Frontal eye fields: Inhibition through competition

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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 disengagement 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 fronto-occipital 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 disengagement 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 SC's subject 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

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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 other schools 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. 1990; Jenner & Wolf 1992; Karmy-Jones & Hallett 1987). In 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)