A model of curved saccade trajectories: Spike rate adaptation in the brainstem as the cause of deviation away

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ABSTRACT

The trajectory of saccades to a target is often affected whenever there is a distractor in the visual field. Distractors can cause a saccade to deviate towards their location or away from it. The oculomotor mechanisms that produce deviation towards distractors have been thoroughly explored in behavioral, neurophysiological and computational studies. The mechanisms underlying deviation away, on the other hand, remain unclear. Behavioral findings suggest a mechanism of spatially focused, top-down inhibition in a saccade map, and deviation away has become a tool to investigate such inhibition. However, this inhibition hypothesis has little neuroanatomical or neurophysiological support, and recent findings go against it. Here, we propose that deviation away results from an unbalanced saccade drive from the brainstem, caused by spike rate adaptation in brainstem long-lead burst neurons. Adaptation to stimulation in the direction of the distractor results in an unbalanced drive away from it. An existing model of the saccade system was extended with this theory. The resulting model simulates a wide range of findings on saccade trajectories, including findings that have classically been interpreted to support inhibition views. Furthermore, the model replicated the effect of saccade latency on deviation away, but predicted this effect would be absent with large (400 ms) distractor-target onset asynchrony. This prediction was confirmed in an experiment, which demonstrates that the theory both explains classical findings on saccade trajectories and predicts new findings.

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1. Introduction

Because of the limited resolution of the retina outside of the fovea, visual perception relies on a stream of rapid eye movements to fixate locations of interest. These eye movements (saccades) are intended to bring the fovea from one location to the next, yet almost never follow a straight line; they are usually curved. Some of this curvature is idiosyncratic to the observer, and some of it seems to be unsystematic noise (Optican and Robinson, 1980). However, curvature is also partly influenced by cognitive factors. In particular, saccade deviation from the optimal path is known to be affected by the presence of non-target elements in the visual scene, so-called distractors. (Van der Stigchel, 2010; Van der Stigchel et al., 2006).

1.1. Saccade deviation, population coding and inhibition

To study curved saccades, a distractor paradigm (Sheliga et al., 1994; Doyle and Walker, 2001) is often used: observers make a speeded saccade to a predefined target as soon as it appears, and

a distractor (or more rarely, several) appears in the scene simultaneously with the target. When the distractor appears close to the target (Walker et al., 1997, within 20°), saccades will tend to deviate[1] towards the distractor. This may result in so-called 'global-effect' saccades, where the gaze lands in the middle between target and distractor. (Coren and Hoenig, 1972; Van der Stigchel and Nijboer, 2011).

In explaining these deviations, it is commonly assumed that the oculomotor system utilizes a saccade map where spatially organized activity is evoked by stimuli. To determine the saccade goal, stimuli compete for selection by means of lateral inhibition, where the losing location is suppressed and the remaining target activity is translated into a motor command. The oculomotor pathway indeed contains multiple structures that could implement such a visuomotor map, and of particular interest is the superior colliculus (SC). The SC is a layered midbrain structure, and its intermediate

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[1] Different studies on saccadic behavior have used variable measures and terminology to characterize saccade trajectories. Throughout this article, 'deviation' is used to indicate the angle between the initial direction of the saccade and a straight line from the starting point to the target. 'Curvature' is used whenever we want to emphasize the trajectory of the saccade, which usually displays a decrease in deviation as the saccade curves back towards the target mid-flight.

layers (a) implement a retinotopic map in which activity in visuo-motor neurons corresponds to the current visual input (Robinson, 1972; Marino et al., 2008); (b) are known to trigger saccades in response to sufficient stimulation, directed to the location of receptive visual field at the stimulated location (Robinson, 1972; Gandhi and Katnani, 2011); (c) integrate dense projections from striate, extrastriate and frontal areas that all implement retinotopic representations (Munoz and Schall, 2004, chap. 3; Schlag-Rey et al., 1992; Sommer and Wurtz, 2000); and (d) constitute the primary source of input for the brainstem burst neurons that drive the eye muscles (Sparks, 2002; Scudder et al., 2002). The central role of the SC in saccade generation is illustrated in Fig. 1a.

Deviation towards and the global effect are well explained in terms of population coding in this map (Lee et al., 1988): when distractor activity is not suppressed completely before the saccade, it contributes to the movement which might then deviate to an intermediate location, and land there as well. This explanation is supported by the findings that simultaneous electrical stimulation at two collicular locations results in averaging saccades (Katnani et al., 2012; Robinson, 1972), and that SC recordings during visually evoked averaging saccades are marked by distributed peaks at short latencies, and activity at an intermediate location for longer latency-saccades (Edelman and Keller, 1998; Glimcher and Sparks, 1993). Various successful computational explorations of this theory have been developed (Arai et al., 1994; Trappenberg et al., 2001; Meeter et al., 2010).

In humans, there is also a set of conditions that make saccades consistently deviate away from distractors. The currently dominant interpretation of deviation away from distractors relies on extending the population coding view with spatially focused distractor inhibition in the saccade map. Excessive suppression of the distractor location would 'deflect' the motor command to the opposite direction, and cause the saccade to deviate away (Godijn and Theeuwes, 2002; McSorley et al., 2004; Van der Stigchel, 2010; Walker and McSorley, 2008). Evidence for such spatial inhibition is mostly behavioral, and can be summarized as these effects:

- The *latency effect* refers to an often found correlation between deviation away and saccadic latency (McSorley et al., 2006; Mulckhuyse et al., 2009; Ludwig and Gilchrist, 2003), with more

deviation away occurring for long-latency saccades. This is then interpreted as attentional inhibition building up over time, mostly affecting saccades with long latencies.
- The distractor *similarity effect* has been reported (Ludwig and Gilchrist, 2003; Mulckhuyse et al., 2009), a finding that distractors similar to the target cause more deviation towards at short latencies than very dissimilar stimuli, yet at longer latencies similar distractors evoke more deviation away. The interpretation is that similar distractors require more and stronger inhibition, but that this inhibition is later than with dissimilar – more easily dissociable – distractors.
- Distractor location is known to affect deviation, with greater angular target-distractor distances, or smaller fixation-distractor distances inducing more deviation away (McSorley et al., 2009a; Van der Stigchel et al., 2007). This *position effect* is often explained through the locus of inhibition in the map: in both cases, inhibition has a larger spatial effect on the initial trajectory of the saccade, resulting in greater deviation away.
- Apart from these exogenous manipulations, several *endogenous effects* have been reported: merely expecting a stimulus to appear, or maintaining a location in working memory can result in deviation away without physical distractors (Godijn and Theeuwes, 2004; Van der Stigchel and Theeuwes, 2006; Theeuwes et al., 2009). Explanations of such findings rely on tenets that endogenous processes like attention and working memory will automatically activate representations in the (oculo) motor system (Rizzolatti et al., 1987; Sheliga et al., 1994; Postle, 2006), which in turn yields similar suppression effects.

From such findings it is often concluded that saccade deviation can be used to probe inhibition in the oculomotor system (McSorley et al., 2006; Van der Stigchel et al., 2006; Theeuwes et al., 2009): the amount and direction of saccadic deviation is taken as a measure of inhibition produced by attention mechanisms. However, strong neuroanatomical or neurophysiological evidence for this view is lacking, and to our knowledge no computational model has thus far successfully incorporated this theory, despite its apparent simplicity. Top-down inhibition has therefore functioned more or less as a deus ex machina, called upon to explain deviation away when it occurs, yet remaining unexplained itself.
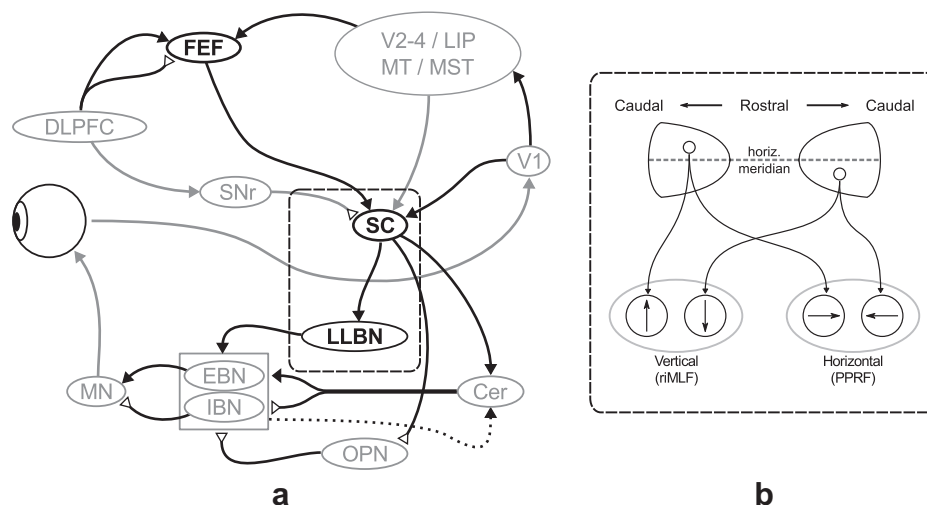

Fig. 1. (a) Schematic representation of the oculomotor system. Markers indicate whether connections are excitatory (solid triangle: ▼) or inhibitory (inverted open triangle: △). Only structures and connections in black are explicitly represented in our model, those in gray are not. See the text for the abbreviations and more detail. (b) Detailed excerpt of the projection from SC to LLBN in (a), schematically outlining how retinotopically organized SC-output is decomposed into the vectorial representation maintained in the brainstem. For two representative neurons in the SC, it is shown how their output is decomposed into directional components for vertical and horizontal eye movements. For example, the top left SC-neuron represents a location in the upper right visual field. Activity at this location projects to brainstem neurons that code for upwards and for rightwards movement. The relative strength of these connections determines the balance between these two components, so that together they produce a movement vector in the appropriate direction.