The influence of image content on oculomotor plasticity

Annegret Meermeier
Institute for Psychology & Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, University of Muenster, Muenster, Germany

Svenja Gremmler
Institute for Psychology, University of Muenster, Muenster, Germany

Markus Lappe
Institute for Psychology & Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, University of Muenster, Muenster, Germany

When we observe a scene, we shift our gaze to different points of interest via saccadic eye movements. Saccades provide high resolution views of objects and are essential for vision. The successful view of an interesting target might constitute a rewarding experience to the oculomotor system. We measured the influence of image content on learning efficiency in saccade control. We compared meaningful pictures to luminance and spatial frequency–matched random noise images in a saccadic adaptation paradigm. In this paradigm a shift of the target during the saccades results in a gradual increase of saccade amplitude. Stimuli were masked at different times after saccade onset. For immediate masking of the stimuli, as well as for their permanent visibility, saccadic adaptation was similar for both types of targets. However, when stimuli were masked 200 ms after saccade onset, adaptation of saccades directed toward the meaningful target stimuli was significantly greater than that of saccades directed toward noise targets. Thus, the percept of a meaningful image at the saccade landing position facilitates learning of the appropriate parameters for saccadic motor control when time constraints exist. We conclude that oculomotor learning, which is traditionally considered a low-level and highly automatized process, is modulated by the visual content of the image.

Introduction

Although saccades serve very important functions in vision, the basic oculomotor processes by which they are controlled are usually studied with simple point targets. Saccade motor control is highly stereotyped and automatized. Its long-term maintenance is served by an oculomotor learning process called saccadic adaptation. Saccadic adaptation is often considered a low-level process that is based primarily on retinal error signals of postsaccadic target position. However, success in reaching a target may mean more than just a small positional error. Since saccades are usually made in order to look at things, a clear view of the target object may hold some value to the visual system. An accurate saccade, in that sense, helps to acquire this value. Hence, the role of saccades in natural vision suggests that the content of the image reached by the saccade is important and that the successful view of the target may even provide a rewarding experience to the oculomotor system. Reward, in this context, refers to an intrinsic value of the image to the observer, as he or she has an intention to look at the image.

Since saccades are too brief to allow online control by visual feedback, any errors relevant for saccadic adaptation become apparent only after the saccade is finished. Saccade adaptation, therefore, has to monitor success after the saccade and learn from observed errors in order to fine-tune planning parameters for future saccades (Hopp & Fuchs, 2004; Pélisson, Alahyane, Panouillères, & Tilikete, 2010). This is studied in the lab by monitoring eye position and shifting the saccade target when the onset of a saccade is detected (McLaughlin, 1967). This procedure introduces an artificial error between the expected and the actual location of the target after the saccade, providing a learning signal to the oculomotor system (Collins & Wallman, 2012; Wong & Shelhamer, 2012). If the error is consistently in one direction—for example, when the target is always shifted forward—the amplitude of saccades to this target increases over several tens of trials. We reasoned that this increase

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should be larger if the target is meaningful—in the sense that it carries positive intrinsic value—and that a successful high-resolution view of this target could be rewarding to the visual system.

Several factors, such as task relevance and social importance, can specify the meaning and value of an image (Anderson, Laurent, & Yantis, 2011; Cerf, Harel, Einhäuser, & Koch, 2008; Pomplun, 2006; Rothkopf, Ballard, & Hayhoe, 2007). In particular, gaze is naturally drawn towards human faces (Bindemann, Burton, Langton, Schweinberger, & Doherty, 2007; Hershler & Hochstein, 2005) and human bodies (Downing, Bray, Rogers, & Childs, 2004; Downing, Jiang, Shuman, & Kanwisher, 2001; Ro, Friggel, & Lavie, 2007). As one of the most salient and evolutionarily important stimuli, faces and bodies might carry positive intrinsic value. Stimulus features and value not only determine where we look, but also how we look there. Extrinsic reward of a target (e.g., in the form of water drops) can increase the velocity and the accuracy of a saccade in monkeys (Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002). But also, expectation of viewing an intrinsically valuable target (e.g., a face) increases saccadic peak velocity (Collins, 2012; Xu-Wilson, Zee, & Shadmehr, 2009). Secondary saccades, needed when the primary saccade does not reach the target, also seem to be influenced by expected target value (Schütz, Trommershäuser, & Gegenfurtner, 2012). Taken together, the expected target value and information about the successful execution and achieved accuracy of the previous saccades are integrated in saccade planning and could enhance the process of saccadic adaptation.

The content of the target image might affect saccadic adaptation in two different ways. First, before the saccade, the peripheral view of an interesting target might increase motivation for an accurate saccade. Second, the high-resolution view of the image after the saccade might constitute a rewarding experience. To distinguish between these possibilities, we introduced masking conditions that would or would not allow a final view of the target. In one condition, the target was masked immediately at saccade onset. In a second condition, the target was masked 200 ms after saccade onset, thus allowing a brief postsaccadic glimpse. In a third condition, the target was never masked, thus allowing a full inspection of the target. The second condition was introduced to control for secondary, corrective saccades. Such corrective saccades are usually made to fully reach the target when the initial saccades fall short. The 200-ms time interval limits the presentation of the target such that no visual processing is possible after the end of the corrective saccade.

Material and methods

Participants

Thirty-six subjects (mean age 24.5 years, $SD = 3.76$, five male, 31 female) participated in the study. All gave informed consent, had normal or corrected-to-normal vision, and were naive to the purpose of the experiment. Sample size was determined via preliminary testing and adjusted to allow for a full counterbalancing of the experimental design. Experimental procedures adhered to the tenets of the Declaration of Helsinki and were approved by the ethics committee of the department.

Apparatus

Participants sat 57 cm in front of an Eizo FlexScan 22-in. monitor (Eizo, Hakusan, Japan) with a visual display size of 40 × 30 degrees of visual angle. Display resolution was 1157 × 864 pixel at a refresh rate of 75 Hz. Eye position was recorded with the Eyelink 1000 (SR Research, Ontario, Canada) at 1000 Hz. Viewing was binocular. Only the left eye was recorded. Movements of the head were minimized by a chin rest. Experimental code was written in MATLAB (Mathworks, Natick, MA) and stimuli were presented via the Psychophysics Toolbox extensions (Brainard, 1997).

Stimuli

To investigate the impact of target content onto saccadic adaptation, we compared meaningful images with meaningless noise images (Figure 1a). We chose images of attractive females (head and body) as are commonly used on magazine covers or in advertisements. All images were presented in grayscale at a size of 50×75 pixels ($1.76° \times 2.63°$). Meaningful images and meaningless noise stimuli were matched for luminance and spatial frequency using the MATLAB SHINE toolbox (Willenbockel et al., 2010). A set of 50 distinct meaningful images was used, and a set of 50 meaningless noise stimuli was constructed accordingly. A further set of 100 noise images of the same size was used as masks. Each meaningful image and meaningless noise image had its own masking image.

The stimulus arrangement and adaptation procedure ensured that adaptation for both types of targets was measured in a single session. This is important in order to avoid differences in overall motivation that might occur between sessions. Furthermore, value of targets may be encoded on a relative scale (i.e., one target being more valuable than another) such that both types of target need to be present in a single experiment. Since adaptation is specific to saccade

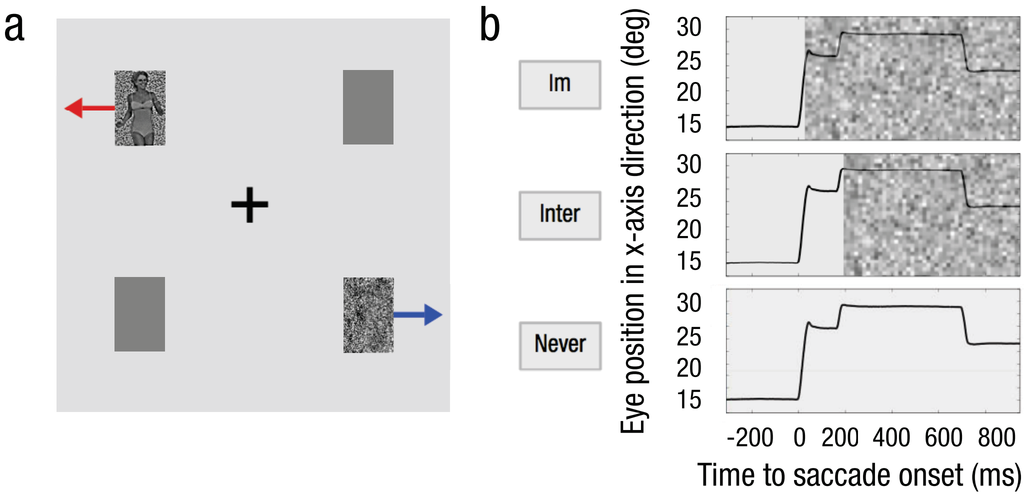

Figure 1. (a) Illustration of the stimulus arrangement in an example trial with counterclockwise scanning direction. The meaningful image is on the left; the noise stimulus is on the right side. Subjects made a saccade from the central fixation cross to the upper right stimulus, then proceeded in counterclockwise direction. Upon detection of the leftward horizontal saccade onset (second saccade in this sequence), all stimuli stepped 4° to the left, into the direction of the current saccade (red arrow). Upon detection of the rightward bottom saccade, stimuli shifted towards the right (blue arrow). Three more manifestations of the experimental task existed, reversing image and noise stimulus and mirroring the setup at its vertical midline, resulting in a clockwise scanning of the stimuli. (b) Timing of the mask onset for the three masking conditions in reference to the eye position trace of a rightward scanning saccade and corrective saccade. In immediate masking (Im) the mask appears at saccade onset. In intermediate masking (Inter), the mask appears 200 ms later.

direction (Hopp & Fuchs, 2004), separating the two target types by the direction of the respective saccade ensured that both adaptations occurred independently of each other.

Behavioral task

At the start of each trial, four stimuli were placed in quadratic arrangement around a black fixation cross (2.3° × 2.3°) on a gray background (Figure 1a). Distances between stimuli in horizontal and vertical direction were 12°. One stimulus was a meaningful image, one was a noise image, and the remaining two were homogenous dark gray rectangles. Participants were instructed to scan the four stimuli beginning and ending on the central fixation cross. Scanning direction was either clockwise or counterclockwise, with the first saccade going to the upper left or upper right corner, respectively. The target of this saccade was always a simple gray rectangle. The meaningful and noise images were used as targets of the two horizontal saccades (i.e., the second or the fourth saccade in the sequence). The position of the meaningful image (on the right or the left side, on the top or on the bottom) resulted in four distinct manifestations of the task, two for clockwise and two for counterclockwise scanning direction. These were counterbalanced across participants.

Adaptation procedure

Each trial started with fixation at the fixation cross for 300 ms. Then, a small red arrow (1.5°) appeared for 200 ms at the fixation point to indicate the direction of the first saccade. Subjects then scanned the stimuli at their own pace. To ensure valid completion of the task, subjects had to establish fixation on each stimulus for at least 100 ms, which was controlled online via position and velocity criteria on the eye data. If the criteria were not fulfilled, the trial was repeated. Repetition of a trial was rare and occurred only in 1.7% of all adaptation trials. Such erroneous saccade amplitudes were not included in analysis.

Saccadic adaptation was introduced for the two horizontal saccades, one of which was directed to the meaningful image and the other to the noise target. For these saccades, the eye tracker detected the onset of the saccade via a position and velocity criterion. First, eye position had to exceed a threshold of 3° distance from the current stimulus and second, eye velocity had to exceed a threshold of 100°/s for at least four consecutive samples. When the onset of the saccade was detected, the entire stimulus arrangement was shifted 4° in the saccade direction, thereby introducing a consistent postsaccadic error. After successful completion of the entire sequence, the fixation cross turned red when the gaze returned to it. Subjects then had a 1.5-s rest interval before the experiment commenced with the next trial.

Masking

The above procedure was performed in three masking conditions (Figure 1b), each with a third of the participants. In the immediate masking condition (Im), the target image (meaningful or noise) was replaced with a noise mask of the same size as soon as the participant had started the saccade. Thus, participants saw the images only in peripheral vision and never in high resolution. In the intermediate masking condition (Inter), the image was replaced by the mask 200 ms after saccade onset. For an average saccade duration of 55 ms, this allowed a brief postsaccadic glimpse of the target but was not long enough to reach and process the target image with a foveal view after the corrective saccade had ended. If one assumes that it takes at least 50–70 ms for visual data to be available for processing, only 0.3% of all corrective saccades finished in time for that. Finally, in the never masking condition (Never), the target was never masked such that participants had the opportunity to make corrective saccades and achieve a full view of the target.

Procedure

Subjects conducted 20 pre-adaptation baseline trials followed by 150 adaptation trials. The pre-adaptation baseline trials were identical to the adaptation trials with the exception that the arrangement of the stimuli on the screen remained stationary throughout the trial and did not shift during any saccade. Target images were selected pseudorandomly in each trial.

Data analysis

From the recorded eye movements, we selected the primary saccades, during which the adaptation procedure took place, as well as any corrective saccades that occurred within 300 ms after the offset of the primary saccade. Cases in which the primary saccade was not in the expected direction or in which its amplitude was below 6° (i.e., 50% of the original stimuli distance) were discarded. This occurred in 1.6% of all trials. Similarly, corrective saccades that were not in the same direction as the preceding primary saccade, or were larger than 6° (i.e., 150% of the target step), were also discarded. This affected 12.4% of all trials.

To estimate the amount of saccadic adaptation, each subject's mean primary saccade amplitude over the last 20 adaptation trials (A_{adapt}) was compared to the subject's mean primary saccade amplitude from the 20 baseline pre-adaptation trials (A_{pre}). Amplitude change (AC) in percent was calculated as in Equation 1 (Panouillères et al., 2009).

$$AC = \frac{(A_{\mathrm{adapt}} - A_{\mathrm{pre}})}{A_{\mathrm{pre}}} \cdot 100 \qquad (1)$$

To quantify the rate of adaptation, we fitted the series of primary saccade amplitudes and corrective saccade amplitudes of each single session with an exponential:

$$y = c + a \cdot exp\left(\frac{x}{-b}\right) \qquad (2)$$

Corrective saccade amplitudes (A_{corr}) were analyzed as percentage of the average primary saccade amplitude in the pre-adaptation trials as in Equation 3.

$$A_{\mathrm{ncorr}} = \frac{A_{\mathrm{corr}}}{A_{\mathrm{pre}}} \cdot 100 \qquad (3)$$

Latencies of corrective saccades were quantified as the time interval between the end of the primary saccade and the onset of the corrective saccade.

Latencies of primary saccades are difficult to define in a scanning paradigm, since they are not separable from voluntary fixation durations. As an approximation, we took the time interval from the onset of the preceding fixation until the onset of the primary saccade (Cotti, Guillaume, Alahyane, Pélisson, & Vercher, 2007; Zimmermann & Lappe, 2009).

Since saccades towards meaningful images and meaningless noise stimuli were measured within one trial, and within one subject, we computed repeated measures analyses of variance (ANOVAs) and paired samples t tests to investigate differences between saccades towards meaningful images versus saccades towards noise. We computed Wilcoxon's signed rank test in cases in which the underlying distribution was skewed. All computations were made with the MATLAB Statistics Toolbox (R2014a).

Results

We were interested in whether meaningful, pleasant-to-look at images of human figures induced a stronger gain of saccadic adaptation than noise images. Before we analyzed the adaptation data, we checked that amplitudes in the baseline trials before adaptation were not different for the two target sets—immediate masking: image 11.90° (0.81°), noise 11.86° (0.59°), $F(1, 11) = 0.25$, $p = 0.88$; intermediate masking: image 11.93° (0.56°), noise 12.05° (0.59°), $F(1, 11) = 0.375$, $p = 0.55$; and never masking: image 12.40° (0.37°), noise 12.22° (0.73°), $t(11) = -0.866$, $p = .41$. In all cases, saccade amplitudes were larger at the end of the adaptation phase—immediate masking: images, $F(1, 11) = 44.745$,

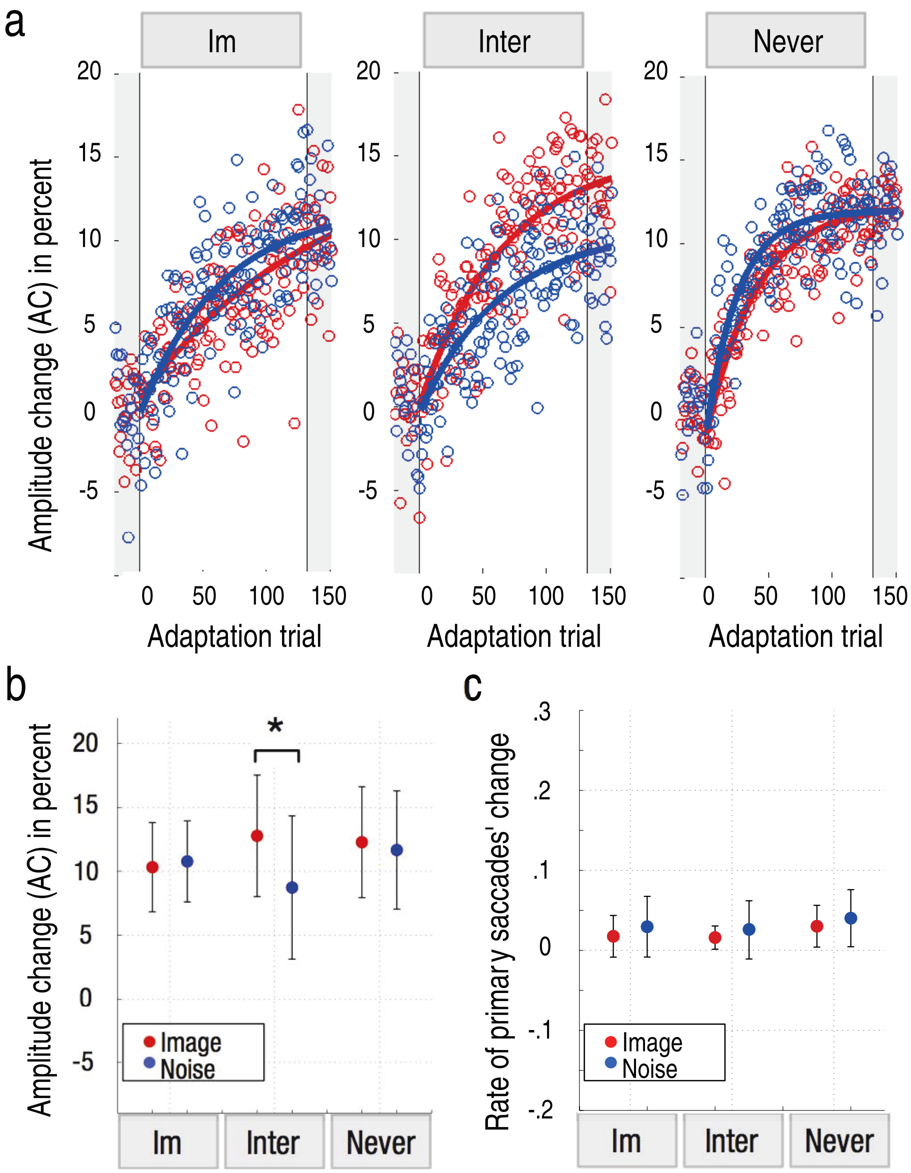

Figure 2. (a) Summary of primary saccade adaptation for the three experimental conditions. Red data points represent averaged saccade amplitudes towards meaningful targets. Blue data points represent averaged saccade amplitudes towards random noise targets. Lines represent an exponential fit. (b) Amount of adaptation (*AC*) for the three experimental conditions. Red points present average amplitude percent change of saccades to meaningful targets. Blue points indicate average amplitude change towards for saccades to random noise targets. Asterisk indicates $p < 0.05$ in repeated measures ANOVA. Bars indicate the 95% *CI*. (c) Average rates of adaptation from exponential fit. Bars indicate standard deviation.

$p < 0.001$, noise, $F(1, 11) = 61.28$, $p < .001$; intermediate masking: images, $F(1, 11) = 37.058$, $p < 0.001$, noise, $F(1, 11) = 11.677$, $p < 0.01$; and never masking: images, $F(1, 11) = 38.099$, $p < 0.001$, noise, $F(1, 11) = 30.495$, $p < 0.001$. We then determined the *AC* produced by the adaptation for each masking condition. Finally, we compared the amplitude changes for meaningful images and noise images. When the stimuli were masked immediately after saccade onset, amplitude changes were the same for both targets. Saccade amplitudes toward images increased by 10.3% (5.49%) and saccade amplitudes toward noise increased by 10.69% (5.1%), $F(1, 11) = 0.043$, $p = 0.84$, $\eta_p^2 = 0.004$. The same was true when stimuli were never masked. Amplitudes toward images increased by 12.28% (6.83%), amplitudes toward noise increased by 11.67% (7.29%), $F(1, 11) = 0.143$, $p = 0.71$, $\eta_p^2 = 0.013$. However, in the intermediate masking condition, when stimuli were masked 200 ms after saccade onset, adaptation amounts were significantly different, $F(1, 11) = 5.904$, $p = 0.03$, $\eta_p^2 = 0.349$. Amplitudes toward images increased by 12.77% (7.49%), whereas amplitudes towards noise increased only by 8.74% (8.82%). The values are shown in Figure 2b.

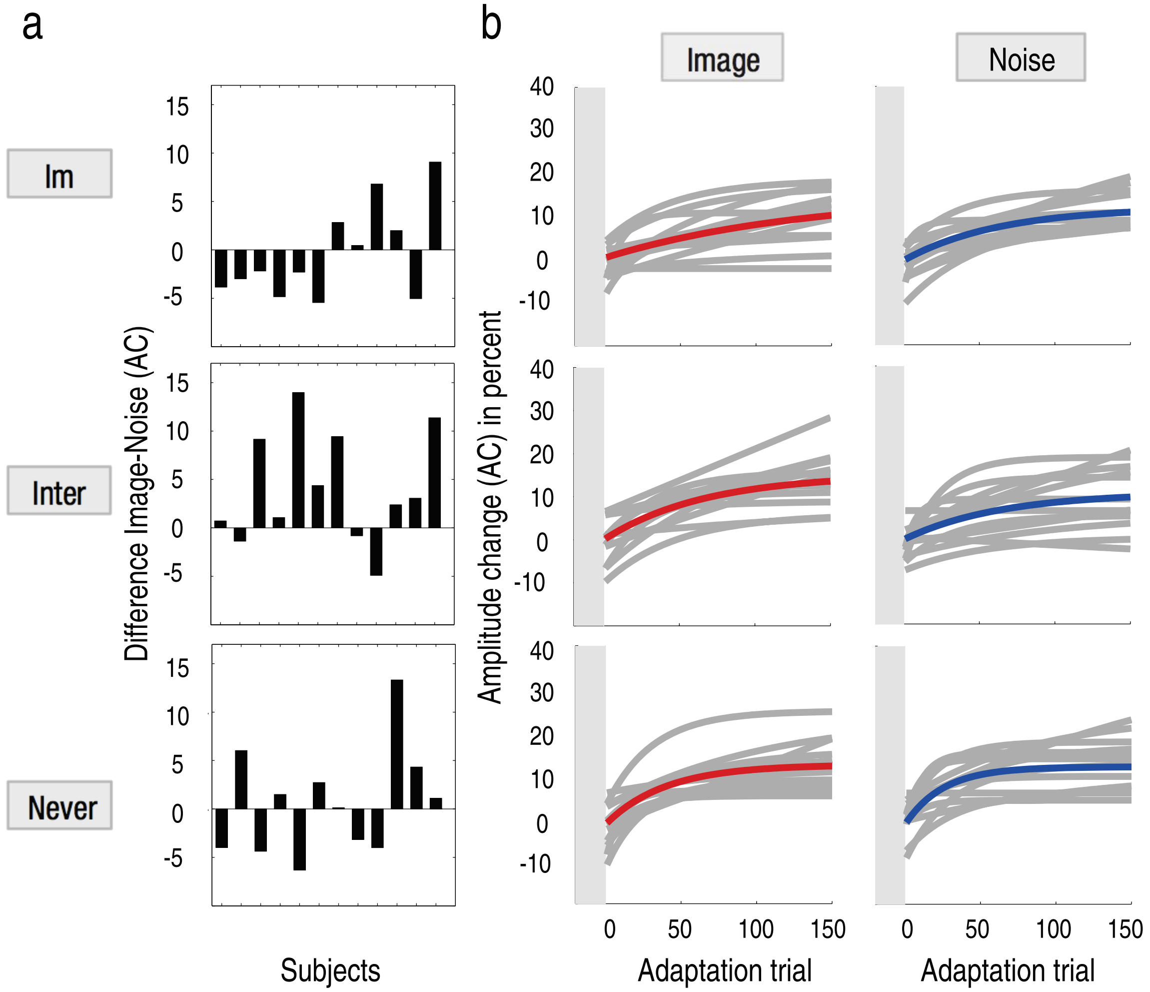

Figure 3. (a) Difference in amount of adaptation in primary saccades towards images and towards noise in the three masking conditions for all individual subjects. (b) Exponential fits of single subject data (gray) and averaged amplitudes of adaptation towards images (red) and noise (blue).

Figure 2a illustrates the development of adaptation for the two targets (images in red, noise in blue) in the three masking conditions. The data points correspond to saccade amplitudes averaged over participants while the lines illustrate an exponential fit to the data. The difference in the amount of adaptation is clearly visible in the intermediate masking condition. The exponential fit allows an estimate of the rate of change of the saccade amplitudes (i.e., the speed of adaptation). To test whether adaptation rates differed between image and noise targets, we fitted each individual's adaptation time course in each condition and for each target and compared the resulting rates (Figure 2c). This analysis indicated that rates of adaptation did not differ significantly in any of the masking conditions—immediate masking: $Z = -0.471$, $p = 0.68$; intermediate masking: $Z = 0.089$, $p = 0.93$; and never masking: $F(1, 11) = 0.661$, $p = 0.43$. Hence, subjects adapted more for saccades to meaningful targets in the intermediate masking condition but with the same speed as in all other cases.

Figure 3 presents the data for all single subjects. Differences in the achieved amount of adaptation (image–noise) are displayed in Figure 3a. In Figure 3b single subjects exponential fits can be seen together with the exponential fit for the averaged data.

These results show that the adaptation of the saccade amplitude to the target shift was stronger for meaningful images than for noise targets when the primary saccade afforded only a brief glimpse of the target. Amplitude changes were not different when the target was visible long enough to inspect it with a corrective saccade. To further investigate the contribution of corrective saccades in these scenarios, we also analyzed their amplitudes over the course of adaptation. The purpose of corrective saccades is to correct for errors of the primary saccade and to bring the fovea onto the target if the primary saccade failed to do so. In the adaptation paradigm, the target is shifted by 4° during

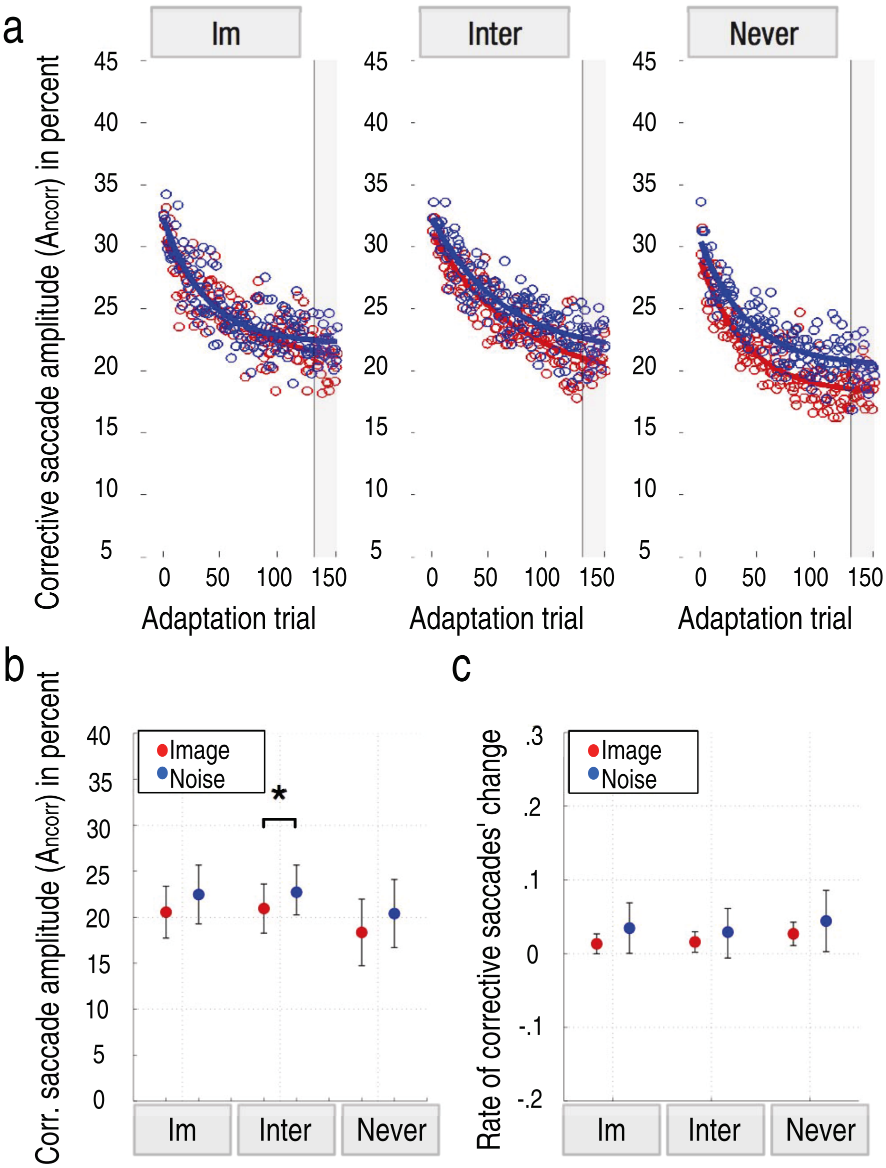

Figure 4. (a) Summary of corrective saccades in percent of primary saccade amplitude for the three masking conditions. Red data points represent averaged corrective saccade amplitudes towards meaningful targets. Blue data points represent averaged corrective saccade amplitudes towards random noise targets. Lines represent an exponential fit. (b) In intermediate masking the last 20 corrective saccade amplitudes were shorter when directed toward meaningful images than toward noise (repeated measures ANOVA, asterisk indicates $p < 0.05$). Bars indicate the 95% *CI*. (c) Rates of adaptation from exponential fit were not different. Bars indicate standard deviation.

the 12° primary saccade and hence the corrective saccade has to bring the eye 4° further to meet the target.

Therefore, corrective saccade amplitude in the first adaptation trials is equivalent to the target step and surmounts to about 33% of the primary saccade amplitude. As the length of the primary saccade increases over the course of adaptation, the amplitude of the corrective saccades decreases respectively. Figure 4a shows that this is the case in all masking conditions. Moreover, the pattern of amplitude changes of the corrective saccades to meaningful images and to noise matched that of the primary saccades.

When the stimuli were masked immediately, there was no difference in corrective saccades' amplitude A_{ncorr} images $= 20.55\%$ (4.44%), A_{ncorr} noise $= 22.47\%$ (5.03%), $F(1, 11) = 0.798$, $p = 0.39$, $\eta_p{}^2 = 0.07$. Also when the stimuli were never masked, there was no difference in corrective saccades' amplitude A_{ncorr} images $= 18.35\%$ (5.69%), A_{ncorr} noise $= 20.40\%$ (5.83%), $F(1, 11) = 1.309$, $p = .28$, $\eta_p{}^2 = .11$. A difference occurred only in the intermediate masking condition.

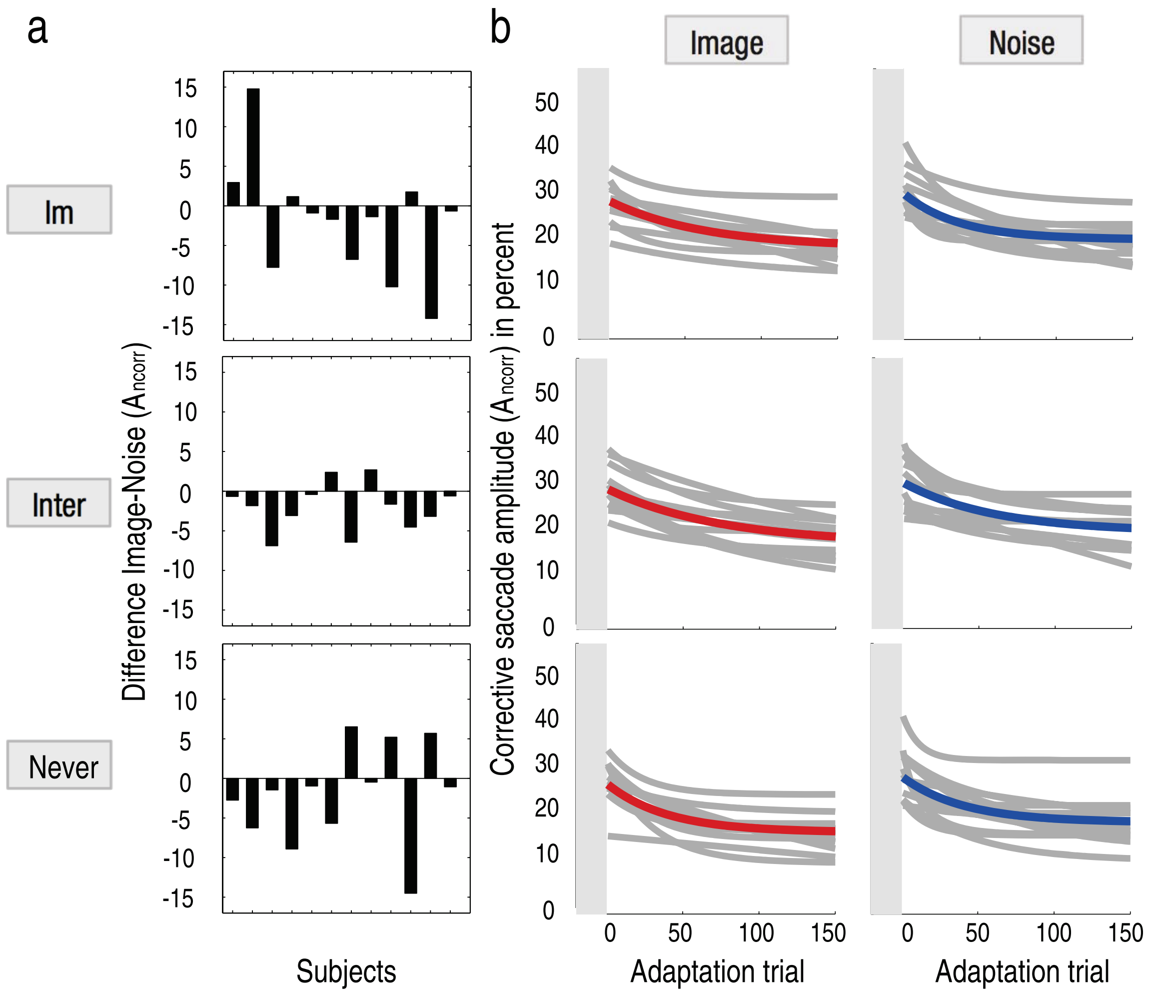

Figure 5. (a) Difference (image–noise) in mean corrective saccades amplitudes in late adaptation (A_{ncorr}) in the three masking conditions for all individual subjects. (b) Exponential fits of single subjects (gray) and averaged corrective saccades' amplitudes towards images (red) and noise (blue).

In that condition, corrective saccades were shorter when directed towards meaningful images than towards meaningless noise A_{ncorr} images = 20.94% (4.20%), A_{ncorr} noise = 22.96% (4.26%), $F(1, 11) = 5.366$, $p = 0.04$, $\eta_p^2 = 0.33$, consistent with longer primary saccades for meaningful images than for noise (Figure 4b). Rates of corrective saccades' decrease did not differ in any masking condition—immediate masking: $t(1, 11) = -2.086$, $p = 0.06$; intermediate masking: $Z = -1.019$, $p = 0.34$; and never masking: $t(1, 11) = -1.419$, $p = 0.18$ (Figure 4c). Figure 5 presents corrective saccades' data for all single subjects. Differences in the decrease of corrective saccades' amplitude in the last 20 adaptation trials (image–noise) are displayed in Figure 5a. In Figure 5b single subjects exponential fits of corrective saccades can be seen together with the exponential fit for the averaged data.

This pattern of results shows that the oculomotor behavior is not entirely driven by image content, consistent with the view that saccadic adaptation is primarily an automatic and stereotyped process. Even when the target does no longer afford an image view, as in the immediate masking condition, or when the corrective saccade does not lead to a better view of the original image, as in the intermediate masking condition, corrective saccades are regularly performed to reach the target location. Moreover, the condition in which the image was always visible does not contain more or better corrective saccades than the other conditions, nor does the meaningful image in this condition draw more or better corrective saccades than the noise image. Hence, corrective saccades appear rather uninfluenced by image content.

However, a difference between conditions was visible in the latencies of corrective saccades (i.e., in the duration of the time interval between the end of the primary saccade and the onset of the corrective saccade). From the early phase of adaptation to the late phase of adaptation, this interval increased for saccades to images in the intermediate masking condition—first

20 adaptation trials: 135.98 ms (25.11 ms), last 20 adaptation trials: 147.3 ms (26.23 ms), $t(1, 11) = 2.701$, $p = 0.02$, $d_z = 0.78$—but not in any of the other conditions—from early to late immediate masking: images 151.32 ms (30.83 ms) to 160.42 ms (33.09 ms), $F(1, 11) = 2.371$, $p = 0.15$, noise 139.98 ms (23.71 ms) to 147.47 ms (24.90 ms), $t(1, 11) = 1.096$, $p = 0.30$; intermediate masking: noise 145.40 ms (27.46 ms) to 146.91 (28.05 ms), $t(1, 11) = 0.185$, $p = 0.86$; and never masking: images 136.36 ms (23.84 ms) to 150.86 ms (44.18 ms), $t(1, 11) = 1.484$, $p = 0.17$, noise 143.28 ms (38.87 ms) to 145.42 ms (31.50 ms), $F(1, 11) = 0.148$, $p = 0.71$.

To approximate the latency of primary saccades, we took the time interval from the onset of the preceding fixation until the onset of the valid adaptation saccade. From early to late adaptation phase, we saw a significant change in primary saccade latencies, but only when saccades went to images in the intermediate condition—413.95 ms (140.46 ms) to 347.26 ms (107.09 ms), $F(1, 11) = 6.613$, $p = 0.03$. In the other conditions the interval did not change significantly during the course of adaptation—from early to late immediate masking: images 371.33 ms (207.29 ms) to 304.14 ms (101.46 ms), $t(1, 11) = 1.649$, $p = 0.13$, noise 348.50 ms (172.23 ms) to 298.76 ms (96.33 ms), $t(1, 11) = 1.188$, $p = 0.30$; intermediate masking: noise 408.52 ms (137.45 ms) to 362.55 ms (153.21 ms), $F(1, 11) = 2.354$, $p = 0.15$; and never: images 315.50 ms (104.65 ms) to 307.01 ms (88.64 ms), $F(1, 11) = 0.119$, $p = 0.74$, noise 313.81 ms (70.52 ms) to 312.02 ms (84.28 ms), $t(1, 11) = 0.008$, $p = 0.93$.

Taken together, therefore, two effects occurred in the intermediate masking condition. First, subjects increased their primary saccade amplitude. Second, they delayed the onset of the corrective saccade, thereby increasing the time spent in the vicinity of the meaningful stimulus before it was masked. Both changes benefit processing of the target image and increase information gain for the meaningful images.

Discussion

Every one of us makes millions of eye movements each day in order to look at things. These eye movements are highly stereotyped and are controlled by basic oculomotor processes. Their accuracy is constantly monitored by the visual system to identify targeting errors and adjust control, respectively. Our results show that not only positional error is used in this adjustment but also the content of the target image. Meaningful target images induce stronger adaptation of saccadic amplitudes than meaningless noise images. This finding provides two important points for discussion. First, the most basic levels of oculomotor control are influenced by image understanding. Second, successful viewing of an interesting image can constitute a reward to the visuomotor system.

Regarding the first point, saccadic adaptation has long been considered an automatic, low-level, motor process that takes place in the cerebellum (Hopp & Fuchs, 2004; Pélisson et al., 2010). Still, saccadic adaptation may exceed the concept or a mere recalibration of the motor system since it can be elicited in the absence of any spatial errors by reinforcement learning (Madelain, Paeye, & Wallman, 2011) and can differ for target stimuli with specific visual properties (Herman, Harwood, & Wallman, 2009).

Our results may be explained through such a reinforcement learning procedure if the meaningful image provides stronger reinforcement than the meaningless image. However, our results may also be explained by classical error-based motor learning, the prevalent model of saccadic adaptation (Ethier, Zee, & Shadmehr, 2008), if the error signal would be weighted by the content of the image.

In either case, information about the content of the image would need to be conveyed to the oculomotor structures responsible for saccadic adaptation. Recent studies (Blurton, Raabe, & Greenlee, 2012; Gerardin, Miquée, Urquizar, & Pélisson, 2012) have shown activity during saccadic adaptation in cortical areas, in addition to the cerebellum, and provided evidence of cortical contribution to adaptation via transcranial magnetic stimulation (Panouillères et al., 2014). The influence of the content of the image, and perhaps its motivational or rewarding character, may be conveyed by this route or, alternatively, by direct influences on cerebellar plasticity. A further possibility is the involvement of basal ganglia circuits that contribute to eye movement control and to reward-based learning (Hikosaka, Kim, Yasuda, & Yamamoto, 2014). The basal ganglia maintain long-term associations between stimuli and rewards and modify eye movement vigor to rewarding stimuli. The caudate nucleus can encode stable as well as flexible stimulus–reward associations at different sites. The coupling of stimuli and reward manifests in a capture of attention and gaze of the rewarded stimuli as well as quick and fast saccades going to high-value targets (Anderson & Yantis, 2013; Kim & Hikosaka, 2013; Takikawa et al., 2002; Yasuda, Yamamoto, & Hikosaka, 2012). Dopaminergic input to the caudate nucleus could account for reward specific plasticity (Kim, Ghazizadeh, & Hikosaka, 2014). Dopamine neurons become active when an outcome is better than expected, and their plasticity in the long run could maximize reward for future trials (Schultz, 1998). However, the role of basal ganglia in saccadic adaptation is poorly understood. A study with patients suffering from Parkinson's disease suggested that dopaminergic mechanisms in the basal ganglia contribute to adaptive lengthening of memory-guided saccades but not reactive saccade (MacAskill et al., 2002). The scanning saccades used in our study share some properties with memory-guided saccades (Hopp & Fuchs, 2004; Pélisson et al., 2010) such that a contribution of the basal ganglia might be conceivable. In either case, the influence of image content on saccadic adaptation shows that the typical procedure to study eye movements, namely by using simplified point targets to concentrate on spatial and temporal aspects of the stimulation, does not cover all aspects of oculomotor control. Even supposedly simple mechanisms can be different for richer stimuli. However, other aspects of the oculomotor behavior in our experiment indeed confirmed the automaticity of the process. For example, the stereotypical performance of corrective saccades occurred in all conditions, irrespective of whether they afforded successful target viewing or not.

Second, only the intermediate masking resulted in a difference between saccades to images and saccades to noise targets. In this condition, the image was masked 200 ms after the onset of the primary saccade. It is known that for simple point targets, a delayed onset or temporally restricted presentation of the postsaccadic target can reduce the amount of saccadic adaptation (Bahcall & Kowler, 2000; Panouillères, Urquizar, Salemme, & Pélisson, 2011). However, in our study, the content of a stimulus was masked while the spatial position error remained unaltered. The difference in adaptation towards images and towards noise shows that not only the target's spatial position, but also its content enters into the adaptation process. It may be that the value of the two stimuli in each session is measured relative to one another, rather than absolutely. In fact, this is the reason why we setup the paradigm so that both types of stimuli, meaningful and meaningless, occurred in the same session. For such relative coding, if one stimulus is higher valued than the other, there should develop a difference between the stimuli, but this can occur by increasing efficiency for one or by decreasing efficiency for the other, or a combination of both.

In comparing meaningful and meaningless stimuli in this way, our study aimed at maximally different categories. We, therefore, chose stimuli of attractive human figures to induce a strong and reliable outcome. These stimuli allow for a very intuitive and fast image understanding as well as intrinsic value association. Possibly the effect could transfer to other stimulus categories that share these features.

The masking puts maximum pressure on the success of the primary saccade because there is no time to perform a corrective saccade to view the image. This, together with the lack of difference in the other two masking conditions, allows some conclusions on the role of image content in saccadic adaptation. Since there was no difference in the immediate masking condition, we can conclude that it is not the attractiveness of the peripheral target in presaccadic view that supports a stronger adaptation. Instead, it is the postsaccadic view of the target that is important. However, since there was also no difference when the target was never masked, we can conclude that it is not the postsaccadic view per se. In the never masked condition, participants performed corrective saccades that allowed a successful target view eventually. In this case, pressure on the immediate success of the primary saccade was reduced. Thus, strong adaptation occurred only when a better adapted primary saccade was the only means to increase the quality of the postsaccadic view of the image. This finding shows that the adaptation is geared to provide a good postsaccadic view of the image if the image is of value to the participant, and that the successful view is a rewarding signal that increases learning efficiency.

Keywords: eye movements, learning, rewards, vision, perception

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Corresponding author: Annegret Meermeier.
Email: meermeier@uni-muenster.de.
Address: University of Muenster, Muenster, Germany.

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