditions; (ii) a reduction in saccade latencies and an increase in the proportion of express saccades; (iii) a reduction in saccade latencies and a complete switch to express saccades in trials with a sufficient gap.

Smith and Findlay (1991) looked for such changes in standard deviations but failed to find evidence for them.

Without such clear evidence of *bimodality* between express and fast regular populations, the possibility remains that the population of saccades with latencies around 140 msec is a practice-improved regular population (R') and the population with very short latencies of around 100 msec, a practice-improved fast regular population (FR').

Are express saccades anticipatory?

Peter West and Christopher M. Harris

Department of Ophthalmology, Hospital for Sick Children, London WC1N 3JH, England

Electronic mail: segxpw1@ucl.ac.uk

Since their discovery by Fischer and Boch (1983), express saccades (E-saccades) have been controversial. Although their existence was initially doubted, the evidence that monkey and

man can make very short latency visually guided saccades is now beyond question. In monkeys it is clear that E-saccades form a separate distribution of latencies from regular saccades. The existence of bimodal latency distributions for man is somewhat more equivocal since some investigators have failed to find bimodality (Wenban-Smith & Findlay 1991). However, we suspect that there are subtleties in the stimulus and training paradigms that have yet to be delineated. In this commentary we accept the existence of bimodality in man and do not dwell upon species differences.

The thesis of the target article is that E-saccades result from the disengagement of high-level attention cued by the fixation light offset before the target light onset. According to Fischer & Weber (F&W), saccades toward a peripheral light cannot be made until attention has been released from the fixation light. The release of attention requires 100 msec or more, so that short latencies can occur if the subject is given an appropriately timed warning signal (visual or otherwise). Although F&W's argument is seductive, we believe it to be flawed for the following reasons:

First, there is an optimum gap for eliciting E-saccades (Mayfrank et al. 1986), with individuals showing a peak proportion of E-saccades for gaps from 100–250 msec but with a rapid fall-off for longer gaps. If attention is disengaged at 200 msec, why is it not still disengaged at say 800 msec, when there is no other external stimulus competing for attention?

Second, the predictability of the target location modifies the latency of E-saccades. When target eccentricity is held constant, randomisation of direction results in an increase in mean latency from 107 msec to 120 msec compared to latencies when direction is predictable (Fischer & Ramsperger 1986). How can the disengagement of attention be slowed by the later-occurring saccade?

Finally, and most important, training of E-saccades is directionally specific. When monkeys were trained with a gap to make E-saccades to targets only at one location, later testing revealed comparatively few E-saccades to other locations (Fischer et al. 1984). According to F&W, the offset of the fixation target cues the disengagement of attention. Since the target location is unknown at the time of offset, why do we not see E-saccades to all locations?

An alternative to the attention disengagement hypothesis is that E-saccades result from some form of facilitation or practice effect (Ruelen 1984). With training, one might expect a gradual but continuous decrease in latency until some minimum is reached. However, as F&W rightly point out, facilitation would not account for the bimodality of latency distributions. Instead, bimodality strongly implies two distinct functional (but not necessarily anatomical) pathways. For this reason, the existence of bimodality is a pivotal point and needs to be further substantiated in man.

Neither attention disengagement nor facilitation appears to give a parsimonious account of E-saccades. We propose a third alternative that overcomes these objections. With suitable training, the saccadic system learns to make anticipatory saccades to frequently used target locations. The cuing event (e.g., the offset of the fixation point) initiates the calculation of a saccade to the most probable anticipated target location, based upon past experience, even though no real target has yet appeared. If the calculation is completed simultaneously with the appearance of the real target *and* the locations of the predicted target and the real target coincide, then the precalculated saccade is executed immediately, with a short latency relative to the target onset. If the predicted and real target locations are different, then saccade calculation is restarted to the real target location. If the real target appears before the calculation is completed (i.e., a short gap) the calculation is restarted to the real target location. If the target does not appear shortly after the completion of the calculation (i.e., a long gap) the precalculated saccade is not executed and the calculation is restarted when the real target appears, resulting in a regular latency.

In the untrained subject, the saccadic system has been exposed to a wide range of target locations and correct precalculation occurs only occasionally. On the majority of trials, saccade target location must be recalculated, yielding normal latencies. However, as training progresses, the saccade system anticipates the correct target location with greater probability, thereby increasing the proportion of E-saccades. Some subjects who have been extensively trained with thousands of identical saccades over many days become so adapted to precalculating that they are able to do so in the absence of an external cue. It is these subjects who can perform E-saccades in the overlap condition.

Thus, we are proposing that E-saccades are anticipatory but not executed when incorrect. The precalculations of the anticipatory saccades are probably distributed with a mode of about 200 msec, corresponding to the most effective gap duration. If this hypothesis is correct, we would expect the proportion of E-saccades to depend on how well the subject can extract the probability of target location, which will in turn depend on the exact stimulus paradigm and degree of training.

Indexing and the control of express saccades

Richard D. Wright^a and Lawrence M. Ward^b

^aDepartment of Psychology, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6 and ^bDepartment of Psychology, University of British Columbia, Vancouver, B.C., Canada V6T 1Z4

Electronic mail: ^arwright@sfu.ca; ^blward@cortex.psych.ubc.ca

Fischer & Weber's (F&W's) demonstration that express saccades occur only during a state of attentional disengagement is an important step in the process of explaining the mechanisms responsible for eye movements and visual attention shifts. Yet there is one puzzling aspect of the data that is not well accounted for in terms of the F&W model as stated. This is that the large practice effects seen in the gap paradigm, which result in increases in the number of express saccades, are specific to the locations to which the saccades are made during the practice, for both monkeys and humans (Fischer & Breitmeyer 1987). Clearly, observers are learning something during this practice, but according to the loop model what they are learning is only how to successfully disengage attention while keeping the eyes fixated on the fixation location during the gap (sect. 7). Although facilitated by the disappearance of the fixation stimulus, this process as described by F&W does not seem to be characterized by target location specificity. Location specificity of practice effects seems at first to be better explained by something like premotor priming but F&W dismiss this for what appear to be good reasons. How then can we account for location-specific practice effects within the loop model?

We propose that an elaboration of the central state F&W refer to as the *dec* or "decision to make a saccade state" will accomplish this task. We propose that the decision to make a saccade is a location-specific decision. How could this be? Such a decision could be location-specific if it involved indexing of spatial locations. By indexing we mean entering the location into a priority stack or queue that guides intermediate level visual processing (Ullman 1984) and attention focusing (Wright & Ward 1992). An index tag, or FINST (for Finger of INSTantiation – Pylyshyn 1989) may be necessary for any intermediate level visual processing (such as counting) directed at specific locations (or objects occupying them) in visual space, including the focusing of attention. Up to four such tags are thought to be inserted into the stack and maintained for subsequent processing, which can act on them in order of priority (Pylyshyn & Storm 1988; Yantis & Johnson 1990). Indexing can occur in a goal-driven manner whenever a computational goal such as counting requires that locations be tagged. This would correspond to activation of the

dec state in the loop model by *c* and some types of *r* inputs, as occurs during express saccades. Indexing can also be triggered in a stimulus-driven manner by a signal from the visual system that an "interesting" visual event, such as an abrupt onset stimulus or a movement, has occurred. This would correspond to activation of the *dec* state by an input from *vis*, as occurs during fast regular saccades.

We accordingly propose that in the typical gap paradigm, which has only one or two locations to which saccades are made, observers could be learning with practice how to index those locations during the gap interval (goal-driven indexing) while at the same time disengaging their attention from the fixation location. Only locations experienced during practice sessions could be indexed in a goal-driven manner during the gap interval since new locations tested during a postpractice session would usually be distributed unpredictably over the visual field. Even if some unpracticed locations recurred, only one or two such unpracticed locations could receive advance, goal-driven indexing during the gap because of the four-tag limit, and since they would recur infrequently, there would be little motivation to index them. The most likely scenario would be that the unpracticed locations receive indexing triggered in a stimulus-driven manner only after the target occurred, as portrayed in the fast regular or slow regular scenarios. The tag assigned to an unpracticed location in this way during a trial when a saccade to it was required would probably remain until the tag was reassigned to another, new, unpracticed location. Thus, the likelihood of an unpracticed location being indexed during the gap on a trial on which a saccade had to be made to it would be very low, precluding a significant number of express saccades to any such location. Even in the Fischer and Breitmeyer (1987) study, in which there was only one unpracticed location, the observer would not be expected to be able to index that location reliably until after further practice. Interestingly enough, in this study there were more express saccades to the single unpracticed location during the test session than during the first session, although many fewer than to the practiced location, indicating that some learning of how to index the unpracticed location probably occurred during the test session itself.

We suggest that Fischer & Weber's *dec* state should be renamed "index" to indicate that the decision to make a saccade is location specific and corresponds to the indexing operation studied by others. Since indexing has also been implicated in the control of visual attention (Wright & Ward 1992), and since disengagement of attention has been proposed as preliminary to attention shifts not accompanied by eye movements (e.g., Posner et al. 1988), we feel that Fischer & Weber's work has lent strength to the view that the control of saccadic eye movements is not only intimately linked to the control of visual attention but may also provide the mechanisms required to shift attention in visual space in the absence of eye movements (cf. Wright & Ward 1992).

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Authors' Response

Modes of saccade generation and their attentional control

B. Fischer and H. Weber

Department of Neurophysiology, University of Freiburg, D-78 Freiburg, Germany
Electronic mail: franz.aiple@sun1.ruf.uni-freiburg.dbp.de

R1. Introduction

Our response to the many interesting and useful commentaries – some in favor, others against our notion of the relationship between express saccades and visual attention – is organized in sections:

Some commentators believe firmly, some have doubts, and others are still not convinced that express saccades are visually guided (not anticipatory) oculomotor responses. The first section takes up again the role of anticipation and prediction in the generation of express saccades and presents the data of an experiment with increased temporal and spatial uncertainty of stimulus presentation. Once it is accepted that visually guided saccades can have latencies in the order of 100 msec in man (70 msec in the monkey) the next question (and section) concerns the relationship between express saccades and the gap effect. How can one identify express saccades as a separate population? Is the gap effect more than just a reduction of reaction time? We treat these two aspects together, because usually the gap task has been used to elicit express saccades and the real controversy is the question of bimodal distributions obtained in this task. However, we must again stress the fact that express saccades also occur in naive subjects with the overlap task. The problem of different modes, their generation by the three-loop model and its neural basis is taken up in the section on modes and model. Here we also treat the problem concerning the second mode – the fast regular saccades – that is, the question of target selection and decision making. Once express, fast regular, and slow regular saccades are accepted as separate populations of visually guided saccades, the question arises how mechanisms of attention are related to the generation of express saccades or to any type of saccade. The pathways involved will be discussed. Finally, aspects of development and dyslexia will be taken into account: What can we learn from the saccadic reaction times produced by children and dyslexics?

R2. Anticipation and prediction

Our position is that anticipatory and express saccades have certain preparatory processes in common; however, the express saccade is visually guided whereas the anticipatory saccade is not. If the spatial or temporal arrangement of the experiment allows the subject to go through all preparatory steps with the exception of the computation of the metrics, the incidence of express saccades is increased. Some commentators still required that the

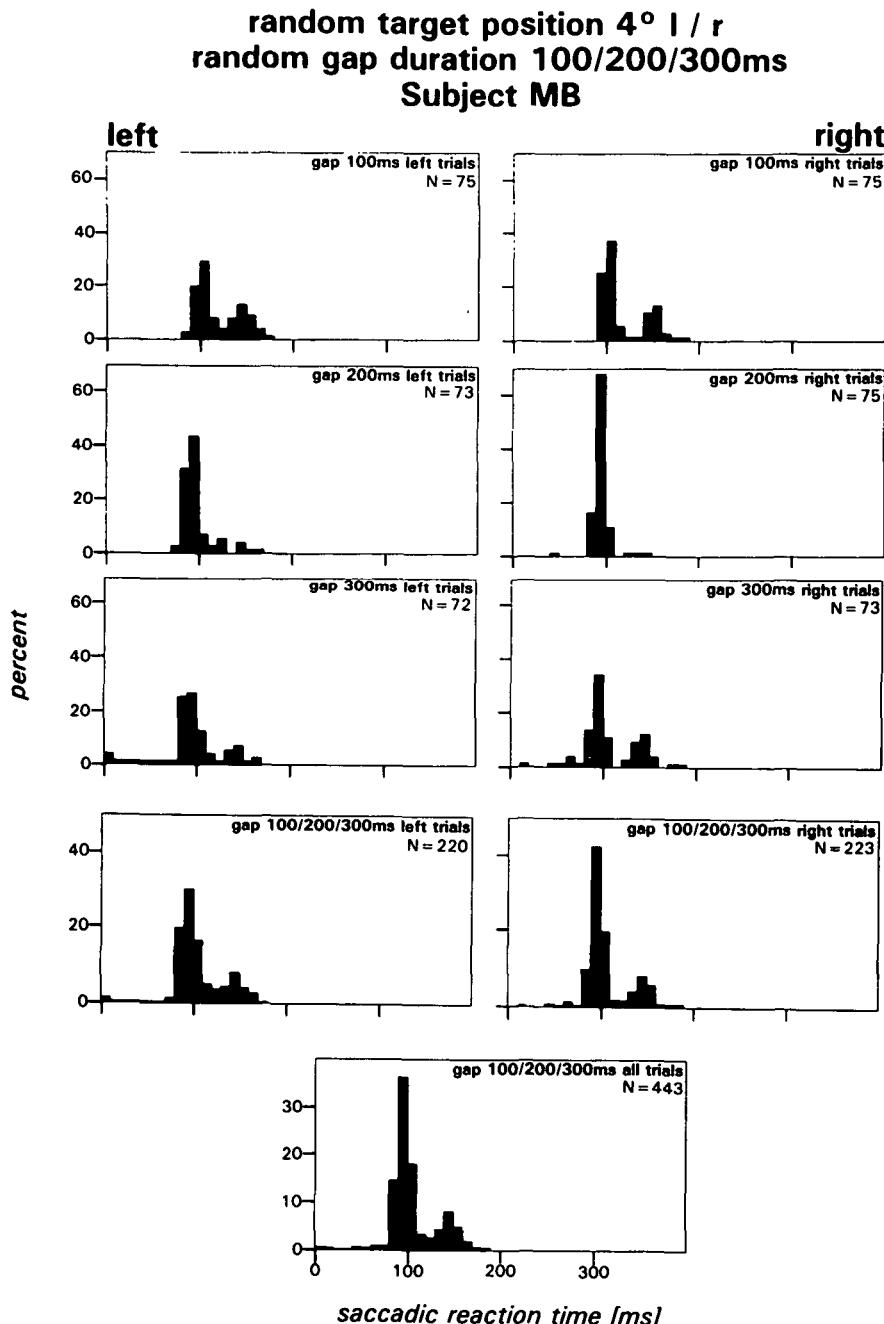


Figure R1. Distributions of saccadic reaction times (bin width = 10 msec) obtained in an experiment with random target location (4° left/right) and random gap duration (100/200/300 msec): data from a single trained subject. The panels in the 3 upper rows consider the 6 randomized conditions separately; left = target on the left, right = target on the right. The different gap conditions are indicated in the respective panels. The fourth row shows the data pooled for all left and all right trials. In the lowest panel the data from all trials have been pooled. Note that the two modes of express and regular saccades are present in all distributions.

spatial and temporal uncertainty of stimulus presentation be increased to ensure that express saccades are indeed visually guided oculomotor responses. The results of such an experiment are presented in Figure R1. Some commentators consider the reduction of the number of express saccades by the introduction of catch trials (Jüttner & Wolf 1992) as further evidence for the anticipatory nature of these saccades. Another important aspect to be considered is the relationship between latency and errors of the saccades. Finally, we will deal with the question of whether the occurrence of express saccades is the result of learning to preprogram saccades to particular locations.

R2.1. Spatial and temporal uncertainty. The use of a single target location or gap condition, as Cameron & Lennie mention, favors the presence of anticipatory saccades that are indistinguishable from visually guided saccades. However, these anticipatory saccades can be readily distin-

guished from express and regular saccades: The normalized velocities of express saccades correspond to those of longer latency saccades, while anticipatory saccades have significantly lower velocities (Fischer & Weber 1992). Scatter plots of saccade amplitude versus reaction time clearly show the transition between anticipatory and express saccades (cf. Fig. 6 of the target article); whereas the amplitudes of anticipatory saccades exhibit a large scatter, those of express saccades make up a compact distribution. Vitu suggests that express saccades are the result of the subject's estimating or guessing the stimulus parameters and that the presence of range and global effects for the express saccades would support this hypothesis. However, these averaging effects were first reported for regular saccades (Findlay 1982; Kapoula 1985), and without applying a gap condition. These saccades can certainly not be considered anticipatory. Furthermore, the global effect can be partly suppressed by

the instruction to select one of the targets as the goal for the saccade. This suppression was about equally effective for regular and express saccades (Weber et al. 1993).

In the early studies (Fischer & Ramsperger 1984) there was indeed a 15 msec latency increase for right-left randomized target positions versus constant target position. It was, however, also shown that randomizing the target position between 4° and 8° to the same side did not lead to a corresponding latency increase. The suggestion of Cameron & Lennie, Schall & Hanes, Vitu, and West & Harris that the occurrence of extremely fast oculomotor reactions – the express saccades – is attributable to spatial certainty must be discarded because it contradicts the experimental results.

Temporal uncertainty of target onset was raised by Schall & Hanes and Vitu. Both consider the experiments of Schiller et al. (1987) and Wenban-Smith and Findlay (1991), who used randomized gap durations ranging from 0 to 300 msec. As a result, the number of short latency (express) saccades increased with increasing gap duration. We have recently performed a series of experiments in which we systematically investigated the effect of stimulus uncertainty on the occurrence of express saccades. The results of an experiment with randomized target location (left/right) and randomized gap duration (100/200/300 msec) are shown in Figure R1: Express saccades (with a peak around 90–95 msec) are present in all 6 randomized conditions. Furthermore, the largest number of express saccades is obtained with a gap of 200 msec, while bimodal distributions of express and fast regular saccades are obtained with gaps of 100 msec and 300 msec. The other two subjects tested in this experiment showed similar results. Schall & Hanes claim that with increasing gap duration the subject's readiness to initiate the movement increases in parallel, resulting in progressively shorter reaction times. If this were correct, then we should expect shortest latencies and largest numbers of express saccades always for the longest gap duration included. Instead, the number of express saccades decreases for gap durations longer than 200 msec. Neither can we support Vitu's suggestion that subjects estimate the moment of target appearance as the mean of the possible gap durations. If one compares the proportion of express and regular saccades obtained in the randomized gap conditions (Fig. 1) with those obtained in the corresponding control experiments with constant gap durations, the distributions with gaps of 200 msec and 300 msec are not affected by randomization, while the number of express saccades with the shortest gap (100 msec) is decreased. If the subjects "synchronized" their response to the mean gap duration one would expect the shortest reaction times and a high number of anticipatory saccades with the longest gap duration. The experimental evidence is again against this notion.

We accordingly maintain that express saccades are obtained when all processes of saccade preparation are completed *except the computation of the metrics*, which is completed after target onset; express saccades are therefore visually guided. The same is true for the fast regular saccades, which occur when only one step (attention disengagement) is completed before target onset, whereas the others (decision-making and computation of the saccade metrics) take place after target onset. Both express and fast regular saccades may therefore have antici-

pative components, that is, part of their preparation can be initiated and completed before target onset. They are not anticipatory saccades as Vitu suggests, however, because the execution of the actual saccade is triggered by target onset.

R2.2. Catch trials. A gap condition with different rates of catch trials randomly intermixed in the trial sequences was used by Jüttner and Wolf (1992). It was found that the number of express saccades decreased with increasing catch trial rate. Jüttner & Wolf attribute this result to the process of decision-making, operating in a short-term mode (in case of an express saccade) or a long-term mode (in case of a fast regular saccade). Tam as well as Vitu explain the finding of Jüttner & Wolf in terms of the subject's inability to anticipate the occurrence of the target because of the uncertainty of target occurrence. Jüttner & Wolf's detailed analysis, however, contradicts this view. They found that express saccades tended to be suppressed mostly in trials following a catch trial, the effect being a local phenomenon depending on the trial history. Furthermore, express saccades did not disappear; Figure 1 of Jüttner & Wolf (1992) shows that their subject GS still made large numbers of express saccades with a 50% catch trial rate and even with 90% catch trials some express saccades were present, while anticipations with reaction times below 80 msec were in fact already absent with a 10% catch trial rate. This suggests that with temporal stimulus uncertainty express saccades survive whereas anticipations disappear.

R2.3. Latency-error tradeoff. Error rates would have been ignored in express saccade research, Cameron & Lennie object. This is actually not the case: On the contrary, looking at direction errors has been very helpful in identifying anticipatory saccades and in distinguishing them from visually guided saccades (Fig. 4 of our target article; Wenban-Smith & Findlay 1991). It is, however, true that express saccades have smaller amplitudes and are more often followed by corrective saccades, as described in more detail in the response section R3.1 on "identification of express saccades."

Cameron & Lennie and Vitu mention that dyslexic subjects produce faster saccadic latencies (more express saccades) at the cost of a higher rate of amplitude errors (Fischer & Weber 1990). It should be noted, however, that, for example, dyslexic teenagers make more errors than age-matched normal subjects in the overlap task too, where their saccadic reaction times are slower. The fact that dyslexic subjects produce more errors should therefore be regarded as a separate phenomenon, independent of the faster reaction times of this subject group.

R2.4. Learning or prediction? Fischer et al. (1984) trained monkeys in the gap task to make saccades to one particular target location in the visual field. Subsequent testing of other (untrained) locations revealed that the monkeys made high numbers of express saccades only to the trained location and not to the others. Another finding from human subjects is the asymmetry with respect to the frequency of express saccades: When tested with right/left randomized target presentation some subjects made many express saccades to one side (mostly to the right) but only a few to the other. These results lead West

& Harris and Vitu to the conclusions that the saccadic system learns to make anticipatory saccades to a frequently used target location, or that subjects adopt a strategy of anticipating and computing saccades to a particular direction. In response to this notion we want to emphasize again that practice or training is not essential for the presence of express saccades. Many naive adult subjects and most children and teenagers produce considerable numbers of express saccades in the gap and even in the overlap task spontaneously without any previous training. Furthermore, some of them show asymmetries in their latency distributions for right versus left target presentation. It is impossible that all these subjects have adopted anticipatory strategies within a single test session, or even within a single trial (see also Fig. R2). We admit, however, that the reasons for such directional asymmetries is still unclear.

R3. Express saccades and the gap effect

In this section we treat first the problem of the identification of the express saccade as belonging to a separate population and then the question of what the gap effect is.

R3.1. Identification of express saccades. It is argued by Klein & Kingstone and Reuter-Lorenz & Hughes that neither the absolute latency nor the occurrence of bimodality helps to identify the express saccade: The absolute latency depends on the physical parameters (such as target luminance or gap duration); the bimodality may consist of two peaks, both well outside the range of the express saccades. Considering only this information, the argument sounds correct: Given a single reaction time of a single saccade (e.g., 125 msec), it is indeed impossible to tell whether or not this is an express saccade. One needs more information. If a subject produces a single peak of reaction times with a gap duration of 200 msec, it is helpful to test whether an additional peak emerges with another gap duration. The results of Figure 4 of the target article show – in agreement with Wenban-Smith and Findlay – that anticipatory saccades have latencies below about 80 msec. Hence if one peak occurs between 80 and 130 msec and a second between 140 and 200 msec, one can be sure one is looking at two types of saccades – the express and the fast regular population. If, finally, the data of a given subject in fact fail to allow such an identification on the basis of the latency distributions, this is still no reason to deny the existence of a separate population of express saccades.

As already pointed out in the target article (e.g., Fig. 6), it is also important to analyze further parameters of the saccades over and above the reaction times (e.g., saccade amplitudes). A recent investigation of corrective saccades (Fischer et al. 1993) has revealed a further identification criterion: Looking at corrective saccades, we found that express saccades do not overshoot the target, whereas overshoots occur more or less frequently with regular saccades. Express saccades, on the other hand, have a stronger tendency to be undershoots. All this information can be made available and should be used to identify a separate saccade population.

Hallett proposes to estimate a set-up time for express saccades by adding the express saccade latency and gap duration (of 200 msec), resulting in an “effective latency”

of about 300 msec. This procedure is rather useless, because it does not account for “set-up times” for express saccades occurring with longer or shorter gap durations, nor for express saccades occurring in the overlap task. The experimental findings suggest that the preparation time for an express saccade is not a fixed value, nor is it initiated exclusively by external events such as the offset of the fixation point. We agree, however, that a time period of about 200 msec is optimal for the completion of the first two processes of saccade preparation, so that the third (computation) process can be accomplished most effectively upon target onset.

R3.2. The gap effect – what decreases the reaction times?

Is the gap effect response specific? It is claimed by Reuter-Lorenz & Hughes that a gap effect exists for prosaccades only, but not for antisaccades or manual reactions. Introducing a warning tone in gap and overlap trials, they found a gap effect for pro but not for antisaccades. Without the acoustic warning signal, however, antisaccade latencies were reduced by the gap. Reuter-Lorenz & Hughes argue that for antisaccades the fixation point offset provides only an alerting signal for the subject, which, when controlled for, provides no benefit. The logic of this argumentation is by no means convincing. From these results it should be assumed that the tone, introduced together with the offset of the fixation point, causes an *overlap effect* for antisaccades. In response to this commentary we have replicated these experiments with three subjects and found a clear gap effect of more than 30 msec for antisaccades both with and without the additional introduction of a warning tone. In the experiment with the tone, however, the incidence of direction errors (saccades to the stimulus, which used to be mostly express saccades) was increased as compared with the experiment without the tone. This suggests that by introducing the tone in addition to the event of fixation point offset, the subjects could use the gap even more effectively to prepare for the following saccade, so that in many (15–20%) trials they made a reflexlike prosaccade (direction error). Reuter-Lorenz et al. (1991), however, report that in their experiments directional errors were rare (<3%). We found that it was indeed possible to avoid such reflexlike errors if subjects “waited” for the appearance of the stimulus and started saccade initiation only after they had actually ensured themselves where it was presented. Subjects thereby voluntarily neglected the presence of the gap. This behavior indeed resulted in a low number of directional errors and in long saccadic reaction times in the range of slow regular saccades or even longer, corresponding to the values reported by Reuter-Lorenz et al. (1991). The same effect may also account for the fact that Reuter-Lorenz et al. (1991), using their paradigm with an additional warning tone, obtained no gap effect with choice-manual reaction times. These authors again report the absence of any errors, whereas Iwasaki (1990), using a choice-manual task without a warning tone, obtained a clear gap effect; this was at the expense of an increased error rate, however.

The idea that the gap effect is response specific and exists for prosaccades only must therefore be rejected. However, we see no great discrepancy with Reuter-Lorenz & Hughes's view that the gap effect can be understood as the release of a reflexive oculomotor re-

ONE NAIVE ADULT SUBJECT

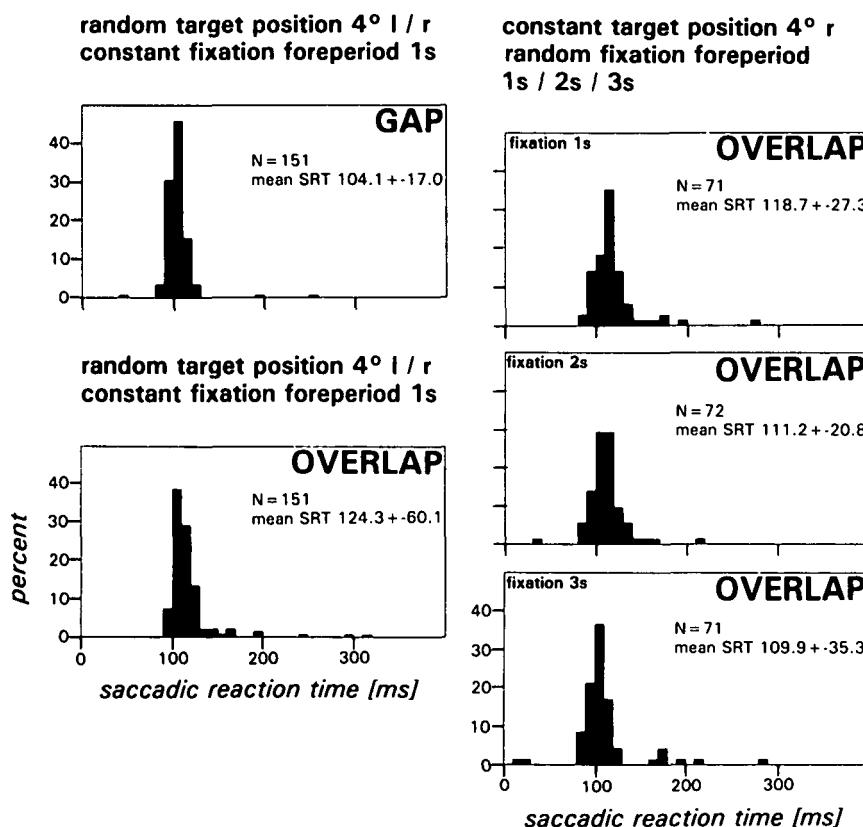


Figure R2. Distributions of saccadic reaction times from 3 experiments with a naive adult subject. Upper left: Data from a gap task with random target location (4° left/right), constant gap duration (200 msec), and constant fixation foreperiod (1 sec); left and right trials have been pooled. Lower left: Data from an overlap task with random target location (4° left/right) and constant fixation foreperiod; left and right trials are pooled. The 3 panels at the right show data from an overlap task with random fixation foreperiod (1/2/3 sec, the 3 conditions are given separately) and a constant target location (4° right). This subject made almost exclusively express saccades in all conditions without any previous training and without receiving any feedback about his performance.

sponse from voluntary fixation: Voluntary fixation can only be attentive fixation; the offset of the attention goal (the fixation point) leads to a disengagement of attention, allowing short-latency (and even reflexlike express) saccades to occur in response to the stimulus. We do not think – as Klein & Kingston suggest – that this release from attentive fixation is mediated mainly by the superior colliculus; but at the level of the superior colliculus it may be manifest as a pause in the firing rate of the rostral collicular fixation neurons (Munoz & Wurtz 1992).

Premotor preparation – a component of the gap effect? It is suggested by West & Harris as well as Klein & Kingston and Reuter-Lorenz & Hughes that the gap effect includes a motor preparation effect. West & Harris, like Kowler (1990), even assume that the offset of the fixation point initiates the calculation of a saccade to a most probable (or most experienced) target location. Coincidence of the anticipated and the actual location would yield an express saccade; if predicted and real target locations were different, saccade calculation would be restarted, resulting in a regular saccade. This idea, however, is incompatible with the data obtained from a naive adult subject (student of biology, age 27 years) shown in Figure R2. The upper left panel gives the saccadic reaction times from the gap task, with a constant gap of 200 msec and right/left randomized target location; the lower left panel shows the result from an overlap task with a 1 sec constant fixation foreperiod. The three panels on the right side consider an overlap task with randomized fixation foreperiods (1/2/3 sec) and constant target location. This subject produced almost exclusively express saccades in all tested conditions, although he had no

experience in eye movement tasks and did not receive any feedback about his performance. The occurrence of express saccades in the overlap task with spatial and/or temporal uncertainty of stimulus presentation cannot be explained in terms of prepared motor programs. We assume that this subject is in a disengaged state of attention and ready to make a reflexlike saccade any time. With this idea in mind we asked him to make antisaccades. As expected, he was unable to follow the instruction to generate a saccade to the side opposite the target. Instead, he produced single express peaks to the right and the left side where the targets were presented in random order. We are currently trying to work out how this subject is able to adopt such a state, but regardless of the origin of this behavior, the present results show that express saccades can be made without any precalculation processes. This general notion is also supported by the observation from children, teenagers, and dyslexic subjects, who spontaneously make considerable numbers of express saccades in the overlap task with random target position (Biscaldi & Fischer 1993; Fischer & Weber 1990).

Furthermore, Figure R2 confirms that the gap effect and the occurrence of express saccades are two different phenomena. Although express saccades are favored by the gap, the external event of fixation point offset is not a necessary prerequisite for their occurrence.

R4. Modes and model

Once it is accepted that the express saccade is visually guided and constitutes a separate mode of saccades, the

question arises how different modes are generated. First, we will consider the alternatives of serial versus parallel processing. We will consider the neural structures and pathways involved as well as the three-loop model and its relation to the neurophysiology and neuroanatomy of the optomotor system. This discussion will bring us directly to the second loop. Does it have to do with spatial selection and decision making? Although it may be accepted that two or three modes exist, the question of how bimodality is generated will be discussed. We will consider the neurophysiology of the superior colliculus, its possible role in the generation of bimodality, and the computation (COM) module's activity in the impulse version of the three-loop model.

R4.1. Serial versus parallel processing. Several arguments have been raised against the notion that the three central processes found to be responsible for the three modes of reaction times act in a strong serial order. First, this is not our view: Strong serial processing would lead to a monomodal distribution of slow regular saccades only. It is instead assumed that serial *and* parallel processing take place within the network outlined by the model. The way the processes interact leads to the multimodality: On some trials parallel processing allow one or the other state to be achieved and the corresponding waiting time is not needed. This type of parallel and serial processing becomes clearer if one implements the three-loop model not by logical operations (the Boolean version) but by neural elements producing, sending, and receiving impulses (the impulse version). In this version of the three-loop model the question of serial or parallel processing no longer requires an alternative answer.

Albano misunderstands the extra input *c* into the attention (ATT) module and thinks it has to do with the computation of the retinal error. This, we propose, is the job of the COM-module. Whereas we agree that the express saccade is generated from a state of readiness, we disagree that in this state the saccade is already preprogrammed. Such a concept would predict antisaccades to be of the express type, because in the corresponding antitask the subjects really could and should (deliberately) have preprogrammed the saccade. Yet express saccades are absent. Albano's idea of preprogramming would also be unable to explain the occurrence of express saccades in overlap trials with randomly varied target position in naive subjects.

A similar misunderstanding has led Jüttner & Wolf to the criticism that the model predicts slow regular saccades where fast regular saccades were actually obtained in the corresponding experiment. The direct inputs from the visual (VIS) module into the decision (DEC) and COM-modules allow short reaction times in cases where the ATT-module is already activated or (in the impulse version) when the two inputs alone are strong enough to activate the motor (MOT) module. Of course the model (in either version) cannot explain the effect of introducing catch trials or any type of learning without being extended. Such an extension should allow the states that have been reached at the end of one trial to influence the chances of transition in the subsequent trials.

Another parallel processing proposal was made by Forman et al. and Van Gisbergen & Minken. They point to the fact that the function of the frontal eye fields must

be more than the inhibition of express saccades. We of course agree, because it is the express and the fast regular populations that are abolished when the superior colliculus is not functioning, whereas slower saccades remain intact. We have not yet considered this possibility explicitly, as will certainly have to be done. Van Gisbergen & Minken mention that silencing the fixation neurons in the superior colliculus allows express saccades. This fact provides no evidence for a direct influence from the ATT-module onto the COM-module, however, and the occurrence of express saccades after the removal of the DEC-module is still explained by the direct connections from the ATT- and COM-modules to the MOT-module. Nevertheless, what remains open is the question of how the slow regular saccades obtained after removal of the superior colliculus find the target without the COM-module. Obviously, spatial information for saccades is available from structures other than the superior colliculus.

R4.2. Spatial selection and decision making. This brings us to the difficult question of the role of the second process, labeled DEC in the three-loop model. We admit that this process is most unclear in its functional identification, as pointed out by Ruhnau & Haase. Their criticism reads as a rather nonspecific one, though. We agree that the saccade system is under much more complicated control than what we could explicitly fit into the simple model. The general feature of the three-loop model in its impulse version together with the possible input from other central brain structures (input *c* at the top of Fig. 13) will, however, take into account that serial and parallel processing play a role in saccade generation and attentive fixation and that the optomotor system is by no means isolated from the rest of the brain. After all, we believe, unlike Ruhnau & Haase, that computer simulation is a very helpful means of testing theoretical concepts. Verbally formulated theories – so often presented in neurosciences – urgently need concrete formulations and simulations to show that they are at all applicable to a solution of a given problem.

Belopolsky, Jüttner & Wolf, Van Gisbergen & Minken, and Wright & Ward raise the question: What makes a stimulus a target for a saccade? Whereas Belopolsky proposes a selection from top, that is, by the *c*-input into the ATT-module, the others assign a spatial component to the DEC-module. Jüttner & Wolf call the DEC-process a "decision to select a stimulus," but they do not say what this really means. How does the system know which stimulus has to be selected? Likewise addressing this question, Van Gisbergen & Minken propose assigning a "selection" aspect to the DEC-operation and raise the problem of the effect of a second target stimulus. We have indeed shown that distracting stimuli inhibit express saccades (Weber & Fischer, submitted). In its present state, the model cannot account for this phenomenon. More concretely, Wright & Ward propose to identify the DEC-module with an indexing operation. This sounds like an attractive extension of the model but it runs into difficulties: The indexing operation would also work for the antisaccade, yet no express saccades are obtained in the antitask. How does the indexing hypothesis cope with the express saccades occurring in the overlap task with spatial stimulus uncertainty in naive subjects? More work is needed to clarify the nature of the second loop, or – to

pose the task in an experimental way – to investigate the nature of the second peak in the SRT (saccadic reaction time) distribution.

R4.3. What is the origin of the bimodality? Proposing a short-term operation (for express saccades) and a long-term one (for fast regular saccades) in the decision module, Jüttner & Wolf argue that the long-term operation includes a selection process that is necessary when saccades must be made to targets embedded in a structured background, or to texture-defined targets. The corresponding finding (absence of express saccades) must be considered in detail, however: If a saccade target is presented in a structured background, the structure being visible all the time, express saccades are readily obtained. If the structure is generated together with the target, express saccades are absent. The reason is that the structure acts as distractor which prevents the generation of express saccades (Weber & Fischer, submitted). Jüttner & Wolf's notion of two operations would, furthermore, fail to explain the bimodality in experiments where only one target is used and a selection is not necessary.

Ruhnau & Haase pick up the idea of Frost and Pöppel (1976), who suggest a connection between neural oscillations and the execution of saccades: If one burst of impulses fails to trigger a reaction, the next burst in the oscillation will do. This account looks attractive at first, but it too has shortcomings: Why do we not see corresponding bimodalities with the same peak separation in manual reaction times? Why do the slow regular saccades scatter much more in their reaction time as compared with the express saccades? The oscillations would have to change their characteristics with practice or a further mechanism must be postulated, such as a shift of a temporal window. We agree, however, that the three-loop model also needs extension and modification to explain the intertrial effects and the effect of training. This may be achieved using the three-loop model in its impulse version by changing the parameters, for example, the coupling constants and the synaptic delay times. Nevertheless, the notion of neural oscillations opens new perspectives for future work.

Sommer et al. and Van Gisbergen & Minken both mention the burst-pause-burst neurons in the superior colliculus as a possible source for the bimodality. In response to this proposal we have looked at the simulated impulse activity of the COM-module using a gap of 300 msec and an appropriate set of parameters. Usually the bimodality is generated by the model because on some trials the ATT- and the DEC-activities are strong enough to allow the immediate triggering of a saccade in response to target onset, whereas on other trials the activity is still too low. However, on some other trials the COM-module activity rises slowly within the gap period, before the target onset produces a burst. This first burst may be strong enough to elicit a saccade, which is of the express type (lower part of Fig. R3). If the first burst fails to trigger a saccade, it is followed by a second burst (after the DEC-delay) eliciting a fast regular saccade (upper part of Fig. R3). Note that in the impulse version of the three-loop model randomness is introduced by the randomness of the impulse trains and by the resulting randomness in the strength of the activity in the different modules.

It must be noted, though, that the superior colliculus

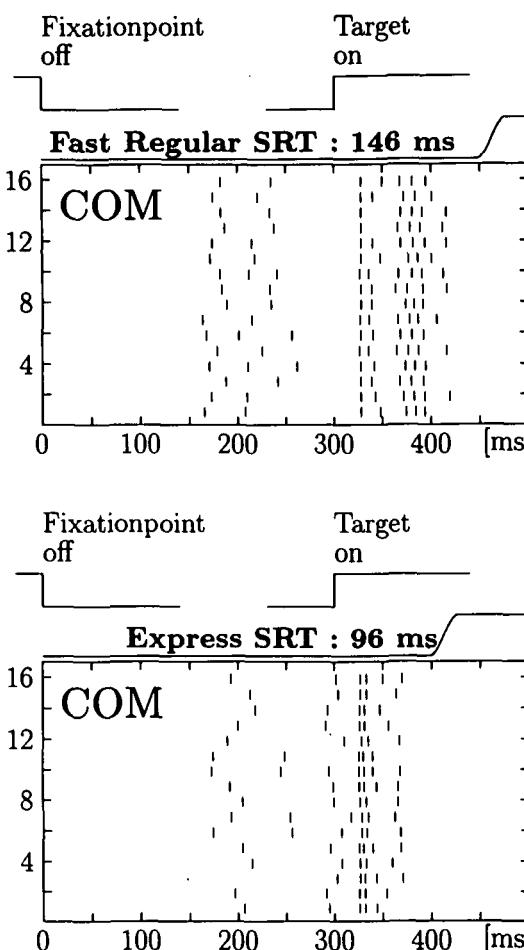


Figure R3. Results from a computer simulation of the impulse version of the three-loop model. The two panels consider 2 runs (selected from a total number of 100 runs) performed with an identical set of parameters and a gap duration of 300 msec. The activities of the 16 neural elements constituting the COM-module are shown for a time interval of 500 msec following fixation point offset. The upper panel illustrates the case of a fast regular saccade, the lower panel that of an express saccade as described in the text.

alone cannot be responsible for the generation of saccade latencies. Rather, and in accordance with the model and experimental findings, it is under control of higher structures that act to prevent or allow the colliculus to generate a saccade.

R5. Attention

Once the various modes of saccadic reaction time are established, the question arises concerning the conditions under which they occur. The introduction of a gap between fixation point offset and target onset is not a necessary condition, because in overlap trials express saccades and bimodality or even trimodality can also be obtained.

In the target article we have proposed the disengagement of visual attention as one of two prerequisites that favor express saccades, the other having to do with decision making. Many commentators have addressed the question of the role of attention in the generation of saccades in general and of express saccades in particular.

Some have considered the possibility that general attention facilitates the reduction of saccadic latency and may eventually lead to express saccades. Others put into discussion the attentional concept of disengagement/move/engagement (DmE) in general, while still others ask the specific question of engagement: When does it take place in relation to the saccade; or the question: disengagement: of what? Another group of commentators, while accepting the two-state (DmE) concept of attention, were concerned with the neural control pathways involved in the engagement or disengagement.

R5.1. Attention: General or specific? Several commentators have suggested that neither the gap effect nor the occurrence of express saccades has to do with visual attention; or that, if anything, it may be some kind of general attention that controls these aspects of saccadic latency. **Bachmann** mentions global *facilitation*, **Findlay** as well as **Reuter-Lorenz & Hughes** speak of a general state of *alertness* or *readiness*, and **Forman et al.** call it *arousal*. We have attributed the first preparatory step of a visually guided saccade to attention, because the instruction "pay attention to . . ." changes the reaction times so drastically. We have furthermore specified attention as visual, because we have so far investigated the effects in the context of visually guided saccades, not saccades triggered through other modalities.

This leaves it open whether or not other sensory modalities have different effects and whether or not nonvisual stimuli can elicit express saccades. We have shown that a tone can trigger the preparation process (which we call the disengagement), but this does not necessarily mean that one deals with a general attentional effect, because the tone may be used to disengage visual attention. As far as we know, there are no reports that show that a tone can be used to elicit an express saccade without a visual target. **Bracewell** discusses this possibility and points to the fact that the superior colliculus contains cells that respond to both visual and auditory stimuli.

We agree that *warning* signals of any kind can cause the above-mentioned general effects which then lead to a reduction of reaction times; these effects are relatively small and would not lead to bimodal distributions but to a shift of the reaction times. Furthermore, if it was a general and nonspecific effect that led to the gap effect and to express saccades, one would not understand the absence of anti-express saccades, with the presence of a gap effect for antisaccades. The suppression of express saccades by distractors would also call for alternative accounts, as mentioned correctly by **Findlay**. Finally, why do we see no express saccades when the targets come close to the fovea? General altering to any other general attentional effects would work for saccades of any size.

We agree that we need more experimental data and a parallel measure of attention effects per se in relation to latency reduction and the occurrence of express saccades.

R5.2. The disengage/move/engage concept (DmE). Here we have two extreme commentaries: **Belopolsky** questions whether the attentional system has such a dual structure. **Nakayama & Mackeben**, working on the attentional system without eye movements, believe firmly in the DmE concept originally proposed by **Posner et al. (1984)**. Most authors accept the DmE structure of atten-

tion, because the experimental data are most consistently described by this concept. The basic experiment by **Mayfrank et al. (1986)** with long reaction times for the attended target location was taken as one more piece of evidence in favor of this notion. Not one of the commentators has addressed the question of attentional shift, or the "move" part. Could it be that there is no such mechanism? It may be that the disengagement from one spatial location and the engagement at another location does not involve any movement.

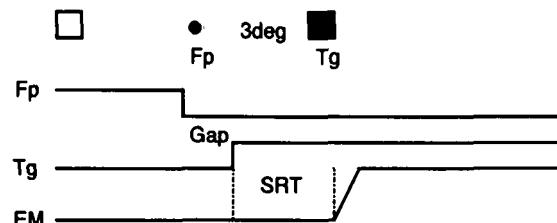
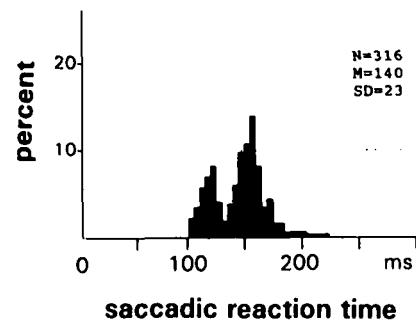
R5.3. Engagement: When? This question was posed directly by **Deubel & Schneider** and by **Henderson**. Whereas Deubel & Schneider in general believe in the DmE concept, Henderson as well as **Bachmann** and **Crawford** argue that attention should be engaged to the new target before the saccade begins, a notion also held by **Henderson** and by **Fischer & Rayner**. Even stronger, **Cavegn** and **Inhoff** suggest the antithesis: Engagement of attention – not disengagement – leads to express saccades.

In response to these commentaries we present in Figure R4 the data of an experiment designed to begin to resolve this problem: A first target for the saccade was extinguished at the beginning of the first saccade, which therefore landed at no target. After a temporal gap, a second target was presented at a different position, which required a second saccade (double target task). The lower part of Figure R4 shows that a gap of only 60 msec duration was sufficient to give a maximum number of express saccades, whereas in the normal single target task the optimal gap duration for a maximum number of express saccades was 200 msec. The upper part of Figure R4 shows the SRT distribution for a gap of 60 msec introduced after fixation point offset (normal gap task). Only a small but clear express peak is obtained. The interpretation of this result could be that after the first saccade the system was still disengaged, but a new decision was necessary, so the minimal gap was correspondingly shorter. If the first target remained visible for only 50 msec, the following second saccade was delayed by about 30 msec (not shown). This would imply that the engagement occurred neither before nor right after the saccade.

After all, however, there must be a time or a condition in which the attentional system goes back into the state of engagement. Having in mind the dead zone for express saccades, we tested the possibility that the engagement takes place when a saccade brings the target close enough or right into the fovea. If this was true one would expect to see small corrective saccades after long intersaccadic intervals, but large corrective saccades after very short (down to zero!) intersaccadic intervals.

The analysis of the data yielded the following results (Fischer et al., submitted): Anticipatory saccades made in the wrong direction and some of the anticipatory saccades made in the direction of the target could be corrected by express saccades. These corrective express saccades occurred about 100 msec *after the onset of the target* (not 100 msec after the end of the anticipatory saccade). This implies that the intersaccadic interval between the primary and corrective saccade can be extremely short. Visually guided saccades (express or regular) that failed to reach the target at once were later corrected following the rule: The smaller the error, the longer the correction

single target/single gap task gap 60ms, right



double target/double gap task second gap 60ms, right/right

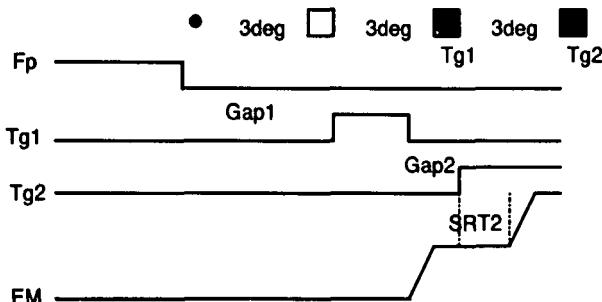
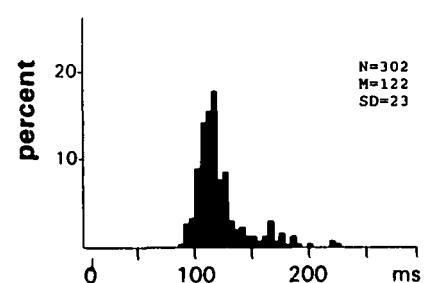


Figure R4. Distributions of saccadic reaction times (left) and schematic representations of the experimental conditions (right) in the single target/single gap task (upper part) and the double target/double gap task (lower part). Data pooled from 4 trained subjects. Single target/single gap task: Target location was randomized between 3° left/right, the gap duration was 60 msec. Only right target trials are shown. Double target/double gap task: The duration of the first gap was 200 msec, the location of the first target was randomized between 3° left/right. The offset of the first target was triggered by the beginning of the saccade. After a gap of 60 msec the second target could appear 3° left or right from the location of the first target. The distribution shows reaction times of second saccades from trials where the first target appeared at the right and the second target appeared 3° farther to the right.

time. We conclude that the disengaged state is preserved after a saccade. A new engagement occurs as soon as the saccade has brought the target into the dead zone.

R5.4. Disengagement: Of what? Some commentators agree that a disengagement is necessary to prepare a saccade, but they do not believe in a disengagement of attention. Breitmeyer, Klein & Kingstone, and Reuter-Lorenz & Hughes propose a disengagement of voluntary fixation, while Tam calls it a disengagement of the ocular system. According to our view, the state of fixation appears as a state of attentional engagement to a foveal stimulus. Therefore, in our view, disengagement of fixation is the same as disengagement of attention to a foveal stimulus. We agree that the fixation point is most effective in attracting attention and its offset is therefore most effective in eliciting the disengagement and the subsequent events that lead to the gap effect and to express

saccades. Not only do we use the fovea for this purpose throughout our lives but the fovea is also the most sensitive part of the visual system. Hence we do not see too much of a disagreement between the notion of disengagement of attention versus disengagement of fixation.

Fischer & Rayner and Henderson consider more natural and complex viewing conditions where one must assume that attention after disengagement from the fixation point is reengaged to the next target. The detailed studies referred to by Henderson and Fischer & Rayner using the elegant technique of moving windows are indeed very suggestive in favor of attention allocation preceding the saccade. We agree that a reengagement to the target can occur before the saccade, but at the cost of an additional time to disengage again with no other preparations necessary for the next saccade. The sequence of attentional events just after the end of a saccade could be "engage, disengage from fovea, engage to next target,

disengage from target, move the eye." Going through the disengagement again may seem useless, but it may nevertheless be a necessary step to enable the saccade. The problem with the engagement preceding the saccade is the express saccade itself: When the subject does not know when and where the next target appears, how can attention be allocated to the new target within 100 msec? One way out could be the assumption of a more complex saccade generating system that is used in complex viewing conditions and in particular when cognition is involved. At this point, however, we would recommend the more parsimonious hypothesis outlined above.

Fischer & Rayner ask why express saccades do not occur often during reading. The reason may be that the dead zone is always in operation in natural viewing conditions and in particular in reading or reading-like situations, because any saccade brings a new target into or close to the fovea, thereby initiating almost reflexlike the engagement.

R5.5. Pathways. In the target article we considered the parietal cortex the main cortical structure in attentional processes, in particular, in the disengagement. We agree that other structures and pathways may also control the saccadic system. Specifically, **Jackson & Lees** point to the role of the basal ganglia. Unfortunately, the Jackson & Houghton (1992) paper is not yet available, but from the commentary it sounds reasonable that there may be a more general system that prevents hyper-reflexive orienting and suppresses distracting stimuli. It will be very interesting to find out why some subjects make spontaneous and almost exclusively express saccades in overlap trials (Fig. 2). Using drugs with these subjects may be one way of finding it out.

Robinson & Cowie consider the role of the pulvinar in engaging attention; they believe that the disengagement is mediated by the parietal cortex. It is certainly very important to study the foveal representations in the parietal cortex and in the pulvinar to further support this view.

R6. Development and dyslexia

Investigating babies, **Atkinson & Hood** failed to see express saccades or bimodal distributions, but their methods (video frames with a 40 msec temporal resolution) may have missed both phenomena if they were present. **Forman et al.**, referring to unpublished work of Johnson, report that the frequency of express saccades decreased from week 6 to month 6. Our own data were collected from children of age 9 to 10 years and we also have a small group of children in the second grade. Hence little can be said about the development of the express mode and any other pathway possibly controlling the reflexlike saccades. As pointed out above, we also believe that the frontal eye fields, as mentioned by Forman et al., contribute more to the generation of "sophisticated" saccades than just to an inhibition of the express mode.

Considering dyslexic subjects we have taken the position that a defect in saccade control – not a defect of the oculomotor system as such – may lead to both difficulties in reading and abnormal latency distributions. We never argued that erratic eye movements cause dyslexia. When **Fischer & Rayner** claim that most – perhaps not all –

dyslexics do not show "erratic eye movement patterns" they should have specified whether latency and size of saccades in noncognitive tasks were included in the analysis of these "patterns." The results of Fischer and Weber (1990) strongly suggest that the timing of visually guided saccades differs from that of normal reading control in children of the same age, as does the size of their saccades (Biscaldi & Fischer 1993). Fischer & Rayner do not see a functional significance for express saccades. A close look at our notion as presented in the target article shows that the express mechanism acts in a reflexlike manner as a final step in the generation of any saccade: It is the cycle of engagement/disengagement/decision making/computation that takes the time of a normal fixation duration. During normal vision, where there is no "target-onset trigger" to measure reaction times, there are no express saccades. Interpreting this concept the way it was presented erases some of the controversies in the context of dyslexia and eye movements.

R7. Conclusions

This exchange has shown that there is convergence and divergence in the field of visually guided saccade generation and its control by attention. The convergence is toward the notion that saccades, after extremely short latencies in the order of 100 msec are visually guided. Under certain conditions their preparation may be facilitated by subjects' ability to anticipate or predict the time or the location of the target. However, these optomotor reactions can also be obtained when there is no possibility of prediction and the preparatory steps are initiated and completed through internal processes. Converging also is the evidence for up to three modes of saccadic reaction times – with the qualification that one mode or the other may not always show up as a separable peak in the distribution or may not be produced by some subjects at all. The express saccade seems to be generally accepted as a real phenomenon. The divergence comes with the question of how the different modes – and particularly the express saccades – are controlled. Although the evidence is in favor of a specific attentional influence on the occurrence of the different modes and it is agreed that the attentional system acts through at least two opposite states – engaged and disengaged – its exact linkage to fixation and saccades is still under discussion. One aspect of this problem may be related to the spatial organization of the decision process. The target article did not consider explicitly the computation of spatial parameters nor does the three-loop model. These aspects are to be addressed by more experimental and theoretical work in the future.

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Letters *a* and *r* appearing before authors' initials refer to target article and response respectively.

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