A gaze-contingent paradigm for studying continuous saccadic adaptation

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Abstract

Saccadic eye movements are used to quickly and accurately orient our fovea within our visual field to obtain detailed information from various locations. The accuracy of these eye movements is maintained throughout life despite constant pressure on oculomotor muscles and neuronal structures by growth and aging; this maintenance appears to be a product of an adaptive mechanism that continuously accounts for consistent post-saccadic visual error, and is referred to as saccadic adaptation. In this paper, we present a new paradigm to test saccadic adaptation under circumstances that more closely resemble natural visual error in everyday vision, whereas previous saccadic adaptation paradigms study adaptation in a largely restricted form. The paradigm achieves this by positioning a stimulus panel atop an identically colored background relative to the gaze position of the participant. We demonstrate the paradigm by successfully decreasing participants' saccadic amplitudes during a common visual search task by shifting the stimulus panel in the opposite direction of the saccade by 50% of the saccadic amplitude. Participants' adaptation reached approximately 60% of the 50% back-shift during the adaptation phase, and was uniformly distributed across saccadic direction. The adaptation time-course found using the new paradigm is consistent with that achieved using previous paradigms. Task-performance results and the manner in which eye movements changed during adaptation were also analyzed.
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Saccadic eye movements, which are used to rapidly orient our fovea within our visual field, are quite accurate to their intended targets (Becker, 1989; Kowler and Blaser, 1995). This accuracy is maintained despite constant influence on extraocular muscles and neuronal structures by growth and aging (Munoz et al., 1998; Warabi et al., 1984). This saccadic plasticity appears to be, in part, a product of a continuous mechanism that evaluates the visual error between post-saccadic gaze position and intended gaze position (Noto and Robinson, 2001; Wallman and Fuchs, 1998). If this post-saccadic visual error remains consistent over multiple saccades, a form of motor learning slowly adjusts the saccadic system towards a smaller visual error. This adjusting of the saccadic system is referred to as saccadic adaptation.

Robust saccadic adaptation has been demonstrated in humans and monkeys using natural visual error involving weakened or damaged extraocular muscles (e.g., Abel et al., 1978; Kommerell et al., 1976; Optican and Robinson, 1980) as well as induced visual error by trans-sacadically displacing the target of the saccade (e.g., Deubel et al., 1986; McLaughlin, 1967; Noto et al., 1999). McLaughlin (1967) introduced a paradigm to test saccadic adaptation by laterally displacing the target of a saccade towards the starting location of the saccade while the saccade was in flight. Such displacements of the saccadic target are possible since human vision is effectively suppressed during saccades (e.g., Brooks and Fuchs, 1975; Matin, 1974; Riggs et al., 1974; Riggs et al., 1982). Consequently, after participants have finished a saccade under this paradigm, it appears to them as though their saccade had overshot the target, which would then, given sufficient visual error, induce a second, corrective saccade to foveate the displaced target. In this way, McLaughlin was able to demonstrate a significant saccadic amplitude reduction after only 5–10 saccades. Many experiments since have used McLaughlin's paradigm to further study saccadic adaptation. In addition to amplitude reduction, amplitude increases (Deubel et al., 1986; Noto et al., 1999) and directional changes (Deubel, 1987; Noto et al., 1999) have been demonstrated using variations of McLaughlin's paradigm. Interestingly, researchers have also shown that one saccadic vector can be adapted independent of other saccadic vectors, given that the vectors involved are sufficiently distinct (Deubel et al.,

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1986; Deubel, 1987; Miller et al., 1981; Semmlow et al., 1987; Weisfeld, 1972).

The paradigm used to demonstrate the aforementioned adaptations begins by having participants foveate a centrally located target. After some time, the central target is extinguished and a new target is presented, usually between 10° and 15° eccentricity, to which the participants are then supposed to saccade. Once the participant's saccadic eye movement has reached a predefined criterion (e.g., a specific saccadic velocity), an adaptation step is triggered (e.g., a 3° step towards the starting location of the saccade). When this procedure is repeatedly administered, the induced visual error causes participants to slowly adjust their saccadic amplitude or direction to compensate for the adaptation step. Adaptation time constants using this paradigm usually range between 5 and 50 saccades (Miller et al., 1981). For example, Miller et al. (1981) demonstrated adaptation to a single target resulting in a time constant of six saccades and adaptation to six targets resulting in a time constant of 57 saccades. While McLaughlin's paradigm is able to demonstrate significant adaptation to one or more predefined saccadic vectors, the conditions of the paradigm make it unrealistic for studying adaptation from natural causes. For instance, it is customary under this paradigm to only apply the adaptation step to the first targeting saccade, while all other saccades (e.g., corrective saccades) are allowed to be executed normally. This type of situation seems quite unlikely to occur naturally, as natural visual error would likely be present for all saccades, including corrective saccades. Consequently, interactions between saccadic vectors are largely ignored. Moreover, it is rare that we would make saccades of the same amplitude and direction many times in a row. It is equally unlikely that the only purpose of our saccades would be to foveate a location without interest in its inspection; as usually, there is another purpose behind any saccade, such as looking for our keys or reading.

In this paper, we present a new saccadic adaptation paradigm that does not use the standard, trans-saccadic adaptation step, but instead induces post-saccadic visual error by continuously shifting a gaze-contingent stimulus panel. Under this paradigm, instead of the target jumping instantly to a predetermined position during a participant's saccade, the target will continuously transition from its pre-saccadic position to its post-saccadic position based on a simple calculation involving the participant's gaze position throughout the saccade. Rather than speaking in terms of an adaptation step, we introduce the term adaptation shift to illustrate the deviation from the standard paradigm. Since participants' vision is effectively suppressed during the saccade, participants in our paradigm should not perceive the movement of the items during their saccades, but only the resulting visual error. This manner of inducing post-saccadic visual error is quite different from previous paradigms, and a thorough account of these differences and their implications is given in Section 3 of this paper.

To demonstrate this new paradigm, we tested participants' adaptation using a pair of simple equations to calculate the position of the stimulus panel such that a 50% back-shift (i.e., during the saccade, the display was shifted towards the starting location by 50% of the saccadic amplitude) was induced while participants performed a simple visual search task. For the task, participants were asked to search a display of visual items for the presence of a pre-specified target item during an initial, adaptation, and recovery phase. The final phase is referred to as a recovery phase, as participants are, in effect, recovering their normal saccadic amplitudes.

1. Method

1.1. Participants

The experiment was performed with the assistance of ten university students from the University of Massachusetts Boston who were paid a $10 honorarium for their participation. All participants had normal or corrected-to-normal vision.

1.2. Apparatus

Stimuli were presented on a 21-in. Dell P1130 monitor using the resolution 1024×768 and a refresh rate of 120 Hz. Participants sat approximately 33 cm from the screen resulting in a horizontal and vertical viewing angle of 57.5° and 44.9°, respectively. Eye movements were recorded using the SR Research Ltd. Eye-Link II eye-tracker system. The average error of visual angle in this system is 0.5°, and its sampling frequency is 500 Hz. During the adaptation phase of the experiment, a gaze-contingent stimulus panel was used to induce the post-saccadic visual error. The parameters of the gaze-contingent stimulus panel were set such that the stimulus panel would shift counter to participants' saccades by 50% of the amplitude of the saccade. The maximum delay between participants' eye movements and the display movement was approximately 11 ms. Participants' responses in the discrimination task (see below) were recorded using a handset, commonly referred to as a gamepad.

1.3. Materials

Displays were created using very similar target and distracter items (average luminance 22.0 cd/m^2) atop a black background (0.2 cd/m^2) as shown in Fig. 1a. In order to facilitate the analysis of saccadic adaptation, items were designed so that participants had to foveate them in order to determine if they were a target or distracter item. Items measured approximately 1.4° in diameter and were composed of a circle intersected by four colored lines of equal length positioned at 0°, 90°, 180°, and 270°, respectively. The target item was identical to the distracter items except that two of the lines on the target item were of the same color, whereas the distracter items contained lines of four different colors. The colors present on each item were randomly chosen from four colors, which were pink (CIE chromaticity coordinates: $x = 0.348$, $y = 0.229$), light brown ($x = 0.378$, $y = 0.386$), blue ($x = 0.254$, $y = 0.264$), and green ($x = 0.296$, $y = 0.480$). The four colors were chosen to attract approximately equal amounts of visual attention based on a recently proposed, spherical color space of saccadic selectivity in visual search (Xu et al., 2007). Half of the displays contained three distracter items and one target item, and the other half contained four-distracter items. The four items
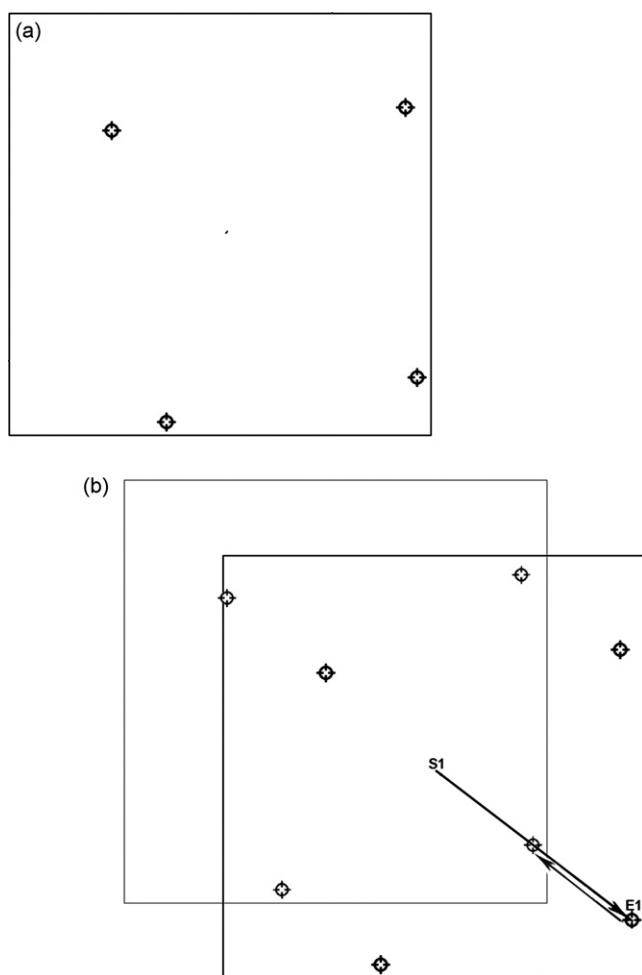
Fig. 1. (a) An example display shown to participants during the visual search task. In the actual trials, the items were colored and the background was black. (b) Example mechanics of the gaze-contingent display presented during the visual search task. An example saccade (black arrow) is shown starting at "S1" and ending at "E1". The black box and items represent the stimulus panel from (a) as it would have been seen by a participant while fixating S1, and the grayed box and items represent the stimulus panel from (a) as it would have been seen by a participant while fixating E1. The separation between the expected location of the intended item after the saccade (black item near E1), and the actual location of the intended item after the saccade (gray item halfway along the example-saccade arrow), represents the adaptation shift for the example saccade. An example corrective saccade is also shown (gray arrow), which would also overshoot the intended item, as the display would also shift during this saccade.

in each display were randomly placed on a $28.6° \times 28.6°$ area, which we refer to as the stimulus panel (Fig. 1a). The minimum distance between items was $12.5°$. The displays were randomly generated, and each participant was subject to the same set of displays.

1.4. Procedure

Prior to the start of a session, each participant was given specific instructions about the task. Participants were also fitted with the eye tracker headpiece and given a quick calibration task at this time. They then completed three consecutive phases composed of 75 trials during the initial phase, 225 trials during the adaptation phase, and 75 trials during the recovery phase;

participants were not pre-notified of phase switches. Participants were asked to search through the items as quickly and accurately as possible to determine if a target item was present in the display and to press one button on the gamepad if a target item was present or press another button if no target item was present. Immediately following a participant's response, a sound was played that indicated whether a correct or incorrect response was made. Prior to the start of the next trial, participants performed a simple drift correction of the eye tracker by foveating a small grey disc presented at the location of their fixation during the button press.

During the trials, the presence of the stimulus panel was not apparent to participants because both the panel background and screen were black. In the initial and recovery phases of the experiment, the stimulus panel described above was centered on the screen. During the adaptation phase however, the stimulus panel was positioned relative to participants' gaze position using the following calculations: $x = 512 - (gx - 512)/2$ and $y = 384 - (gy - 384)/2$ where gx and gy, respectively, represent participants' horizontal and vertical gaze position in pixels from the upper-left corner of the screen, and x and y, respectively, represent the corresponding horizontal and vertical position for the center of the stimulus panel, also in pixels. For example, Fig. 1b shows the position of the stimulus panel under two different gaze positions, S1 and E1. The first gaze position (S1) is located at the center of the screen ($gx = 512$, $gy = 384$) and corresponds to the first position of the stimulus panel (black box and items; $x = 512$, $y = 384$), which is also centered on the screen. This condition can be viewed as the 'home' condition, that is, a screen-centered gaze position corresponds to a screen-centered stimulus panel. The black arrow from S1 to E1 represents an example saccade directed toward the item located at E1. During this faux saccade, the stimulus panel is continuously shifted from its initial position when the participant was fixating S1 (black box and items; $gx = 512$, $gy = 384$; $x = 512$, $y = 384$) to its new position when the participant is fixating E1 (gray box and items; $gx = 756$, $gy = 576$; $x = 390$, $y = 288$). Since the stimulus panel is gaze-contingent and designed to counter participants' saccades by 50% of their amplitude, during the saccade from S1 to E1, which has an amplitude of $13.6°$ rightward and $11.4°$ downward, the display was smoothly shifted $6.8°$ leftward and $5.7°$ upward. The consequence of this shift is that during the subsequent fixation, participants perceive that they have overshot the item. A sample corrective saccade is also indicated in Fig. 1b as a gray arrow, which would also overshoot the intended item since the display is also shifting during this saccade.

1.5. Data collection

For easier reference, we will refer to the item nearest the landing location of the saccade as the intended target of the saccade. The amount of adaptation measured during the trials was only computed for saccades that fit three specific criteria. One; the saccade's starting and landing locations were not nearest to the same item. Two; the post-saccadic visual error was between -20% and 20% during the initial phase, or between -20% and 120% during the adaptation phase or between -60% and 10%

during the recovery phase. Visual error is calculated using the formula:

$$\text{Visual error} = \left(\frac{\text{Saccadic amplitude}}{\text{Correct amplitude}} - 1 \right) \times 100$$

where Saccadic amplitude is the amplitude of the saccade and Correct amplitude is the amplitude needed to correctly foveate the target. Three; the direction of the saccade did not deviate by more than $15°$ from the direction of the intended item from the saccade's starting point. These criteria were designed to restrict analysis to saccades that were made strictly from one item to another, which we refer to as scanning saccades; saccades that have a starting and landing location that are nearest the same item are referred to as corrective saccades.

2. Results and discussion

Following the experiment, participants reported they were somewhat "confused" by the initial imposition of the adaptation shift, but additionally reported that after running a few trials they had regained visual stability (i.e., they did not perceive the motion of the display at all). This could likely be avoided altogether by using a smaller adaptation shift (e.g., 25% of the saccadic amplitude). A plot of saccadic eye movements for a single trial and participant during the initial phase (Fig. 2a), adaptation phase (Fig. 2b), and recovery phase (Fig. 2c) is given in Fig. 2. The plot of saccadic eye movements for the initial phase (Fig. 2a) shows that the landing locations of scanning saccades (black arrows) are very near their intended item (black items). In the plot of eye movements for the adaptation phase (Fig. 2b) however, the stimulus panel is gaze-contingent and the location of the intended item prior to a saccade is different from the location of the intended item after a saccade (gray items). The saccadic eye movements in Fig. 2b demonstrate exactly how participants overshoot their intended target due to the adaptation shift; the subsequent corrective saccades (gray arrows) to foveate the displaced target are also illustrated in Fig. 2b. Finally, following the adaptation phase, participants should have partially adjusted their saccadic amplitudes to the imposed visual error during the adaptation phase, which, as shown in Fig. 2c, causes their saccades to fall well short of the intended item. Fig. 2c also demonstrates that adaptation has additionally occurred for short saccades (i.e., corrective saccades) as it takes up to two corrective saccades following the initial scanning saccade to effectively foveate the target.
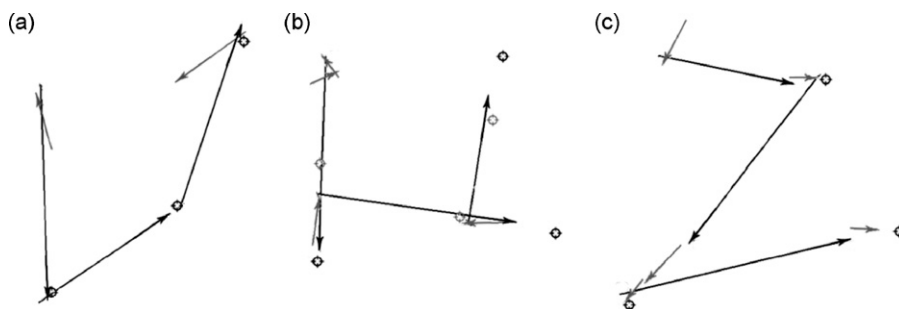

Fig. 2. Eye movement during the initial phase (a), adaptation phase (b), and recovery phase (c). Following Fig. 1, black arrows represent scanning saccades and gray arrows represent corrective saccades. Although during the adaptation phase, all items in the stimulus panel appeared at different locations corresponding to every gaze position during the trial, displayed items represent only the locations before and after the associated scanning saccade made to them. The locations of the intended items as seen from the start of the scanning saccade made to it are shown as black items, and the locations of the intended item as seen from the landing location are shown as gray items (only applicable for the adaptation phase).
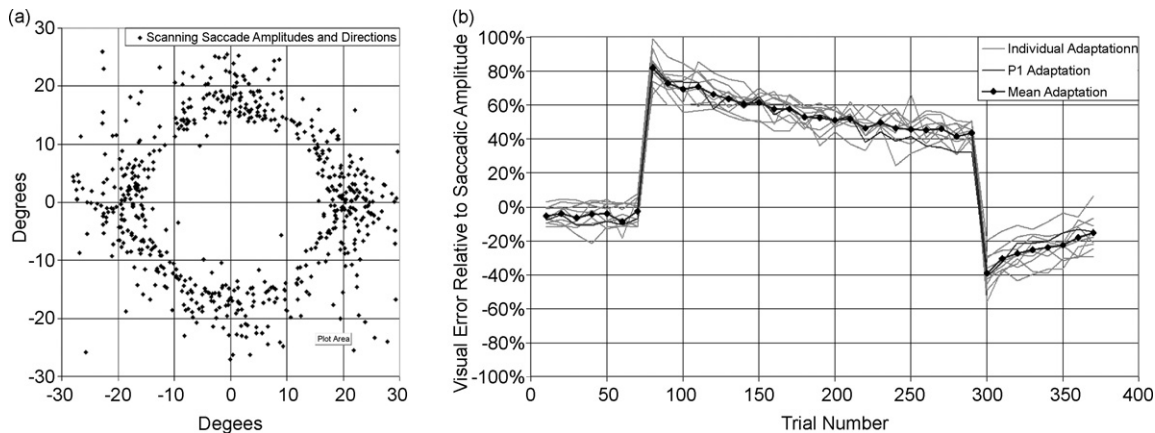

Fig. 3. (a) Amplitude and direction for all scanning saccades of a single participant (P1) made during the adaptation phase. (b) The visual error as calculated using the equation listed in Section 3 averaged across every 10 trials; these values are given for each of the 10 participants (thin gray lines, except for participant P1 which is in black) as well as the mean visual error for all 10 participants (thick black line with data points).

2.1. Analysis

Fig. 3a shows a plot of the amplitudes and directions of all scanning saccades made by a participant (P1) during the adaptation phase, and Fig. 3b shows the results from plotting the visual error of scanning saccades that were identified using the criteria outlined in Section 3 in all three phases for all 10 participants as well as the mean visual error for all participants. If we look at the data from the initial trials, we see that participants collectively tend to undershoot the target location by approximately 5%. This is in line with what we would expect as it has been theorized that the saccadic system is naturally slightly hypometric (Henson, 1978; Hopp and Fuchs, 2004; Miller et al., 1981). No significant difference in the visual error measure was found between the first half of trials (5.4% undershoot), referred to as early trials, and the second half of trials (4.4% undershoot), referred to as late trials, during the initial phase, $t(9) = 1.26$, $p > 0.1$. Fig. 3b also clearly demonstrates that participants do in fact adapt over time to the induced visual error (i.e., the 50% back-shift) during the adaptation phase, as participants went from overshooting the target by 81.7% during the first ten trials to overshooting the target by 43.5% during the last ten trials. In this phase, the visual error measured during the early trials (67.2% overshoot) is significantly greater than that measured during the late trials (48.4% overshoot), $t(9) = 10.79$, $p < 0.001$. Finally, Fig. 3b shows that participants also recover their normetric saccadic amplitudes over time during the recovery phase. They went from undershooting the target by 38.9% during the first ten trials to undershooting the target by 15.3% during the last ten trials, and that participants undershoot the target significantly more during the early trials (16.0% undershoot) than during the late trials (11.3% undershoot) of the recovery phase, $t(9) = 8.97$, $p < 0.001$. From this data it appears that recovery follows a similar course of change as adaptation because in the first 75 adaptation trials, participants went from overshooting by 81.7% to overshooting by 61.6% (a difference of 20.1%), and during the 75 recovery trials, participants went from undershooting by 38.9% to undershooting by 15.4% (a difference of 23.5%).

As previously mentioned, it is possible for saccades to be adapted independently if their directions or amplitudes are sufficiently different. However, nearby adapted saccadic vectors likely still influence each other depending on their similarity (Hopp and Fuchs, 2004). We tested for any such influence by averaging the post-saccadic visual error every 45° (see Fig. 4) for participants during their last 25 trials of the adaptation phase; Fig. 4a and b, respectively, show the directional distribution of visual error and the corresponding scanning saccades for all 10 individual participants as well as the mean for all participants. Despite some differences between directions for single participants, no pattern of influence, such as the mutual inhibition of adaptation in opposite directions, could be evidenced from our data. The differences between individual participants are not surprising, as it has been previously reported that adaptation can vary significantly between participants (Hopp and Fuchs, 2004).

Participants' saccadic adaptation can also be seen by the effect it has on their basic eye-movement variables. Fig. 5
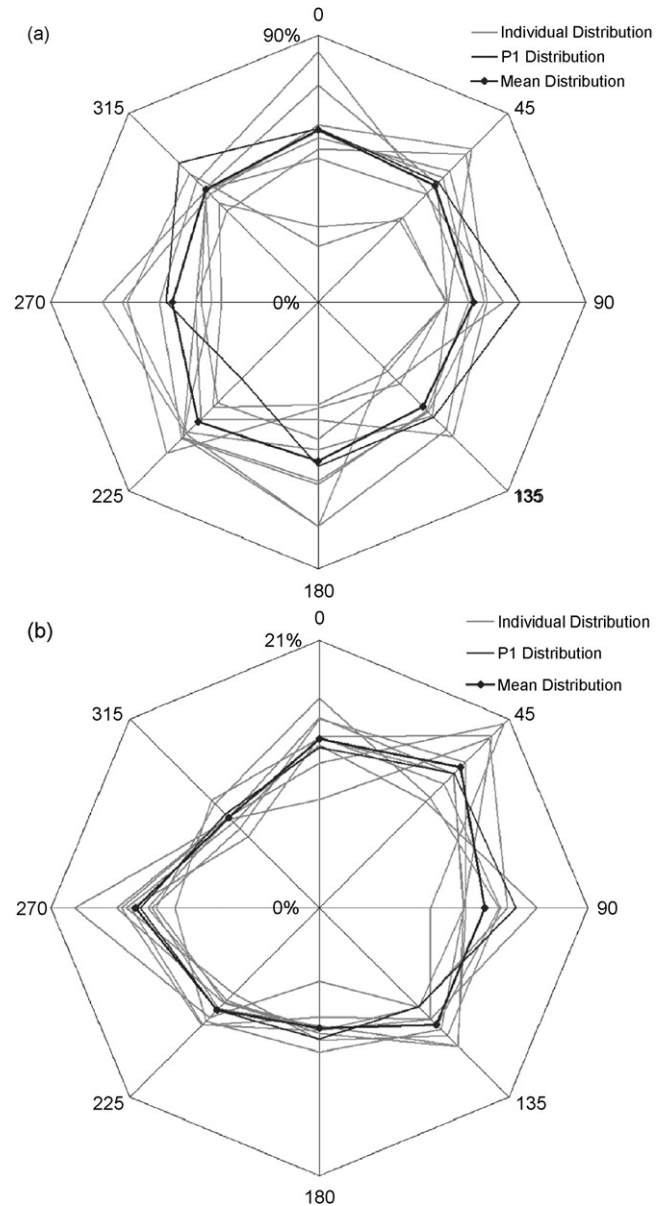

Fig. 4. (a) The individual (gray lines, P1 in black) and mean (thick black line with data points) visual error averaged for every 45° during the last 25 trials of the adaptation phase. (b) The individual and mean percentages of scanning saccades averaged for every 45° during the adaptation phase.

demonstrates how the distribution of saccadic amplitudes changes over the course of the experiment. The white curve shown in Fig. 5 presents the distribution of saccadic amplitudes during the initial phase, and from this, we can identify two primary amplitude intervals that dominate the distribution. First is the large percentage of saccades with very small amplitudes (less than 2.8°), which represents corrective saccades (corrective region). Next, is the "hill" of saccades with larger amplitudes (14° through 23°), which represents scanning saccades (scanning region). The effects of saccadic adaptation are most pronounced in the changes that occur to these two areas. During the first third of the adaptation phase, the scanning region is nearly obliterated due to the incursion of a greater number of – previously unnecessary – corrective saccades, which is embod-
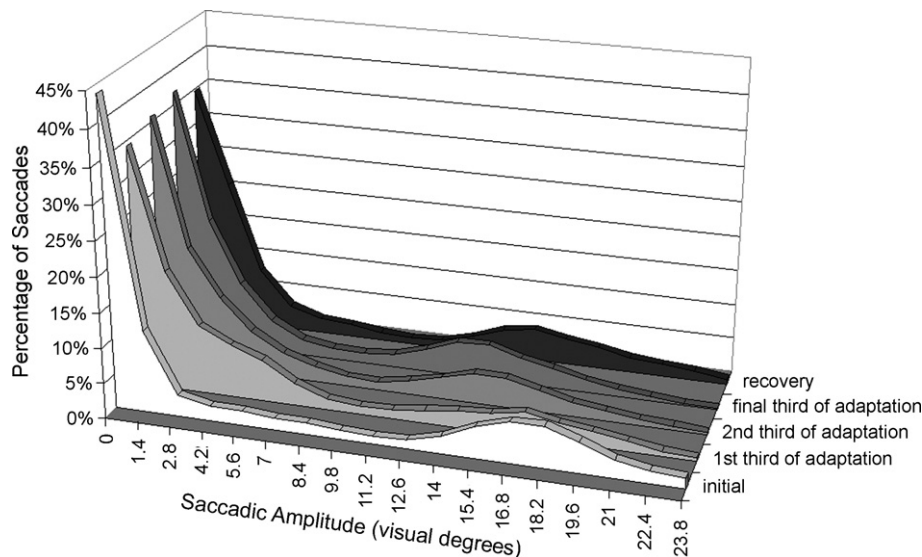
Fig. 5. Percentage of saccades at different saccadic amplitude intervals during the initial phase, first third of the adaptation phase, second third of the adaptation phase, final third of the adaptation phase, and recovery phase; each period represents 75 trials.

ied as the widening of the corrective region (from less than 2.8° to less than 8.4°). As the remaining two thirds of the adaptation phase pass, the scanning region is progressively rebuilt in contrast to the shrinking of the corrective region, indicating that corrective saccades become fewer and shorter. As we would expect, the scanning region is also shifted towards shorter saccades during the adaptation phase as a direct consequence of participants' saccadic adaptation. Finally, during the recovery phase, the scanning region is shifted back towards longer saccades as participants recover their normetric saccades; however, a slightly wider corrective region that is absent during the initial phase still remains as evidence that corrective saccades are still needed.

A two-way analysis of variance with phase (initial trials vs. adaptation trials vs. recovery trials) and time (early trials vs. late trials) as within-subject factors was used to analyze trial accuracy, which is the percentage of trials responded to correctly, and trial duration, which is the time between trial onset and trial cessation. Trial accuracy varied minimally, but significantly across phase (initial: 91.6%; adaptation: 95.2%; recovery: 93.9%), $F(2, 18) = 5.16$, $p < 0.05$, but not across time (early: 92.9%; late: 94.2%), $F(1, 9) = 1.10$, $p > 0.10$. Response times, which were computed only for correctly classified, target-absent trials, varied significantly across phase (initial: 5020 ms; adaptation: 4879 ms; recovery: 4173 ms), $F(2, 18) = 4.68$, $p < 0.05$, and were significantly longer for early trials (4941 ms) than late trials (4441 ms), $F(1, 9) = 7.85$, $p < 0.05$. Improvements in response time appear to stem from two primary sources: a practice effect and an adaptation effect.

3. General discussion

In this study we introduce a new paradigm aimed at examining saccadic adaptation under conditions more akin to those of natural saccadic adaptation. This is accomplished by continuously shifting a gaze-contingent stimulus panel during each saccade made by participants. The position of the stimulus is calculated using a pair of simple equations that relate the current gaze position to the current stimulus panel position. Consequently, the target of a given saccade does not instantly jump as with previous saccadic adaptation paradigms, but instead, smoothly transitions to its post-saccadic position. However, since participants' vision is effectively suppressed during a saccade, participants do not perceive the smooth motion of the display, but only the resulting visual error.

To demonstrate the effectiveness of this new paradigm, we presented an experiment in which participants' saccades were subjected to 50% back-shift while they performed a simple visual search task. In this way, we were able to successfully reduce participants' saccadic amplitudes by 60% of the imposed back-shift. This is approximately equal to the adaptation elicited using previous saccadic adaptation paradigms. For example, Desmurget et al. (1998) introduced a 7.5° backstep during participants' saccades to a peripheral target, and produced an adaptation of approximately 36% after around 30 saccades. In our study, participants adapted to approximately 50% of the 50% back-shift for a single 45° interval after around 40 scanning saccades. Comparable adaptation time-courses have been demonstrated in experiments similar to Desmurget's (Hopp and Fuchs, 2004). One important difference between Desmurget's experiment and ours is that Desmurget's does not involve adaptation to multiple saccadic vectors, whereas our experiment involved many saccadic vectors. However, the results from our experiment demonstrate that in general, participants adapt evenly across all directions. In addition to saccadic adaptation measures, we found evidence that adaptation did have a significant effect on trial response time, as response times similar to those seen at the end of the initial phase could be found after participants had adapted to approximately 40% of the adaptation step.

Our experiment is not the first to study saccadic adaptation using multiple targets, but unlike previous experiments involv-

ing multiple targets, our experiment allows participants to search the targets in any arbitrary order, and furthermore, applies the trans-saccadic shift to all saccades made. For instance, Deubel (1995) tested saccadic adaptation by asking participants to count the number of full T's in a rectangular arrangement of six items that were to be searched in a clockwise or counter-clockwise order. In this experiment, only the first saccade to each target was subjected to the adaptation step. This type of setup, as with McLaughlin's paradigm, was effective for what was being studied, but is unrealistic for studying saccadic adaptation under natural visual error.

This particular demonstration exhibits some of the unique properties of the new paradigm. First of all, since the stimulus panel location is dependent upon participants' gaze position, all saccadic eye movements will be subjected to the adaptation shift, including corrective saccades. Additionally, since the display movement does not need to be calculated prior to testing, the task is not limited to a few, pre-calculated saccadic vectors, without which the experimentation of saccadic adaptation during this type of concurrent visual task would be infeasible. Additionally, this new paradigm also has some other interesting features that add to its potential for studying saccadic adaptation under natural visual error. For instance, in the demonstration experiment we presented, the stimulus panel position was computed using two simple calculations dependent upon the current gaze position; however, these calculations need not be so elementary and could be used to elicit any number of adaptation shifts dependent on many more variables. Furthermore, these calculations could be setup to simulate real-world situations, such as injury to a specific extra-ocular muscle. For instance, a lateral rectus muscle injury would likely hinder abducting eye movements, the effects of which could be simulated using a slightly modified version of the current equations.

Finally, the choice of positioning a stimulus panel further allows the exploration of saccadic adaptation using much different stimuli than traditionally used. For instance, given some clever computer programming, this paradigm could be setup to study saccadic adaptation using real-world scenes captured in an image or video file. Other interesting stimuli include real-time rendered 3D scenes, interactive displays, real-time video feeds, and many others.

Based on the current results, we believe that our paradigm offers certain unique advantages that could afford researchers a tool for studying properties of saccadic adaptation that cannot be studied under previous paradigms. Future research will be aimed toward exploiting the benefits of our paradigm.

Acknowledgement

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