Adaptation and adaptation transfer characteristics of five different saccade types in the monkey

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Kojima Y, Fuchs AF, Soetedjo R. Adaptation and adaptation transfer characteristics of five different saccade types in the monkey. J Neurophysiol 114: 125–137, 2015. First published April 8, 2015; doi:10.1152/jn.00212.2015.—Shifts in the direction of gaze are accomplished by different kinds of saccades, which are elicited under different circumstances. Saccade types include targeting saccades to simple jumping targets, delayed saccades to visible targets after a waiting period, memory-guided (MG) saccades to remembered target locations, scanning saccades to stationary target arrays, and express saccades after very short latencies. Studies of human cases and neurophysiological experiments in monkeys suggest that separate pathways, which converge on a common locus that provides the motor command, generate these different types of saccade. When behavioral manipulations in humans cause targeting saccades to have persistent dysmetrias as might occur naturally from growth, aging, and injury, they gradually adapt to reduce the dysmetria. Although results differ slightly between laboratories, this adaptation generalizes or transfers to all the other saccade types mentioned above. Also, when one of the other types of saccades undergoes adaptation, it often transfers to another saccade type. Similar adaptation and transfer experiments, which allow inferences to be drawn about the site(s) of adaptation for different saccade types, have yet to be done in monkeys. Here we show that simian targeting and MG saccades adapt more than express, scanning, and delayed saccades. Adaptation of targeting saccades transfers to all the other saccade types. However, the adaptation of MG saccades transfers only to delayed saccades. These data suggest that adaptation of simian targeting saccades occurs on the pathway common to all saccade types. In contrast, only the delayed saccade command passes through the adaptation site of the MG saccade.

saccade; adaptation; motor learning; plasticity; monkey

PLASTICITY is an important property of the nervous system. In the case of movement, it helps to overcome persistent motor errors caused by growth, injury, and aging. Such motor plasticity or adaptation can be investigated quite handily for saccadic eye movements, which shift the direction of gaze between visual targets of interest. To cause adaptation, the target can be displaced during the saccade so that the saccade appears to have the wrong amplitude or direction. When faced with such repeated apparent errors, the oculomotor system gradually adapts the size and/or direction of its saccades so that gaze eventually lands near the displaced target (McLaughlin 1967). This adaptation paradigm has been used in primates to infer the site(s) and mechanism of adaptation in the saccade system.

Primate saccades can be elicited in a variety of situations. We consider five types here. The most natural type is the scanning saccade, which we use to redirect our gaze from one interesting, usually stationary, object in space to another, e.g., during reading. The remaining types are elicited primarily in the laboratory in response to jumping spots, whose timing generally produces different response latencies. Express saccades, which have the shortest latencies (80–120 ms) (Fischer et al. 1993; Fischer and Boch 1983; Fischer and Ramsperger 1984), occur if a target that is being fixated disappears before a distant target appears. Typical latencies for targeting saccades to sequentially illuminated spots are ~150 ms or greater in highly trained monkeys. Saccades to a distant target can be delayed if the monkey is required to maintain fixation until the fixation target is extinguished. Memory-guided (MG) saccades occur when the distant target appears only briefly and the monkey again must maintain fixation until the disappearance of the fixation target instructs it to saccade to the remembered location of the extinguished target. Although targeting saccades in the monkey have been shown to undergo adaptation, adaptation of the other simian saccade types has not been studied systematically. Therefore, the first goal in this study was to remedy that gap in our knowledge by documenting and comparing the characteristics of adaptation for all five saccade types.

Knowledge of the pattern of adaptation transfer or generalization between saccade types allows us to speculate whether sites of adaptation are shared by different saccade types or whether an adaptation site is unique for a particular type. Adaptation transfer between several saccade types has been studied in humans. For example, although results differ somewhat between laboratories, the adaptation of targeting saccades transfers to express, scanning, delayed, and MG saccades (Alahyane et al. 2007; Collins and Doré-Mazars 2006; Cotti et al. 2007; Deubel 1995, 1999; Fujita et al. 2002; Hopp and Fuchs 2002, 2010; Panouillères et al. 2014; Zimmermann and Lappe 2009; for reviews see Table 1 in Hopp and Fuchs 2004; Pélisson et al. 2010). However, the adaptation of MG saccades transfers only to delayed saccades (Deubel 1995, 1999; Fujita et al. 2002; Hopp and Fuchs 2002, 2010). Therefore, the adaptations of targeting and MG saccades occur at different neuronal loci. Although this information does not allow us to identify specific neural adaptation sites, it suggests that the saccade commands for all of the other four types pass through the targeting saccade adaptation site. In contrast, only the delayed saccade command passes through the MG saccade adaptation site.

The only simian transfer study thus far revealed that targeting saccade adaptation also transfers robustly to the other four types (Fuchs et al. 1996), again suggesting that their saccadic commands pass through the targeting saccade adaptation site.
Neurophysiological studies indicate that targeting and delayed saccade occurrence downstream of the superior colliculus (SC) (targeting saccade: Edelman and Goldberg 2002; Frens and Van Opstal 1997; Melis and van Gisbergen 1996; cf. Takeichi et al. 2007; delayed saccade: Quessy et al. 2010). Neurophysiological studies during adaptation suggest that one downstream structure that likely participates in targeting saccade plasticity is the oculomotor vermis (OMV) of the cerebellum (Barash et al. 1999; Catz et al. 2005, 2008; Kojima et al. 2010b, 2011; Soetedjo et al. 2008; Soetedjo and Fuchs 2006; Takagi et al. 1998). In contrast, nothing is known about the sites or the neuronal substrate for the adaptation of any other saccade type. To locate these different sites and to determine the mechanisms that underlie the adaptations of the different saccade types, we require similar transfer data in an experimental primate. Therefore, our second goal was to determine the mechanisms that underlie the adaptations of the sites or the neuronal substrate for the adaptation of any other saccade type. To locate these different sites and to determine how adaptation of each saccade type affects the other four types. Such data provide a behavioral platform from which to launch the various neurobiological techniques that can be applied to the behaving monkey.

MATERIALS AND METHODS

Surgery and Training

We measured eye movements in two rhesus monkeys (Macaca mulatta, male; monkey B: 7.4 kg, monkey W: 5.0 kg) with the electromagnetic search coil method (Fuchs and Robinson 1966; Judge et al. 1980; Robinson 1965). Briefly, in an aseptic surgery, we implanted a three-turn coil of fine Teflon-coated stainless steel wire on one eye of each monkey. The ends of the wire terminated in a small connector fixed to the top of the skull with titanium screws and dental acrylic. In the same surgery, we attached three receptacles to the monkey’s skull to stabilize the head during eye movement recordings. For more details see Fuchs et al. (1996).

After recovery from the surgery, each monkey was placed in a dimly lit booth and trained to follow a small visual target with its eyes. The monkey sat in a primate chair with its head restrained. We surrounded the animal with a semicircular array of light-emitting diodes (LEDs), which were spaced every 1° along the horizontal meridian, and illuminated them sequentially to produce target jumps. Each LED subtended 0.25°. The LEDs could be programmed to emit light either a red or a green light. We used the green LEDs only to elicit delayed and MG saccades (see below). After the monkeys had been trained to fixate an illuminated LED, i.e., the target, we trained them to make saccades between sequentially stepping LED targets. If the monkey’s gaze arrived within ±2° of the target within 0.8 s of the target step and stayed there for at least 0.5 s, the monkey was continually rewarded every 1–1.2 s. Note that 0.8 s allows the occurrence of a corrective saccade. We applied the same reward schedule for all saccade types during preadaptation, adaptation, and postadaptation sessions.

Saccade Types and Their Adaptation

The data gathered in this study were obtained before we started the cerebellar single-unit recording experiments reported in Kojima et al. (2010b), where the procedures for eliciting the five types of saccade are described in detail. Briefly, after the monkeys made targeting saccades continually for at least 1 h, we attempted to generate express saccades. For each animal, we determined which target amplitude elicited a high incidence of saccades with express latencies (for more detail, see Express saccades below). Monkey B made a high rate of express saccades to a 10° horizontal target step and monkey W to a 15° target step. For each monkey, these same step sizes were used for adaptation and testing of all five types of saccade. Once the animal reliably made saccades with express latencies, we trained it on the delayed, MG, and scanning saccade paradigms.

Targeting saccades. After the monkey had fixated a red LED for at least 0.6 s, another LED was illuminated within the next 0.7–0.9 s and the first went out. This sequence created a target step to either the right or the left that remained within ±22° of straight-ahead.

Adaptation of targeting saccades was induced by a modified version of the intrasaccadic step (ISS) paradigm (McLaughlin 1967). In the McLaughlin paradigm, the target jumped along the horizontal meridian and then, during a targeting saccade, jumped backward so the eye appeared to overshoot the target. The subject then made a corrective saccade backward to acquire the target. This procedure, when repeated over several hundred trials, caused a gradual decrease in the size of the initial saccade. In this study, we did not examine the gradual gain increases that are produced by a forward ISS. In our modified version of the paradigm, we caused the error of the targeting saccade to remain a constant percentage of its amplitude. We employed this adaptation strategy to provide the same percentage ISS to all five saccade types, which had different accuracies. For example, MG saccades were less accurate than targeting saccades (White et al. 1994). A computer detected the saccade end position (when the eye velocity decelerated to <20°/s) and moved the target back 25% of the target step amplitude from the saccade end position. Because the LEDs were placed every 1°, the target position was rounded down to the nearest integer. The schematic at the top of Fig. 1A shows the schematic target movement and elicited saccade that occurs in the “targeting” saccade paradigm.

Express saccades. To elicit express saccades, we extinguished the fixated red LED briefly (gap paradigm) before illuminating a second LED at a distance of either 10° for monkey B or 15° for monkey W (Fischer et al. 1993; Fischer and Boch 1983; Fischer and Ramsperger 1984). We varied the duration of the extinction gap in 10-ms steps from 80 to 200 ms to determine which duration elicited the highest incidence of saccades with express latencies. The most effective gap was 100 ms for monkey B and 160 ms for monkey W. With these gaps, the distribution of latencies was bimodal, with the trough occurring at ~100 ms for monkey B and ~110 ms for monkey W (Fig. 1B). We considered as express saccades only those with latencies from 50 to 100 ms for monkey B and from 50 to 110 ms for monkey W.

To adapt express saccades, we measured saccade latencies online and applied an adapting step only if the latency was <100 ms for monkey B and <110 ms for monkey W (Fig. 1A, Express). The target was stepped backward 25% of the saccade size from the saccade end position. If a saccade latency was greater than the maximum accepted express value, there was no back step and instead the target was turned off for 300 ms. We used this short duration here to gather the maximum number of saccades before the monkey became fatigued.

Scanning saccades. To elicit scanning saccades, we simultaneously illuminated three red LEDs, each separated by either 10° (monkey B) or 15° (monkey W) along the horizontal meridian, and rewarded the monkey whenever it made, at its own pace, more than three consecutive saccades between any of the three LEDs. Monkeys most often made a saccade to the adjacent LED, i.e., 10° (monkey B) or 15° (monkey W).

To adapt scanning saccades, all three illuminated LEDs were extinguished at the end of the saccade and three other LEDs located short of each LED target were illuminated to produce a backward step of the entire three-LED array by 25% of the saccade amplitude from the saccade end position (Fig. 1A, Scanning). The occasional (~1%) saccades that were made between the two most eccentric LEDs were not analyzed. However, the back step also occurred for those saccades.

Delayed saccades. To elicit a delayed saccade, we required the monkey to continue to fixate an illuminated red LED for 0.3 s before a peripheral green LED was illuminated continuously to show the destination for the future saccade. We required the monkey to delay its
To elicit adaptation, the green LED was stepped backward by 25% of the saccade amplitude to the peripheral, illuminated green LED. After the monkey had fixated the green LED for 0.6 s, the red LED was turned on in place of the green LED to serve as the initial fixation LED for the next trial. We used short fixation durations here to maximize the number of saccades before the monkey became fatigued.

To elicit adaptation, the green LED was stepped backward by 25% of the saccade amplitude from the saccade end position (Fig. 1A, Delayed).

**MG saccades.** To elicit a MG saccade, we required the monkey to fixate a red LED for 0.3 s and then we turned on a green LED briefly for 0.2 s at the next target location. After the green LED was extinguished, 0.3 s later the red fixation LED was also turned off, serving as a signal for the monkey to saccade to the remembered location of the green LED. When the saccade landed at the remembered target location, the green LED came on at the actual location. After the monkey had fixated the green LED for 0.6 s, the red LED was turned on in its place to serve as the initial fixation LED for the next trial.

To produce MG saccade adaptation, the green LED was stepped backward by 25% of the saccade amplitude from the saccade end position (Fig. 1A, Memory guided).

**Experimental Conditions**

Once the monkey had demonstrated its ability to perform the various saccade tasks and adapt all types of saccade, we began the transfer experiments. In each experiment, we induced adaptation of one saccade type (the adapt saccade) and tested whether that adaptation transferred to one or more (up to 4) of the other types (the test saccades).

Figure 1C illustrates the time course of an experiment in which one saccade type was adapted and three other types were tested. Before adaptation (Fig. 1C, Pre), we collected ~30 of the saccades to be adapted and ~30 of each of the three saccade types to be tested. We then reduced the amplitudes of the adapted saccade by jumping the targets backward as the monkey made saccades toward them. The backward step was applied for saccades in both the left- and rightward directions. After each ~10-min segment of adaptation, we collected ~20 of one of the three test saccade types so that by the end of the entire adaptation each test saccade had been sampled three times. During an ~10-min segment of adaptation, a monkey adapted approximately 370 targeting saccades, 180 express saccades, 280 delayed or MG saccades, and 550 scanning saccades in each direction. The backward step was not applied during the collection of test saccades.

After the ~20 test saccades, the amplitude of the adapt saccade had shown little or no recovery. Across both monkeys, the average gain recovery was 0.020 ± 0.028, 0.014 ± 0.016, 0.012 ± 0.024, 0.017 ± 0.015, and 0.022 ± 0.026 for targeting, express, scanning, delayed, and MG saccade adaptation, respectively. Gain recovery did not differ significantly between saccade types (unpaired t-test, P > 0.05 with Bonferroni correction). Therefore, we ignored it in further analyses.

Finally, we discontinued the backward step and monitored the recovery of the adapted saccade gain (Fig. 1C, Recovery). For most experiments with monkey B, we were able to test four types of saccade in each adaptation experiment. For most experiments with monkey W, who did not work as long, we could test only two types of saccade in each experiment.

**Data Analysis**

We did the initial data acquisition and the online data processing as described in Kojima et al. (2010a). Briefly, eye and target position
signals were digitized at 1 kHz and stored on a hard disk through an interface [Power1401, Cambridge Electronic Design (CED)]. During the experiment, we used a custom program running in Spike 2 (CED) to control the data acquisition box (Power1401, CED) and to analyze the incoming data online. The data were saved after the experiment and analyzed off-line on a computer using custom programs that ran analysis software (Spike 2, CED). Saccade onset and end were identified by an eye velocity criterion of 20°/s. Saccades elicited by the initial (not intrasaccadic) target jump were selected for analysis. Parameters of saccades and target jumps, e.g., latency, onset, offset, amplitude, duration, peak velocity, etc., and the saccade traces for every trial were exported to other programs (MATLAB, MathWorks) for subsequent analysis. We eliminated saccades with a vertical component that was ≥ 3 standard deviations from the mean and if the horizontal and vertical initial eye positions differed from the initial target positions by ≥ 1°. These restrictions eliminated <5% of the trials.

We calculated gain as [saccade size/target step size]. Before adaptation, the gain of some saccade types in both monkeys was idiosyncratically different. In monkey B, scanning saccades showed significantly higher gains than the other four types (unpaired t-test, P < 0.05 with Bonferroni correction). In monkey W, delayed saccades showed significantly higher gains than express saccades (unpaired t-test, P < 0.05 with Bonferroni correction, here and for all other t-tests). Therefore, in each monkey we normalized the gain of each saccade type as [saccade gain/mean preadaptation gain].

The gain change of the adapted saccade was calculated as [mean normalized gain of first 15 saccades of adaptation (Fig. 1C, First15) – mean normalized gain of last 15 saccades (Fig. 1C, Last15)]. To assess whether the adaptation was significant, we compared the mean normalized gain of the first and last 15 adapt saccades (unpaired t-test, P < 0.05). Saccades in all of the data sets used in this study showed a significant gain reduction during adaptation (unpaired t-test, P < 0.05). We treated rightward and leftward saccades as independent data sets because adaptation in one horizontal direction does not produce adaptation in the opposite direction (humans: Deubel et al. 1986; Miller et al. 1981; Semmlow et al. 1989; cf. Rolfs et al. 2010; monkeys: Noto et al. 1999; Scudder et al. 1998; Straube et al. 1997), so each adapted direction provides a separate data set. The average number of rightward saccades during the adaptation session was 827 ± 321, 593 ± 292, 945 ± 584, 411 ± 108, and 429 ± 103 for targeting, express, scanning, delayed, and MG saccades, respectively. For leftward saccades, it was 767 ± 216, 569 ± 232, 945 ± 598, 435 ± 104, and 482 ± 105 for targeting, express, scanning, delayed, and MG saccades, respectively.

To compare adaptation characteristics across saccade types, we also fit the course of adaptation with an exponential function:

\[ f(x) = a \times \exp(-b \times x) + c \]  

Because all adaptations had at least 300 adapt trials, we determined the gain change after 250 saccades as [mean normalized gain of first 15 saccades of adaptation – f(250) of exponential fit]. Finally, we calculated the initial jump of the adaptation as [mean normalized gain of last 15 saccades of preadaptation – mean normalized gain of first 15 saccades of adaptation] and the recovery jump at the onset of recovery as [mean normalized gain of first 15 saccades of recovery – mean normalized gain of last 15 saccades of adaptation].

To assess the adaptation transfer to the test saccades, we applied an unpaired t-test to the last 15 test saccades during preadaptation and the first 15 test saccades of the third test saccade block (see Fig. 1C). If the normalized gain of saccades in the third test block was not significantly different from the normalized gain of preadaptation test saccades (unpaired t-test, P > 0.05), we considered that adaptation had not transferred to the test saccade, i.e., the percent transfer was 0% (Fuchs et al. 1996). On the other hand, if the normalized gain of the test saccades was smaller and the normalized gain changes of the adapted and test saccades were not significantly different (unpaired t-test, P > 0.05), we considered that adaptation transfer was complete, i.e., the percent transfer was 100%. If the latter t-test was significant (unpaired t-test, P < 0.05), we then calculated the percent transfer as

\[ \text{Percent transfer} = \left( \frac{G_{\text{preT}} - G_{\text{adaT}}}{G_{\text{firstA}} - G_{\text{lastA}}} \right) \times 100 \]  

In this equation, GpreT is the mean normalized gain of the last 15 test saccades of preadaptation, GadaT is the mean normalized gain of the first 15 test saccades of the third test, GfirstA is the mean normalized gain of the first 15 saccades of adaptation, and GlastA is the mean normalized gain of the last 15 adapted saccades before the third test (Fig. 1C, box 1, 2, or 3 for Transfer test). We chose these gain measures so that the ways the target stepped were always the same for the test saccades (GpreT and GadaT, without ISS) and the adapted saccades (GfirstA and GlastA, with ISS).

As shown in RESULTS, there often is an immediate drop in gain at the beginning of adaptation. Therefore, we also calculated the percent transfer in a second way, which took the drop into account by changing the denominator of Eq. 2 to (GpreA – GadaA), where GpreA is the mean normalized gain of the first 15 adapt saccades of preadaptation (use of this modification 1 of Eq. 2 produced the gray bars in Fig. 5). In this case, the target condition differs between GadaT (without ISS) and GlastA (with ISS).

To avoid drawing conclusions based only on nonsignificant results (see the description of Eq. 2), we used the same equation to calculate the actual percent transfer without applying the adjustment for no (0%) or complete (100%) transfer (use of this modification 2 of Eq. 2 produced the striped bars in Fig. 5). These calculations did not change the conclusions of our results.

Because the transfer of adaptation varied from experiment to experiment (Fuchs et al. 1996), we collected 10 data sets for each pair of adapt and test saccade types for each monkey so that the total permutation of the transfer data sets was 10 (data sets) × 5 (adaptation saccade types) × 4 (other test saccade types) × 2 (monkeys) = 400. To infer whether the adaptation transferred to a particular test saccade on average, we tested the mean percent transfer obtained from the two monkeys (n = 20 data sets, t-test). If it was significantly different from 0 (unpaired t-test, P < 0.05 with Bonferroni correction), we inferred that the adaptation had transferred to the test saccade type. Because the number of saccade types tested in each adaptation experiment varied, the number of adaptation data sets for each saccade type did as well. For monkey B, the sets numbered 20, 18, 24, 10, and 10 for targeting, express, scanning, delay, and MG saccades, respectively. For monkey W, they numbered 22, 20, 20, 20, and 24, respectively.

All experiments were performed in accordance with the Guide for the Care and Use of Laboratory Animals (1996) and exceeded the minimal requirements recommended by the Institute for Laboratory Animal Research and the Association for Assessment and Accreditation of Laboratory Animal Care International. All procedures were evaluated and approved by the local Animal Care and Use Committee of the University of Washington (ACC no. 2602-01).

RESULTS

We induced gain decrease adaptation of targeting, express, scanning, delayed, or MG saccades and tested the transfer of that adaptation to one or more of the other four types. We first describe the adaptation characteristics of each type of saccade and then the transfer of that adaptation.

Course of Adaptation of Different Saccade Types

All types of saccade showed significant adaptation. However, the amount of gain change during adaptation varied from one saccade type to another. Figure 2, A–E, show representative courses of adaptation and recovery of the five types of J Neurophysiol • doi:10.1152/jn.00212.2015 • www.jn.org
saccades for monkey B. Note that although other types of saccade were inserted and tested during the adaptation (see Fig. 1C), we have plotted only the adapted saccades. Also recall that the 20 test saccades inserted at various times during adaptation caused very little recovery of the adapted saccade (see MATERIALS AND METHODS).

As described in Straube et al. (1997), the course of targeting saccade adaptation (Fig. 2A) was nicely fit with an exponential function ($r = 0.73$, rate constant = 646). There was an initial jump in gain when we stopped the target back step (vertical dashed line between Adapt and Recovery; Fig. 2A), and the subsequent recovery was gradual. The adaptation courses of express, scanning, delayed and MG saccades (Fig. 2, B–E) were qualitatively similar but exhibited some quantitative differences. For example, express, scanning, and delayed saccades adapted less than targeting saccades, whereas MG saccades adapted the same amount as targeting saccades but in fewer trials. Also, scanning saccades showed an initial jump decrease in gain at the onset of adaptation, whereas the other types did not.

Figure 2F shows representative courses of adaptation for each saccade type in monkey W. They were qualitatively similar to their counterparts from monkey B.

We compared five measures that describe adaptation for the five different types of saccade. The mean gain decrease at the 250th saccade of adaptation was greater for targeting and MG saccades than for the other three types in both monkeys (Fig. 3A). For the average from both monkeys, MG saccades exhibited a significantly greater reduction than did scanning saccades (unpaired t-test, $P < 0.05$ with Bonferroni correction; Fig. 3A). In monkey B, the initial jump at the onset of adaptation was larger for scanning saccades than for the other four types; however, it was the smallest among all test saccades in monkey W (Fig. 3B). Finally, the jump at the beginning of recovery was significantly larger for MG saccades than for delayed, scanning, and express saccades in both monkeys (Fig. 3C).

To analyze the time course of adaptation for the different saccade types, we compared the rate constants ($1/b$ in Eq. 1) and the absolute gain changes ($a$ in Eq. 1) of the exponential fits of adaptation. Because we did not always collect adaptation data until the gain change had reached a plateau, rate constants and the absolute gain changes might be slightly inaccurate in some experiments. Figure 3D shows the distribution of the width of the 95% confidence interval for the rate constants of the exponential fits of all adaptations. Because the width of the 95% confidence interval was <1,000 in most data sets, we excluded those with larger widths in our consideration of rate constants and absolute gain changes. The number of experiments remaining after this exclusion was 32, 18, 33, 18, and 27 for targeting, express, scanning, delayed, and MG saccade adaptation, respectively. Across saccade types, the rate constant was significantly greater for targeting saccades and smaller for MG saccades than for the other four saccade types (unpaired t-test, $P < 0.05$ with Bonferroni correction; Fig. 3E). The absolute gain changes for targeting and MG saccades were larger than those of the other saccade types (Fig. 3F). In summary, targeting and MG saccades exhibited the greatest amount of adaptation, but MG saccade adaptation was faster and showed a larger recovery jump. Other saccade types were not significantly different from each other.

Transfer of Adaptation from One Saccade Type to Another

Adaptation transfer from targeting to other saccade types. Figure 4 shows data on the transfer from adapted saccades to test saccades from representative experiments in monkey B. Although we tested three types of saccade during every experiment (see MATERIALS AND METHODS), each panel in Fig. 4 shows the data associated with only the adapted saccade and one type of test saccade examined three times during the course of adaptation. For example, in column T in Fig. 4, the plots in rows E, D, and MG are from the same experiment, i.e., B627. Because test saccade 1 was MG, 2 was delayed, and 3 was express (see Fig. 1C), the number of adapt saccades is smallest for the first-tested MG saccades and largest for the last-tested express saccades.

As the gain of targeting saccades decreased (Fig. 4, column T), the gains of all types of test saccades exhibited a gradual decrease as well, albeit smaller. The mean percent gain decrease of the adapted targeting saccades calculated from data taken just before and just after the third set of data from the test saccade (see MATERIALS AND METHODS) ranged from 21.6 ±
7.7% to 27.0 ± 11.3% (Fig. 4, 4 data sets in column T) and was always highly significant ($P < 0.05$, unpaired t-test). In contrast, the mean gain decrease for tested express, scanning, delayed, and MG saccades was only 16.1 ± 9.0%, 19.5 ± 10.3%, 8.4 ± 6.6%, and 13.5 ± 6.6%, respectively (Fig. 4); however, each decrease was significant ($P < 0.05$). The percent gain decreases of all test saccade types were significantly less than those of the adapted targeting saccade. For these exemplar experiments, the percent gain transfer from targeting saccades was 70.9%, 72.2%, 38.9%, and 57.9% to express, scanning, delayed, and MG saccades, respectively.

Figure 5 shows the percent transfer from adapted targeting saccades to the various test saccades. In column T, each open bar represents data calculated with Eq. 2 and averaged across the 10 experiments performed on each monkey and the filled bar represents the data averaged across both monkeys. Across the monkeys, the average percent gain transfer from adapted targeting to express, scanning, delayed, and MG saccades was 73.6 ± 18.1%, 58.1 ± 16.7%, 63.8 ± 20.5%, and 34.6 ± 16.7%, respectively, and was significantly different from zero. Thus adaptation of targeting saccades transferred significantly to each of the other four types of saccade. The thin gray and striped bars represent the percent transfer evaluated by modifications 1 and 2 of Eq. 2, respectively (see Data Analysis).

Adaptation transfer from express to other saccade types. Figure 4, column E, shows data for the transfer of adaptation from express saccades to the four other saccade types taken from an exemplar experiment in monkey B. The mean gain decreases of the adapted express saccades before the third tests of the different types were ~20% and always significant ($P < 0.05$, unpaired t-test). Although targeting saccades showed a significant gain decrease, scanning, delayed, and MG saccades did not. The gain changes of all the test saccades differed significantly from that of the adapted express saccade; the gain transfer was 25.6%, 0%, 0%, and 0% for targeting, scanning, delayed, and MG saccades, respectively.

Across both monkeys (Fig. 5, column E), the average percent gain transfer from adapted express saccades to targeting, scanning, delayed, and MG saccades was 71.5 ± 22.3%, 22.1 ± 19.4%, 23.3 ± 20.6%, and 18.8 ± 19.9%, respectively, but the transfer was significantly different from zero only for targeting saccades. Thus adaptation of express saccades transfers only to targeting saccades.

Adaptation transfer from scanning to other saccade types. Figure 4, column S, shows data for the transfer of adaptation from scanning saccades to the four other saccade types taken from representative experiments in monkey B. The mean gain decrease of the adapted scanning saccades was always significant. Targeting and express test saccades also showed significant gain decreases, but delayed and MG saccades did not. The gain decreases of targeting and express saccades were not significantly different from that of the adapted scanning saccade. Therefore, the percent gain transfer was 100%, 100%, 0%, and 0% for targeting, express, delayed, and MG saccades, respectively.

Across both monkeys (Fig. 5, column S), the average percent gain transfer from adapted scanning saccades to targeting, express, delayed, and MG saccades was 67.1 ± 21.5%, 68.6 ± 27.0%, 33.0 ± 22.8%, and 22.8 ± 20.5%, respectively; however, the transfer was significantly different from zero only for targeting and express saccades. Thus adaptation of scanning saccades transferred only to targeting and express saccades.
Adaptation transfer from delayed to other saccade types. Figure 4, column D, shows data for the transfer of adaptation from delayed saccades to the four other saccade types taken from a representative experiment in monkey B. The mean gain decrease of the adapted delayed saccades was always significant, as was the mean gain decrease of all types of test saccades. The gain decreases of targeting and scanning saccades were significantly less than those of the adapted delayed saccade. Therefore, the percent gain transfer was 48%, 100%, 72%, and 100% for targeting, express, scanning, and MG saccades, respectively.

The average percent gain transfers from adapted delayed saccades to other test saccades across both monkeys were 68.8 ± 20.7%, 80.2 ± 17.5%, 43.6 ± 23.1%, and 38.9 ± 24.1% for targeting, express, scanning, and MG saccades, respectively (Fig. 5, column D). The transfer to each type of test saccade was significantly different from 0. Thus adaptation of delayed saccades transferred to all types of saccades.

Adaptation transfer from MG to other saccade types. Figure 4, column MG, shows data for the transfer of adaptation from MG saccades to the four other saccade types taken from representative experiments in monkey B. The mean gain decrease of the adapted MG saccades was always significant. The tested targeting, express, and scanning saccades showed no significant gain decrease, but delayed saccades did. The gain decrease for each type of test saccade was significantly different from that of the adapted saccade, and the percent gain transfer was 0%, 0%, 0%, and 80.1% for targeting, express, scanning, and delayed saccades, respectively.

In summary (Fig. 5, column MG), the average percent gain transfer from adapted MG to targeting, express, scanning, and delayed saccades was 14.0 ± 15.8%, 15.5 ± 15.9%, 18.8 ± 16.4%, and 40.3 ± 24.3%, respectively, but was significantly different from 0 only for delayed saccades. Thus adaptation of MG saccades transfers only to delayed saccades.
DISCUSSION

The objective of this study was to test the adaptation characteristics of different types of saccade in the monkey and to determine the degree to which the adaptation of one type generalized to other types. First, we compare the adaptation characteristics such as gain decrease, initial and recovery jumps, and the rate constant for the five types of saccade we examined. Then we consider the adaptation transfers between different types and draw inferences as to the existence of common and distributed adaptation sites. Finally, we conclude by comparing our data with similar data collected in nonhuman primates and humans by our lab and others.

Adaptation Characteristics of Different Saccade Types

The ISS adaptation paradigm, which has been used to reduce the amplitude of simian targeting saccades, also produced a significant adaptation of MG, delayed, scanning, and express saccades (Fig. 2). However, the adaptation characteristics of the different saccade types often were not the same. In particular, MG saccades showed the fastest and greatest amount of adaptation and the greatest recovery jump (Fig. 3). These results suggest that MG saccades are able to undergo the greatest adaptation and to switch rapidly back to the unadapted state when the adaptation paradigm is discontinued.

It has been suggested that saccade adaptation consists of both a rapid and a slow process (Ethier et al. 2008; Smith et al. 2006; for review see Tian et al. 2009). Smith et al. (2006) showed that it is the jump in gain after error clamps or a break that is a marker of the fast process. Unfortunately, our experimental protocol does not allow a direct evaluation of these two processes. If, however, the recovery jumps in gain (Fig. 4) reflect the rapid components and the subsequent gradual gain changes represent the slow component, MG saccades might have adaptation mechanisms with especially robust rapid and slow components because they exhibited a greater recovery jump and faster gradual gain change.

The differences in adaptation characteristics suggest that the neuronal mechanisms that produce adaptation of the various saccade types could be different. Moreover, the mechanisms might, at least in part, lie in different pathways within the saccade circuitry. Whether an adaptation pathway might be specific to a single saccade type or be shared by several types can be inferred from the transfer of adaptation among different saccade types.

Adaptation Transfer Between Different Saccade Types

Adaptation transfer depended strongly on which saccade type was adapted. In agreement with a previous study on monkeys (Fuchs et al. 1996), our study shows that the adaptation of targeting saccades transfers to express, scanning, delayed, and MG saccades (Fig. 6A, column T). In addition, the present study showed that adapted delayed saccades also transferred to all other types of saccades. Adaptation of express saccades transferred only to targeting saccades, whereas scanning saccade adaptation transferred to both targeting and express saccades. Adaptation of MG saccades transferred only to delayed saccades.

Our transfer data suggest that the adaptation sites of some types of saccade are shared with other types, whereas some sites are not. Figure 6B shows how these sites might be configured based on our data. Each saccade type can be adapted, and therefore each has an adaptation site through which its saccade signal flows. If adaptation of one kind of saccade transfers to another, the tested saccade pathway traverses the adaptation site of the
adapted saccade. For example, the adaptation of MG saccades transferred to delayed saccades, so the delayed saccade pathway traverses the MG adaptation site in Fig 6B. Similar logic can be applied for the remaining transfers of saccade adaptation. Because adaptation of both targeting and delayed saccades transferred to all other saccade types (Fig. 6A), the saccade pathway for the other types must traverse the adaptation site for both targeting and delayed saccades, suggesting that they have a common adaptation site (Fig. 6B). Indeed, when either targeting (Frens and Van Opstal 1997; cf. Takeichi et al. 2007) or delayed (Quessy et al. 2010) saccades undergo adaptation, the neuronal activity in the SC does not change, indicating that both targeting and delayed saccades use an adaptation site that is downstream of the SC.

The short-latency express saccade is often considered to be a reactive saccade like a targeting saccade (for reviews see Hopp and Fuchs 2004; Pélisson et al. 2010). Therefore, it might be expected to be one of the last types to join the common final saccadic pathway. However, because we show here that scanning saccades transfer to both targeting and express saccades, targeting and express saccade commands must traverse the site for scanning saccade adaptation (Fig. 6B). Similarly, delayed saccades are considered to be voluntary saccades that require cortical processing (for reviews see Hopp and Fuchs 2004; Pélisson et al. 2010). However, because delayed saccades transferred to all other saccade types, the site for delayed saccade adaptation must lie on the saccade command pathway for all other saccade types. Just because delayed saccades apparently involve cortical processing, their adaptation site does not have to lie in the cortex. On the basis of our transfer data, it seems plausible that the adaptation sites for both the reactive targeting saccade and the voluntary delayed saccade could lie downstream of the adaptation site for the reactive express saccade.

From this simple schematic, we suggest that the adaptation sites of targeting and delayed saccades are shared and likely are located the farthest downstream along the saccade command pathway. In contrast, the adaptation sites for express, scanning, and MG saccades are likely to be separate and located more upstream. Please note that the adaptation sites depicted in the signal flow schematic of Fig. 6B do not necessarily refer to specific structures in the brain; they could represent different groups of cells in the same neural structure or different synapses on the same cell. Moreover, adaptation transfer between any of the saccade types was never 100%, suggesting that, in addition to the site indicated in Fig. 6B, each type also may have a site specific to its own adaptation.

Could Experimental Conditions Account for Any of the Differences in Transfer Between Saccade Types?

We consider three possible factors here. Although there may be others, these have been explicitly suggested in the review process.

In humans, the amount of forward but not backward adaptation transfer between saccade types depends on the preview duration of the saccade target (Zimmermann 2013). In our study of backward adaptation, the target preview duration for scanning saccades was the intersaccadic interval (~1 s), for delayed saccades the delay + the saccade latency (300 + ~150 = ~450 ms), for MG saccades 300 ms, and for targeting and express saccades the saccade latency (~150 and ~80–120 ms, respectively). Although the preview duration for targeting saccades was twice that for express saccades, they transferred to each other. Also, although the preview duration for targeting saccades was less than half that for the delayed saccade, they still transferred to each other. Thus preview duration also is not a factor in the transfer of backward adaptation in the monkey.

Does the amount of transfer depend on the velocities of the different saccade types? Across both monkeys, the average preadaptation peak velocity was fastest for scanning saccades (~370°/s) and slowest for MG saccades (~280°/s). Targeting, express, and delayed saccades had similar, intermediate peak velocities (~340°/s). If the transfer were dictated by the similarity of saccade peak velocity, express saccade adaptation would have transferred to delayed saccades, but it did not (Fig. 6A). Also, if transfer preferentially occurs from faster to slower saccades (or vice versa), scanning saccade adaptation would have transferred to MG saccades (or MG saccade adaptation would have transferred to scanning saccades); again, this was not the case.

The characteristics of the adaptation process itself also did not appear to be a factor in the adaptation transfer between...
saccade types. For example, transfer did not always occur between saccade types with similar adaptation speeds, e.g., express to scanning (Fig. 3, A and E). Nor did transfer always occur from faster to slower adapting saccades, e.g., MG to express, or from slower to faster adapting saccades, e.g., express to MG (Fig. 3).

Comparison with Previous Studies

Nonhuman primates. Our lab’s earlier study on the transfer of targeting saccade adaptation in the monkey also demonstrated substantial, but somewhat greater, transfer to all the other saccade types tested here (Fuchs et al. 1996). One possible explanation for the modest quantitative difference between the studies is that Fuchs et al. (1996) used an adapt step that was a fixed percentage of the target step, whereas this study employed an adapt step that was a fixed percentage of the actual saccade (see Materials and Methods). A study in humans suggested that the adaptation process indeed might be different when elicited by different back step paradigms (Zimmermann and Lappe 2010). A direct comparison of the results of these adaptation paradigms in the monkey might shed some light on the adaptation process itself.

Humans. In Fig. 6A, we compare the transfer between pairs of saccade types in the monkey with the transfer between the same two pairs in humans. As Fig. 6A shows, there are mostly similarities but some differences.

Targeting saccade adaptation. In both monkeys and humans, adapted targeting saccades transferred to express saccades (Fig. 6A, column T). Adapted targeting saccades also transferred to scanning saccades in the monkey, but not consistently in humans. A possible extenuating factor might have been the different numbers of fixed target spots used to elicit scanning saccades in the two species. When seven (Alahyane et al. 2007), six (Deubel 1995, 1999), or four (Zimmermann and Lappe 2009) spots were used with humans, there was no transfer; however, when two spots were used with either humans (Cotti et al. 2007) or monkeys (Fuchs et al. 1996) or three spots were used with monkeys (this study), transfer occurred. However, one study on humans (Panouilères et al. 2014) produced no transfer when three spots were used (only supplementary data).

In the monkey, adaptation of targeting saccades transferred to both MG and delayed saccades, whereas transfer was inconsistent in the human. For human MG saccades, transfer depended on the delay before the saccade “go” signal. If MG saccades were executed after delays >1 s (Deubel 1995, 1999), no transfer occurred; however, after shorter delays transfer did occur to MG saccades (Fujita et al. 2002; Hopp and Fuchs 2010). Our delay (0.3 s) was similar to that of these last two human studies, so the transfer to MG saccades was consistent between the two primate species when similar conditions were used. For human delayed saccades, targeting saccade adaptation produced no transfer whether the delay was long (>1 s; Deubel 1995, 1999) or short (0.3 ms; Collins and Doré-Mazars 2006).

Express saccade adaptation. Express saccade adaptation transferred to targeting saccades in both monkeys (Fig. 6A, column E) and humans (Deubel 1995, 1999; Hopp and Fuchs 2002, 2010). To the best of our knowledge, transfers of express saccade adaptation to scanning or delayed saccades have not been investigated in humans. Express saccade adaptation did not transfer to MG saccades in this study, but there was significant transfer in humans (Hopp and Fuchs 2010).

There are several differences between this monkey study and the human studies. In our study, we used shorter gap durations to elicit express saccades. Second, the distribution of latencies was bimodal in our study but unimodal in the human study (Hopp and Fuchs 2010). Therefore, in our study fewer total saccades were in the latency range of express saccades, so the average gain change was smaller. However, when we selected the subset of our experiments with the largest gain changes [16 ± 3.6% (n = 3) compared with 14 ± 0.7% in Hopp and Fuchs 2010], there still was no significant transfer to MG saccades; therefore, the lower average gain change in monkeys did not explain the lack of transfer.

Scanning saccade adaptation. Scanning saccade adaptation transferred to targeting saccades in both monkeys (this study) and humans (Alahyane et al. 2007; Cotti et al. 2007; Deubel 1995, 1999; Erkelens and Hulleman 1993; Panouilères et al. 2014; Zimmermann and Lappe 2009) (Fig. 6A, column S). Scanning saccade adaptation also transferred to monkey express saccades, but transfer to human express saccades has not been tested. Scanning saccade adaptation transferred to neither delayed nor MG saccades in monkeys and showed only a weak transfer to those saccade types in humans (Deubel 1995, 1999).

To provide a data set with gain changes more comparable with those of Deubel (1999), we selected the subset of our experiments with the largest gain changes [12.3 ± 1.3% (n = 4) compared with 20.5% in Deubel 1999]; however, there still was no transfer (0 ± 0%) from scanning to MG saccades.

Delayed saccade adaptation. Delayed saccade adaptation transferred to all other types in the monkey (Fig. 6A, column D). In humans, no data are available for the transfer of delayed saccades to express or scanning saccades. Adapted delayed saccades transferred to targeting and MG saccades in both monkeys (this study) and humans (targeting: Collins and Doré-Mazars 2006; MG: Fujita et al. 2002; Hopp and Fuchs 2010). MG saccade adaptation. Adaptation of simian MG saccades transferred only to delayed saccades (Fig. 6A, column MG). In humans, the transfer of MG saccade adaptation to other types was rather modest, if present at all. There was either weak transfer to targeting, express, and delayed saccades (Fujita et al. 2002; Hopp and Fuchs 2010) or none at all (Deubel 1995, 1999). There was no transfer to scanning saccades in either monkeys (this study) or humans (Deubel 1995, 1999).

In summary, there is substantial agreement regarding the transfer of adapted saccades to test saccades across nonhuman primates and humans (Fig. 6C). 1) Adapted targeting saccades transferred to express saccades, to MG saccades elicited with short delays, and to scanning saccades elicited with only a few target spots in both species and to delayed saccades in monkeys but not humans. 2) Adapted express saccades transferred to targeting saccades in both species and to MG saccades in humans but not monkeys; other saccade types were not tested in humans. 3) Adapted scanning saccades transferred to targeting saccades in both species and showed little if any transfer to delayed or MG saccades in either species. In monkeys, there also was a transfer to express saccades, but this transfer has not been tested in humans. 4) Adapted delayed saccades transferred to all saccade types in the monkey; transfer to express and scanning saccades has not been tested in humans. 5) Adapted MG saccades showed little if any transfer to targeting,

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express, or scanning saccades but transferred to delayed sac-
cades in both primate species.

Speculation on Possible Neuronal Sites of Adaptation

Because the generation of different saccade types is thought
to involve different brain regions (for reviews see Gaymard et al.
1998; Hopp and Fuchs 2004; Lynch and Tian 2006; Pélis-
son et al. 2010; Pierrot-Deseilligny et al. 2004), it seems
logical to expect that the sites where they undergo adaptation
may also be distributed.

Considerable progress has been made in understanding the
adaptation mechanisms for the extensively documented simian
targeting saccade. Studies using a variety of techniques have
placed the site of adaptation of targeting saccades downstream
of the SC. First, SC saccade-related activity does not change
during adaptation of targeting saccades (Frens and Van Opstal
1997; Takeichi et al. 2007). Second, there is significant adap-
tation transfer from targeting saccades to saccades evoked by
low-current electrical stimulation of the SC (Edelman and
Goldberg 2002; Melis and van Gisbergen 1996). Finally, stim-
ulation of the SC to act as a surrogate error signal induces
saccade adaptation artificially (Kaku et al. 2009; Soetedjo et al.
2009).

Unit recording together with inactivation, lesion, and ana-
tomical evidence have identified the OMV as an important
component of the downstream adaptation pathway. The grad-
ual change in amplitude that occurs during saccade adaptation
is associated with gradual changes in the discharge patterns
of neurons of the OMV (Catz et al. 2008; Kojima et al. 2010b), its
output, the caudal fastigial nucleus (cFN) (Inaba et al. 2003;
Scudder and McGee 2003), and the brain stem burst generator
to which cFN neurons project (Kojima et al. 2008). Moreover,
the error signal for targeting saccade adaptation reaches the
OMV over climbing fiber inputs to OMV Purkinje (P) cells that
originate in the SC (Catz et al. 2005; Kaku et al. 2009; Soetedjo
et al. 2008, 2009; Soetedjo and Fuchs 2006). However, even
targeting saccade adaptation apparently has a cortical compo-
nent because it can be influenced or driven by cognitive
processes, such as reinforcement (Madelain et al. 2011), atten-
tion (Khan et al. 2014), or the nature of a perceptual task
(Schutz et al. 2014).

There are a few scattered studies concerning possible sites of
adaptation for delayed, MG, and scanning saccades. When
delayed saccades are adapted, SC saccade-related activity also
does not change (Quessy et al. 2010), indicating that the adap-
tation site for delayed saccades also is downstream of the
SC. Because OMV P cells discharge for all the saccade types
examined in the present study (Kojima et al. 2010a), it is possi-
ble that the OMV could constitute at least part of the final
common adaptation site of targeting and delayed saccades
hypothesized in Fig. 6B. Neurons in the lateral intraparietal
(LIP) of the simian cortex show no change in activity during
adaptation of either MG or targeting saccades in the monkey
(Steenrod et al. 2013). Therefore, the site of MG saccade
adaptation is likely downstream of the LIP. Finally, human
studies have suggested that the adaptation of scanning saccades
involves some part of the parietal cortex (Cotti et al. 2007,
2009; Gerardin et al. 2012; Panouillères et al. 2014) and the
lateral cerebellum (Alahyane et al. 2008; Panouillères et al.

Conclusions

Before this report, the detailed characteristics of adaptation
in the monkey had been extensively documented only for
targeting saccades. With the help of those behavioral data,
significant progress has been made during the last 20 years in
understanding the neuronal basis of targeting saccade adapta-
tion. In this report we provide comprehensive adaptation data
for four other types of simian saccade. Equipped with this
foundation, we can expect similar progress to be made in
understanding the neuronal basis of adaptation of express,
scanning, delayed, and MG saccades. A logical place to begin
such studies would be the OMV, whose P cells discharge for
all five saccade types.

Our second contribution documents for the first time the
transfer of adaptation between five types of saccade in the
monkey. These data allow us to create a simple hierarchical
model of how adaptation sites might be roughly configured for
the different saccade types. For some of the reasons mentioned
above, it currently is premature to equate the adaptation sites in
Fig. 6B with actual neuronal structures, with the possible
exception of the most downstream site that probably involves
the cerebellum. The rough correspondence of the adaptation
transfer data in monkeys and humans provides some optimism
that the neuronal mechanisms revealed in the monkey may
have relevance when extrapolated to humans.

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AUTHOR CONTRIBUTIONS

Author contributions: Y.K. and A.F.F. conception and design of research;
Y.K. performed experiments; Y.K. analyzed data; Y.K. interpreted results of
experiments; Y.K. prepared figures; Y.K. drafted manuscript; Y.K., A.F.F.,
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