Saccadic adaptation shapes visual space in macaques

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[1]*Department of Psychology, University of Münster, Münster, Germany;* [2]*Otto Creutzfeld Center for Cognitive and Behavioral Neuroscience, University of Münster, Münster, Germany;* and [3]*Department of Human and General Physiology, University of Bologna, Bologna, Italy*

Gremmler S, Bosco A, Fattori P, Lappe M. Saccadic adaptation shapes visual space in macaques. *J Neurophysiol* 111: 1846–1851, 2014. First published February 12, 2014; doi:10.1152/jn.00709.2013.—Saccadic eye movements are an integral part of many visually guided behaviors. Recent research in humans has shown that processes which control saccades are also involved in establishing perceptual space: A shift in object localization during fixation occurred after saccade amplitudes had been shortened or lengthened by saccadic adaptation. We tested whether similar effects can be established in nonhuman primates. Two trained macaque monkeys localized briefly presented stimuli on a touch screen by indicating the memorized target position with the hand on the screen. The monkeys performed this localization task before and after saccade amplitudes were modified through saccadic adaptation. During localization trials they had to maintain fixation. Successful saccadic adaptation led to a concurrent shift of the touched position on the screen. This mislocalization occurred for both adaptive shortening and lengthening of saccade amplitude. We conclude that saccadic adaptation has the potential to influence localization performance in monkeys, similar to the results found in humans.

eye movements; localization; motor learning; spatial cognition

SACCADES ARE SO BRIEF that the visual information is not fully processed until the movement has ended. To keep saccades accurate, their motor commands are continuously adjusted. If a saccade consistently overshoots its target, the amplitude is shortened and if the saccade undershoots its target, the amplitude is lengthened. This saccadic adaptation is driven by the mismatch between the observed visual input after the saccade and the expected visual input predicted when the saccade was planned (Collins and Wallman 2012; Wong and Shelhamer 2011). In the laboratory, a postsaccadic error can be induced artificially by shifting the saccade target during the eye movement (McLaughlin 1967). Studies using this paradigm showed that saccadic adaptation occurs in humans and in monkeys with different time scales (Albano 1996; Deubel 1987; Frens and Van Opstal 1994; Straube et al. 1997; Watanabe et al. 2003).

In humans, saccadic adaptation not only changes saccade amplitude but also can affect the perceived location of objects. Such mislocalization has been found in hand pointing and in perceptual reports, depending on the type of saccade that is adapted and the adaptation direction (Awater et al. 2005; Bahcall and Kowler 1999; Bruno and Morrone 2007; Collins et al. 2007; Cotti et al. 2007; Hernandez et al. 2008; Moidell and Bedell 1988; Schnier et al. 2010; Zimmermann and Lappe 2009). These findings suggest that internal representation of the environment is not exclusively constructed from the visual input collected on the retina but that knowledge about the eye movement that is required to look at an object contributes to its perceived position (Collins et al. 2007; Zimmermann and Lappe 2010). Saccadic adaptation causes a dissociation between the physical location of an object on the retina and the end point of the saccade that targets that object. This separation might be due to either a modified calculation of the saccadic motor command or adjustments of the target representation during saccadic adaptation. In the latter case, saccadic adaptation does not just change amplitudes of eye movements but changes already the representation of the surrounding scene during fixation. In Zimmermann and Lappe (2010) human subjects were first adapted by shifting the saccade target during the saccade. When adaptation was established, the subjects had to localize briefly presented peripheral targets while they held fixation on a presented fixation spot during the whole trial. No saccade was executed in the localization trials, and hence no motor output was produced. The subjects localized the targets by indicating the perceived position on the presentation display with a mouse pointer. After adaptive saccade lengthening, subjects reported the objects more eccentric. After adaptive shortening, the effects on the perceptual report depended on the adaptation procedure. Subjects reported the perceived location less eccentric when the adaptation procedure involved a strong and persistent postsaccadic error. Since amplitude shortening in humans is faster and more efficient than lengthening, it reduces the postsaccadic errors quickly during the adaptation process. Different time courses of saccadic shortening and lengthening are also seen in monkeys [see Hopp and Fuchs (2004) and Pelisson et al. (2010) for review], but since overall saccadic adaptation is slower in monkeys, the development of the postsaccadic error likely differs between humans and monkeys. Therefore, we were interested in testing potential effects of adaptation on localization in monkeys.

MATERIALS AND METHODS

Experiments were performed in accordance with national laws on care and use of laboratory animals and with the European Communities Council Directives of 24th November 1986 (86/609/EEC) and 22nd September 2010 (2010/63/EU) and were approved by the Bioethical Committee of the University of Bologna.

The head-restraint system on the head of the trained *Macaca fascicularis* was surgically implanted in asepsis and under general anesthesia (thiopental sodium, 8 mg·kg^{-1}·h^{-1} iv) following the procedures reported by Galletti et al. (1995). Adequate measures were taken to minimize pain or discomfort. A full program of postoperative analgesia (ketorolac tromethamine, 1 mg/kg im immediately after surgery, and 1.6 mg/kg im on the following days) and antibiotic care [Ritardomicina (benzatinic benzylpenicillin plus dihydrostreptomycin plus streptomycin), 1–1.5 ml/10 kg every 5–6 days] followed the surgery.

Recording of eye movements and stimulus presentation. During the experimental sessions, signals from both eyes were recorded simultaneously with an infrared oculometer (ISCAN) at a sampling rate of 100 Hz. The monkey sat in a primate chair with its head restrained and faced a 19-in. touch screen monitor (ELO IntelliTouch 1939L) with a visible display size of 37.5 × 30.0 cm and 15,500 touch points/cm². The viewing distance of 28 cm from the animal's eyes to the screen resulted in a visual field of 53.3 × 47.0 deg. The display had a resolution of 1,152 × 864 pixels and a frame rate of 60 Hz. For stimuli presentation we used MATLAB with the psychtoolbox extension (Brainard 1997). The stimuli were green and red dots with a radius of 0.2 deg and yellow vertical bars (0.2 × 2.2 deg).

Behavioral task. The two monkeys were trained to make memory-guided reaching movements to a briefly presented target stimulus on a touch screen. During localization training sessions, to be rewarded the monkeys had to hold gaze fixation on a fixation spot and, after a go signal, indicate the position of a briefly presented eccentric target stimulus on the touch screen with the right hand. The position of the target stimulus varied between 5 and 25 deg to the right of the fixation spot. The animal needed to touch the screen at the horizontal position of the target stimulus ±1.0 deg and hold the fixation on the fixation spot at the same time to receive the reward. Both monkeys used all four fingers of the right hand to touch the screen. The training ensured that they were able to indicate the flashed position with a precision of <1 deg.

After training we measured touch locations before and after manipulation of saccadic amplitude by adaptation. The measurements were completed in two conditions. In the first condition the saccadic amplitude was shortened, and in the second condition the amplitude was lengthened. In the beginning of each session, the animal performed 20 localization trials in which it had to touch the target location during fixation. The setup of a localization trial is described in Fig. 1, preadaptation phase. The monkey pressed a button in front of its chest to start the trial, and a green fixation spot appeared. After a randomized time between 1.0 and 1.7 s, a yellow bar was flashed for 50 ms 18 deg to the right of the fixation spot. The monkey was trained to keep fixation on the green spot. If the monkey broke fixation when the bar was presented, the trial was aborted and the monkey did not receive any reward. After another randomized time between 1.0 and 1.7 s, the fixation spot changed color to red. This was the signal for the monkey to touch the screen in the position where it had seen the

flashed bar before. The monkey used its hand to indicate the position of the flashed bar on the screen while still holding fixation on the red spot. In training sessions, before the experiment started, the monkey had to touch the screen in a small window of 1 × 1 deg around the horizontal position of the flashed bar to receive the reward. During the experiment, in which we expected that the touch location might vary because of the prior adaptation, the monkey was allowed to touch the screen at any position to receive reward. In this way, we avoided having to reinforce any bias of touched position while the data were collected. Furthermore, in localization trials the monkey did not execute any saccade but had to hold fixation.

Our experiment tested localization for a bar flashed at the saccade target location. We chose this position because it is known that adaptation is a local phenomenon that spreads only moderately to neighboring locations (Frens and Van Opstal 1997) and because the same is true for the associated localization effects in humans (Collins et al. 2007; Schnier et al. 2010). To ensure that the monkeys continue to report the perceived bar position accurately, the animals performed several training sessions with hundreds of localization trials in the weeks before the measurements and also in between the measurements. In these training sessions, the bar appeared at many different positions, and to be rewarded the monkey had to localize the flashed position within a margin of 1 deg. Therefore, the monkey was reinforced to continue accurately reporting the perceived bar position without any strategic offsets during the whole time of the experiment.

After measuring the baseline localization performance of the monkey in the preadaptation phase, we manipulated the saccadic amplitude in the adaptation phase. This phase consisted of 400 adaptation trials. The setup of adaptation trials is pictured in Fig. 1, adaptation phase. After the monkey pressed the button to start the trial, a green fixation spot appeared for a randomized time between 0.7 and 1.5 s. If the monkey's gaze did not enter a 4 × 4-deg window around the fixation spot in less than 300 ms after the appearance of the fixation spot, or if the monkey's gaze left that window for longer than 150 ms after entering, the trial was aborted, the screen became black, and the monkey did not receive any reward in that trial. Provided that the monkey's gaze successfully entered the fixation window and that it was detectable inside the window for the last 300 ms, the fixation spot disappeared again after a randomized time between 0.7 and 1.5 s, and simultaneously a green target spot was presented 18 deg to the right of the fixation spot. The monkey then had to make a saccade to the
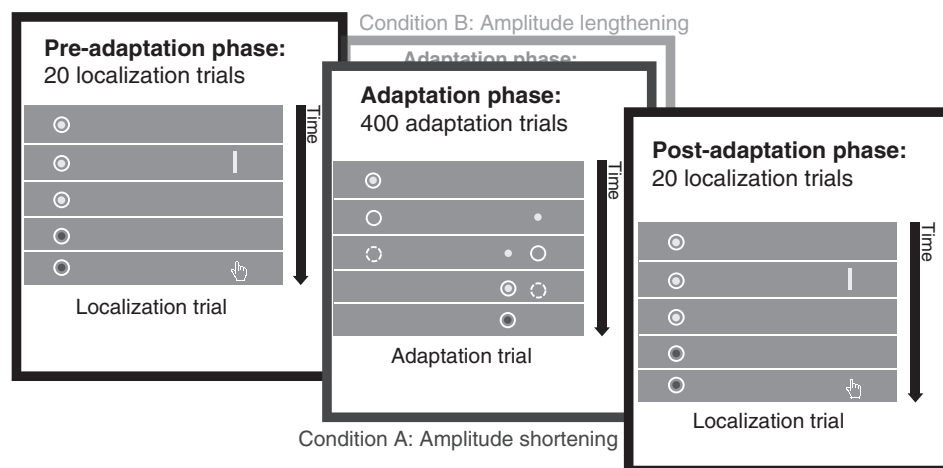

Fig. 1. One session consisted of 3 phases. In the preadaptation phase the animals completed 20 localization trials. In the localization task the monkey had to fixate on a green spot presented at the eye level of the monkey and at a 9-deg viewing angle to the left. After a randomized time, a yellow bar was flashed at 18-deg eccentricity. After a subsequent color change of the fixation spot, the monkey indicated the target position on the touch screen while he maintained fixation. The following adaptation phase consisted of 400 saccadic adaptation trials. In these trials the target spot was shifted during the saccade, and thus a mismatch between calculated postsaccadic retinal target position and actual postsaccadic retinal target position was induced. After the saccadic amplitude had been shortened or lengthened during the adaptation phase, the animal had to complete another 20 localization trials in the postadaptation phase so that we could measure the deviation from the localization baseline determined in the preadaptation phase. White circle, gaze position; dashed white circle, previous gaze position; light/dark gray dot, fixation spot and saccade target position; vertical bar, localization stimulus; hand, position of the correct manual response on the touch screen.

target. Saccade onset was detected when the gaze movement exceeded a distance of 3 deg from the fixation spot. As soon as saccade onset was detected, the target was shifted to a new position to induce a postsaccadic error. The maximum elapsed time between saccade onset and target shift thus was composed of the time the eyes need to travel the first 3 deg of the saccade, the sample time of the oculometer, and the frame duration of the screen. The eyes typically exceeded a distance of 3 deg to the fixation spot in less than 30 ms after saccade onset, and sample time and frame duration added up to a maximum of 27 ms. Hence, the target shift occurred about 57 ms after saccade onset and thus before the 18-deg amplitude saccade was finished.

The target reappeared shifted to either the right or the left, depending on the condition that was tested in the session. In the first condition, the target was shifted 4 deg leftward toward the fixation point. In this way, the monkey overshot the new target position and the amplitude became shorter during the adaptation phase. In the second condition, the target jumped 4 deg farther to the right so that the saccadic amplitude increased during the adaptation phase. In each session only one condition was tested, and thus the amplitude was either shortened or lengthened. The structure of these trials was the same as the structure of the training trials that the monkey had made to learn the saccade task. The only differences were the intrasaccadic target jumps to induce the adaptation and the reward contingencies. In training trials without the intrasaccadic target jump, the monkey's gaze had to enter a 6×6-deg window around the target position in less than 150 ms after saccade onset detection and stay in that window for 200 ms. Otherwise, the trial was aborted and the monkey did not receive any reward. In adaptation trials, reward was not contingent on the monkey's final gaze position, since we expected gradual change of amplitude and thus saccadic end position due to adaptation during the session. However, in training as well as in adaptation sessions, the target turned red after a randomized time between 600 and 1,000 ms after it had appeared or was shifted. The color change was the signal for the monkey to release the button that he had to press since the start of the trial. If the monkey released the button within a maximum time of 1,000 ms, the trial was ended successfully and a defined amount of water was given as reward.

After the amplitude was successfully altered in the 400 adaptation trials, we again tested the monkey's object localization in a postadaptation phase. This phase was built up identically to the preadaptation phase. In the end, we compared the mean touched position in the preadaptation phase before the saccadic amplitude was modified with the mean touched position in the postadaptation phase after the saccadic amplitude had been adapted. We refer to the difference between the two mean touched positions as the adaptation-induced mislocalization. Two sessions were separated by at least 48 h to extinguish the induced adaptation before the next session started.

Data analysis. Saccade trajectories during the adaptation phase were used to calculate the amplitude of each saccade by determining gaze position directly before the saccade onset at the time when the target was presented and the saccade ending position when the velocity of the saccade dropped under the threshold of one-tenth of the maximal velocity reached in that saccade. For the offline data analysis we used MATLAB. Changes of localization position and saccadic amplitude were tested for significance by employing two-tailed *t*-tests with independent and paired samples.

To determine the adaptation time constants during saccadic shortening and lengthening, the time course of adaptation in every session was fit with an exponential function (see Fig. 2): $A(trial) = A_0 + G \cdot e^{-trial/t}$, where A_0 is the asymptotic amplitude the monkey is approaching, G is the difference of the baseline amplitude and the asymptotic amplitude, and t is the rate constant of decay and increment during saccade shortening and lengthening, respectively.

In the first 10 trials of the adaptation phase, the target stayed in place and was not shifted in any direction. These first 10 saccadic amplitudes were used to calculate the mean preadaptation amplitude, i.e., the baseline amplitude. Likewise, the last 10 trials of this phase were used to calculate the mean postadaptation amplitude. This postadaptation amplitude was then used to calculate the deviation of the amplitude from the baseline after the adaptation.

RESULTS

In every session we first measured a baseline mean touched position for the flashed bar before we altered the saccadic amplitude via saccadic adaptation. Moreover, before calculating the saccadic amplitudes in the 400 trials of the adaptation phase, we checked that the start positions at the beginning of the adaptation phase and the end of the adaptation phase did not differ, to ensure that any amplitude change during the adaptation phase could be ascribed to landing point modifications rather than a shift of the monkey's fixation position inside the tracker window in the direction of the future position of the saccade target. There was no significant difference between the mean fixation position in the first 10 adaptation trials of each session and the last 10 trials in both monkeys. *Monkey I* showed an insignificant mean shift in fixation position of -0.18 ± 0.6 deg (2-tailed paired *t*-test, $P = 0.74$), and *monkey II* showed an insignificant opposed shift of 0.16 ± 0.5 deg (2-tailed paired *t*-test, $P = 0.43$). In Fig. 2, two adaptation curves with saccadic shortening (*A*) and saccadic lengthening (*B*) are presented. The time course of adaptation was fit with an exponential function, to determine the time constants of adaptive change of the saccadic amplitude.

Saccadic shortening is usually much faster than saccadic lengthening (Hopp and Fuchs 2004; Pelisson et al. 2010),

Fig. 2. Examples of the adaptation phase. In one condition the animal's saccadic amplitude was shortened (*A*), and in the other condition the amplitude was lengthened (*B*), via saccadic adaptation. The plots show the size of the saccadic amplitude in every trial of 1 session (dots). The line represents a fit of the data with the exponential function $A(trial) = A_0 + G \cdot e^{-trial/t}$, where A_0 is the asymptotic amplitude the monkey is approaching and G is the difference of the baseline amplitude and the asymptotic amplitude. The rate constants of the adaptation course in these 2 example sessions are $t = 112.5$ saccades for amplitude shortening and $t = 471.2$ saccades for amplitude lengthening.

A Amplitude shortening

B Amplitude lengthening

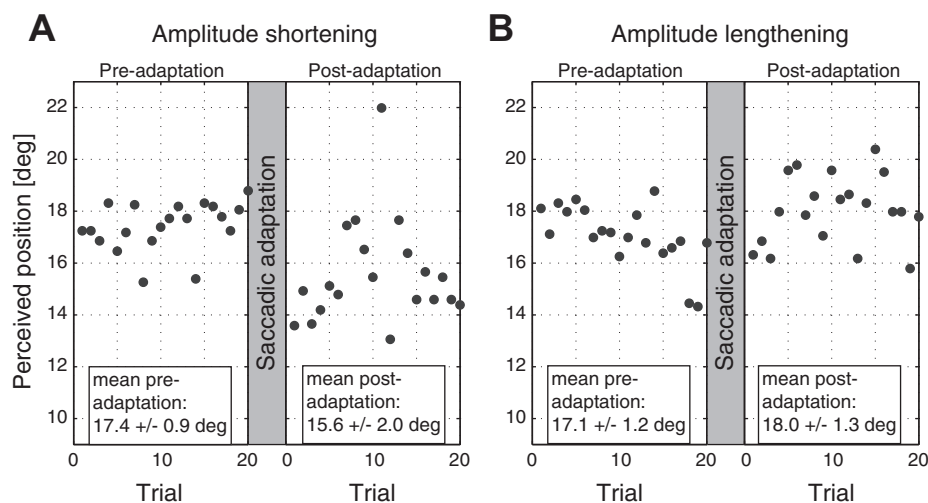t = 112.5 saccades

t = 471.2 saccades
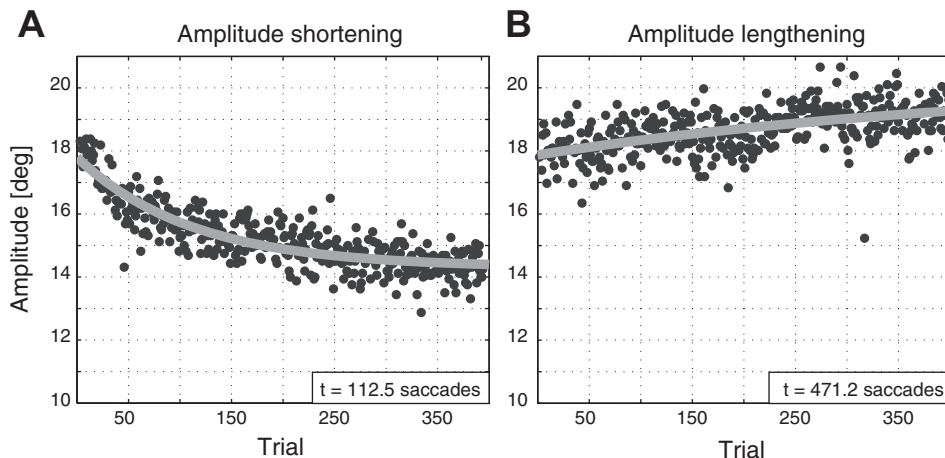
Fig. 3. Positions of the flashed stimulus as indicated by 1 animal by touching the screen in 2 example sessions. *A*: the indicated positions of a flashed stimulus at 18-deg viewing angle before and after shortening of the saccadic amplitude via saccadic adaptation. The preadaptation mean indicated position in this session was 17.4 ± 0.9 deg, and the postadaptation mean indicated position was 15.6 ± 2.0 deg. *B*: the indicated positions before and after lengthening of the saccadic amplitude. The preadaptation mean indicated position was 17.1 ± 1.2 deg, and the postadaptation mean indicated position was 18.0 ± 1.3 deg.

and this was also the case in our data. In Fig. 2, the time constants that are given for the two presented example sessions show that the monkey adapted faster in the saccadic shortening session. The mean rate constant for all sessions of both monkeys was $t = 72.7 \pm 58.2$ saccades for saccadic shortening, whereas for saccadic lengthening it was $t = 249.3 \pm 196.6$ saccades. The higher rate constant for saccadic lengthening indicates that lengthening adaptation might not be fully saturated after 400 trials. A higher number of adaptation trials would thus lead to stronger amplitude modification in amplitude lengthening but would have only little or no effect on the induced amount of adaptation in amplitude shortening. After the saccadic amplitude had been modified, we again measured the touched position on the screen in the localization trials. In Fig. 3, the positions that were touched by one monkey in the localization trials before and after the saccadic adaptation phase are shown for two example sessions. In the session displayed in Fig. 3*A*, the saccadic amplitude was shortened, and in Fig. 3*B*, the saccadic amplitude was lengthened. The 20 trials in the preadaptation phase were used to calculate a mean preadaptation baseline position, and the 20 trials of the postadaptation phase were used to calculate the mean deviation in located position from the baseline.

The results from both monkeys are presented in Fig. 4. *Monkey I* completed three sessions with amplitude shortening and four sessions with amplitude lengthening. In the three sessions with saccadic shortening, a significant mean saccadic amplitude change of -2.9 ± 0.7 deg (2-tailed *t*-test, $P = 0.02$)

was induced. The adaptation induced also a significant mislocalization compared with the baseline localization of -1.4 ± 0.5 deg (2-tailed *t*-test, $P < 0.05$). The amount of induced mislocalization was significantly smaller than the saccadic amplitude change (1-tailed paired *t*-test, $P = 0.04$).

In the four sessions with amplitude lengthening, we found significant saccadic amplitude change of 1.0 ± 0.4 deg (2-tailed *t*-test, $P = 0.01$) and also an adaptation-induced mislocalization of 0.6 ± 0.2 deg (2-tailed *t*-test, $P = 0.01$). In contrast to amplitude shortening, there was no significant difference between saccadic amplitude change and mislocalization (2-tailed paired *t*-test, $P = 0.15$) after amplitude lengthening. The total amount of mislocalization was 2.3 times higher after amplitude shortening than after amplitude lengthening (2-tailed paired *t*-test, $P = 0.04$).

In the condition of adaptive amplitude shortening, we found stronger adaptation than in the condition of amplitude lengthening (2-tailed paired *t*-test, $P = 0.01$). The amplitude change in the condition of amplitude shortening accounted for 70% of the 4-deg target step, whereas the amplitude change after amplitude lengthening accounted only for 25% of the 4-deg target step. Thus the saccades ended much closer to the shifted target during amplitude shortening, inducing a smaller postsaccadic error during the major part of the adaptation phase compared with amplitude lengthening. The results from *monkey II* are presented in Fig. 4, *right*. This animal completed four sessions with amplitude shortening and three sessions with amplitude lengthening. Saccadic adaptation induced a signifi-
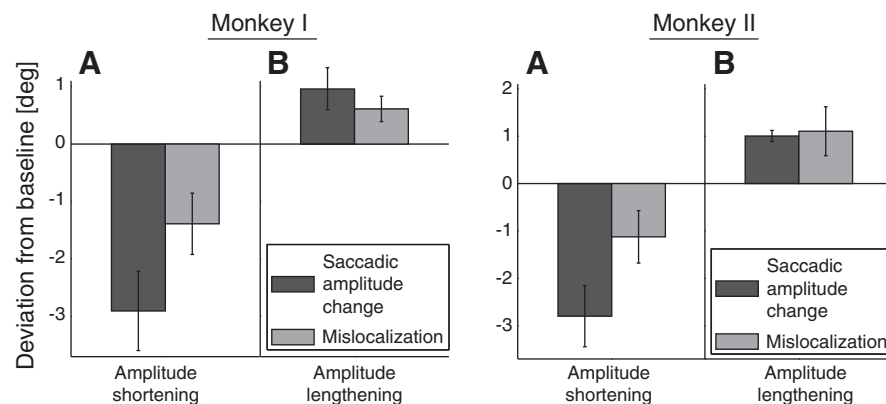

Fig. 4. Mean localization results from both animals. Dark gray bars represent the mean adaptation level of each monkey in the inward adaptation sessions in *A* and the outward adaptation sessions in *B*. Light gray bars represent the mislocalization of the flashed stimulus in both adaptation sessions.

cant mean saccadic amplitude change of -2.7 ± 0.6 deg (2-tailed t-test, $P < 0.01$) in the four sessions with saccadic shortening. The adaptation also induced a significant mislocalization of -1.1 ± 0.5 deg (2-tailed t-test, $P = 0.03$). Similar to findings in *monkey I*, the amplitude change and the mislocalization differed significantly (2-tailed paired t-test, $P < 0.01$) in the condition of amplitude shortening.

In the three sessions of *monkey II* with amplitude lengthening, we found significant saccadic amplitude change of 1.0 ± 0.1 deg (2-tailed t-test, $P < 0.01$) and also an adaptation-induced mislocalization of 1.1 ± 0.5 deg (2-tailed t-test, $P < 0.05$). As in *monkey I*, there was no significant difference between saccadic amplitude change and mislocalization (2-tailed paired t-test, $P = 0.8$) after amplitude lengthening. In contrast to *monkey I*, *monkey II* showed the same total amount of mislocalization after amplitude shortening and lengthening (2-tailed paired t-test, $P = 0.9$).

Finally, in the condition of adaptive amplitude shortening, we again found stronger adaptation than in the condition of amplitude lengthening in this monkey (2-tailed paired t-test, $P < 0.01$).

DISCUSSION

Two monkeys were trained to indicate the position of a briefly flashed stimulus with the hand on a touch screen while holding fixation on a presented fixation spot during the whole trial. Both animals showed a significant offset in touched position after their saccadic amplitudes had been altered, even though no saccade was executed during these localization trials. We regard the positions at which the monkey touched the screen as a measure of localization of the presented target, and thus as an indicator of perceived position, similar to experiments in humans (Collins et al. 2007; Schnier et al. 2010; Zimmermann and Lappe 2009, 2010). Alternatively, one may consider the touch position as the end point of a reaching movement, i.e., the result of another motor action. In this case, our findings demonstrate that saccadic adaptation transfers to reaching movements, or that saccade and reaching movements share a common representation of target location. However, in humans, effects of saccadic adaptation on perceived location have been shown with several different methods [pointing (Bruno and Morrone 2007; Cotti et al. 2007; Hernandez et al. 2008), verbal or perceptual report (Awater et al. 2005; Moidell and Bedell 1988), or probe placement with a mouse pointer (Collins et al. 2007; Schnier et al. 2010; Zimmermann and Lappe 2009)], suggesting that a common representation of object location in all these cases is affected by saccadic adaptation.

The results of our study can be summarized in the following way. First, we found an adaptation-induced change in saccade amplitude in both conditions in both monkeys. Second, mislocalization of the flashed stimulus occurred after adaptation in both conditions in both monkeys. Third, this mislocalization was in all cases in the same direction as the saccade amplitude change. Fourth, the saccadic amplitude change was stronger after amplitude shortening than after amplitude lengthening in both monkeys. Fifth, in one monkey the change of localization position was stronger after amplitude shortening than after amplitude lengthening. This was not the case in the other monkey. Finally, after amplitude shortening, the change in

localization position was smaller than the change in saccade amplitude, whereas both changes were of comparable magnitude after amplitude lengthening. This was true in both monkeys.

The differences in amplitude change between amplitude shortening adaptation and amplitude lengthening adaptation provide further support for the view that saccadic lengthening and shortening are based on partial different mechanisms within the adaptation process (Catz et al. 2008; Cecala and Freedman 2009; Cotti et al. 2009; Ethier et al. 2008a; Hernandez et al. 2008; Miller et al. 1981; Panouilleres et al. 2009; Semmlow et al. 1989; Straube and Deubel 1995; Straube et al. 1997; Zimmermann and Lappe 2009).

Our findings on mislocalization show agreement with earlier results in human subjects, but they also show some interesting differences. In the first experiment of Zimmermann and Lappe (2010), which used the same adaptation paradigm as our study, human subjects showed mislocalization only after lengthening adaptation but not after shortening adaptation. Our findings in monkeys agree very well for saccadic lengthening, but in contrast to findings in humans, saccadic shortening also influenced localization.

However, the second experiment of Zimmermann and Lappe (2010) showed that mislocalization also can occur after shortening adaptation provided that a constant error was applied throughout the adaptation trials. In this constant-error adaptation, the saccadic landing end point was calculated online while the saccade was executed and the target was shifted to a position with a constant offset from the landing position.

Zimmermann and Lappe (2010) proposed that saccade adaptation for amplitude shortening is so fast that the postsaccadic error is reduced too quickly to establish effects on localization. Adaptive lengthening, which follows a slower time course in both humans (Ethier et al. 2008a; Hernandez et al. 2008; Miller et al. 1981; Panouilleres et al. 2009; Straube and Deubel 1995) and monkeys (Cecala and Freedman 2009; Straube et al. 1997), can lead to localization errors through an adaptive change of saccade target representation that is slow and takes effect only if a large postsaccadic error persists over a large number of trials. The constant-error paradigm also established this situation for saccade shortening in humans and hence also leads to mislocalization also in this situation. This explanation would be consistent with our result that normal saccadic shortening influences localization in monkeys, since adaptation is generally slower in monkeys than in humans (Albano 1996; Deubel 1987; Frens and Van Opstal 1994; Straube et al. 1997; Watanabe et al. 2003), leading to a longer persistent error during saccade shortening adaptation in monkeys compared with humans.

It is well established that saccadic adaptation is not a singular mechanism but affects multiple stages of the oculomotor transformation and that fast adaptive amplitude shortening and comparatively slow adaptive lengthening must involve at least in part different stages [see Hopp and Fuchs (2004) and Pelisson et al. (2010) for review]. Studies on adaptation time courses and dynamics suggested on the one hand a forward model with adaptation via modifications of internal monitoring as a possible adaptive mechanism and, on the other hand, direct modification of the saccade steering motor command and thus of a target representation stage (Chen-Harris et al. 2008; Ethier et al. 2008b; Xu-Wilson et al. 2009). In the model of Chen-

Harris et al. (2008), a large postsaccadic error size, which occurs enduringly in slow adaptive lengthening, leads with increased probability to modifications of the target representation stage. Moreover, these modifications might result in modified target localization. Thus this size-dependent error assignment could account for the differences between adaptive shortening and lengthening and, furthermore, for the differences between fast-adapting humans and slow-adapting monkeys in adaptation-induced mislocalization.

We conclude that saccadic adaptation affects localization in monkeys in a way comparable to how it affects localization in humans. Slower adaptation in monkeys than in humans might lead to a stronger contribution of target representation stage modifications to the adaptation process in monkeys that yields mislocalization after both adaptive shortening and lengthening. Furthermore, the slower amplitude change during amplitude lengthening than during shortening leads to longer remaining large postsaccadic errors. These errors in turn may lead via error assignment to modifications of the target representation stage and associated changes in localization.

GRANTS

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.G., A.B., P.F., and M.L. conception and design of research; S.G. and A.B. performed experiments; S.G. and A.B. analyzed data; S.G., P.F., and M.L. interpreted results of experiments; S.G. prepared figures; S.G. drafted manuscript; S.G., A.B., P.F., and M.L. edited and revised manuscript; S.G., A.B., P.F., and M.L. approved final version of manuscript.

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