



# Effect of visual background on saccade adaptation in monkeys

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## Abstract

The brain maintains saccade accuracy by modifying saccades that are consistently inaccurate (e.g. hypermetric). To determine whether this adaptation is influenced by the visual background we used several different target and background movements to elicit changes in saccade gain. In almost all cases, the target spot drove gain changes. The background had no effect on, or slightly reduced, adaptation. We conclude that the saccade adaptation mechanism is driven almost entirely by stimuli on or near the fovea and is affected very little by visual stimuli falling more peripherally. © 2000 Elsevier Science Ltd. All rights reserved.

**Keywords:** Plasticity; Motor learning; Oculomotor; Primate; Eye movement

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## 1. Introduction

Saccades are so brief that there is not enough time for visual feedback to guide the eye to its target. Nonetheless saccades are quite accurate. The brain maintains this accuracy by correcting the commands that produce consistently inaccurate (e.g. hypermetric) saccades. Such corrections are called saccade adaptation. Some investigators propose that corrective movements made after an inaccurate saccade could contribute to driving adaptation (Albano & King, 1989; Schweighofer, Arbib & Dominey, 1996). Recent work indicates, however, that the drive for saccade gain adaptation is primarily the visual error after the saccade, not the corrective movement (Wallman & Fuchs, 1998).

In a normal visual setting targets for saccades appear against a rich visual background. A saccade that is too large will overshoot the background as well as its intended target. Thus, information from the background could provide a drive for adaptation. To date there are no published studies on the effect of visual background on saccade adaptation.

We characterized the way in which a visual background affects adaptation by causing saccades to seem too large. To do this we employed a technique first used by McLaughlin (1967) in which a target steps back during a saccade so that the saccade seems to end beyond its target. We measured the adaptation of saccade size elicited by four conditions: (1) when no background was present; (2) when the target spot and the background moved together; (3) when the target spot moved across a stationary background; and (4) when the spot did not step back but the background did. We found that the adaptation mechanism is driven almost exclusively by the target spot and very little by the background.

## 2. Methods

### 2.1. Animal preparation

Two juvenile male rhesus macaques (*Macaca mulatta*) were prepared for eye-movement recording via the electromagnetic search coil technique (Robinson, 1963; Fuchs & Robinson, 1966). In aseptic surgery with the monkey under deep anesthesia, we implanted a three-turn coil of Teflon-coated stainless-steel wire around one eye and attached three small acrylic sockets to the animal's skull to hold the head steady during eye-movement recording.

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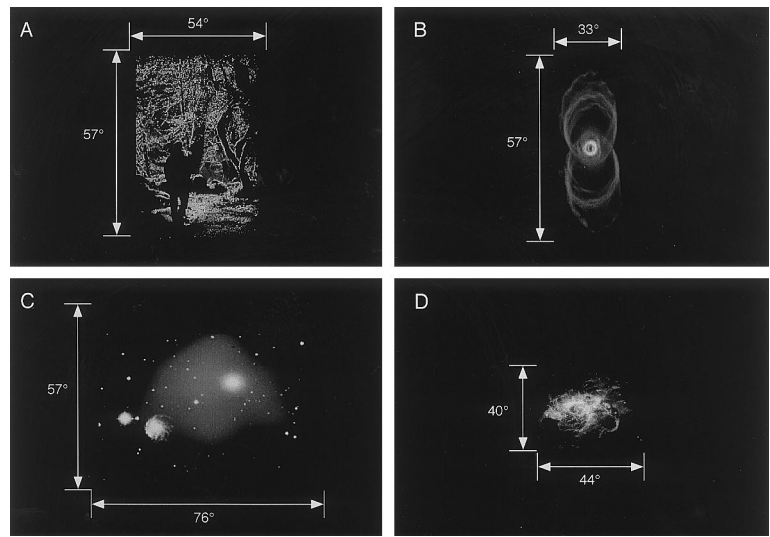


Fig. 1. Four background images used in these experiments. (A) A man walking in a forest. (B–D) Astronomical objects.

A week after surgery we started training each monkey to track a target with its saccades. The target, a spot of red light  $\sim 0.3^\circ$  across, was back-projected from a laser diode onto a frosted screen 57 cm in front of the monkey. The image of the spot reflected off two galvanometer mirrors before reaching the screen. We controlled the horizontal and vertical position of the target spot by changing the position of the mirrors. The monkey received applesauce from a feeding tube near its mouth when it tracked the spot successfully. After about 6 weeks of training the monkeys reliably made 4000–5000 targeted saccades per day.

2.2. Saccade adaptation

In these experiments we reduced the size of saccades by making them seem too large. An electronic circuit detected the start of a monkey’s saccade by signaling when eye velocity exceeded  $\sim 50$  deg/s. This signal caused the target to move back toward the saccade’s starting position during the movement. Thus each saccade seemed to end beyond its target. When a human (McLaughlin, 1967; Miller, Anstis & Templeton, 1981; Deubel, Wolf & Hauske, 1986) or monkey (Straube, Fuchs, Usher & Robinson, 1997) makes many saccades that seem to overshoot, saccades become smaller. In humans saccade size falls significantly within about 100 saccades, in monkeys within about 1000.

When we used back-stepping targets to reduce saccade size, the spot stepped randomly to the left or right by  $10^\circ$  or  $13^\circ$ . We used two sizes of target step to make final target position less predictable to the monkey. These two sizes are similar enough that reducing the size of one with back-stepping targets also significantly reduces the size of the other (Miller et al., 1981; Frens & van Opstal, 1994; Albano, 1996; Straube et al., 1997;

Noto, Watanabe & Fuchs, 1999). The spot never moved to more than  $20^\circ$  away from straight ahead horizontally and never moved vertically. The target spot stepped back toward its starting position by 30% of its initial size ( $3.9^\circ$  for  $13^\circ$  target steps and  $3^\circ$  for  $10^\circ$  target steps). Adapting both leftward and rightward saccades allowed us to measure two separate adaptations in one experimental session because adapting saccades in one direction does not affect saccades in the opposite direction (Weisfeld, 1972; Miller et al., 1981; Deubel et al., 1986; Frens & van Opstal, 1994; Albano, 1996; Straube et al., 1997).

The monkeys were rewarded with a drop of apple sauce every few seconds for continuously keeping their eyes within  $\sim 2^\circ$  of the target spot. After every target step the monkeys had  $\sim 250$  ms to redirect their eyes to the target before they were registered as off target. In tests during which we extinguished the target spot the monkeys usually waited for the spot to reappear to redirect their eyes if necessary.

During some tests the monkey tracked the target spot in the presence of a visual background that, like the target spot, was back-projected onto the screen. The

Table 1  
Luminance of the target spot and the backgrounds (cd/m<sup>2</sup>)<sup>a</sup>

	Luminance (cd/m <sup>2</sup> )	
	Brightest	Darkest
Target spot	0.5	—
Background A	1.02	0.07
Background B	1.04	0.02
Background C	1.51	0.02
Background D	1.77	0.03

<sup>a</sup> Letters refer to the backgrounds pictured in Fig. 1.

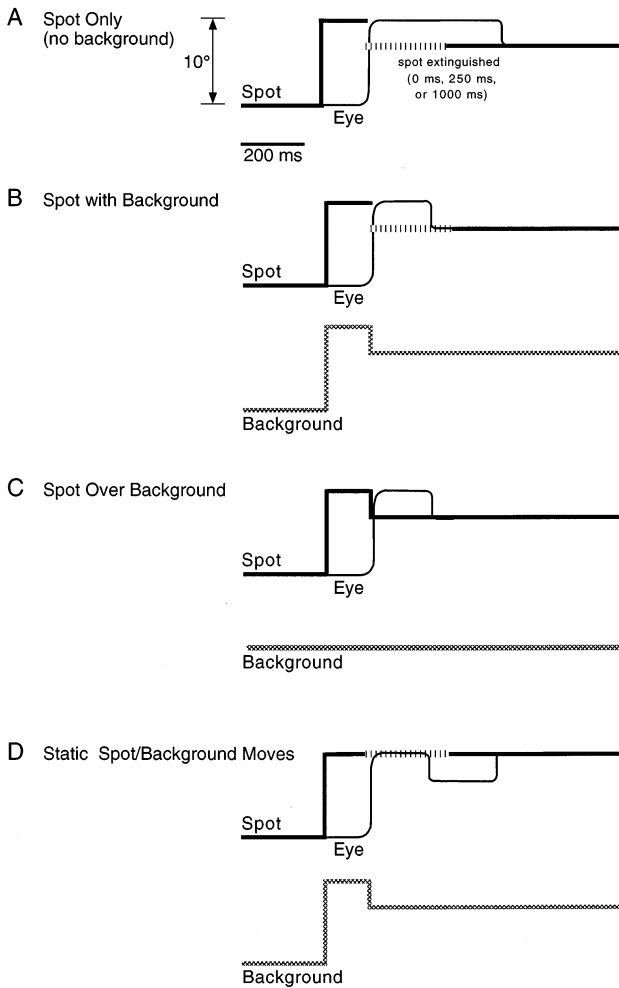


Fig. 2. Schematic representations of the four conditions used to adapt saccadic size. Shown are  $10^\circ$  initial target and background movements. Each experiment also included an equal number of  $13^\circ$  target and/or background movements. (A) Spot-only: the target spot moved to a new location and then stepped back 30% of its initial step size during the saccade. (B) Spot-with-background: the target spot moved as in A, and the background moved with it, as if they were one stimulus. (C) Spot-over-background: the target spot moved as in A across a stationary background. (D) Static-spot/background-moves: the target spot and background moved together to a new location. The spot did not step back 30% during the saccade but the background did. In conditions A, B and D, adaptation experiments were run with the target spot extinguished for 0 (i.e. was continuously visible), 250 or 1000 ms.

background was one of the four images shown in Fig. 1. Table 1 summarizes the luminances of the target spot and backgrounds. The images were in color and occupied a region  $\sim 1800$ – $4300$  square degrees on the screen. We moved the background image by controlling a mirror galvanometer that intersected the light path between the projector and the screen.

### 2.3. Testing

We compared the amount of adaptation caused by each of four conditions (Fig. 2). In the spot-only condition (Fig. 2A), the target spot made both its initial step and the intrasaccadic back-step on a dark screen. This condition is commonly used to cause saccade adaptation in monkeys and humans. In the *spot-with-background* condition (Fig. 2B), the target spot and background made both the initial step and the back-step together as a single stimulus. Thus the spot always appeared on the same part of the background. In the *spot-over-background* condition (Fig. 2C), the target spot made both its initial step and back-step against a stationary background. In this condition saccades seem to overshoot the spot but not the background. Finally, in the *static-spot/background-moves* condition (Fig. 2D), the target spot and background made the initial step to a new location together. During the saccade the background stepped back 30% of the size of its initial step. In this condition saccades seem to have overshoot the background but not the target.

We tested each of these four conditions with the target spot continuously visible. We also tested three of them when the target spot was extinguished for 250 or 1000 ms after the start of a saccade (i.e. spot-only, spot-with-background, and static-spot/background-moves). In these conditions, the monkeys could not use the target spot's position as a cue to saccade accuracy until the spot was visible again 250 or 1000 ms after the start of the saccade. We presented every adaptation condition to each monkey one to three times in each horizontal direction. In Figs. 4 and 5 we distinguish repetitions of identical conditions with the letters A, B or C.

To describe the size of a monkey's saccades we used saccade gain (saccade amplitude/target amplitude). Fig. 3 shows the gains of saccades to  $10^\circ$  target steps during two different adaptation experiments, one that caused a large gain reduction (Fig. 3A) and one that caused no gain reduction (Fig. 3B). As the figure shows, at the start of each experimental session we recorded several 'pre-adapt' saccades to normal (i.e. not back-stepping) targets. We then presented  $\sim 1000$  leftward target steps intermixed with  $\sim 1000$  rightward back-stepping target steps to elicit 'adaptation'. Finally, we recorded several 'post-adapt' saccades to normal targets.

### 2.4. Data analysis

During pre-adapt and post-adapt saccades we recorded voltages proportional to eye and target position on video tape with a PCM converter (Vetter 4000A). We digitized these records at 1 kHz and analyzed saccades with an interactive program that marked, or allowed the user to mark, the beginning and

end of each movement. The program measured the amplitude of the saccade and of the target step and calculated saccade gain.

We measured changes in saccade gain by comparing the gain of pre-adapt and post-adapt saccades. For each post-adapt saccade we measured how different its gain was from the average gain of pre-adapt saccades. We calculated the percentage gain change using the formula:

$$\text{Percent gain change} = \frac{(\text{average gain of pre-adapt saccades}) - (\text{gain of single post-adapt saccade})}{(\text{average gain of pre-adapt saccades})}$$

We then averaged the percentage of gain change of all of the post-adapt saccades in an experiment. These averages and their standard deviations are shown in Figs. 4 and 5.

We compared the percentage gain change caused by different conditions with a one-way ANOVA using the Bonferroni/Dunn correction for repeated tests. We considered  $P < 0.05$  to be significant. Because adaptations of leftward and rightward saccades were independent of one another we compared leftward adaptations only to other leftward adaptations and rightward adaptations only with other rightward adaptations.

### 3. Results

We measured the percentage gain change in 38 adaptation experiments in monkey M1 and 42 in monkey M2. The data were virtually identical for 10° and 13° step sizes so this report presents only data from the 10° steps.

Fig. 4 shows the percentage gain change caused by the four different conditions tested when the spot was continuously visible. Contrary to our expectation, adaptation using a back-stepping target spot with no background image (Fig. 2A) caused gain reductions that were often larger than those in any other condition. Adaptation in which the target spot and background always moved together (Fig. 2B) caused gain reductions that were the same as or smaller than those caused by the spot-only condition. For both leftward and rightward saccades in monkey M1 (Fig. 4) the spot-with-background adaptation caused significantly less gain change than did spot-only adaptation of saccades in either direction (each  $P < 0.0001$ ). In monkey M2, one spot-with-background adaptation, leftward B, caused gain changes that were significantly smaller than those caused by the spot-only adaptation ( $P < 0.003$ ). M2's other spot-with-background adaptations elicited gain reductions that were indistinguishable from those elicited by spot-only adaptation. Thus the condition in which saccades overshoot the target spot alone drove the adaptation mechanism as well as, and sometimes better than, the condition in which saccades overshoot both the target spot and the background.

If, as normally happens, a visual background is present during inaccurate saccades, does the adaptation mechanism use the information that saccades are overshooting the background to aid adaptation? We tested this by comparing the gain reductions caused by the spot-and-background condition (Fig. 2B) with those caused by the spot-over-background condition (Fig. 2C). In the spot-over-background condition the target spot back-stepped just as in the spot-only condition and the background never moved. In both monkeys the spot-over-background condition elicited gain changes

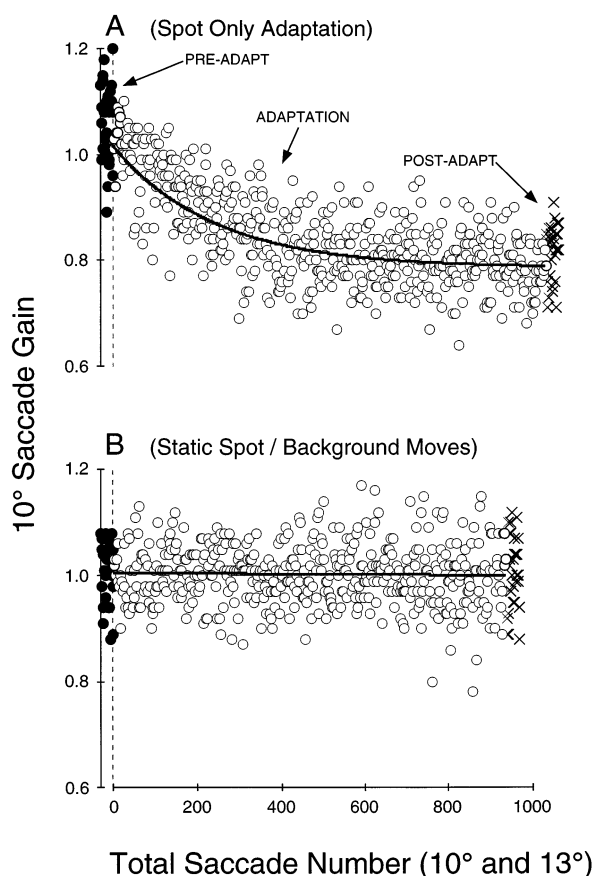


Fig. 3. Examples of saccadic gain change elicited by two types of adaptation used in this study. Saccades were adapted with both 10° and 13° target steps; data shown are for saccades to 10° target steps. ● show the gain of saccades before adaptation to normal target steps (i.e. not followed by intrasaccadic back-steps). ○ show gain of saccades to repeated adapting target steps (i.e. followed by intrasaccadic back-steps). Xs show gain of saccades to normal target steps after adaptation. Curve through open circles is exponential fit. (A) Adaptation to target spot making both its initial and intrasaccadic back-step on a dark screen (condition A in Fig. 2). (B) Adaptation to the spot and background making the initial step together followed by a back-step by the background but not the target (condition D Fig. 2). Arrows in Fig. 4 mark bars that show the percentage of gain change calculated from these two adaptations.

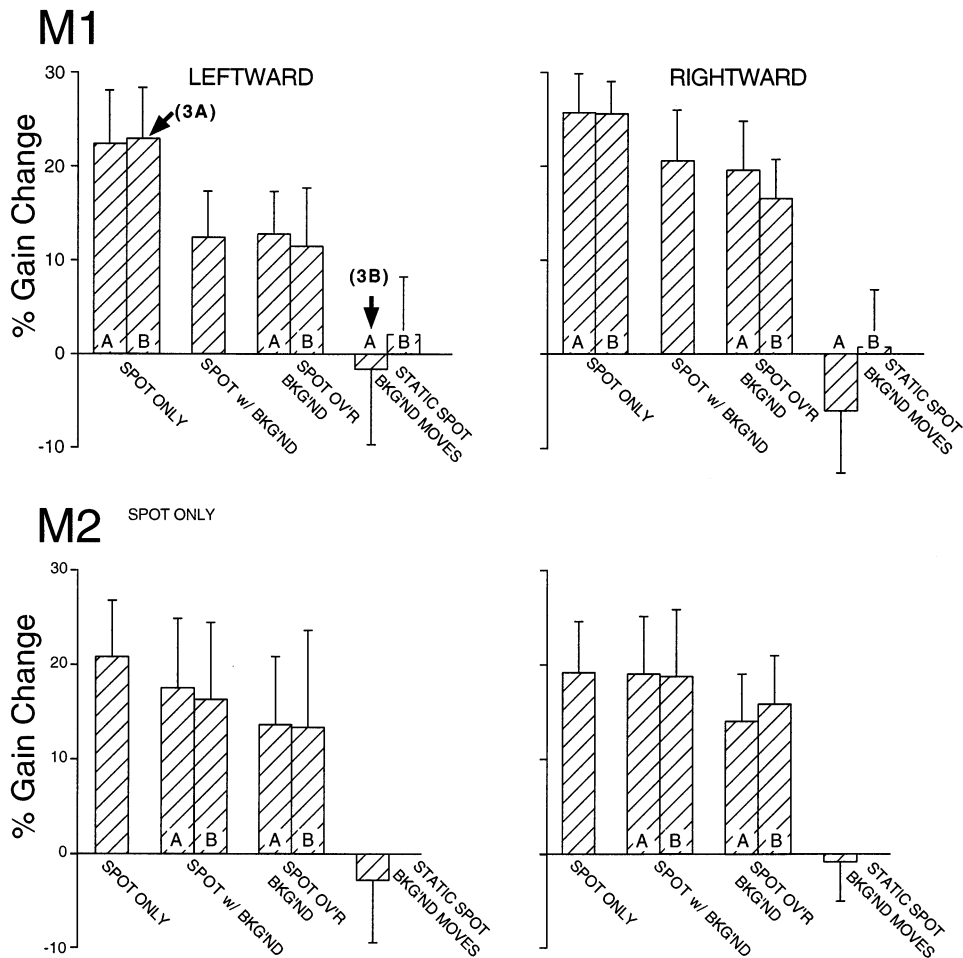


Fig. 4. Bar graphs showing the percentage of gain change caused by the four adaptation conditions shown in Fig. 2. In every experiment shown here the target spot was continuously visible. Each bar represents the results from one adaptation like the examples in Fig. 2. Bars representing experiments that presented identical conditions are labeled A and B. Data shown separately for leftward and rightward saccades in monkeys M1 and M2. Arrows in the panel showing adaptation of M1's leftward saccades (upper left) show the bars representing the gain changes calculated from the examples in Fig. 3A,B.

that were indistinguishable from, or smaller than, those in the spot-with-background condition. In both monkeys, one spot-over-background adaptation elicited a smaller gain change than did spot-with-background (right B in M1,  $P < 0.0001$ ; right A in M2, each  $P < 0.002$ ). The other three spot-over-background adaptations in each monkey caused gain changes that were indistinguishable from those caused by spot-with-background adaptations. This result indicates that entirely eliminating the overshoot of the background has a small and often insignificant effect on the gain change elicited. Together this and the first result indicate that saccades overshooting their target drive adaptation much more strongly than saccades overshooting the background.

The dominance of the target spot in driving adaptation is also reflected in adaptation elicited by the last condition, static-spot/background-moves (Fig. 2D). In this condition the target spot steps normally, without

back-stepping, but the background back-steps during the saccade. This creates a direct conflict between the signal from the spot ('no adaptation necessary') and that from the background ('reduce saccade size'). All adaptations in this condition elicited smaller gain reductions than those elicited in any other condition (each  $P < 0.0001$ ). Four of the six static-spot/background-moves adaptations caused a small adaptation in the wrong direction, i.e. they increased saccade size. Like the gain changes of the spot-over-background adaptations, the gain changes of the static-spot/background-moves adaptations indicate that when there is a conflict between the signals from the background and the spot, it is the signal from the spot that dominates the performance of the adaptation mechanism.

Despite its evident insignificance during saccade adaptation, information from the background may be able to influence adaptation if information from the target spot is unavailable to the adaptation mechanism.

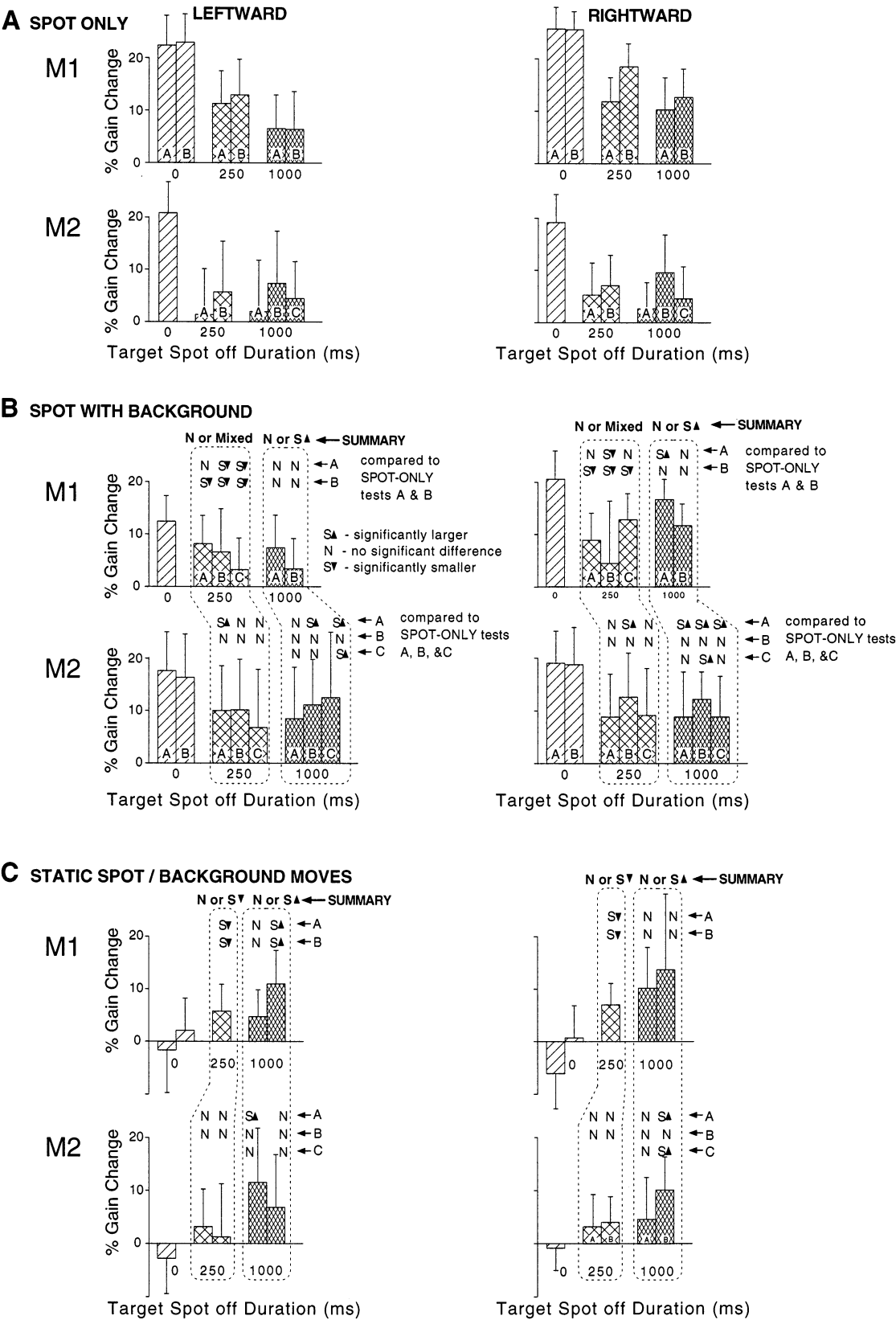


Fig. 5. Bar graphs showing effect of extinguishing the target spot for 0, 250 and 1000 ms on the percentage of gain change elicited by adaptations in three conditions: (A) spot-only; (B) spot-with-background; and (C) static spot/background-moves. Letters over bars in B and C show how the gain change is different from that elicited by the corresponding spot-only experiments in A. Summaries appear at the top of each group of the same experiment. N, no significant difference; S with upward arrowhead, significantly larger; S with downward arrowhead, significantly smaller.

We tested this possibility by measuring the size of gain changes when we deprived the adaptation mechanism of the spot, but not the background, soon after the start of each saccade. To do this we extinguished the spot for 250 or 1000 ms beginning when eye velocity reached  $\sim 50$  deg/s in three types of adaptation: spot-only (Fig. 2A), spot-with-background (Fig. 2B), and static-spot/background-moves (Fig. 2D).

Extinguishing the spot often elicited corrective saccades different from those when the spot was always on. When the target was continuously visible monkeys made corrective saccades that were nearly always accurate and had normal latencies (150–250 ms). When the target was extinguished for 250 or 1000 ms during the spot-only and spot-with-background conditions, the monkeys usually made no corrective saccade until the target was visible again. During this time they usually maintained their gaze at the position where the target was last visible. Occasionally, however, the monkeys would make a second saccade after their initial saccade to a region other than that where the target would appear, i.e. they would look away. The monkeys did this more often when the target was off for 1000 ms than when it was off for 250 ms. When the target was extinguished in the static-spot/background-moves condition the monkeys usually made a corrective saccade to follow the background movement (illustrated in Fig. 2D).

Fig. 5A shows the size of gain changes elicited in spot-only adaptations when the spot was continuously visible (target spot off duration = 0 ms) and when it was extinguished for 250 or 1000 ms. Extinguishing the spot for either 250 or 1000 ms caused gain changes that were significantly smaller than when the spot was continuously visible. This was true in both monkeys for adaptations of saccades in both directions (each  $P < 0.0001$ ). However, even these conditions, during which we extinguished the spot, often caused a clear reduction in saccade gain.

Movement of the background with the spot (Fig. 5B) did not consistently cause gain reductions that were any larger than those caused by moving the spot alone. The letters above each bar in Fig. 5B indicate how that gain change was different from that elicited in each spot-only condition when we extinguished the spot for the same duration. A separate letter compares each spot-with-background adaptation with each spot-only adaptation. Summary statements above the bars of each graph describe the combined results for both monkeys. Even when it was extinguished for 250 or 1000 ms, the spot alone caused gain changes that were not consistently distinguishable from those caused by the spot and background together. Thus, movement of the background during the 250 or 1000 ms absence of the spot did not drive adaptation any better than when the screen was simply dark for this period in the spot-only condition.

Despite its apparent inability to aid gain reduction during spot-with-background adaptations, background movement did elicit gain reduction in one condition. Fig. 5C shows the size of gain reductions elicited by static-spot/background-moves adaptations (illustrated in Fig. 2D). In this condition background movement was the only possible drive for gain reduction because the spot did not step back during the saccade but the background did. When the target spot was extinguished for 250 or 1000 ms this kind of adaptation elicited gain reductions that were indistinguishable from those elicited by spot-only adaptations when the spot was off for the same durations. Thus, if the target spot is extinguished for 250 or 1000 ms and re-illuminated without stepping back, the back-stepping of the background can reduce saccade gain.

#### 4. Discussion

The major finding of this study was that, in every condition but one, information from a visual background did not significantly contribute to causing gain changes elicited by an apparent overshoot of saccades. Indeed the presence of a visual background moving with a target spot often reduced the size of gain changes elicited by saccade overshoot. Our current data do not tell us why this is so, but they do clearly indicate that a back-stepping target with no background is the best stimulus, of the four we tested, with which to cause adaptation of saccade size.

Once a background is present, it makes little difference if it moves with the spot or is stationary (the middle two sets of bars in each panel of Fig. 4 are similar). If the spot remains static after its initial movement to a new location but the background moves during a saccade, little gain change occurs, i.e. the effect of the static spot dominates the effect of the back-stepping background (the rightmost bars in each panel of Fig. 4 are small).

The spot dominated the background even when we reduced the ability of the spot to drive gain change by extinguishing it for 250 or 1000 ms. We know that extinguishing the target spot does, in fact, reduce the spot's ability to drive adaptation because doing so elicited smaller gain changes in the spot-only condition (Fig. 5A). The gain changes elicited in the spot-with-background condition when we extinguished the spot were about the same as those elicited by the spot alone, i.e. the movement of the background during the absence of the spot added nothing to the adaptation.

Paradoxically, static-spot/background-moves adaptations elicited gain changes when we briefly extinguished the spot. Why did background movement elicit gain reductions in this condition but not in any other? We propose that it is because, after the spot disappears,

some feature of the background appears in place of the spot. When the background steps back in the absence of the spot, the revealed feature steps back, thus taking the place of the spot in driving adaptation.

If the revealed background feature were exactly equivalent to the spot, the static-spot/background-moves adaptations would have elicited gain reductions as large as those for spot-only adaptations when the spot was continuously visible. They did not. There are two possible reasons for this. The revealed background feature may not provide a perfect illusion of spot movement. Additionally, the appearance of the true target spot, even after 1000 ms, may provide the adaptation mechanism with a belated 'no adaptation necessary' signal that mitigates the effect of background movement. We know that illumination of the spot after 250 or 1000 ms can influence the adaptation mechanism because spot-only adaptations in which the spot is off for these durations can elicit gain reductions (Fig. 5A).

The belated appearance of a 'no adaptation necessary' signal may explain the pattern of gain changes evident in Fig. 5C. In both monkeys, for adaptation in both directions, there was a clear increase in the size of the gain change as we increased the time the spot was extinguished. We interpret this pattern to mean that the sooner a signal reaches the adaptation mechanism the more influence it has. Another of our findings indicates that this is so. Extinguishing the spot during spot-only adaptation (and thereby delaying visual information about saccade size from reaching the adaptation mechanism) reduces the size of elicited gain changes (Fig. 5A). Thus, in our view, the increasing size of elicited gain changes as we moved from spot-off durations of 0–1000 ms (Fig. 5C) reflects the increasing influence of the signal from the revealed background feature ('reduce saccade size') and the decreasing influence of the signal from the target spot ('no adaptation necessary').

If, as we propose, movement of a revealed background feature can elicit gain reductions, why did spot-with-background adaptations (in which the background stepped back in the absence of the spot) elicit the same gain changes as spot-only adaptations (in which there was no background)? This similarity indicates that when the spot and the background provide the same signal to the adaptation mechanism ('saccade was too large, reduce saccade size') the two signals do not add linearly.

Four of the six static-spot/background-moves adaptations we tested with the spot continuously visible caused small gain changes in the wrong direction, i.e. saccade gain increased. The simplest explanation for this is that the back-step of the background created the illusion that the target spot had moved forward during the saccade. Consistent forward movement of the target during saccades causes an increase in saccade size in humans (Miller et al., 1981; Albano & King, 1989;

Albano, 1996) and monkeys (Straube et al., 1997). It is plausible that our monkeys misinterpreted the back-stepping of the background as forward stepping of the target because humans can confuse background and target movement. Human subjects report that a saccade target seems to step back when, in fact, it has been blanked for 200 ms and the background has stepped forward. However, despite reporting this illusion, these subjects did not reduce the size of their saccades (Deubel, personal communication).

Conditions in which the target is always visible elicit a pattern of corrective saccades different from that when we extinguished the target. This difference raises the possibility that different corrective saccades contributed to causing different gains. We think that this is very unlikely because corrective saccades contribute much less to adaptation than visual stimuli (Wallman & Fuchs, 1998). Nonetheless our current data cannot entirely eliminate the possibility that extinguishing the target spot caused different gain changes at least in part because it caused different corrective saccades.

No previous work has directly examined the role of a visual background on saccade adaptation. A visual background was present in experiments that studied adaptation to the dysmetria caused by weakened extraocular muscles in humans (Kommerell, Olivier & Theopold, 1976; Abel, Schmidt, Dell'osso & Daroff, 1978; Optican, Zee & Chu, 1985) and monkeys (Optican & Robinson, 1980). In these experiments saccade size took much longer to change than in experiments that simulated saccade dysmetria with intrasaccadic target movement (i.e. several days vs. 45 min). A large part of this difference was a consequence of the fact that experiments using weakened eye muscles usually require adaptation of a much wider variety of saccade sizes and directions. Weakened eye muscles and intrasaccadic target movement cause similar rates of adaptation if both methods adapt the same variety of saccade sizes and directions (Scudder, Batourina & Tunder, 1998). Our finding that the presence of a background often reduces the size of the induced gain change raises the possibility that the visual backgrounds that are usually present in experiments studying adaptation of subjects to weakened eye muscles may also contribute to the slower gain change elicited by weakened eye muscles.

In summary, the presence of a visual background often reduces the gain change elicited by apparent saccade overshoot. Once a background is present it makes little difference if the background moves with the spot or is stationary. In the only condition in which the background elicited gain reductions, it is plausible that the image of a small feature of the background fell near the fovea and substituted for the spot. We interpret our results to mean that the target spot, appearing on or near the fovea, is much more influential in driving adaptation than the background.



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