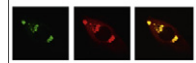


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Research Report

Long term retention of saccadic adaptation is induced by a dark environmental context

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ARTICLE INFO

Article history:

Accepted 9 October 2012

Available online 15 October 2012

Keywords:

Saccadic adaptation

Environmental context

Motor learning

Motor memory

ABSTRACT

Under many circumstances, motor memory needs to be retained for a long period of time to enable accurate behavior. Since the first introduction of the saccadic adaptation paradigm in 1960s, saccadic adaptation protocols have been widely used to study the mechanisms of motor learning and motor memory. However, previous studies reported that the effect of saccadic adaptation on the oculomotor system was rather short (minutes to hours) in human and non-human primates. Here we ask whether the fast decay of the effects of saccadic adaptation is due to the influence of environmental context. To test this hypothesis, we asked human subjects to perform a saccadic adaptation task in a very dark environment. Our data showed that saccade gain remained at the post-adaptation level 24–72 h after exposure to the saccadic adaptation task without significant recovery, and that the effect of saccadic adaptation on saccade gain could still be found 2 months later, much longer than previously reported. Our results indicate a vital role for environmental context in the retention of saccadic adaptation.

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1. Introduction

Adapting our behavior to compensate for changes either in ourselves or in the surrounding environment relies on the brain's ability to modify behavioral output for a given sensory input when either internal or external circumstances change. For instance, if a subject has weakened extraocular muscles in one eye, they will experience diplopia because of the incongruence of the two eyes. This diplopia can be corrected either by patching the intact eye or by wearing a prism goggle in front of the weakened eye (Abel et al., 1978; Kommerell et al., 1976; Lewis et al., 1999). The two eyes resume congruence by adjusting the oculomotor parameters of

the weakened eye (motor learning/adaptation). Adaptation protocols have served as useful behavioral models to study motor learning and motor memory in both clinical and laboratory research settings (Choi and Bastian, 2007; Reisman et al., 2007). Saccadic adaptation is considered an ideal paradigm because of the relatively simple structure of the extraocular muscles (only six muscles controlling each eye), as well as our relatively extensive understanding of the neural control of saccadic eye movements (Barash et al., 1991a; Dorris et al., 1999; Goldberg et al., 2002; Munoz and Wurtz, 1995a, 1995b; Schall and Hanes, 1993; Schlagrey et al., 1992; Snyder et al., 2000; Zhang and Barash, 2000). The most frequently used saccadic adaptation paradigm in

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the laboratory is the so called double-step target task (McLaughlin, 1967). In this task, the visual saccade target is surreptitiously and systematically displaced during the saccade providing misleading feedback to the oculomotor system. Because of the reduction of visual sensitivity during saccades (saccadic suppression), subjects rarely notice the displacement of the saccadic target if the changed eccentricity is less than 1/3rd of the target's original eccentricity (Campbell and Wurtz, 1978; Jeffries et al., 2007). As a result, the amplitudes of saccades adjust (adapt) based on the continuous existence of the post-saccadic retinal error signal, i.e. the difference between the endpoint of executed saccade and the visual target. Usually, it takes hundreds of trials in human and 1000–3000 trials in monkey for saccadic adaptation to develop (Alahyane and Pelisson, 2005; Pelisson et al., 2010; Straube et al., 1997).

It has been argued that in order to keep movements accurate, the effects of adaptation must endure over a long time scale (Robinson et al., 2006). However, studies of adaptation in healthy human and non-human primates have found that the effect of saccadic adaptation only lasts for a brief period of time (minutes to hours) (Deubel et al., 1986; Edelman and Goldberg, 2002; Seeberger et al., 2002; Straube et al., 1997). Even placing subjects in a dark environment after exposure to the saccadic adaptation task, monkeys showed significant recovery of saccadic gain after 20 min (Seeberger et al., 2002). Several more recent studies focused on the retention of saccadic adaptation in human and monkeys (Alahyane and Pelisson, 2005a, 2005b; Robinson et al., 2006). In one study, five human subjects showed significant saccade gain reduction up to 5 days after a single exposure to the backward double-step target task (Alahyane and Pelisson, 2005a). In another study, three rhesus monkeys were trained in a similar task every day for up to 19 days. The effect of saccadic adaptation was marginally longer (7–10 days) compared to a single exposure to the same task (Robinson et al., 2006). Nevertheless, the retention of saccadic adaptation was still not as long as required to maintain accurate behavior over a long time scale. Here we examine why the duration of retention demonstrated in previous experimental conditions is less than that required for long term changes in motor memory. Is it because the decay of motor memory is too fast, or because the influence of other visual signals interferes with motor memory?

It has been demonstrated previously that saccadic adaptation is context specific (context-specific adaptation), i.e. different saccadic gains can be induced by different stimulation paradigms (context states) (Alahyane and Pelisson, 2004; Herman et al., 2009; Shelhamer and Clendaniel, 2002; Shelhamer et al., 2005; Tian and Zee, 2010). This form of “context-specific adaptation” also has been found in other motor systems, such as pointing (Welch et al., 1993) and the vestibulo-ocular reflex (Welch et al., 1998), which suggests that “context-specific adaptation” is a common ability for primates to deal with the complex, dynamic circumstances under natural conditions. When the environment changes, one needs to immediately adapt with an appropriate response. Therefore, it has been suggested that contextual learning of a saccadic adaptation state associated with specific experimental condition could result in persistent

retention despite the influence of normal saccades performed outside the experimental environment (Madelain et al., 2010; Tian and Zee, 2010). We therefore hypothesize that contextual learning plays a vital role in the long-term retention of saccadic adaptation, such that once a state is robustly established, it should persist for a considerable period of time. However, previous studies of “context-specific adaptation” did not address the effect of repeated training. To test this hypothesis, we asked human subjects to perform a backward double-step target task in an extremely dark environment. We measured the change of saccadic gain (saccade-amplitude/target-eccentricity) throughout the experiments. Six out of seven subjects showed no recovery of saccade gain between sessions of saccadic adaptation training, and the effect of saccadic adaptation lasted much longer (more than 2 months) than previously reported. Our results are consistent with previous findings that saccade adaptation is highly context specific, and further demonstrates that repeated training over several days can enhance contextual learning. We found that saccadic adaptation induced in a specific environmental context can persist up to 2 months when subjects are re-exposed to the specific environmental context even when there was no adaptation cue presented.

2. Results

The baseline saccadic gain for each subject was set as saccade gain in the single visual target task (Fig. 1(B)) before exposure of double-step target task. The values of baseline saccade gain of six subjects were 0.93–0.98, which were consistent with previous reports (0.9–0.95) (Becker, 1989). We first analyzed the characteristics of saccade gain in sessions of the double-step target task. Our data showed that, in darkness, there was no significant recovery of saccade gain at the beginning of a training session compared to the previous training session, even when the interval between the two sessions exceeded 3 days. The long-term effect of saccadic adaptation was also reflected in the change of saccade gain in a single target task; during exposure to the double-step target task, the saccade gain in the single target task gradually decreased and was consistently smaller than the baseline saccade gain. More than 2 months after the last exposure to the double-target task, the saccade gain in the single target task was still significantly smaller than the baseline saccade gain.

2.1. Characteristics of saccade gain in the double-step target task

To assess the effect of the backward displacement of the adaptation cue on saccadic amplitude, we calculated the saccade gain of each trial and plotted its value against the time since the first exposure to the double-step task in Fig. 2. Data from each individual subject was presented in a different panel respectively. The short vertical lines in the x-axis of each panel mark the beginning of each session. Day 1 refers to the first day the double-step target task was introduced to the subjects. Subsequent numbers indicate the experiment date relative to day 1. Gray circles represent the saccade gain

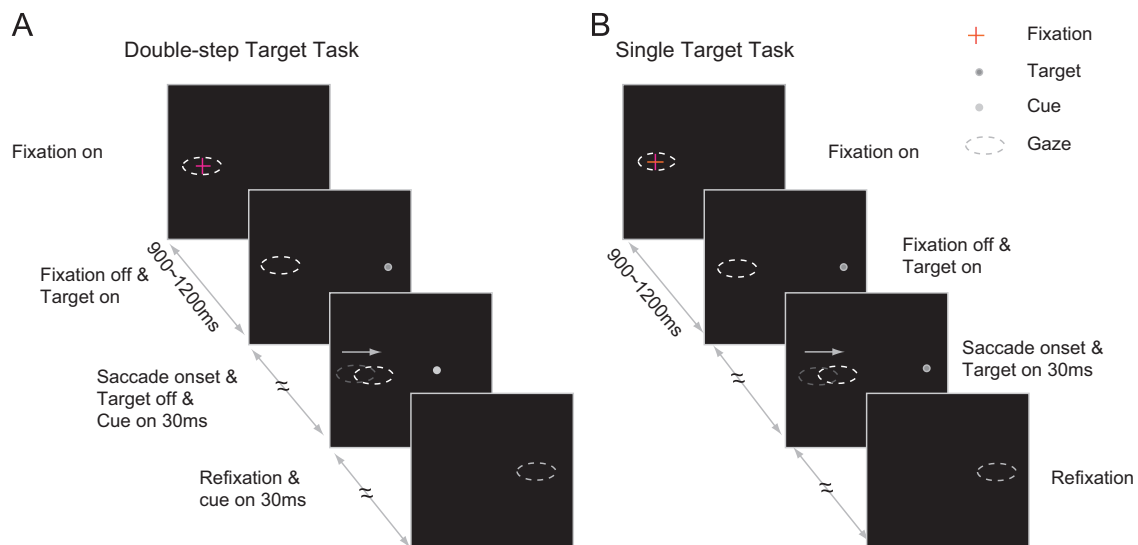


Fig. 1 – Behavioral task. (A) Double-step target task. A trial begins with a fixation cross appearing 7° to the left of the center of the screen. After a variable period (900–1200 ms), the fixation cross would vanish. Simultaneously, a visual target appears randomly at either 12° or 15° horizontally to the right of the fixation cross. As soon as an on-line detection of the initiation of a saccade, the visual target would turn off and the adaptation cue would appear at a position 2/3rd of the eccentricity of the saccadic target away from the fixation and remained on for 30 ms. **(B) Single target task.** Events are similar to the double-step target task but are without an adaptation cue. Also, the possible locations of saccadic target were increased to six, i.e. 9° , 10° , 11° , 12° , 13° and 15° to the right of the fixation cross.

in baseline condition, whereas gray squares depict the saccade gain in double-step target task. All subjects show a transient and fast reduction of saccade gain in the first session of double-step target task. Then, the saccade gain gradually decreases in the following sessions. Comparing saccade gain between two neighboring sessions, five out of six subjects show no significant recovery of saccade gain in the beginning of each session. A single subject (MLN), shown in panel F, does show some recovery of saccade gain in the beginning of each session. To better visualize the profile of the saccade gain distribution for each subject, we calculated the average values of the saccade gain by using a sliding average function (see Section 4). The black and gray line connects the average values respectively. To further analyze whether there is significant recovery of saccade gain in the beginning of each session, we compared the mean value of saccade gain of the beginning 30 trials in a session with the last 30 trials of the previous session. Fig. 3 shows the result of the comparison in a scatter plot. Colored triangles represent data from each individual subject. Qualitatively, all data points are distributed close to the diagonal line without systematic bias. We further statistically tested whether there is biased distribution of data points for each subject by doing two-tailed Wilcoxon test of mean saccade gain. Five subjects show no significant difference between the two sets of data (smallest P value = 0.20). Only one subject (MLN) exhibited a mean value of saccade gain in the first 30 trials of a session that was significantly greater ($P = 2.65 \times 10^{-10}$) than that of the last 30 trials of the previous session. The population data of all six subjects have no significant bias with $P = 0.8398$. These results indicate that there is no significant recovery of saccade gain between sessions of adaptation training in a dark environment.

2.2. The long-term effect on saccade gain in the single target task

To dissociate the long-term effects of saccadic adaptation from the short-term effects, we always started experiments with session(s) of the single target task followed by the double-step target task. The values of saccade gain of the six subjects in single target task are shown in panels of Fig. 4. Gray circles represent the baseline saccade gain whereas gray squares represent saccade gain after exposure to the double-step target task. All six subjects show a transient and quick reduction of saccade gain in the first session after the first exposure to double-step target task. Then, in the following days, some subjects (Subject LY and MLN) show continuous reduction of saccade gain, whereas the other four subjects remain at a constant level. Nevertheless, after initial training of saccadic adaptation, the saccade gain in the single target task is remarkably smaller compared to the baseline saccade gain. Gray squares within the dashed rectangle in each panel depict trials in which the saccadic target's luminance is slightly increased (the value could not be measured by the photometer). All subjects showed an increase of saccade gain in the increased luminance condition. The ratio between the mean saccade gain of each session (with low target luminance) and that in baseline condition is shown in Fig. 5. Symbols with the same color represent data from an individual subject. All of the data points are distributed under the value of 1. A statistical comparison reveals that the saccade gain ratio of population data is significantly less than 1 ($P = 0.0014 - 10^{-52}$, Wilcoxon test). These results indicate that the effect of saccadic adaptation on the oculomotor system is long lasting, and can be measured after more than 24 h and even up to 120 h.

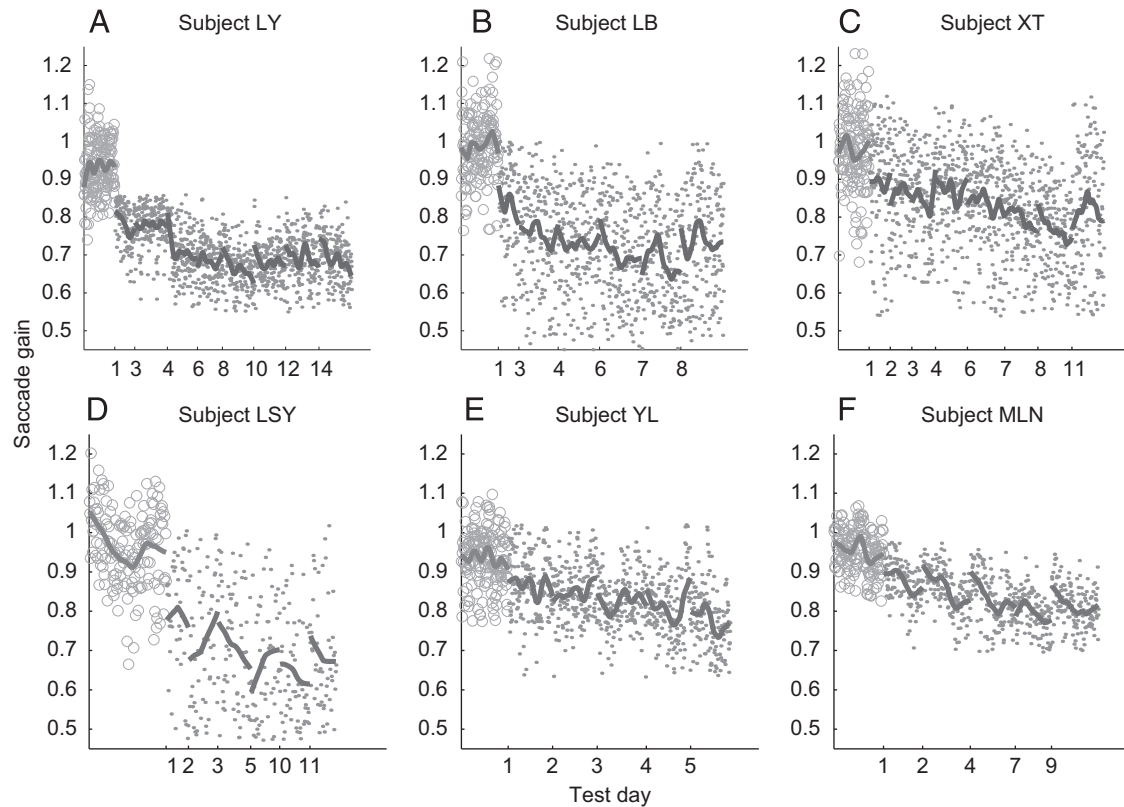


Fig. 2 – Characteristics of saccadic gain in double-step target task. (A–F) Plot the values of saccade gain of each subject as a function of data collection time. The short vertical lines in the x-axis of each panel mark the beginning of each session. Day 1 is the first day of presenting the double-step target task to subjects. Subsequent numbers indicate the experiment date relative to day 1. Gray circles represent the saccade gain in baseline condition, whereas gray squares depict the saccade gain in sessions of double-step target task. A dark gray line connects the average values of saccade gain respectively. Five out of six subjects (A–E) show no significant recovery of saccade gain in the beginning of each session. One subject (F) shows some recovery of saccade gain in the beginning of each session.

Finally, three of the six subjects were available to re-test saccade gain in the single target task more than 2 months after the last exposure to the double-step target task. Each subject's saccade gain data are compared with the baseline saccade gain in Fig 6(A). Gray triangles represent saccade gain in the baseline condition whereas dark circles represent saccade gain 2 months later. The dark gray lines indicate the linear fits (least squared method) of the two data sets respectively. The values of the coefficient of determinacy (R^2) for the regression range from 0.8572 to 0.999. Data from all three of the subjects show that saccade gain after 2 months is significantly smaller than saccade gain in the baseline condition ($P < 0.001$, Wilcoxon test). The two linear regressions are separate from each other and have slopes that are close to zero ($\theta = -3.6223 \times 10^{-5} - 7.2893 \times 10^{-5}$). Although the above analysis indicates that saccade gains do not recover to baseline value after 2 months, it does not provide information about whether the saccade gain is partially recovered. To answer this question, we compared saccade gain in the last day of adaptation training with saccade gain 2 months later. Data are shown in Fig 6(B). The difference between these two sets of data is variable among subjects, but taken as a whole indicate that the effects of saccadic adaptation under these experimental conditions are long lasting. For subject XT, the saccade gain 2 months later is still significantly lower than

that of the last data collection ($P = 3.5523 \times 10^{-18}$, Wilcoxon test); For subject LB, the two sets of data overlapped with each other ($P = 0.9424$, Wilcoxon test). For subject LY, the values of saccade gain two months later are greater than that in the last exposure ($P = 4.7883 \times 10^{-9}$, Wilcoxon test). Such results indicate that the effect of saccadic adaptation on saccade gain is retained over a significantly longer period of time than previously described.

In our present experiments, the luminance of saccadic target was very dim but adaptation cue was relatively bright. It is therefore possible that in the test sessions following saccadic adaptation, the subjects may have made saccades to the remembered location where the relatively bright adaptation cue appeared rather than making visually guided saccades. In other words, subjects might perform saccadic eye movements that were guided by a deliberate strategy. In our double-step target task, the saccadic target randomly appeared either 12° or 15° horizontally away from the fixation point, and the adaptation cue always appeared horizontally with $2/3$ rd of the eccentricity of the target. The larger the eccentricity of the saccadic target was, the greater the distance between the adaptation cue and the target. Therefore, although saccades to both targets exhibit similar saccadic gain, the amplitude of saccades undershoot made to the 15° target was greater than that of those made to the 12° target. To further test whether the

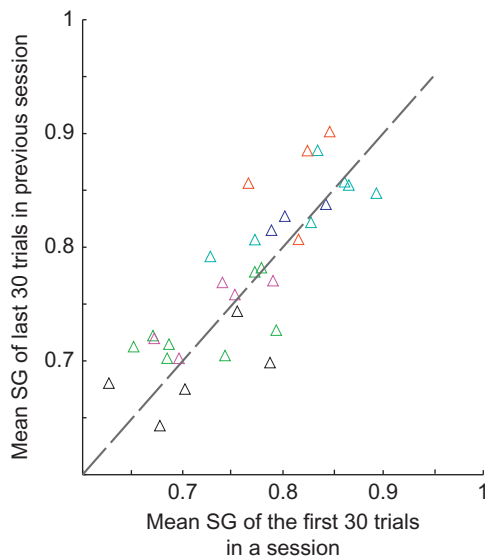


Fig. 3 – Comparison of saccade gain between the first 30 trials of a session with the last 30 trials of previous session. (A–F) Same colored symbols represent data from an individual subject. While one subject (F) exhibits a mean value of saccade gain in the first 30 trials of a session that is significantly greater ($P=2.65 \times 10^{-10}$, Wilcoxon test) than that of the last 30 trials of the previous session, the other five subjects show no statistical difference. The population data of the six subjects have no significant bias with $P=0.8398$ (Wilcoxon test). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

post-adaptation reduction of saccadic amplitude we observed in test was due to the adaptation procedure and not a deliberate strategy, we analyzed the relationship of saccade amplitude with target eccentricity. If the reduced saccadic amplitude was due to the effect of the adaptation procedure, we would expect to see two results: First, a linear relationship between the target eccentricity and saccadic amplitude; Second, the difference between the target eccentricity and the saccadic amplitude gradually increases with increasing target eccentricity. Just as we predicted, the saccade amplitudes linearly increased with increasing target eccentricities (Fig. 7). In addition, when we compared the linear fit between baseline and test condition, six subjects showed a smaller slope in test condition. These results demonstrate that the saccades were guided by the saccadic target.

3. Discussion

In our study, we successfully induced a much longer-lasting adaptation of saccades in a very dark environment. Compared to previous saccadic adaptation studies, our experiments showed two remarkable findings: (1) 24–72 h after exposure to the double-step target task, the saccade gain remained at a similar level as immediately after the saccadic adaptation; and (2) the effect of saccadic adaptation lasted as long as 2 months. Such results suggest that oculomotor memory can indeed persist for a long period, which meets the demand of long-

term retention of motor memory. Our results suggest a vital role of contextual learning in invoking the appropriate adaptation state, and it can be enhanced by repeated training.

Although saccadic adaptation paradigms have been widely used to study the mechanisms of motor learning and memory in both humans and monkeys, most of the previous studies focused either on addressing the characteristics of saccadic adaptation or on addressing the neuronal mechanisms underlying the development of saccadic adaptation (Barash et al., 1991a; Desmurget et al., 1998; Edelman and Goldberg, 2002; Optican and Robinson, 1980; Straube et al., 1997; Thier and Prsa, 2011). Only a few studies address the issue of the retention of saccadic adaptation (Deubel et al., 1986; McLaughlin, 1967; Seeberger et al., 2002; Straube et al., 1997). It was commonly observed in previous studies that the saccadic gain recovered either entirely or partially soon after exposure to the saccadic adaptation task (minutes to hours). This conflict between the theoretically proposed long-term retention and experimentally observed short-term effect of adaptation has attracted researchers' attention recently. In fact, several studies have focused on testing whether there is a long-term effect of saccadic adaptation on the oculomotor system (Alahyane and Pelisson, 2005a, 2005b; Robinson et al., 2006). These studies found that the effect of saccadic adaptation could last for several days after exposure to double-step target task, which was much longer than other reports (Deubel et al., 1986; Seeberger et al., 2002). In a more recent study, Robinson et al. (2006) proposed two distinct memory systems being involved in mediating short-term and long-term saccadic adaptation respectively. Results in these studies showed evidence of longer retention of saccadic adaptation in human and monkeys. However, the retention reported in these studies was still relatively short (several days), which would not fulfill the requirement of a long-term effect of adaptation. In the present study we have provided new evidence to show that the retention of motor memory is actually long. We believe that the differing observations in our study and these two previous studies are mainly due to the special experimental context. Presumably, subjects with normal extraocular muscles would recover from the adapted state and demonstrate normal saccade gain after exposure to visual stimuli in normal daily life. This phenomenon has been demonstrated previously in other studies (Robinson et al., 2006; Seeberger et al., 2002). However, in our study, even after 2 months of presumably un-adapted saccades in a normal visual environment, once re-exposed to the experimental context, saccade gain changes after training can still be observed. This indicates that various saccadic adaptation states can be learned and stored simultaneously. Then, when necessary, a specific adaptation state can be recruited depending on the particular context. Such a strategy is appropriate for producing accurate behavior in a complicated and ever-changing normal visual environment, which is not as constrained and artificial as a laboratory setup. Because saccadic adaptation is a subtype of motor learning, it should involve general learning mechanism. Indeed, context-specific adaptation was not only found for saccades but also pointing movements (McGonigle and Flook, 1978; Welch et al., 1993) and vestibulo-ocular reflex (Welch et al., 1998), which suggest a universal context-specific adaptation in motor learning.

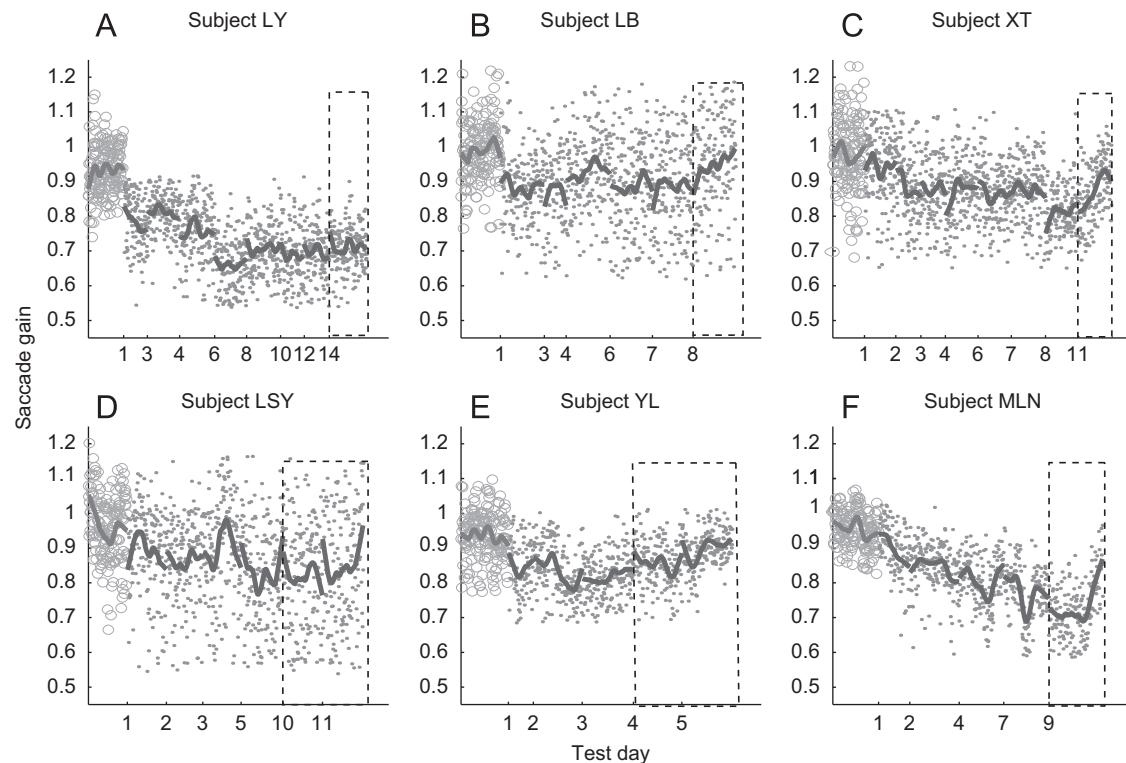


Fig. 4 – Change of saccade gain in the single target task. Same format as in Fig. 2. (A–F) The six subjects show a transient and fast reduction of saccade gain in the first session after the first exposure to double-step target task. Although the change of saccade gain varies among subjects in the following days, saccade gains for all of the subjects are remarkably smaller compared to the baseline saccade gain. Dashed rectangles indicate saccade gain in the higher contrast target condition.

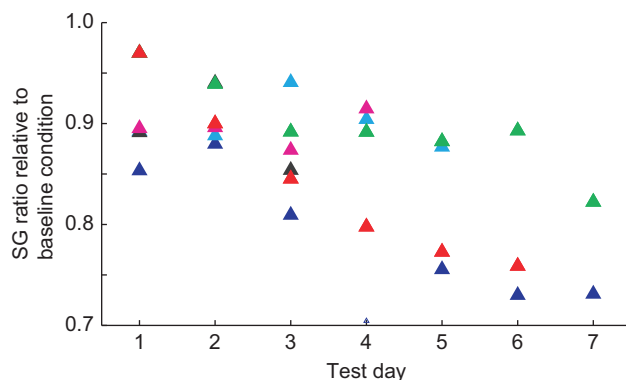


Fig. 5 – Ratio of saccade gain between mean saccade gain of each session and that in baseline condition. Symbols with the same color represent data from one individual subject. All of the data points are less than 1 (in the population data $P=0.0014-10^{-52}$, Wilcoxon test). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Our result suggests that the influence of experimental context and the amount of training affect the adaptation state. Over-training and strong contextual cues can reinforce the storage of the corresponding adaptation state, a potentially efficient method of selecting and storing behaviorally relevant motor memories. Compared with the normal conditions in daily life, experimental training was a marked

transient event, so the oculomotor system may allocate less resources to storing the adaptation state in this condition. Either the lack of over-training or the lack of a special experimental context in these studies may explain the fast decay saccadic adaptation observed.

There were sharp reductions of saccade gain at the very beginning of exposure to double-step target task in our experiments, and it took only a few trials to reach an adapted level of saccade gain (see Fig. 2). These results are quite different from observations from previous studies (which required several hundreds of trials to achieve saccadic adaptation). The possible explanations are following: first, the contrast of saccadic adaptation cue was much higher than that of the original visual target in our task. The brighter adaptation cue might modify the saccadic trajectory online and attract the saccadic endpoint to it; second, the loss of visual reference in complete darkness might increase the difficulty of localizing the visual target, which in turn shortens the process of adaptation.

4. Experimental procedures

4.1. Participants

Seven college students, recruited from local colleges (three male, four female, aged from 23 to 26) participated in our experiments and three of them were available to participate

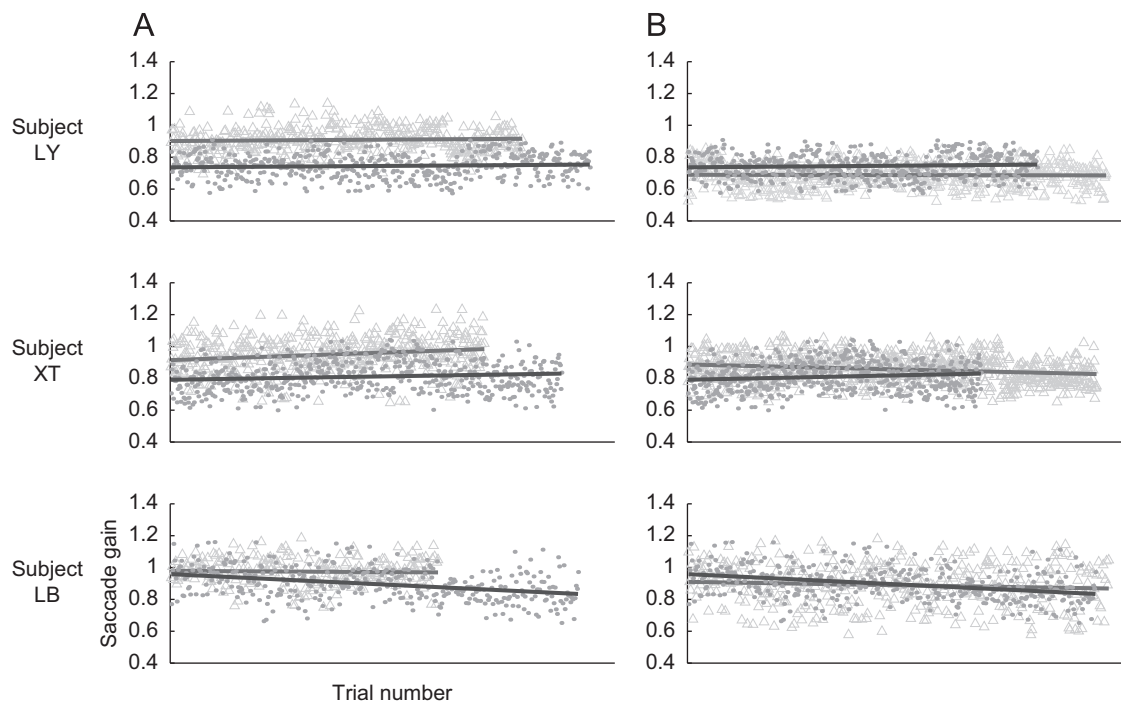


Fig. 6 – Saccade gain after more than 2 months. (A) Three subjects' saccade gain data are shown together with his/her baseline saccade gain in Fig. 5(A) respectively. Gray triangles represent saccade gain in baseline condition, dark circles represent saccade gain 2 months later. The two sets of data are fitted with linear model (least squared method) respectively. Three subjects show that the saccade gain 2 months later is significantly smaller ($P < 0.001$, Wilcoxon test) than the saccade gain in baseline condition. **(B)** Comparison of saccade gain between 2 months later and the last day of data collection. The difference between these two sets of data is not significant in all three subjects.

in data collection 2 months after the last exposure to the backward double-step target task. All subjects had normal or corrected to normal vision, and were never trained in psychophysical or saccade-related tasks. They were introduced to and consulted about the experimental procedure by the experimenter before agreeing to participate. All subjects received payment for their participation. Experiments were conducted under a protocol approved by Institute of Neuroscience, Shanghai Institute for Biological Sciences, Chinese Academy of Sciences.

4.2. Apparatus

Visual stimuli were presented on a 21-inch CRT color monitor (Sony Multiscan G520) with vertical refresh rate of 100 HZ and spatial resolution of 1280×960 pixels. Experiments were performed in a very dark booth: All of the subjects claimed that they could not see anything (including the frame of the monitor) except for the stimuli throughout the experiment. Subjects were seated 80 cm in front of the monitor with their heads restrained with a chin and forehead set. The position of the subject's right eye was monitored by an infrared eye tracker (Eyelink 1000 Desktop, SR Research) with a sampling rate of 1 KHZ. Matlab software (The MathWorks, Inc.) with Psychtoolbox (PTB-3, Brainard and Pelli) running under Mac OS X was used to control the experiment and analyze the data both on-line and off-line.

4.3. Procedure, task and procedure

4.3.1. Procedure

The objective of the present study requires that all experiments be performed in a very dark environment. To avoid the change of eye position between light and dark environment (known as up-shift) (Barash et al. 1998), subjects were required to sit in the dark booth for at least 5 min to adapt to the darkness. A 6-point eye-tracker calibration procedure was performed before each block of the experiment. Only if the maximum spatial deviation from the calibration target was less than 1° and the average was less than 0.5° , were the experiments were carried out. Before running the adaptation experiments each day, the level of target's luminance (lowest luminance with 100% correct performance) for each subject was measured in a visually guided saccadic task. Each session lasted less than 12 min to avoid fatigue. The inter-session interval was about 5–10 min. In the first 2–3 days of data collection, subjects only performed two sessions of the single target task per day. In the following days, subjects first did a session of the single target task followed by two sessions of the double-step target task. Each session consisted of 90 trials. All of the data collected in the single target condition was collected prior to performing the double step task in each session. Data was not required to be collected on successive days, usually it was collected every other day, and the longest interval reached was 5 days.

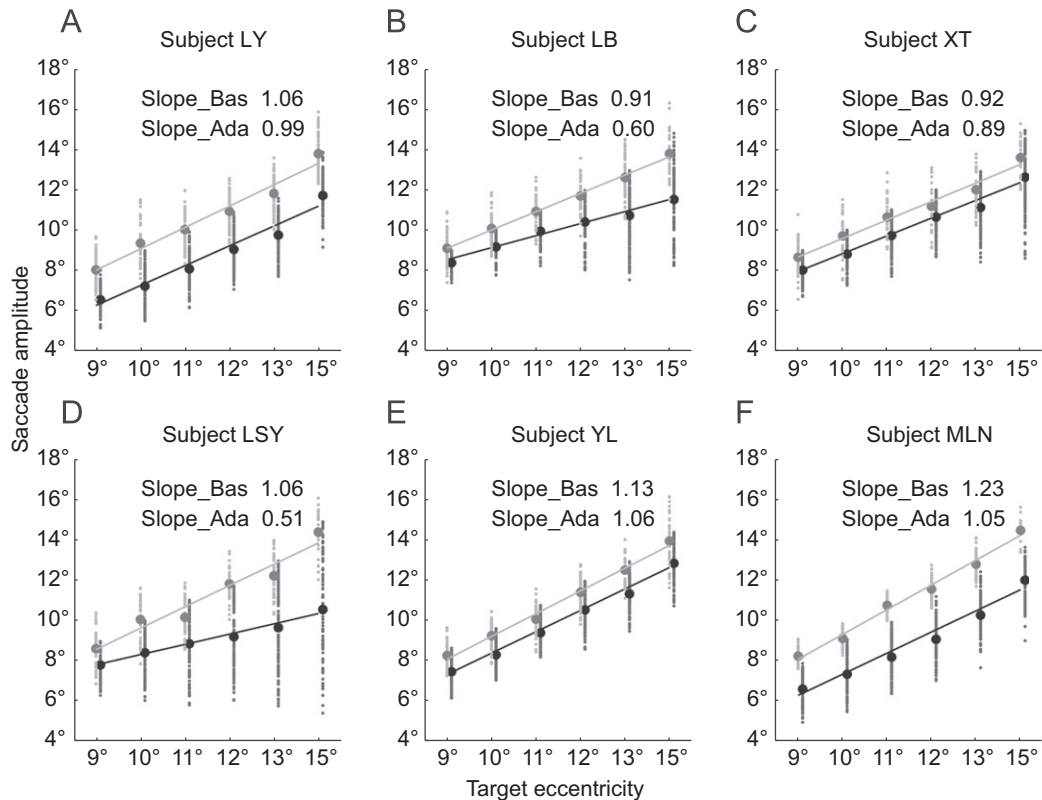


Fig. 7 – The relationship between the saccade amplitude and the target eccentricity. (A–F) All the six subjects show a linear raise on the saccade amplitude as the target eccentricity increased both in the baseline condition and after the exposure to the double-step target task. Gray and dark dots in each panel represent individual saccade amplitude with a designated target eccentricity in baseline and after exposure condition, dark asterisk indicates the mean value and fitted with linear model (least squared method). Slope_Bas and slope_Ada in each panel demonstrate regression in baseline and after exposure condition respectively. R^2 are all larger than 0.97.

Finally, three out of the six subjects were tested on the single target task 2 months after the last exposure to the backward double-step target task.

4.3.2. Visual stimuli and eye position detection

The background of screen was completely black with luminance of 0 measured by the photometer (Konica Minolta LS-110). A red orthogonal cross (0.5° in length, $\sim 0.15 \text{ cd/m}^2$ in luminance) served as the fixation point. To guarantee proper fixation, we set an invisible $3^\circ \times 3^\circ$ square window centered at the fixation cross from 500 ms after trial beginning to the fixation offset. If the eye position moved out of this window during the fixation interval, the fixation cross would turn green and the trial would be terminated. The saccadic target was a white 0.3° dot which varied in luminance based on the individual subject's perceptual threshold. This manipulation was used to diminish the influence of the residual image of the saccade target on saccade gain. In order to avoid phosphor persistence of the target point against the dark background interfering with the induction of saccadic adaptation, we set the luminance of the target point based on each subject's perceptual threshold (tested prior to the experiment). The luminance of the saccadic target used in our experiments was so low so that it could not be measured by the photometer

(its measurement range starts at 0.001 cd/m^2). However, after more than 5 min sitting in the dark booth, all of the subjects claimed that they could detect the stimuli with no problem. The adaptation-inducing cue had same size and shape as the saccadic target but with higher luminance (0.85 cd/cm^2), because a lower luminance cue would not induce saccadic adaptation due to saccadic suppression.

4.3.3. Behavioral tasks

Two saccadic paradigms were used in the present study, the double-step target task and the single target task (Fig. 1).

Double-step target task: we slightly modified the standard double-step paradigm (McLaughlin 1967) in order to induce saccadic adaptation in darkness. A trial begins with a fixation cross appearing at an eccentricity of 7° horizontally left to the center of the screen. To initiate a trial, subjects had to look at the cross and maintain fixation on it. After a variable period (900–1200 ms), the fixation cross was extinguished. At the same time, a saccade target randomly appeared at either 12° or 15° horizontally to the right of the fixation cross. Subjects needed to make a saccadic eye movement to the target as quickly as possible. Immediately after on-line detection of the initiation of a saccade (see methods for detailed explanation), the saccadic target turned off and the

adaptation cue appeared at a location 2/3rd of the eccentricity of the saccadic target away from the fixation and remained on for 30 ms. Each trial was required to be completed within 2000 ms.

Single target task: We used a modified version of the classical, visually-guided saccade paradigm as our single target task. In this protocol, the possible locations of saccadic target were 9°, 10°, 11°, 12°, 13° and 15° to the right of the fixation cross. To keep stimulus parameters consistent with trials of the double-step target task, the saccadic target disappeared 30 ms after online detection of the initiation of a saccade.

4.4. Data analysis

4.4.1. Detection of saccade

(1) Online detection of saccade: The EyeLink detected the initiation of saccades online when the velocity of eye trace exceeded 30°/s and lasted for more than 4 ms. (2) Off-line detection of saccade: we set the following criteria for properly detecting saccades. (i) Eye position must be kept within a 3° fixation window within 500 ms after the fixation cross was present; (ii) saccade latency was 100–600 ms; (iii) saccade duration was 10–100 ms; (iv) saccadic velocity exceeded 30°/s and lasted more than 5 ms; (v) the eye position difference in the ordinate axis between the saccadic endpoint and fixation point was less than 3°. Based on these criteria, 149 (2.12%) out of total 7052 trials in single target task, and 134 (2.73%) out of 4932 trials in double-step target were excluded from further analysis.

4.4.2. Calculation of saccadic gain

Saccadic gain was calculated as the ratio between saccadic amplitude in abscissa axis and the eccentricity of saccadic target. Since the saccadic endpoints were distributed more widely in the dark environment, we excluded some trials from further analysis if their saccade gain values exceeded two times the standard deviation. Further, for subject LSY, saccade adaptation with a target eccentricity of 15° was not significant, so we excluded 344 (7.8%) trials in this condition from further analysis.

4.4.3. Calculation of the average value of saccade gain

To better visualize changes in saccade amplitudes over time, we averaged saccade gain for each subject by employing a sliding average filter function that averaged saccade gain of trial “x” by calculating the mean of the adjacent saccade gain of 30 trials centered at trial “x”, as shown in the following equation: $\text{Mean Gain}(x) = (1/30) \sum_{x-14}^{x+15} \text{Gain}(k)$.

Acknowledgments

This study was supported by the State Key Laboratory of Neuroscience, Chinese Government (Nos. SKLN-2010A05 and SKLN-201203). We thank Dr. Michael E. Goldberg and Dr. Sara Steenrod for their comments to improve the manuscript and Dr. Sara Steenrod for her language help.

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