# SELECTIVE REWARD AFFECTS THE RATE OF SACCADE ADAPTATION

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Abstract—In this study we tested whether a selective reward could affect the adaptation of saccadic eye movements in monkeys. We induced the adaptation of saccades by displacing the target of a horizontal saccade vertically as the eye moved toward it, thereby creating an apparent vertical dysmetria. The repeated upward target displacement caused the originally horizontal saccade to gradually deviate upward over the course of several hundred trials. We induced this directional adaptation in both right- and leftward saccades in every experiment ($n = 20$). In half of the experiments ($n = 10$), we rewarded monkeys only when they made leftward saccades and in the other half ($n = 10$) only for rightward saccades. The reaction time of saccades in the rewarded direction was shorter and we, like others, interpreted this change as a sign of the reward's preferential effect in that direction. Saccades in the rewarded direction showed more rapid adaptation of their directions than did saccades in the non-rewarded direction, indicating that the selective reward increased the speed of saccade adaptation. The differences in adaptation speed were reflected in changes in saccade metrics, which were usually more noticeable in the deceleration phases of saccades than in their acceleration phases. Because previous studies have shown that the oculomotor cerebellum is involved with saccade deceleration and also participates in saccade adaptation, it is possible that selective reward could influence cerebellar plasticity. © 2017 The Author(s). Published by Elsevier Ltd on behalf of IBRO. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Key words: saccade, adaptation, reward, cerebellum.

## INTRODUCTION

Growth, injury and aging may cause movements to become inaccurate. When inaccuracies occur, the dysmetric movement gradually changes so it lands on target. This improvement in movement accuracy has been called motor adaptation. The characteristics of motor adaptation have been extensively studied for saccadic eye movements, which rapidly shift the direction of gaze from one object of interest to another. Saccades provide an attractive motor system model because dysmetrias can be produced behaviorally by surreptitiously displacing the target as the eye moves toward it, thereby causing the initial saccade to miss the target (McLaughlin, 1967). During many repetitions of this apparent dysmetria, the metrics of the initial saccade, e.g., amplitude, direction or both, gradually change so that the line of sight eventually lands near the displaced target. The subject, either a human or monkey, need not be explicitly encouraged to engage in this motor adaptation. Rather, it occurs automatically when the subject is following the jumping target (Frens and van Opstal, 1994; Hopp and Fuchs, 2004).

However, evidence in humans suggests that adaptation might be susceptible to some forms of motivation. Although saccade adaptation occurs without specific motivation, clinical studies suggest that general motivation does affect the adaptation speed. In patients with Parkinson's disease, where apathy is a major non-motor symptom, saccade adaptation is slower than in age-matched healthy control subjects (MacAskill et al., 2002; Abouaf et al., 2012). Also, motivation in the form of a differential reward can affect saccade characteristics in some non-adaptation tasks. For example, if saccades made to simple target steps in one direction are rewarded more than those in another direction, saccades associated with the larger reward have both shorter reaction times and faster velocities in both monkeys and humans (Takikawa et al., 2004; Hikosaka et al., 2006; Milstein and Dorris, 2007, 2011; Collins, 2012). These studies suggest that the motivation provided by a differential reward can influence saccadic responses. Therefore, we test here whether the specific motivation of a selective reward also has an effect on saccade adaptation. In this study, we examine adaptation in the monkey to provide a potential model for future neurophysiological experiments.

To test the effect of selective motivation on saccade adaptation, we induced adaptation of both right- and leftward saccades simultaneously, but rewarded the monkeys only when they made a saccade either to the left or right. We found that saccades in the rewarded direction adapted faster than did those in the non-rewarded direction. Moreover, the differences in saccade metrics were much more likely to be expressed in their deceleration than acceleration phases. This observation is discussed in the context of the neural circuitry in the oculomotor cerebellum, which has been

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*Abbreviations:* cFN, caudal fastigial nucleus; OMV, oculomotor vermis; SC, superior colliculus.

implicated in saccade adaptation (Catz et al., 2005; Soetedjo and Fuchs, 2006; Catz et al., 2008; Soetedjo et al., 2008b,a; Kojima et al., 2010b).

## EXPERIMENTAL PROCEDURES

### Surgery and training

We measured eye movements in two rhesus monkeys (*Macaca mulatta*, male, 6.0–7.5 kg, monkeys D and A) with the electromagnetic search coil method (Robinson, 1963; Fuchs and Robinson, 1966; Judge et al., 1980). Our previous paper (Kojima et al., 2010b) describes the surgical, recording and training procedures in detail. Briefly, in an aseptic surgery we implanted each monkey with head stabilizing fixtures and an eye coil. After each monkey had recovered from the surgery, it was trained to fixate a small target spot with its eyes in a dimly lit booth, where it sat in a primate chair with its head fixed. We rewarded the monkeys with applesauce for keeping their gaze within $\pm 2°$ windows of the horizontal and vertical positions of the target spot for at least 0.5 s. Once they were trained to fixate the target spot, we trained them to make targeting saccades to a stepping spot that moved on a tangent screen within $\pm 18°$ of straight-ahead. We delivered the applesauce reward ($\sim$0.16 ml per drop, $\sim$200 ml/h) by a pump (masterflex tubing pump, Cole-Parmer, Vernon Hills, USA) every 2 s regardless of the saccade amplitude, direction or timing as long as the monkey made a saccade that landed within the $\pm 2°$ window surrounding the target. The targeting saccade was required to occur within 0.6 s of the target step and the subsequent fixation had to be maintained for 0.3 s ("timed reward").

The visual target for saccades was a red laser spot that was back-projected on a ground glass screen facing the monkey by a pair of X-Y mirrors attached to computer controlled galvanometers. The diameter of the red spot was $\sim$0.4°. It took less than 1 ms for the computer to start the galvanometers, and the target arrived in its new position within 6 ms.

After the monkeys had learned this basic tracking task, we presented the reward only after a saccade in one horizontal direction but not in the other ("scheduled reward"). For these $\sim$2 h daily training sessions, we used a "scheduled reward" for the first hour and a "timed reward" for the second. The rewarded direction was reversed in the next training session. The amount of applesauce earned per hour was the same in both reward conditions ($\sim$200 ml).

### Behavioral paradigms

To induce adaptation, we used a cross-axis adaptation paradigm (Deubel, 1987; Frens and van Opstal, 1994; Noto et al., 1999; Chen-Harris et al., 2008) to gradually change the direction of the saccade from horizontal to slightly upward. After the monkey had fixated the target spot for 600 ms (arrow #1 in Fig. 1A, B-1), 900–1200 ms later, the spot stepped by either 10 or 12° randomly to the right or left (primary target step) (arrow #2 in Fig. 1A, B-2), but always remained within $\pm 18°$ of

straight-ahead. When the subsequent targeting saccade (primary saccade) had decelerated to a vector velocity ($\sqrt{\text{horizontal velocity}^2 + \text{vertical velocity}^2}$) of 20°/s, the target stepped a constant 3° upward from that eye position measured at that point in time so the primary saccade landed $\sim$3° below the displaced target (arrow #3 in Fig. 1A, B-3). The subject then made an upward corrective saccade to acquire the target (arrow #4 in Fig. 1A, B-4). Because the visual error that was created by the intra-saccadic step (ISS) was held constant at 3° (Robinson et al., 2003), the size of the corrective saccade also remained at about 3° during adaptation. Monkeys always made corrective saccades in response to this visual error. Across all 20 experiments, the actual median distances between the displaced target and the primary saccade's end position in the rewarded and non-rewarded directions (2.74 vs. 2.76, respectively, with a 0.50 interquartile range) were not significantly different (Fig. 2A, Wilcoxon rank sum test, $p > 0.05$). Also, the reaction times of the corrective saccade in the rewarded and non-rewarded directions across all experiments were not significantly different (Fig. 2B, Wilcoxon rank sum test, $p > 0.05$) (see *Data analysis* below for calculation of normalization of the reaction time distribution prior to the statistical test).

In contrast to the conventional adaptation paradigm (McLaughlin, 1967) in which the ISS occurs at the onset of the primary saccade, we caused the ISS to occur at the end of the primary saccade (when it had decelerated to a vector velocity of 20°/s) in order to create a constant visual error when the saccade landed (Robinson et al., 2003; Zimmermann and Lappe, 2010; Kojima et al., 2015). This modified paradigm induces adaptation comparable to the conventional McLaughlin paradigm in both humans and monkeys (Robinson et al., 2003; Zimmermann and Lappe, 2010; Kojima et al., 2015). To minimize the effect, if any, of small differences in the timing of the ISS, we turned off the target during the saccade, i.e., when vector saccade velocity first exceeded and subsequently dropped below 20°/s. Eight hundred ms after the corrective saccade, the target returned to its location prior to the ISS (arrow #5 in Fig. 1A, B-5), so the target and eye always started from the horizontal meridian on each trial (arrow #6 in 1A, B-6).

We used a cross-axis adaptation because in preliminary control adaptations where selective reward was not employed, our monkeys exhibited asymmetrical *amplitude* adaptations, i.e., somewhat greater adaptation for right- than leftward saccades (not shown). In contrast, cross axis adaptation caused symmetrical *directional* adaptation for left- and rightward saccades (control experiment, see Fig. 6). We used an upward ISS because it induced a somewhat greater adaptation than did a downward ISS in our monkeys. This cross-axis paradigm, when repeated over several hundred trials, caused the originally horizontal primary saccade to acquire an upward component (Fig. 1A, bottom, blue arrows, see also Fig. 3).

To make some saccades potentially more rewarding than others, we gave the applesauce reward at the end of a trial, i.e., 300 ms after the corrective saccade