How does saccade adaptation affect visual perception?

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Three signals are used to visually localize targets and stimulate saccades: (1) retinal location signals for intended saccade amplitude, (2) sensory-motor transform (SMT) of retinal signals to extra-ocular muscle innervation, and (3) estimates of eye position from extra-retinal signals. We investigated effects of adapting saccade amplitude to a double-step change in target location on perceived direction. In a flashed-pointing task, subjects pointed an unseen hand at a briefly displayed eccentric target without making a saccade. In a sustained-pointing task, subjects made a horizontal saccade to a double-step target. One second after the second step, they pointed an unseen hand at the final target position. After saccade-shortening adaptation, there was little change in hand-pointing azimuth toward the flashed target suggesting that most saccade adaptation was caused by changes in the SMT. After saccade-lengthening adaptation, there were small changes in hand-pointing azimuth to flashed targets, indicating that 1/3 of saccade adaptation was caused by changes in estimated retinal location signals and 2/3 by changes in the SMT. The sustained hand-pointing task indicated that estimates of eye position adapted inversely with changes of the SMT. Changes in perceived direction resulting from saccade adaptation are mainly influenced by extra-retinal factors with a small retinal component in the lengthening condition.

Introduction

Neural control of the oculomotor system is calibrated to enable the ocular-muscle plant to produce accurate eye movements that match intended eye movements. Uncalibrated eye movements would result in differences between intended and actual position of the retinal image and errors in perceived direction that are similar to space distortions that can be demonstrated by pressing gently on the side of an eye. Calibration is especially critical for saccadic eye movements that are ballistic in nature and lack visual feedback to guide their ongoing responses. The mapping between a target location and the muscle commands that are required to move the eye changes over time because of normal growth of the plant, neurological, or muscular damage, optical distortions due to spectacles, instability of neural control, and other factors (Abel, Schmidt, Dell'Osso, & Daroff, 1978; Kommerell, Olivier, & Theopold, 1976; Optican, 1985). Thus, the oculomotor system must constantly be recalibrated to maintain accurate saccadic eye movements. We are interested in knowing how this recalibration influences perceived visual direction.

To study the recalibration process, one has to introduce a change in the sensory-motor mapping. This can be done by using a saccadic adaptation paradigm such as the McLaughlin, or double step, paradigm in

which a saccade target is presented and then displaced before the saccade is completed. Prior to adaptation, the displacement introduces an error between the perceived location of the final target position of the double-step stimulus and the muscle command intended to move the eye to the initial target position (Hopp & Fuchs, 2004; McLaughlin, 1967). Within a few trials, the initial saccade amplitude is adjusted to minimize the visual error produced by the displacement. The perceived direction of a flashed saccadic stimulus is also affected by saccade adaptation (Bahcall & Kowler, 1999). We used the double-step paradigm to adapt saccades and a pointing task to investigate how such adaptation affects perceived direction.

Two control signals determine saccade amplitude: the estimates of retinal localization for intended saccade amplitude and the sensory-motor transform of retinal signals into muscle innervation signals (Grossberg & Kuperstein, 1986; Kawato, 1999). This transformation process can be characterized by a feed-forward model similar to those described by Bullock, Cisek, and Grossberg (1998) and Robinson (1975). In those models, a target is first represented as a retinal localization signal for intended saccade amplitude. Then the intended movement is converted to a motor innervation signal for execution. Neural correlates (efferent or reafferent) of eye position provide estimates of current eye position, and these must be calibrated to match the intended saccade amplitude in order to maintain perceptual stability during and immediately following a saccade.

To understand how perception is affected by saccade adaptation, we had people point with an unseen hand to a flashed target while holding fixation straight ahead (flashed condition) or while maintaining fixation on an eccentric target (sustained condition). The relevant signals are the estimate of the retinal position of the target ($\hat{R}$, which is in retinal coordinates), the estimate of eye position from extra-retinal signals ($\hat{E}$, head coordinates), and the sensory-motor transform of sensed retinal position to motor innervation. We assume a proportional mapping between actual and estimated positions, which is appropriate for our simple experimental situations but has been shown to be problematic under more complex circumstances (Awater, Burr, Lappe, Morrone, & Goldberg, 2005; Collins, Doré-Mazars, & Lappe, 2007; Ross, Morrone, & Burr, 1997). We assume that those estimates are subject to random and systematic error, and that the systematic error is multiplicative (Freeman & Banks, 1998). Thus,

$$\hat{R} = \rho R \tag{1}$$

$$\hat{E} = \varepsilon E, \tag{2}$$

where R and E are the actual positions of the retinal stimulus and the eye, respectively, and ρ and ε are the scale factors that transform the physical positions to the

estimated positions. Eye-position estimates could be computed by scaling either efference copy or proprioceptive signals by ε. The estimate of target eccentricity in head coordinates ($\hat{T}$) is given by the sum of the retinal and the extra-retinal estimates: $\hat{T} = \hat{R} + \hat{E}$. To move the eye to an estimated target location, the system must estimate retinal eccentricity and apply the sensory-motor transform to the eye (μ):

$$E = \mu \hat{R}. \tag{3}$$

To point the hand to an estimated location, the system must estimate eccentricity relative to the head and apply the appropriate sensory-motor transform to the hand (α):

$$A = \alpha(\hat{R} + \hat{E}). \tag{4}$$

We were interested in determining which of these parameters change during saccade adaptation. Is the change in saccade amplitude due to changes in the sensory-motor transform, to changes in retinal localization, or both? We were also interested in determining if saccade adaptation is associated with changes in perceived visual direction, and if so, are changes in perceived direction a consequence of changes in estimates of retinal localization, of sensed eye position, or of a combination of changes in both estimates? We measured the saccade amplitude and the direction of hand pointing to flashed and sustained targets before and after adaptation to quantify changes in the parameters ρ, ε, and μ in the above equations and to determine which signals are involved in saccade adaptation. Because our adaptation paradigm does not involve the hand, we assumed that α does not adapt and that changes in hand pointing are due to changes in the other signals.

From Equations 1 and 3, the amplitude of a saccade to a target flashed at position R is $E = \mu \rho R$. Thus, a change in the motor or retinal gain (μ or ρ) affects the amplitude of the resulting saccade. We can only measure E and R, so we can only estimate the product of the two gains and not the individual gains from the ratio of saccade amplitude before and after adaptation. Freeman and Banks (1998) made the same point for estimating the gains of retinal-motion signals and extra-retinal, eye-velocity signals. We circumvented this problem by using a hand-pointing task toward fixated and eccentric targets.

Bahcall and Kowler (1999) conducted a study that is related to ours. They examined how saccade adaptation affects perceived location of saccadic targets using the double-step paradigm. After adaptation, subjects made saccades to the remembered location of a briefly flashed target. Once they were fixating at the remembered location, subjects indicated whether the original saccade target had been to the left or right of a flashed visual probe. After saccade-lengthening adaptation, the probe had to be

positioned more eccentrically, and after saccade-shortening adaptation, it had to be placed less eccentrically than the original target location. Thus, subjects mislocalized the original target location in the same direction that the saccade had adapted. Bahcall and Kowler noted that subjects perceived the probe as being in the same direction as the remembered saccade-target location (once it was fixated). From this, they concluded that saccade adaptation was of the sensory-motor transform, and that post-adaptation localization errors resulted from estimates of eye position based on an adapted efference copy signal or on an unadapted planned eye movement signal that was upstream from the site of adaptation. However, it is possible that the retinal signal for intended saccade amplitude was also adapted and that the efference copy signal was recalibrated to match the adapted retinal signal. Adaptation of retinal localization could cause a change in the length of the saccade to the remembered target (Hopp & Fuchs, 2004) without changing the gain of the sensory-motor transform. However, physiological studies indicate that saccade adaptation includes adjustments of the sensory-motor transform at the level of the cerebellum, which adjusts the activity of saccade signals in the brainstem (Desmurget et al., 1998). Thus, saccade adaptation could involve all three levels of saccade control, and perceptual distortions could involve both the estimates of retinal signals for intended saccade size and the estimates of eye position from extra-retinal signals.

Some studies have investigated adaptation of retinal signals for saccade adaptation and their influence on perceived direction by having subjects point with an unseen hand to a flashed target without making an eye movement (de Graaf, Pélisson, Prablanc, & Goffart, 1995; Kröller, de Graaf, Prablanc, & Pélisson, 1999; McLaughlin, Kelly, Anderson, & Wenz, 1968). They found little if any effect of adaptation suggesting that the retinal signal was not adapted. There has been no direct test for adaptation of the sensed extra-retinal eye-position signals. We developed procedures for measuring changes in estimated retinal localization and changes in sensed eye position.

In our first experiment, we had subjects point with the unseen hand to a briefly flashed target without moving the eyes. We call this the *flashed-pointing task*. Because the eyes did not move, we assume that $\hat{E} = 0$ and therefore that Equation 4 becomes

$$A = \alpha \rho R. \tag{5}$$

Any change in perceived direction after saccade adaptation had to have been caused by changes in retinal localization. This experiment is similar to that of Kröller et al. (1999). They found small changes in retinal localization, which suggests that most of saccade adaptation is caused by recalibration of sensory-motor-transform signals.

In our second experiment, we had subjects make a saccade to a double-step target whose final position was

sustained at the same location as the pre-adapted saccade stimulated by a single step (compare Figure 2C with Figure 2D, respectively). Thus, the amplitudes of the pre- and post-adapted saccades were the same. One second after the second step was presented, subjects pointed an unseen hand at the final target. We call this the *sustained-pointing task*. Because the eyes were fixated on the target when the pointing occurred and because of the length of the delay, changes in pointing were attributable to changes in sensed eye position rather than retinal localization. Kröller et al. (1999) conducted a similar experiment, but in their case, saccade amplitudes were different before and after saccade adaptation, so differences in eye position could have affected pointing, making it impossible to isolate the effect of changes in extra-retinal signals for sensed eye-position.

Adaptation of retinal and motor-transform gains

We have estimated the adapted gain ratio for the retinal signal from experiments that measure pointing of an unseen hand to a flashed target. In this task, observers keep their eyes still and point to a flashed target position, so that the eye position signal (E) and its corresponding estimate $\hat{E} = \varepsilon E$ are both zero. We assume that because the eye remains still, the eye position is normalized to zero and that this does not change during adaptation. Adapted gain ratio is measured as the ratio of pre- and post-adapted hand-pointing responses. Thus, the estimated hand posi-tion should correspond to the estimated retinal location of the target: $\hat{A}_f = \hat{T}_f = \hat{R}_f$. Subscript f denotes that this is the flashed task, and * indicates that a measurement, estimate, or gain is post-adaptation. Using Equations 1 and 4 and taking the ratio of the pre A_f and post A_f* tests, we have

$$\frac{A_f^*}{A_f} = \frac{\alpha \rho^* R_f}{\alpha \rho R_f} = \frac{\rho^*}{\rho}. \tag{6}$$

Thus, our task allows us to directly measure the ratio of the adapted and unadapted retinal gains.

Because eye position is computed from the product of retinal and motor-transform gains, the adaptation in gain of the combined retinal and motor signals ($\rho^* \mu^* / \rho \mu$) can be estimated directly from measures of adapted saccades. The adaptation of the sensory-motor-transform gain (μ^*/μ) can be calculated from the ratio of the saccade amplitudes to the initial step size before (E) and after (E^*) adaptation and the retinal gains before (ρ) and after (ρ^*) adaptation:

$$\frac{E_f^*}{E_f} = \frac{\mu^* \rho^* R_f}{\mu \rho R_f} = \frac{\mu^*}{\mu} \cdot \frac{\rho^*}{\rho}. \tag{7}$$

It is reasonable to assume that pointing movements to visual stimuli presented to a stationary eye are directed by the same retinal or perceptual signals that control voluntary saccades (Cotti, Guillaume, Alahyane, Pelisson, & Vercher, 2007). We assume that before the experiment, the sensory-motor transform of retinal signals for pointing the hand has been calibrated with visual feedback and that the calibration of the hand is not affected by saccade adaptation because there was no feedback for accuracy of hand pointing during the experiment. The posterior parietal cortex has been shown to be involved in integrating cues for both saccade and reach planning (Andersen, Essick, & Siegel, 1985; Cohen & Andersen, 2002; Pouget & Sejnowski, 1997), suggesting that hand pointing would be a useful tool for dissociating changes in visual sensory-motor signals.

Adaptation of estimated eye position

The motor plan for pointing the unseen hand is computed from the difference between perceived target direction and an estimate of the hand's current direction. Ideally, estimated eye-position would equal actual eye position because the estimates are continuously recalibrated whenever the plant is changed by fatigue, injury, aging, or development. Note that in our experiments, we change visual signals to mimic the effects of an altered physical plant (Scudder, Batourina, & Tunder, 1998). If saccade adaptation causes estimated eye position to be recalibrated, then estimated eye position would become unequal to actual eye position, and the mismatch would produce errors in pointing the unseen hand. In our experiments, it is possible that changes in estimated eye position could be calibrated based on changes in estimated saccade size, changes in the gain of retinal or sensory-motor-transform signals for saccades or their combination as described in the model.

The errors in hand pointing in the sustained-pointing task were used to measure changes in the gain of extra-retinal eye-position estimates ($\varepsilon^*/\varepsilon$): The subscript s indicates that this is a sustained task.

$$\frac{A_s^*}{A_s} = \frac{\alpha \varepsilon^* E_s}{\alpha \varepsilon E_s} = \frac{\varepsilon^*}{\varepsilon}. \tag{8}$$

Methods

Subjects

Seven subjects, three males and four females, ages 23–33, took part in the experiments. All were right-handed and had normal or corrected-to-normal vision with contact lenses. KC and JW were the only ones who were not naïve to the experimental goals. None of the subjects had prior experience with the pointing apparatus. All subjects gave written informed consent before beginning the experiment. Because subjects were either emmetropes and did not wear glasses or had ametropia corrected with contact lenses, neither of these refractive conditions would produce optical distortions that would stimulate saccade adaptation.

Apparatus

Eye position was recorded with the Eyelink II tracking system, which has a sampling rate of 500 Hz. The subject's head was stabilized using a bite bar and a forehead rest. Figure 1 depicts a side and plan view of the apparatus. An unseen arm–hand-pointing apparatus was placed directly below the perceived location of the targets.

Pointing direction was measured by having subjects rotate an unseen vertical metal rod (pointer) beneath the perceived location of a visual target. Holding the rod near its tip, subjects rotated its far end with their dominant hand. The pointer's pivot was directly below the midpoint of the interocular axis (i.e., the cyclopean eye). Position was measured with an optical encoder (A2 Absolute Encoder from US Digital) and converted to units equivalent to visual angle.

Visual stimulus

The binocular visual stimulus was displayed using a Wheatstone-mirror haploscope composed of two 20-inches. monochrome CRTs (Monoray Model M20ECD5RE; Clinton Electronics, IL, USA), operating at a 120-Hz non-interlaced frame rate with 1280 × 1024 resolution. The
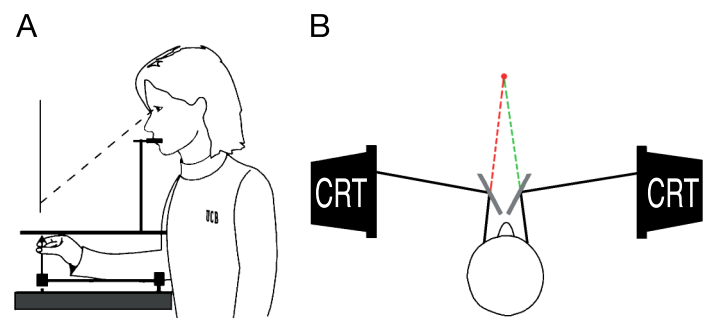

Figure 1. Experimental apparatus. (A) Side view. Visual targets were displayed −17° below straight-ahead, and the hand and arm were hidden by a board. Subjects used a pointing rod located below the board that rotated horizontally about a pivot to indicate perceived target direction. (B) A plan view of the display apparatus. An image is displayed to each eye individually via two CRTs and two mirrors.

haploscope allowed us to present pure version stimuli along the isovergence circle without any change in binocular parallax. The monitors have a fast DP-104 phosphor, which decays to 0.1% of the peak luminance in 0.6 ms, which is critical to preventing ghost images with flashed stimuli. The optical distance and the binocular convergence distance of the visual stimuli were closely matched at 36 cm for subjects KC, JW, AC, and AL. The optical distance was 32.3 cm, and the vergence distance was 29 cm for EP, LC, and SS (the change being required by a modification of the apparatus for another experiment).

The visual stimulus was a small 5-pixel dot, which subtended 0.17°. It was displayed at various azimuths in Helmholtz coordinates along the isovergence circle at an elevation of −17° below primary position. Points along an isovergence circle stimulated pure vergence angles of either 9.53° (36-cm vergence distance) or 11.8° (29-cm vergence distance) and pure version movements of 12°. Vergence varied slightly with individual subjects' inter-pupillary distance (IPD). The curved horizontal movement (azimuth) of the pointer placed it at the same distance as the binocular visual target. The pointer had a constant distance from the cyclopean eye but the viewing distance of the Vieth–Muller circle measured from the cyclopean eye becomes reduced as azimuth increases. In the straight-ahead position, the distance of the pointer and the binocular vergence were the same. At the largest target eccentricity (11° azimuth), the distance of the Vieth–Muller circle was reduced by 0.5 cm. The experiments were conducted in a dark room to prevent subjects from using other images as a frame of reference and to maintain the adapted state.

Paradigm

Subjects performed two pointing tasks with an unseen hand before and after adapting saccades to the double-step stimulus. In the flashed-pointing task, they pointed at a briefly flashed peripheral target without moving the eyes from the starting fixation point. In the sustained-pointing task, they made a saccade from the starting position to a sustained peripheral target resulting from the double-step stimulus described above, and after 1 sec, they pointed their unseen hand at the fixated sustained target. Subjects were instructed to point at the perceived location of the visual targets, and they were not given feedback about the accuracy or position of the pointer during the experiment. Both tasks were run in the same session before (pre) and after (post) adapting the amplitude of saccades to the double-step stimulus. The flashed-pointing task was designed to measure adapted gain (ρ^*/ρ) of the estimated retinal signal (see Equation 6), and the sustained-pointing task was designed to measure adapted gain of estimated eye position ($\varepsilon^*/\varepsilon$) (see Equation 8). Adapted gain of the sensory-motor-transform signal (μ^*/μ) was calculated from the combination of eye-position information, measured in

the sustained-pointing task, and the measured adapted gain of the retinal signal from the flashed-pointing task (see Equation 7). The details of the tasks are described in the subsections below.

The experiment was run in three stages: pre-adapted-pointing trials, saccade adaptation, and post-adapted-pointing trials. At least 75 flashed-pointing trials were presented in both pre- and post-adapted stages. At least 110 sustained-pointing trials were presented in the pre-adapted stage, and 95 in the post-adapted stage. The trials in the post-adapted stage contained a double step in order to maintain the adaptation. Because some trials were discarded due to inappropriate eye or hand movements, additional trials were presented to ensure that we would have sufficient trials for analysis. There were more sustained-pointing trials than flashed-pointing trials because the pre-adapted sustained trials were used to obtain baseline data for saccade size and post-adapted sustained-pointing trials were used to maintain the double-step adapted response. Each pointing task was presented in blocks of 10 trials. The blocks alternated between the flashed- and sustained-pointing tasks. The adaptation stage (described below) had 450 saccades in which subjects were instructed to aim their eyes at the jumped target and not move their unseen pointing hand.

Separate experiment sessions were run for two saccade-adaptation conditions: (1) saccade-shortening (hypometric) adaptation and (2) saccade-lengthening (hypermetric) adaptation. Hypometric adaptation resulted in decreased amplitude of rightward saccades. Hypermetric adaptation resulted in increased amplitudes of rightward saccades.

Adaptation stage

During the adaptation stage of the experiments, subjects fixated a dot at −5° azimuth and pressed a button to begin each trial. The fixation point remained visible for 400–600 ms, after which the target jumped either −6° (to the left of fixation) or 12° (to the right). In trials containing a leftward step, the target remained fixed. In trials containing a 12° rightward step, the target remained visible until a saccade was detected (on-line version velocity of 40 deg/s or more), and then the target was stepped either −4° (hypometric adaptation) or +4° (hypermetric adaptation). Figure 2A depicts a sample hypometric target stimulus and resulting saccade from the adaptation phase of the experiment.

Although all subjects reached a stable hypometric adaptation endpoint in fewer than 200 trials, approximately 300 double-step trials were needed to achieve a significant and stable hypermetric adaptation endpoint. In order to provide a comparison between adaptation sessions of equal duration for the two conditions, 300 double-step trials were included in the adaptation stage for both hyper- and hypometric conditions. One hundred fifty single-step trials (−6° azimuth) were used to prevent
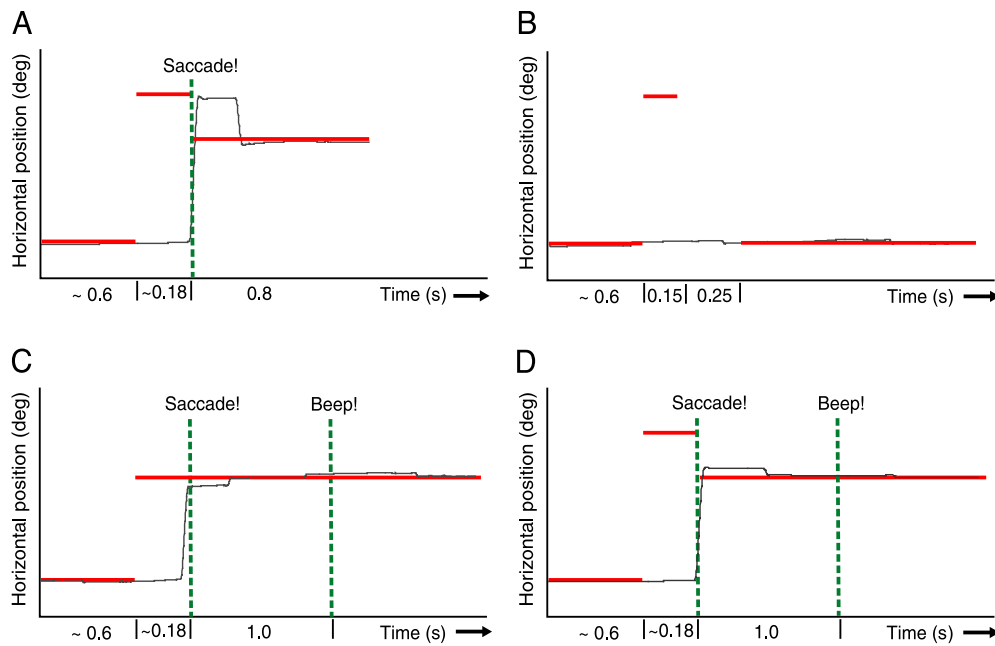
Figure 2. Time courses of the visual stimuli and examples of saccadic responses. Red lines indicate target position. Black lines are sample eye-position traces. (A) Double-step hypometric adaptation trials. (B) Targets in the flashed-pointing task. (C) Pre-adaptation targets for pointing in the sustained-pointing task. (D) Post-adaptation hypometric targets for pointing in the sustained-pointing task. The eye trace in panel A is from an early trial in the adaptation stage. The dotted green lines labeled *Saccade* indicate that the tracker has detected an eye movement. In the flashed-pointing task, subjects pointed after seeing the flash. In the sustained task, they pointed after hearing a beep that occurred 1 s after detection of the saccade.

anticipatory saccade movements. Following adaptation, subjects performed two pointing tasks.

Point to a briefly flashed target

On each trial, a fixation point was first presented at −5° (to the left of straight ahead), and subjects positioned the pointer below its perceived location. They then pressed a button to begin the trial. As illustrated in Figure 2B, the fixation point remained visible for 400–600 ms after which it was extinguished, and then another target was flashed for 150 ms at −11°, 3°, or 7° (step sizes of −6°, 8°, and 12°, respectively). Two hundred fifty milliseconds after the flash, the fixation point reappeared to help subjects maintain a steady eye position while pointing the unseen hand at the perceived location of the flashed target. Subjects pressed a button, and the pointing response was recorded. After every trial, the screen was blanked for 1 s before a new fixation point appeared at −5°. Twenty-five trials of each step size were recorded. Trials in which the subject blinked or made a saccade were automatically discarded by the computer and placed back into the trial queue. Likewise, trials in which pointing movements began less than 150 ms after the flash (classified as anticipatory hand movements) or those taking longer than 2.5 s were also automatically discarded. Some trials were discarded offline due to eye drift or

button-press error. Average pointing response time for this task was 1.05 s after the flash.

Point to a sustained target

In this task, a fixation dot was presented at either −5° or −11°. As in the flashed-pointing task, subjects were asked to position the pointer below the perceived location of the fixation point. As illustrated in Figure 2C (pre-adapted stimulus), the subject pressed a button to start the trial and then the fixation point remained visible for 400–600 ms. Immediately after the fixation point disappeared, a target was displaced −6°, 8°, 12°, or 16° from the fixation point. The fixation positions of −5° and −11° were used to extend the range of step sizes within the available field of view and were used for both the hypo- and hypermetric adaptation conditions. Once the displaced target appeared, subjects made a saccade to it and maintained fixation on it for 1 s. One second after the saccade was detected, a brief beep sounded indicating that the subject should point in the perceived direction of the target. Trials in which subjects moved their unseen pointing hand before the beep or took longer than 2.5 s to complete the movement were discarded and placed back in the trial queue.

The pre-adaptation fixation stimulus (Figure 2C) was designed to produce baseline data for unadapted saccade sizes. The hypometric adaptation stimulus (Figure 2A)

jumped 12° and then back to 8° from fixation (−4° change), and the hypermetric adaptation stimulus (not shown) jumped 12° and then to 16° from fixation (4° change). Baseline measures of pre-adapted saccade amplitude were taken with single-step stimuli. The pre-adapted hypometric test stimuli (Figure 2C) had 15 single-step trials with 12° steps and 70 with 8° steps. The pre-adapted hypermetric test stimuli had 15 single-step trials with 12° steps and 70 with 16° steps. The 8° and 16° pre-adaptation steps equaled the final post-adapted sustained eye position of the sustained-pointing condition. Twenty-five 6° steps were also included in both hyper and hypometric pre-adaptation conditions to prevent anticipatory eye movements. The pre- and post-adapted stimuli also presented −6° steps to prevent anticipatory saccades to the right.

The post-adapted hypometric test stimuli illustrated in Figure 2D had 95 hand-pointing trials. Double-step saccade stimuli were presented to preserve the adaptation response in the post-adapted test trials. Seventy double-step trials were presented in which a target was jumped rightward 12° from fixation and then stepped backward 4° (hypometric condition) or forward 4° (hypermetric condition) once the subject's initial saccade had been detected by a computer algorithm. The sustained-pointing task was performed for the same final sustained eye position in the pre (Figure 2C)- and post-adapted (Figure 2D) test conditions. As with the pre-adapted test stimuli, 25 trials were included to a single target step of −6° to prevent anticipatory movements. Because there was no eye movement in the flashed-pointing task, adapted saccade amplitude was calculated from the initial saccadic response to the 12° step in the sustained trials.

Data analysis

Data were recorded and analyzed using customized software and Matlab applications. Statistical tests were performed with Microsoft Excel's Data Analysis Add-In library.

Horizontal-version eye position and velocity traces for each trial were calculated and analyzed off-line. For the purpose of off-line data analysis, saccade onset was automatically identified with a velocity criterion above 25 deg/s. A velocity criterion below 35 deg/s was used to identify saccade-end locations. Saccade starting and ending positions were then verified by inspection. Final eye position was the same in the pre- and post-adapted conditions for the sustained-pointing task; we wanted this to occur so that we could quantify the adapted gain of estimated eye-position.

All hand positions were recorded as the angular rotation about the pivot point located directly beneath the midpoint between the two eyes. Pointing amplitude was defined as final pointer azimuth minus the initial azimuth. This process is referred to as a bias normalization. Because continuous sampling of pointer position interfered with

sampling of eye position (and by extension, with on-line saccade detection), only start and final pointer positions were recorded.

We assumed that unadapted retinal signals for all subjects had no bias. Note, however, that retinal-gain errors for guiding open-loop pointing at peripherally viewed targets can vary with retinal position. Specifically, retinal errors are exaggerated in the periphery and can cause the hand to point beyond targets by as much as 13% (Bock, 1986; Enright, 1995; Henriques, Klier, Smith, Lowy, & Crawford, 1998). We corrected for the varying gain of such signals by taking the ratio of adapted and unadapted response amplitudes for both pointing and saccades.

The ratio analysis quantifies adapted gain of sensory signals (retinal and estimated eye position) within the saccadic system using pointing response of an unseen hand. The values of interest are the ratios of adapted and unadapted gain. For all retinal and sensory-motor trans-forms, we have assumed that adaptation did not produce bias changes in the system, and that any changes in saccade amplitude or hand pointing to our rightward test target were due to adaptation in gains associated with sensory (ρ^*/ρ and $\varepsilon^*/\varepsilon$) and motor ($\mu^*/\mu$) signals. We assume that pointing gain remained constant throughout the experiment because the unseen hand did not move or attempt to point at targets during the adaptation phase of the experiment.

Results

Overview

We calculated the mean normalized pointing and saccade responses for all seven subjects in the hypo- and hypermetric sessions. Figure 3 (top panels) show the mean pre- and post-adapted response amplitudes for (1) initial saccades to the rightward test target, (2) pointing amplitudes to the flashed target, and (3) pointing amplitudes to the sustained target. In both hyper- and hypometric conditions, saccadic adaptation was significant but not complete. We examined pointing responses for each subject in each condition and found that they were unimodally distributed.

Statistical significance was evaluated using a paired, two-tailed t test. In the hypometric trials, the change in saccadic amplitude was significant ($t(6) = 12.88$, $p < 0.0001$). The change in pointing to a flashed target was not significant ($t(6) = 0.16$, $p = 0.88$), but the change in pointing to a sustained target was significant ($t(6) = 5.73$, $p < 0.05$). In the hypermetric trials, change in saccadic amplitude was significant ($t(6) = 7.95$, $p < .001$). The change in pointing to a flashed target was also significant ($t(6) = 3.06$, $p < 0.05$), and the change in pointing to a sustained target was not significant ($t(6) = 1.46$, $p = 0.20$).
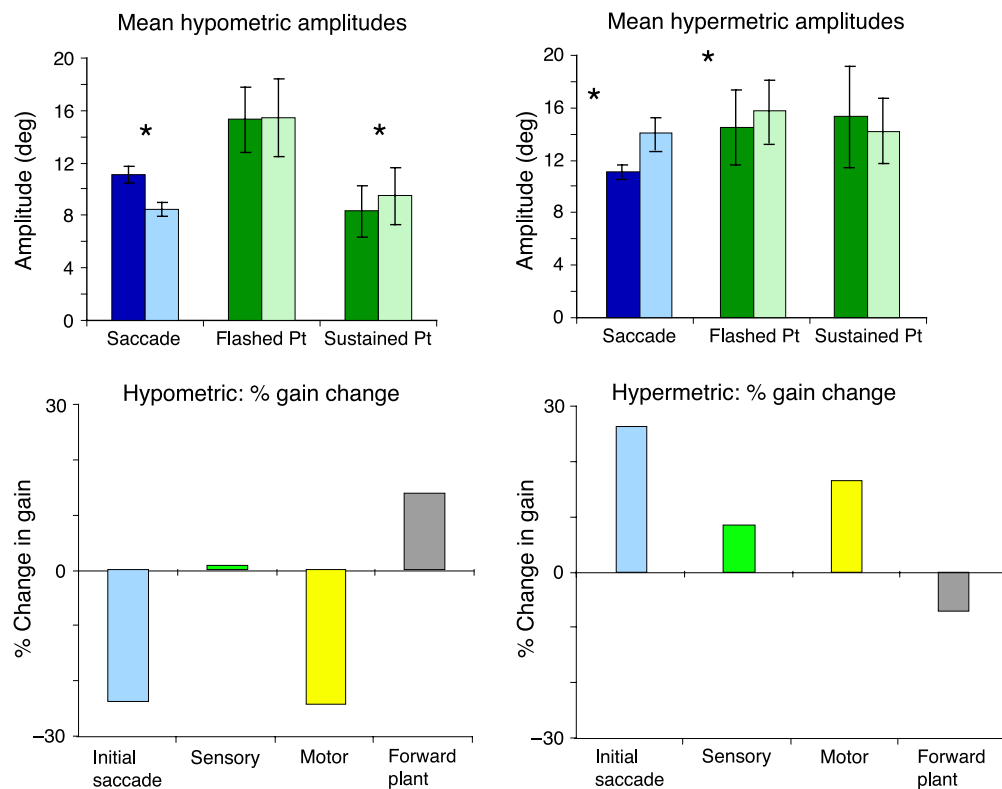
Figure 3. Mean bias-normalized response amplitudes and gain changes (1-adapted gain). Values for the hypometric session are shown in the left column, and values for the hypermetric session are shown in the right column. For all subjects, mean pre-adapted saccade and pointing amplitudes were matched to the location of the visual stimulus. Corresponding post-adapted mean movement amplitudes for each subject were calculated using the relationship between hand and eye movements calculated in the pre-adaptation phase. The top panels show the mean normalized pointing amplitude in the pre-adapted (dark bars) and post-adapted (light bars) conditions. Error bars represent standard deviations of the mean. The bottom panels show the percentage increase or decrease in saccade amplitude (blue bars), retinal gain ρ (green), motor gain γ (yellow), and eye-position gain ε (gray) as calculated from the change in gains in the hypo- and hypermetric conditions. Asterisks in the graphs denote statistically significant changes.

If there were no retinal adaptation in the flashed-pointing task, meaning that all saccade adaptation resulted from changes in gain of the sensory-motor-transform signal (μ), the pre- and post-adapted hand-pointing amplitudes to the flashed target would be equal. We observed this in the hypometric adaptation condition. In contrast, we observed adaptation of both the retinal gain and motor gain in the hypermetric adaptation condition. If the extra-retinal estimated-eye-position gain did not change in the sustained-pointing task, the pre- and post-adapted hand-pointing responses to the sustained target would be equal. Note that in the sustained-pointing task, the final target position, and therefore the sustained eye position were the same in both pre- and post-adapted trials. For both hyper- and hypometric adaptation conditions, the sustained-pointing amplitudes were shifted in the opposite direction from the adapted saccade amplitudes, although the shift was not statistically significant in the hypermetric condition. Thus, when they occurred, shifts in the extra-retinal eye position gain (ε) were inversely related to changes in motor-transform gain (μ).

Figure 3 (bottom panels) illustrate the percentage of adapted gain change (1-adapted gain) for the bias-normalized data. The gains for the sensory-motor transform and estimated eye position adapted in opposite directions for both hypo- and hypermetric adaptation conditions. Retinal gain adapted in the same direction as the sensory-motor-transform gain for the hypermetric condition. There was no adaptation of retinal gain in the hypometric condition.

Saccade adaptation: Individual subjects data

We used the eye movement recordings in the sustained-pointing trials to determine the amplitudes of the initial saccades to the stepped stimulus. By comparing the magnitude of these saccades in the pre- and the post-adapted stages, we were able to quantify the effect of the adaptation on saccade amplitude. Figure 4 shows an example of the time course of adaptation from one subject. Initial saccade amplitudes to the initial 12° step of the double-step target are shown for both the
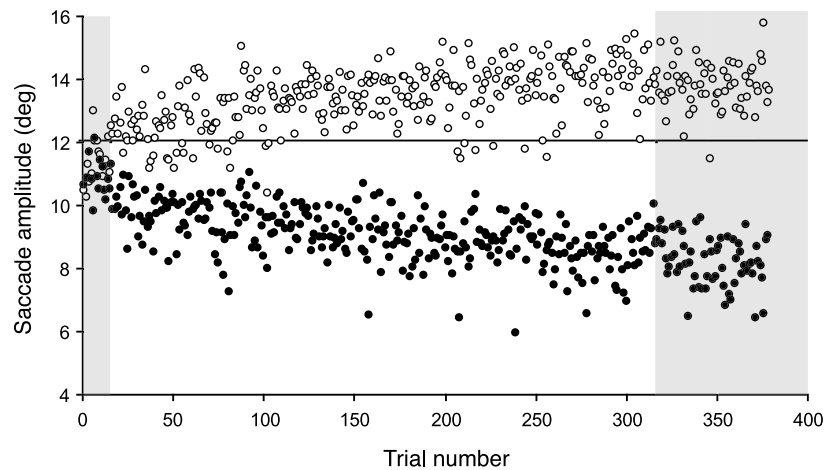
Figure 4. Time course of saccade amplitude during adaptation. Example time course of double-step adaptation, hypometric (filled circles), and hypermetric (empty circles) for subject JW. The left shaded area represents pre-adapted saccade amplitude to targets stepped 12°. The white area shows initial saccade amplitudes during the adaptation stage, and the right shaded area represents post-adapted amplitudes. All subjects adapted more slowly in the hypermetric condition, regardless of the amount of adaptation achieved.

hypometric and the hypermetric adaptation conditions. Note that unadapted saccade amplitudes at time zero exhibited the normal hypometric responses in which the amplitudes were ~10% smaller than the 12° target eccentricity (Becker & Fuchs, 1969). The different time courses observed for adaptation to hypo- and hypermetric stimuli are consistent with previous studies utilizing the double-step paradigm (Hopp & Fuchs, 2004; Kröller et al., 1999; Miller, Anstis, & Templeton, 1981). Significant changes in initial saccadic amplitude were observed for all subjects following the double-step adaptation stage ($p = 0.01$).

Figures 5A and 5B show the mean initial saccade amplitudes for pre- and post-adapted stages in both hyper- and hypometric sessions. Following hypometric adaptation, an average percentage decrease of 23.6° (±3.3°) in rightward saccadic amplitude was observed. Hypermetric adaptation produced a mean amplitude increase of 26.2 (±8.6%). Ratios of post- to pre- adapted initial saccade values for each subject are shown in Table 1.

Flashed hand-pointing task

The flashed-pointing task was designed to measure changes in the gain of the retinal signal following double-step saccade adaptation. Subjects pointed to a briefly flashed target without moving their eyes from the starting position. Mean pre- and post-adaptation-pointing amplitudes for the two directions of saccade adaptation are shown in Figures 5C and 5D. Note that the unadapted-pointing responses to peripheral targets exhibited the normal hypermetric responses in which the amplitudes were larger than the 12° target eccentricity (Bock, 1986; Enright, 1995; Henriques et al., 1998). Mean pre- and post-adapted amplitudes for each subject were compared

using a *t* test ($p = 0.01$). Three subjects showed significant differences in pointing behavior following hypometric saccade adaptation. Subjects AS and AC increased their hand-pointing amplitudes to the target, and EP made smaller hand movements in the post-adapted condition.

Fatigue or criterion changes were accounted for by analyzing pointing to leftward stepped targets. A global change such as fatigue should affect pointing to both leftward and rightward targets. In the hypometric adaptation session, no subject showed a significant change in pointing amplitudes to the leftward −6° stepped target. The shift in mean starting location between pre- and post-adapted stages was also analyzed for each subject. In this session, none of the subjects showed a significant change in starting location between test stages.

Adaptation of retinal gain (ρ^*/ρ) and sensory-motor-transform gain (μ^*/μ) were calculated for each subject and are given in Table 1. Figures 5E and 5F show percentage increase or decrease (1-adapted gain) of the saccadic gain, retinal gain (ρ^*/ρ), and sensory-motor-transform gain (μ/μ^*) for each subject. Adapted gain of the sensory-motor-transform was computed from the ratio of adapted saccade gain and adapted retinal gain (Equation 7). For example, in the hypometric condition, subjects KC, JW, LC, and SS showed no significant change in pointing to the flashed target. These subjects had no measurable change in the gain of their retinal signal so hypometric adaptation can be entirely attributed to a change in sensory-motor-transform gain.

During the experiment, there were two different rightward saccade stimuli that could potentially interact with saccade adaptation. One was the final position of the rightward double-step stimulus, and the other was the refixation saccade from the control target back to the fixation point between each trial. Although saccade adaptation can transfer to non-adapted saccade sizes for
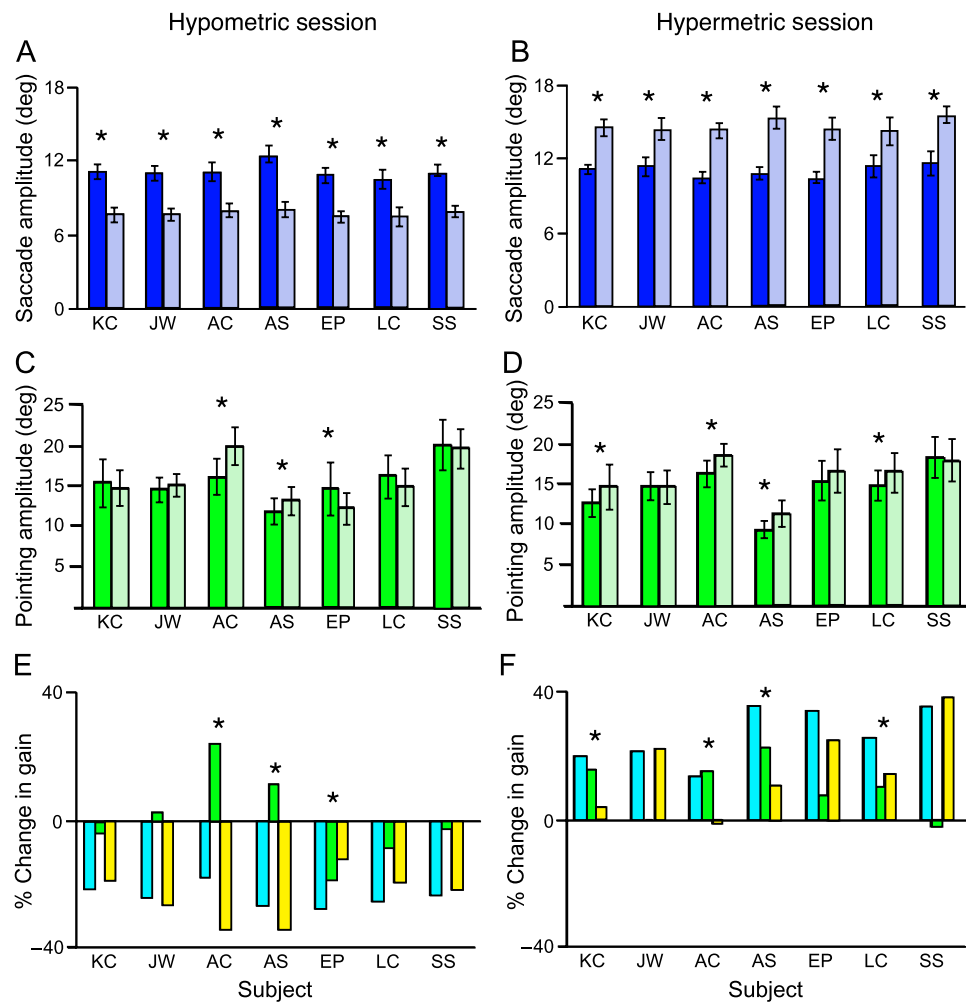
Figure 5. Individual results for the flashed-pointing task. Left column: individual subject results during the hypometric saccade adaptation session. Error bars represent standard deviations. Right column: individual results for hypermetric adaptation. Panels A and B show the mean initial saccade amplitudes to a 12° jumped target during the pre-adapted (dark bars) and post-adapted (light bars) conditions. Adaptation was significant for all subjects. Panels C and D show mean pointing amplitudes to the 12° flashed target in the pre-adapted (dark bars) and post-adapted (light bars) conditions. Panels E and F show the percentage increase or decrease for each subject in saccade amplitude (blue bar), retinal gain (green bar), and motor gain (yellow bar) following double-step adaptation. Asterisks indicate statistically significant changes.

targets presented at the same starting point (Noto, Watanabe, & Fuchs, 1999), there is little transfer to saccades with different starting and ending points that lie outside of the adaptation field (Collins et al., 2007; Deubel, 1987; Frens & van Opstal, 1997; Noto et al., 1999). The starting position of our rightward refixation saccade and adaptation stimulus differed by 6 degrees, and the endpoints for these two saccades were 11 degrees apart, and the saccades occurred in non-overlapping regions of space. Thus, it is unlikely that the refixation saccade from the leftward jump would enter and interfere with saccade adaptation field to the double-step stimulus that is localized about the saccade endpoint (Collins et al., 2007; Deubel, 1987; Frens & van Opstal, 1997; Noto et al., 1999).

Sustained hand-pointing task

The sustained-pointing task was designed to measure recalibration of eye-position estimates due to changes in the gain of extra-retinal signals ($\varepsilon^*/\varepsilon$). Subjects made saccades to a double-step stimulus whose second step was sustained. After fixating the second step for 1 s, they pointed in the perceived direction of the fixated stimulus. Figures 6A and 6B show mean pre- and post-adapted-pointing amplitudes for each subject in the hypo- and hypermetric sessions, respectively. Note that in the sustained-pointing task, the pre-adapted hand-pointing responses for most subjects were not hypermetric as they were for peripheral-pointing amplitudes in the flashed-pointing task. This is because the retinal error in the

	Hypometric				Hypermetric			
Subject	Adapted saccade gain (E*/E)	Adapted retinal gain (ρ^*/ρ)	Adapted motor gain (μ^*/μ)	Adapted EEP gain ($\varepsilon^*/\varepsilon$)	Adapted saccade gain (E*/E)	Adapted retinal gain (ρ^*/ρ)	Adapted motor gain (μ^*/μ)	Adapted EEP gain ($\varepsilon^*/\varepsilon$)
KC	0.784	0.966	0.811	1.208	1.196	1.153	1.037	1.133
JW	0.763	1.029	0.742	1.119	1.210	0.995	1.216	0.863
AC	0.824	1.244	0.662	1.143	1.135	1.150	0.987	0.984
AS	0.735	1.117	0.658	1.194	1.352	1.222	1.106	1.086
EP	0.725	0.825	0.879	1.066	1.336	1.075	1.243	0.925
LC	0.746	0.919	0.812	1.059	1.255	1.099	1.141	0.858
SS	0.770	0.977	0.788	1.189	1.352	0.982	1.378	0.801

Table 1. Calculations of adapted gain for each observer. The adapted saccade gain was calculated by taking the ratio of the sizes of the initial saccades before and after adaptation. The adapted retinal gain ratio (ρ^*/ρ) was calculated as in Equation 6 as the ratio of the hand-pointing amplitudes in the flashed-pointing task. The adapted motor gain (μ^*/μ) was calculated as in Equation 7 as the adapted saccadic gain divided by the retinal gain. The adapted gain of estimated eye position (EEP) ($\varepsilon^*/\varepsilon$) was calculated as in Equation 8 as the ratio of the hand-pointing amplitudes in the sustained-pointing task. Asterisks indicate post-adapted states.

sustained-pointing task was zero and the hypermetric response in the flashed-pointing task was due to an exaggerated gain of peripheral retinal signals (Henriques et al., 1998).

Figures 6C and 6D show the percentage change in estimated eye-position gain for each subject (1-adapted gain). In five of the seven subjects, pointing amplitudes in

the sustained task increased significantly after hypometric saccades ($p = 0.01$). The observed shift is in the opposite direction to the change in the saccade lengths. The adapted gain for estimated eye position for each subject, calculated with Equation 8, is shown in Table 1. Following hypermetric adaptation, pointing amplitudes to the sustained target decreased for four of seven subjects
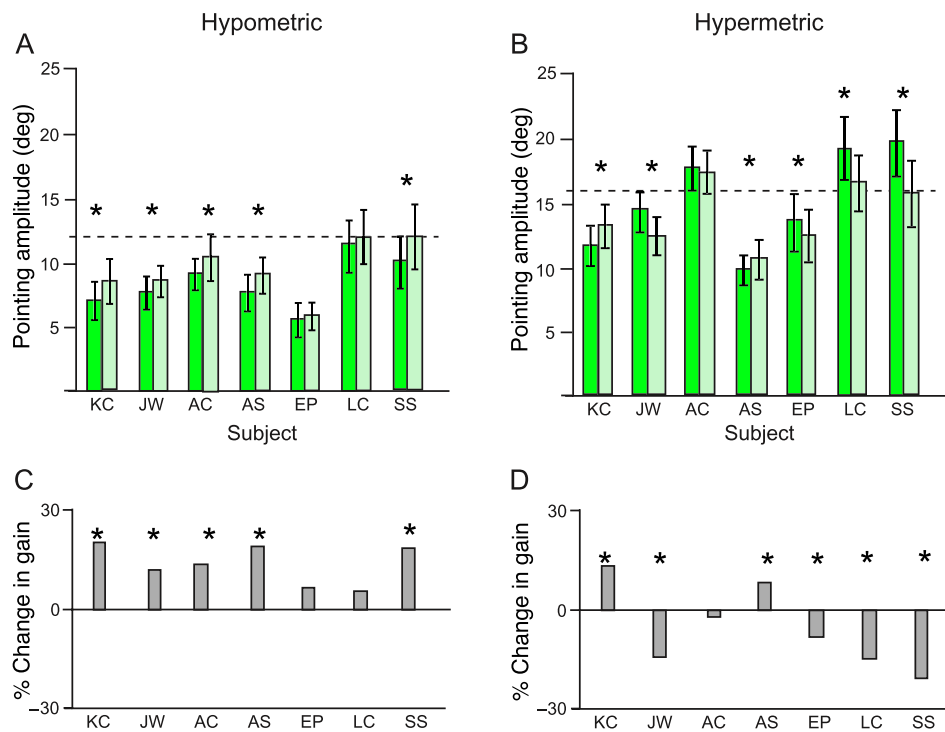

Figure 6. Individual results for the sustained-pointing task. Left column: pre-adapted and post-adapted results for individual subjects during the hypometric experiment session. Error bars represent standard deviations. Right column: Hypermetric session results. Panels A and B show mean pointing amplitudes to a sustained visual target for the pre-adapted (dark bars) and post-adapted (light bars) conditions. Target location is represented by the horizontal dashed line. Panels C and D show the percentage increase or decrease in eye-position gain (ε) for each subject. Asterisks show statistically significant changes.

and increased for two. In this session, subjects AS and KC exhibited a global outward shift with a significant increase in pointing amplitude in the post-adapted stage.

Discussion

We used two pointing tasks with an unseen hand to investigate the effects of saccade adaptation on perceived direction. To measure changes in the retinal and extra-retinal signals, we had to isolate them. We did so by using two pointing tasks. In the flashed-pointing task, we limited the source of target location information for the hand to retinal signals. The resulting shifts in pointing in this task suggest changes in gain for the retinal signals for controlling saccades. In the sustained-pointing task, the final target was at the same pre- and post-adaptation location, so subjects' fixation direction was the same before and after adaptation. In this case, the target is on the fovea, so the error associated with the retinal signal is presumably zero. Changes in pointing suggest adapted changes of gain of the extra-retinal, estimated eye-position signal. Changes in the transformation from retinal signals to a motor command were inferred from the amount of saccadic adaptation not accounted for by adaptation of retinal signals, implying that most of the adaptation in the saccadic shortening paradigm was due to this transformation. In the saccade lengthening condition, about 2/3 of the adaptation was caused by changes of the sensory-motor transform. The sustained hand-pointing task indicated that estimates of eye position adapted inversely with changes of the sensory-motor transform. Changes in perceived direction resulting from saccade adaptation are mainly influenced by extra-retinal factors with a small retinal component in the lengthening condition.

There are three possible sites in the control pathway for saccades that may be recalibrated during saccade adaptation (retinal signals for intended eye position, sensory-motor-transform signals, and extra-retinal eye-position signals). The posterior parietal cortex (PPC) contains areas that have been shown to be involved in saccade and reach responses (Cohen & Andersen, 2002; Snyder, Batista, & Andersen, 2000). Because the PPC receives sensory signals from vision, proprioception, and auditory signals (Andersen, Snyder, Bradley, & Xing, 1997; Batista, Buneo, Snyder, & Andersen, 1999), this area is thought to facilitate motor planning for both the oculomotor and the reaching systems by transforming perceptual information into a common coordinate system (Cohen & Andersen, 2002). This close physiological connection between saccade and reach responses suggests that open-loop pointing (unseen hand) is a useful tool to measure changes in sensory signals related to saccade adaptation. In the open-loop arm-hand-pointing task, the visual system provides an estimate of target direction from a retinal signal and an extra-retinal eye-position signal.

Previous studies

Most of our subjects showed some gain change in their sensory-motor-transform signal for both directions of adaptation. This is consistent with previous studies that attributed the bulk of saccade adaptation to low-level motor signals (Desmurget et al., 1998; Frens & van Opstal, 1994; Wallman & Fuchs, 1998). Our experiment also shows that it is possible for the gain of retinal signals that control saccade amplitude to undergo modification. Several prior studies have also measured the transfer of saccade adaptation to pointing (Cotti et al., 2007; Kröller et al., 1999; McLaughlin et al., 1968). McLaughlin et al. (1968) found no transfer of adaptation to pointing movements and concluded that saccade adaptation did not affect the perceived location of a visual target. However, the duration of their adaptation period was brief (12 trials). While there were enough trials to induce a significant change in saccadic amplitude, they may not have been long enough to induce retinal adaptation or changes in estimated eye position as observed by Moidell and Bedell (1988). Kröller et al. (1999) examined pointing to an eccentric flashed target while maintaining central fixation (similar to our flashed-pointing task) and pointing to remembered target locations when accompanied by a saccade. Following hypometric saccade adaptation, they observed a small transfer of saccade adaptation to pointing movements without eye movement and no change in pointing when saccades preceded the pointing movement. Our analysis of their data indicates that most of the hypometric saccade adaptation was due to adaptation of the sensory-motor-transform gain, and there was also a smaller adaptation of retinal signal gain. They also reported no significant transfer of saccade adaptation to pointing the unseen hand in either task following hypermetric adaptation. They attributed this to fatigue. However, our analysis indicates that hypermetric saccade adaptation in their experiment was entirely attributable to changes in the gain of the sensory-motor transform. Cotti et al. (2007) also measured perceptual localization following hypometric adaptation of voluntary saccades using a pointing task that was similar to our flashed-pointing condition. Their subjects pointed an unseen hand at the saccade target while fixating straight ahead, and they found significant changes in pointing following adaptation to large 30-degree saccades, but not to smaller 20-degree saccades.

Several other studies have used visual probes to estimate retinal gain changes following saccade adaptation. Following a double-step saccade adaptation paradigm, with the eye fixating straight ahead, Moidell and Bedell (1988) used a flashed visual probe to estimate the location of a target flashed at the same horizontal

eccentricity (8.3 degrees) as the saccade adaptation stimulus. They observed 14.9% and 8.8% shifts, respectively, of estimated target location that were in the same direction as the adapted hypometric and hypermetric saccades. Using a similar technique, Collins et al. (2007) used a visual probe after hypometric saccade adaptation to measure perceptual localization. While fixating straight ahead, the location of the visual probe was adjusted to appear at various locations about a 12-degree saccade target, and they found no change in localization judgments before and after saccade adaptation. Using a different probe technique, Bahcall and Kowler (1999) reported that subjects mislocalized remembered targets in a direction toward their adapted saccadic eye position following hypometric and hypermetric adaptation to a double-step 4-degree saccade. Their subjects made saccades to a remembered target location and then reported whether the original target had been to the left or right of a visual probe. They observed that direction estimates of the location of a flashed probe were shifted in the direction of saccade adaptation such that targets flashed at the (adapted) saccade landing position were perceived as aligned with the pre-saccade target. They suggested two possible signals for estimating eye position and perceived direction. One signal represented a "high-level" planned eye movement upstream from the adapted sensory-motor transform. This would be an afferent signal similar to an unadapted pre-saccade retinal signal in the current study that would be used to estimate post-saccadic eye position. The other proposed signal was an adapted efference copy signal downstream from the adapted sensory-motor transform. The efference copy signal would be adapted to match estimates of post-saccadic eye position with the retinal signal prior to the saccade. The unadapted high-level signal would be a more parsimonious explanation because it would only require adaptation of the sensory-motor transform and not efference copy signals.

Both groups of studies suggest similar interpretations for our observation of no or small change in retinal gain following saccade adaptation. Our novel result is that we observed larger changes in spatial localization after hypermetric than hypometric adaptation, and we interpret these as changes in retinal gain (i.e., changes in afferent signals to the sensory-motor transform). Our results indicate that estimates of perceived direction are mainly influenced by adaptation of extra-retinal signals for eye position and also a small retinal component that was observed in the lengthening (hypermetric) condition.

Differences between hypometric and hypermetric saccade adaptation

We observed differences between the two types of saccade adaptation that have been reported before (Hopp & Fuchs, 2004; Kröller et al., 1999; Miller et al., 1981). Most of our subjects showed some gain change in their

sensory-motor-transform signals for both directions of adaptation. This is consistent with previous studies that attributed the bulk of saccade adaptation to low-level motor signals (Desmurget et al., 1998; Frens & van Opstal, 1994; Wallman & Fuchs, 1998). However, our experiment shows that it is also possible for the gain of retinal signals that control saccade amplitude to undergo modification as well. The amount of retinal adaptation induced by the double-step paradigm varied across subjects and with direction of adaptation (hypometric vs. hypermetric). Saccadic-gain changes for four of seven subjects in the hypometric direction can be attributed entirely to adaptation of sensory-motor-transform signals. The retinal signal was unchanged. Subjects AC and AS exhibited an unexpected increase in retinal gain, even though their saccade size decreased. Pointing to a control saccade target in the leftward direction revealed no evidence of fatigue or other global change in either of these subjects. The shift might be explained if the decreased gain of sensory-motor-transform signals had overcompensated during the 300-trial adaptation stage and required an increase in retinal gain to produce the hypometric saccade. In the hypermetric session, a large portion of saccade adaptation remained in the motor-transform signals, but four of seven subjects showed a smaller but significant increase in the gain of the retinal signals.

The presence of retinal gain adaptation in the hypermetric adaptation could result from an asymmetry in ability to adapt gain of the sensory-motor transform to hypometric and hypermetric stimuli. Inspection of the bar graph in Figures 5E and 5F illustrates greater gain changes (1-adapted gain) of the sensory-motor transform (μ) in the hypometric than hypermetric adaptation conditions but similar overall amplitudes of saccade adaptation. This resulted from more adaptation of the retinal gain in the hypermetric condition. It is possible that the retinal gain changes occur to supplement the limited adaptation of the sensory-motor transform to hypermetric stimuli. The asymmetry of retinal gain adaptation to hypermetric and hypometric adaptation stimuli could also be related to elevated gain of retinal signals that are normally present for peripheral stimuli (Henriques et al., 1998) that cause exaggerated pointing responses to peripherally flashed targets.

Thus, we infer that adapted changes in retinal gain improved accuracy of saccades to the double-step adaptation stimulus; however, they did not necessarily improve accuracy of pointing responses with the unseen hand. In a natural viewing situation, saccade adaptation to conditions such as muscle paresis occurs when the hand is seen. Under those conditions, visual feedback is used to teach the sensory-motor-transform signals for both the eye and the hand to calibrate accurate pointing responses. Otherwise, if only retinal gain were adapted, it would produce accurate saccades, but inaccurate hand pointing. In contrast, adjusting saccade amplitude by adapting the gain

of the sensory-motor transform will only change saccade gain but will not influence the accuracy of hand-pointing initiated by retinal signals. Thus, under natural viewing conditions in which the hand is visible, it would be more parsimonious to adapt saccades by only changing the sensory-motor transform. Retinal gain adaptation is more complex because it also requires an additional adaptation of the sensory-motor transform for the hand. Thus, retinal gain adaptation may only supplement weak sensory-motor adaptation.

Adaptation of estimated eye position

Optical distortions and changes in muscle morphology are two general problems that produce errors of saccade amplitude and associated estimates of direction. In contrast, adaptation to disorders involving the sensory-motor transform that produced errors or instability of saccade amplitude would not necessarily produce errors of estimated direction that were based on extra-retinal signals. Optical magnification distortions can be produced by spectacle lenses or any magnifiers placed before the eyes. Because the eye rotates behind a stationary spectacle lens, prismatic distortions increase as the visual axis moves away from the optical axis of the spectacle lens. With a magnifier, eye rotations must be larger than the angular eccentricity sensed while viewing along the optical axis of the lens. This discrepancy will result in hypometric errors of saccade amplitude and overestimation of target eccentricity following completion of the inaccurate saccade. Changes in muscle morphology that restrict eye mobility such as muscle paresis also produce hypometric errors of saccade amplitude and overestimation of target eccentricity following the inaccurate saccade. Both of these effects require increased innervation to achieve accurate eye movements. If extra-retinal estimates of eye position were unaffected by saccade adaptation, this would lead to errors in perceived direction that were based on estimated of eye position. Ideally, eye position estimates should change inversely with changes in saccadic gain to preserve accurate estimates of direction. For example, if a muscle was weakened by 50%, some combination of retinal gain and the sensory-motor transform gain would be increased by a factor of two to restore normal movement. This increase would cause errors in estimated eye position unless the gain of the eye position estimate were reduced by 50%. Although the change in saccade size and the change in estimated eye position were not significantly correlated, it is possible that the adaptation of sensed eye position would have been more complete in both hypermetric and hypometric conditions if subjects had received visual feedback about the hand-pointing accuracy. Indeed, before estimated eye position has adapted, recent muscle paresis produces anomalous perceptual shifts during changes in eye position known as oscillopsia, and errors of pointing

an unseen hand, known as past pointing (Matin et al., 1982; Perenin, Jeannerod, & Prablanc, 1977). These errors decline in time (Abel et al., 1978), presumably with adaptation of estimated eye position in response to visual feedback.

The second part of our study (the sustained-pointing task) was designed to reveal changes in extra-retinal estimates of eye position which are based on neural correlates of eye position including reafference and/or efference copy signals. In our saccade adaptation task, pre- and post-adapted innervation signals for controlling eye position were the same so that any changes in pointing could result from scaling these signals.

Ideally, eye position estimates should change inversely with saccade gain, which varies with the gain of both the sensory-motor transform and of retinal signals. Changes in sensory-motor transform dominated the changes in adapted saccade amplitude, and additional retinal changes mainly occurred in the hypermetric condition (see Table 1). Accordingly, an inverse correlation is expected with changes in estimated eye position and changes in sensory-motor transform in both hypermetric and hypometric conditions and with retinal changes in the hypermetric condition. This analysis assumes that estimates of eye position use an efference copy signal originating downstream from the site of saccadic adaptation. No changes in efference copy signals would be necessary if eye position estimates were based on an afferent site that was upstream from the adapted sensory-motor transform or on proprioceptive signals. However, the changes observed in the sustained-pointing task indicate that efference copy signals have been adapted.

Indeed, in both hyper- and hypometric saccade adaptation, estimated eye position gain changed for the majority of subjects in the opposite direction to saccade adaptation and the changes in sensory-motor-transform gain (see Table 1). In both hypo- and hypermetric adaptation, the estimates of eye position adapted inversely to the gain change in the sensory-motor transform and the direction of saccade adaptation. However, the change in estimated eye-position gain was not significantly correlated to the magnitude of the saccadic adaptation in the hypometric condition ($r = 0.375$, $p > 0.05$) or the hypermetric condition ($r = -0.223$, $p > 0.05$). The changes in estimated eye-position gain and sensory-motor-transform gain were not significantly correlated in the hypometric condition ($r = -0.450$, $p > 0.05$) or the hypermetric condition ($r = -0.744$, $p > 0.05$; however, note that $p = 0.055$ in the hypermetric condition).

Changes in estimated eye position were highly correlated with changes in retinal gain in the hypermetric but not the hypometric condition (hypermetric condition: $r = 0.855$, $p < 0.05$; hypometric condition: $r = 0.450$, $p > 0.05$). However, the correlations were positive rather than in the expected negative direction. The positive correlation between changes in retinal gain and estimated eye position appears to result from the negative correlation

between changes in retinal gain and sensory-motor transform (hypermetric condition: $r = -0.952$, $p < 0.001$; hypometric condition: $t = -0.798$, $p < 0.05$). The negative correlation indicates that retinal gain changed most when changes in sensory-motor transform gain were smallest.

Individual differences

While all subjects adapted their eye movements, they differed in which specific signals changed and in how they responded in the two adaptation conditions. In the hypometric condition, two subjects showed a statistically significant increases in gain for both the flashed-pointing and sustained-pointing tasks, one subject showed a significant decrease in gain in the flashed-pointing task only, three showed significant increases in the sustained-pointing task only, and one showed no change in gain for either task. In the hypermetric condition, one subject showed a significant increase in gain for the flashed-pointing task only, two showed increases in both tasks, one showed an increase for the flashed-pointing task and a decrease for the sustained-pointing task, and three showed decreases in the sustained-pointing task only. Despite the heterogeneity of pointing responses, all of the subjects showed significant changes in saccadic amplitude. We contend that this demonstrates the plasticity of the brain in responding to changes in the world. Our task did not indicate to subjects which signal to adapt, and thus it is not surprising that they took different pathways to achieve the same end.

Acknowledgments

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