Integration of competing saccade programs

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Abstract
Reflexive responses are often in direct competition with voluntary control. We test two opposing explanations for how this competition is resolved with respect to eye movements. One states that the quickest activation wins. The other states that the strongest activation wins. We show that an eye movement is executed according to the strongest activation, with the competition being staged at a common subcortical site.

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At any given moment, there are numerous behaviors that one could perform. Some behaviors are signaled by the environment. For instance, braking a car is signaled by a traffic light changing from green to yellow. Other behaviors are guided by internal states, and they often compete with those signaled by the environment. For instance, a hurried driver might accelerate rather than brake a car to pass through a yellow light before it turns red. These competitions between externally and internally triggered behaviors play out time and again in one’s everyday life. This is especially true for eye movements, made on average four times every second. Only one location can be fixated at any given moment, so one must choose to look at some items to the exclusion of others. The subset of items that are fixated can be characterized as “winners” of a competition for control of the eye movement system.

The goal of the present study is to discover how and where this competition is resolved. Until recently, the assumption has been that eye movements elicited by the external environment (often called reflexive saccades) and eye movements generated internally (often called voluntary saccades) are programmed independently but at the same time [1,8]. The eye movement program that is completed first wins the competition, and the corresponding eye movement is generated. The physiology of the eye movement system is certainly consistent with this account. There are two separate pathways that can be activated at the same time; a subcortical pathway associated with reflexive eye movements runs through the superior colliculus (SC), and a cortical pathway associated with voluntary eye movements runs through the frontal eye fields (FEF) [7]. Both pathways converge on subcortical eye movement control structures (see Fig. 1A).

An alternative to this “race model” account has recently been proposed [4,9]. Rather than a race between independent eye movement systems, the competition between reflexive and voluntary saccades is fought head-to-head within the SC. The winner gains control of eye movements. The physiology also supports this conflict model, as there are strong connections between the FEF and the SC [5].

As the physiology supports either account, a direct behavioral test of these two proposals is required. It is well established that turning off a fixated light influences activity within the SC and causes eye movements to be made more rapidly [2]. According to the race model, only the reflexive eye movement program passes through the SC. Thus, only reflexive eye movements should benefit when a fixated light is extinguished. In contrast, according to the conflict model, both reflexive and voluntary eye movement programs converge and compete directly in the SC. Thus, extinguishing the fixated light would affect both reflexive and voluntary saccades equally.

Past research has tried to assess the two models by examining the effect of fixation offset (FO) on voluntary saccades directed away from targets (antisaccades). Using
We instead turned to the oculomotor capture phenomenon [8] as a promising avenue for understanding saccade competition in a more natural task than the antisaccade task. The display consisted of six orange circles surrounding a central fixation (see Fig. 1B). After 1000 ms, all the circles except one changed to red. The task was to saccade to the uniquely colored item (the singleton)\(^1\). Concurrent with the color change, an additional red circle appeared in the display on half the trials. This sudden onset can trigger ("capture") reflexive saccades, often outside the observer’s awareness [8], thus eliciting a competition between a voluntary saccade to the target singleton and a reflexive saccade to the sudden onset. On half the trials, the fixation was removed as the target was revealed. The absence of a temporal gap between fixation offset and target onset minimizes the potential for warning effects, which may not be specific to the SC, to influence the results. For each trial, we classified the first saccade as (1) voluntary if it landed within a 30° wedge centered around the target; (2) reflexive if it landed within a 30° wedge around the distractor onset, or (3) an error if it went elsewhere.

\(^1\) Half the subjects also performed a discrimination task on an item inside the target singleton. The other half just fixated the target as quickly as possible. Results from the two versions were similar, except that saccades tended to be faster and less precise in the latter version. The results are combined in further analyses.

The reflexive eye movement often won out over the voluntary one, resulting in a saccade to the irrelevant onset on 22% of the trials. To measure the effect of fixation offset (FO) on the competition between reflexive and voluntary eye movement programs, we examined the proportion of saccades that were captured by the abrupt onset distractor as a function of FO once the effect of FO on reaction time (RT) had been accounted for using an RT binning procedure\(^2\). The analysis revealed that the proportion of reflexive saccades

\(^2\) Faster saccades are associated with an increase in capture [4,8], independent from any specific effect of the fixation stimulus on competition for control. To isolate the effect of fixation offset on saccade destination from an effect of overall reduced RT, we removed RT differences between fixation-on and fixation-off conditions using a quartile splitting procedure. For each subject, all onset trials where the fixation remained on were divided into quartiles, regardless of saccade destination. After establishing these quartiles for each subject, the fixation-off trials were divided into these four predetermined bins. Because fixation-off trials tended to be faster than the fixation-on trials, there were more fixation-off trials in the fastest RT bin (38.8% of all the fixation-off trials), with a decreasing proportion in the slower bins (to 16.8% in the slowest bin). This procedure approximately matches RT for fixation-on and fixation-off trials within each bin.
increased in faster RT bins, $F(3,81)=32.76$, $p<0.01$, but neither the effect of FO, $F(1,27)<1$, nor the interaction between FO and RT bin, $F(1,27)<1$, approached significance. This indicates that fixation offset does not influence the proportion of saccades directed to the onset (see Fig. 1C), suggesting that the competition between different potential saccade targets is resolved in a common site.

Contrary to the predictions of the race model, removing the fixation did not tip the odds in favor of the reflexive program. This was not due to the fixation offset failing to produce a significant behavioral effect. An analysis of variance (ANOVA) on saccadic RT revealed a significant FO effect of 28 ms, $F(1,27)=23.34$, $p<0.01$, demonstrating its classic facilitative effect on saccadic RT [2]. There was no interaction between FO and the type of saccade [$F(2,54)=2.04$], indicating that the significant effect of FO was present for both reflexive saccades and for voluntary saccades. Among voluntary saccades, the FO effect was not decreased by the occurrence of the sudden onset, suggesting that competition between saccade goals does not influence the magnitude of the FO effect (see Fig. 1D).

The race model predicted that reflexive saccades would be selectively facilitated by removing fixation resulting in an increase in capture in this condition. Instead, we observed that saccades are just as likely to be captured by the onset when fixation is on than when it is off (Fig. 1C), supporting the existence of a common saccade map that is influenced by the inhibitory effects of the fixated stimulus. This direct behavioral test converges with other behavioral evidence [4] confirming the predictions of theoretical and computational models that place the competition between voluntary and reflexive saccades within the SC [6,9]3. Although our results suggest that voluntary and reflexive saccade programs in our experiment converged on a common map, we are not claiming that an extracollicular route for eye movement control does not exist. In fact, an alternative route must exist, given that, in primates, saccadic eye movements are observed even when the SC is ablated [7]. We have, however, found evidence that competition between sensory targets takes place on a common collicular map. The important implication of this finding is that voluntary control can compete with automatic processes subcortically. It remains open whether this principle is specific to the eye movement system or if it also applies to other motor systems.

References


3 In general, RTs were slower than some of those reported previously [4,8], perhaps because the orange target was more similar to the red distractors in our experiments than the gray/red combination used previously. The fact that the RT differences between the two versions of our experiment (see footnote 1) did not influence the overall results suggests that this is not a critical factor.