



## Research paper

# Corrections in saccade endpoints scale to the amplitude of target displacements in a double-step paradigm



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## HIGHLIGHTS

- Primary saccade endpoints adapted to target displacements.
- Magnitude of endpoint adaptations scaled to amplitude of target displacements.
- Online corrections modify primary saccade trajectories.

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## ABSTRACT

It is widely held that discrete goal-directed eye movements (saccades) are ballistic in nature because their durations are too short to allow for sensory-based online correction. Recent studies, however, have provided evidence that saccadic endpoints can be mediated via online corrections. Specifically, it has been reported that saccade trajectories adapt to the eccentricity of an unexpectedly perturbed target location (i.e., target 'jump' paradigm). If saccades are subject to online correction mechanisms, then the magnitude of such changes should scale to the amplitude of the target jump. To test this hypothesis, saccadic endpoints for trials on which the target jumped one of three amplitudes (Small: 2.5°, Medium: 5.0°, and Large: 7.5°; i.e., Jump trials) immediately after saccade onset were compared with the endpoints of trials in which the target location did not change (i.e., Reference trials). Results showed that primary saccade endpoints for Jump trials were longer than for Reference trials. Importantly, the magnitude of this increase in endpoint scaled with the amplitude of the target jump. Thus, these results support emerging and coalescent evidence that saccade trajectories are subject to online corrections.

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## 1. Introduction

The successful and accurate completion of goal-directed limb movements in humans seems to rely on two distinct but inter-related processes [1]. The first process consists of a feedforward movement plan developed prior to movement initiation (i.e., offline). The purpose of this process is to plan the initial ballistic phase of a response. The second process involves the use of response-produced sensory feedback and is engaged to adjust (cor-

rect) for errors in the initial movement trajectory as the response unfolds (see [2] for a review).

In contrast to goal-directed reaches, it is typically argued that rapid goal-directed eye movements (i.e., saccades) are ballistic in nature and are executed without online control [3,4]. This argument is based, in part, on the idea that saccade movement times (MTs) are shorter than the time required for visual information to travel through cortical neural networks—a proposed necessary step in making sensory information available for use in feedback-based trajectory corrections. Specifically, it is thought that if information from the retina must travel to the extra-ocular muscles via cortical pathways, the visuomotor delay involved in this feedback loop may be longer than a typical saccadic MT [5]. Thus, a cortical pathway and the resulting visuomotor delay inherent to that pathway should preclude online trajectory amendments.

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Recent work, however, has revealed that online saccade amendments could occur [6,7]. A model of saccadic control proposed by Robinson [8] could provide a starting point for understanding such online corrections. According to Robinson's model, saccadic generation centers in the superior colliculus do not fully preprogram saccade trajectories; rather, these centers generate an initial plan and then rely on input, such as efferent copies of the plan, from sub-cortical structures to detect and correct for trajectory errors during the saccade. If, as Robinson proposed, the superior colliculus can receive additional input to amend ongoing trajectories, it is possible that one source of input is retinal information that travels through a sub-cortical pathway; perhaps a reintro-collicular-pontine pathway [6]. Such a direct sub-cortical route would avoid a time-consuming cortical visuomotor feedback loop, potentially permitting online updating of extra-ocular muscle activity via visual information.

Behavioral evidence supporting the role of online saccade corrections has emerged from several studies [7,9–13]. Of particular relevance to the present study, Gaveau et al. [6] asked participants to execute saccades of varying amplitudes from left-to-right space in a double-step (i.e., 'target jump') paradigm. During Reference trials, participants fixated an LED at an eccentricity  $10^\circ$  to the left of midline and executed a saccade to a target that was  $20^\circ$  to the right of midline. Jump trials used the same fixation and initial target locations, but at saccade onset (velocity  $> 30^\circ/\text{s}$ ) the initial target was extinguished and another target was presented at an eccentricity  $7.5^\circ$  to the right or left of the initial target. Thus, participants' initially planned saccadic amplitude was now incongruent with the final required amplitude on Jump trials. Results showed that – even though participants were not consciously aware of the target displacement or 'jump' (likely due to saccadic suppression [14]) – final saccade amplitudes were amended in the direction of the new target. Thus, Gaveau et al. [6] concluded that saccadic trajectories were mediated via online corrections, perhaps through a retino-collicular-pontine circuit. They suggested that this circuit may operate in as little 50 ms, though some estimates are as low as 30 ms [7].

Although Gaveau et al.'s [6] results are insightful and provide empirical support for the online control of saccades, there may be two limitations to their design. First, Gaveau et al. examined only one jump amplitude. Hence, it is unclear if the observed change in amplitude was a generic response to a change in the environment, or reflected a corrective process that was sensitive to the amount of trajectory amendment needed. Second, Jump trials occurred predictably on every 10th trial. Due to the consistent order and amplitude of target jump presentation, it is possible that mechanisms other than online corrections – such as offline motor plan adaptation – could have accounted for the shift in primary saccade amplitudes on Jump trials. To elucidate, when target jumps of consistent amplitude occur, participants can make offline corrections for discrepancies between the movement endpoint and the target by adapting their movement plan on subsequent trials. Through this offline planning process, saccadic amplitudes that are inaccurate on initial trials are adapted to land on the "new" jumped target location over the course of several trials [15,16]. Thus, the consistent presentation of the target jump could have led to changes in amplitude that are not reflective of online correction; rather, amplitude changes may have reflected offline adaptation to the movement plan.

The present study was designed to further test if saccades are corrected online by determining if the magnitude of a trajectory correction scales in relation to the absolute amplitude of a target jump. To determine if the correction in saccadic endpoint scales to the amplitude of the target jump, Gaveau et al.'s [6] rightward jump protocol was adapted to include three randomly ordered jump amplitudes (Small  $2.5^\circ$ , Medium  $5.0^\circ$ , and Large  $7.5^\circ$ ). The presence (or absence) of online corrections was evaluated by comparing

primary saccade endpoints of Reference trials with endpoints of the three types of Jump trials. We predicted that, if online control mechanisms play a corrective role in saccades, then primary saccade endpoints should be displaced in a manner consistent with the amplitude of the jump; that is, there should be larger shifts in endpoint on Large trials than on Medium and Small trials. Such a finding would indicate that the oculomotor system is sensitive to error in the initial saccadic plan and engages online corrective processes to increase endpoint accuracy. If, however, the jump-reference endpoint differences observed in the Gaveau et al. study were spurious in nature and/or due to the consistent order of target jump presentation employed in that study, then either no change in saccadic endpoints will be observed across the different Jump conditions, or a consistent change in endpoint, that is not scaled to the amplitude of the jump, will be observed.

## 2. Materials and methods

### 2.1. Participants

Twelve participants (5 female; aged 18–26 years) were recruited from the University of Toronto community. Participants were right-handed, reported normal or corrected-to-normal vision, and were naive to the purpose of the experiment. Participants provided written informed consent prior to beginning the study and received monetary compensation (\$10CAD) for their time. Procedures complied with the ethical standards established in the 1964 Declaration of Helsinki and were approved by the Research Ethics Board at the University of Toronto.

### 2.2. Apparatus and stimuli

Participants positioned their heads in the chin rest of an EyeLink 1000 (SR Research, Ottawa, ON) that sampled the spatial position of participants' right eye at 250 Hz. A 110 cm-radius semi-circular black stimulus presentation board was centered 110 cm from participants' cyclopean eye with 3 mm-diameter red LEDs arranged  $2.5^\circ$  of visual angle apart horizontally, in series on the board (see Supplementary online Fig. 1). The LED that was positioned in-line with the participants' cyclopean eye, in the mid-sagittal plane, was defined as  $0^\circ$ . LEDs located to the left and right of the  $0^\circ$  target were defined as negative and positive space, respectively. The presentation of visual events and recording of gaze location was controlled via custom Matlab (The MathWorks, Natick, MA) software.

### 2.3. Tasks and procedure

A 3-point horizontal calibration and validation procedure was completed prior to commencing the experiment, after every 36 trials, and any time the participant took a break. Errors exceeding  $0.5^\circ$  at any single point, or an average error exceeding  $0.25^\circ$ , were rejected and calibration and validation procedures were re-run.

The experiment consisted of 20 blocks of 12 trials each. Participants were allowed to take breaks at the end of any block and were instructed to rest to prevent fatigue. Each block of trials consisted of the random presentation of 8 Distractor trials, 1 Reference trial, and 3 Jump trials (details below). The random presentation was included to conceal the theoretically-relevant Jump and Reference trials and to eliminate any potential learning that might occur with a constant presentation schedule [cf. [6]].

At the beginning of each trial, a fixation LED was illuminated in left (negative) space. After participants fixated on this LED for  $2000 \pm 300$  ms, the fixation LED was extinguished and a target LED was simultaneously illuminated in right (positive) space. Participants were instructed to plan and execute a single rightward

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