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Express saccades and visual attention

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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

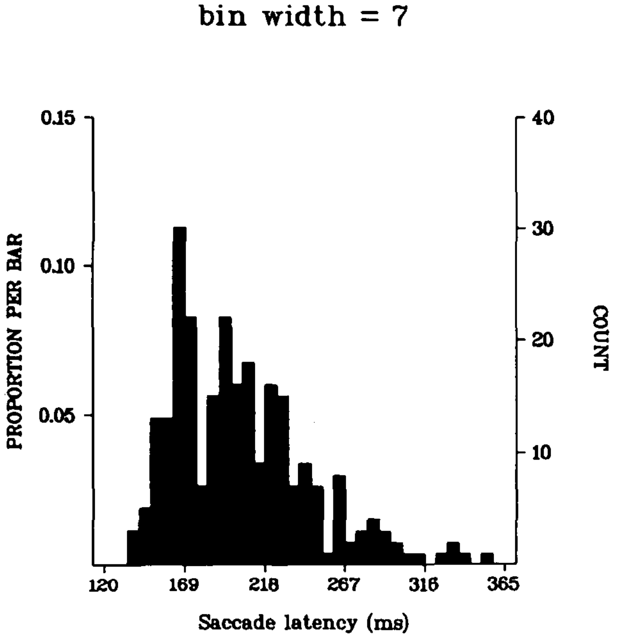

Figure 1 (Ruhnau & Haase). Example of periodic multimodal distribution in visually elicited saccadic reaction times with the overlap paradigm. Modes are estimated as being around 163.75, 198.66, and 220.99 msec respectively. N = 266, median = 198 msec, Subject 4, 15th session. Eccentricities used were 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 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.

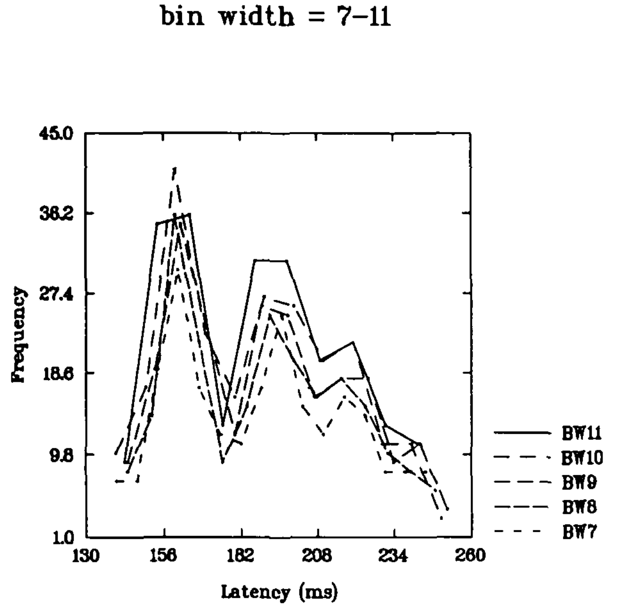

Figure 2 (Ruhnau & Haase). Periodic multimodal distributions of saccadic reaction times are not contingent upon the bin widths used to construct the histogram. Peaks remain constant regardless of the different bin widths. (Data are the same as in Fig. 1.)

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

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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

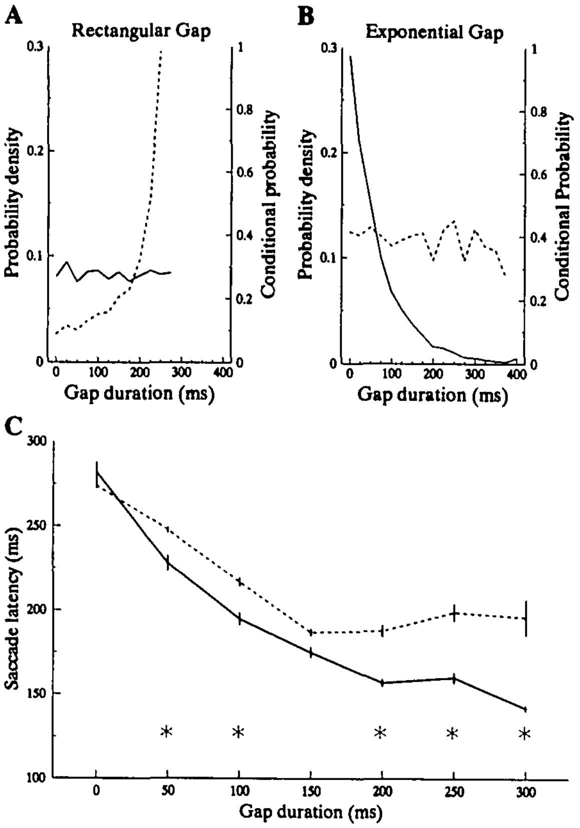

Figure 1 (Schall & Hanes). Saccadic performance with aging and nonaging gap durations. Gap delay was varied in two ways. A: Probability density (solid line) and conditional probability (dashed line) for gap delays sampled from a rectangular distribution ranging from 0–300 msec. With a constant probability 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., Baumeister & 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?

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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).

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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