

The reward of seeing: Different types of visual reward and their ability to modify oculomotor learning

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Saccadic adaptation is an oculomotor learning process that maintains the accuracy of eye movements to ensure effective perception of the environment. Although saccadic adaptation is commonly considered an automatic and low-level motor calibration in the cerebellum, we recently found that strength of adaptation is influenced by the visual content of the target: pictures of humans produced stronger adaptation than noise stimuli. This suggests that meaningful images may be considered rewarding or valuable in oculomotor learning. Here we report three experiments that establish the boundaries of this effect. In the first, we tested whether stimuli that were associated with high and low value following long term self-administered reinforcement produce stronger adaptation. Twenty-eight expert gamers participated in two sessions of adaptation to game-related high- and low-reward stimuli, but revealed no difference in saccadic adaptation (Bayes Factor₀₁ = 5.49). In the second experiment, we tested whether cognitive (literate) meaning could induce stronger adaptation by comparing targets consisting of words and nonwords. The results of twenty subjects revealed no difference in adaptation strength (Bayes Factor₀₁ = 3.21). The third experiment compared images of human figures to noise patterns for reactive saccades. Twenty-two subjects adapted significantly more toward images of human figures in comparison to noise ($p < 0.001$). We conclude that only primary (human vs. noise), but not secondary,

reinforcement affects saccadic adaptation (words vs. nonwords, high- vs. low-value video game images).

Introduction

To see things clearly is not only a common metaphor but often also a necessity in its literal meaning. Visual acuity is maximal in the fovea, which only measures approximately 1° in diameter. Hence, eye movement accuracy is a prerequisite for clear vision. Saccades are very fast movements of the eyes that take only 50–60 ms on average. In fact, they are so fast that their execution cannot be visually controlled online. Different theories about how saccade error is evaluated proposed either the spatial position of the target on the retina after the saccade (Robinson, Noto, & Bevans, 2003; Wallman & Fuchs, 1998), a comparison of the planned (predicted) saccade vector and the actual performed saccade (Collins & Wallman, 2012; Wong & Shelhamer, 2012) or a more complex comparison of predicted and actual post-saccadic images (Bahcall & Kowler, 2000). If a systematic error is experienced repeatedly after several saccades, the preplanned saccade vector will be adjusted during the course of a couple of tens of repetitions. In this way the oculomotor plant is able to ensure saccadic accuracy in

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the presence of adverse events such as aging of the eye muscles, fatigue, or disease. In the lab, these kinds of systematic errors can be administered by stepping the saccade target while the eyes are in flight (McLaughlin, 1967). After a couple of tens of repetitions the saccade will aim more for the new stepped target. The process of saccadic adjustment is called saccadic adaptation.

As evidenced by this adaptation procedure, the clear vision of a target might constitute a valuable commodity to the perceptual system (Collins, 2012; Collins & Wallman, 2012; Madelain, Herman, & Harwood, 2013; Meermeier, Gremmler, & Lappe, 2016). Looking at saccade accuracy from an operant perspective, the clear vision of a target might work as a reinforcer for oculomotor learning. In reinforcement learning, the reinforcer strengthens the behavior upon which it is contingent (Skinner, 1938; Wyckoff, Jr., 1952). Typically, positive reinforcers lead to appetitive behaviors, such as orientation and approach response. Two different types of reinforcers can be distinguished. Primary reinforcers serve basic needs of an organism, such as feeding, drinking, or social interaction, whereas secondary reinforcers do not serve any needs on their own but obtain their reinforcing ability by prior conditioning to a primary reinforcer. A subjects' recent reward history, their experiences, and their dispositions can greatly affect reinforcers (Killeen & Jacobs, 2017).

In previous studies we have shown that meaningful visual images can act as reinforcers for saccades, as saccadic adaptation was stronger to images of human bodies (head and torso) than to noise patterns (Meermeier et al., 2016). Moreover, when the saccade target displayed a novel image in every trial rather than always the same image, adaptation was even stronger (Meermeier, Gremmler, & Lappe, 2017). If visual inspection, curiosity, or social interactions are considered basic needs, the described images of humans might be categorized as primary reinforcers. Social orientation, the drive to mate and make friends, is a human key feature. When viewing a scene special attention is given to features of human bodies or faces, often triggering an orientation or approach response (Bindemann, Burton, Langton, Schweinberger, & Doherty, 2007; Downing, Bray, Rogers, & Childs, 2004; Downing, Jiang, Shuman, & Kanwisher, 2001; Hershler & Hochstein, 2005; Ro, Friggel, & Lavie, 2007; Rothkopf, Ballard, & Hayhoe, 2007). Humans orient to other humans even in the presence of other more salient features (End & Gamer, 2017) and from a very young age (de Schonen, Mathivet, & Deruelle, 1989; Johnson, Dziurawiec, & Morton, 1991). Therefore, the orientation toward images of humans might be a primary mechanism.

In comparison, secondary reinforcers gain their reinforcing qualities by association with primary

reinforcers and thus are learned. In the brain, reinforcement learning has been linked to dopaminergic signaling. The dopaminergic system becomes active if the outcome of an action is surprising or good or surprisingly good. In fact, the behavior of dopamine neurons replicates the predictions of operant learning schemes (Schultz, Tremblay, & Hollerman, 1998). Also, the shift from primary reward to secondary reward can be modeled linearly in dopaminergic signaling (Schultz, 2016). This implies that, after successful association, secondary reward might be processed exactly as primary reward in the brain. Looking from the point of an image one may, therefore, ask what might constitute a primary or secondary reinforcer. On the one hand, the basic experience of clear vision may have a primary reinforcing quality. On the other hand, the content of the image may contribute to the reinforcing quality of viewing it. In our previous study (Meermeier et al., 2016), we compared images of humans with spatial-frequency-matched noise patterns, expecting that such images of humans have a stronger reinforcing quality as meaningless patterns, which turned out to be the case. If we accept that such images may be considered primary reinforcers, either because of their content or simply because they convey meaning, we might go further and ask which images one might consider as secondary reinforcers (i.e., as having acquired reinforcing qualities through prior experience). Such images should essentially convey little or neutral meaning on their own but become meaningful through prior conditioning. In two experiments in the present study, we have chosen to test images from a computer game—with experienced gamers as subjects—in which images of words that convey literal meaning with meaningless images of jumbled characters. In each case, these images by themselves (i.e., in terms of the image) do not represent much meaning, but they have acquired meaning after excessive gaming or learning to read. In both cases, we find no influence of meaning on saccadic adaptation. A third experiment used meaningful images of human bodies similar to Meermeier et al. (2016), and showed that adaptation of reactive saccades is stronger for such images than for noise patterns.

Experiment 1

Experiment 1 tested images constructed from high and low reward configurations in a popular video game. Candy Crush Saga is a three-match puzzle game for mobile phones that is played extensively by many young people. Players are presented with screens consisting of a two-dimensional grid of a set of stylized

candy images (Figure 1a) in different arrangements. The player's task is to identify certain spatial arrangements and then make moves that would remove and rearrange some candies, which would reward the player with points. The aim is to collect as many points as possible before advancing to the next level. Different combinations of candies will score different amounts of points such that low reward and high reward configurations can easily be constructed from the same set of basic image elements.

We conducted this study in routine Candy Crush gamers who were able to play the game well and identify high and low reward configurations. Our participants had played Candy Crush consistently over many weeks or months. Candy Crush has an infamous reputation of a potentially addictive character; in fact, about 7% of all gamers fulfill the psychological criteria of an addiction (Chen & Leung, 2016). This suggests that dopaminergic mechanisms of reward-based learning of goal-directed behavior are activated in Candy Crush players. The behavior of dopamine neurons suggests that secondary rewards should gain comparable reinforcing qualities to the primary rewards (Schultz et al., 1998). Thus, if Candy Crush players learn to associate meaning with different candy configurations, we might consider these stimuli as secondary reinforcers. In Experiment 1 we want to find out whether high and low value images (allowing moves or not allowing moves) modeled after the game Candy Crush could induce the effect of increased adaptation in experienced Candy Crush players.

Methods

Participants

Twenty-eight subjects [average age = 22.5 (2.27) years; seven male, 21 female] participated in two sessions of scanning outward adaptation. Subjects were recruited from various faculties of the University of Muenster via an online social network. We explicitly asked for Candy Crush players who play the game regularly. We asked potential participants to report the level at which they were currently playing and the amount of time they spent playing the game. We confirmed their proficiency during a short Candy Crush playing session prior to the beginning of the experiment. The average level at which our participants played Candy Crush was 611.2 (546.93) points. The average frequency and duration of playing was 16.7 (45.06) times per week and 3.8 (4.47) hours per week. All participants gave written informed consent to participate and were naïve to the purpose of the experiment. The subjects had no history of musculoskeletal or neurological disorders. Procedures were approved by the Ethics Commission of the Department

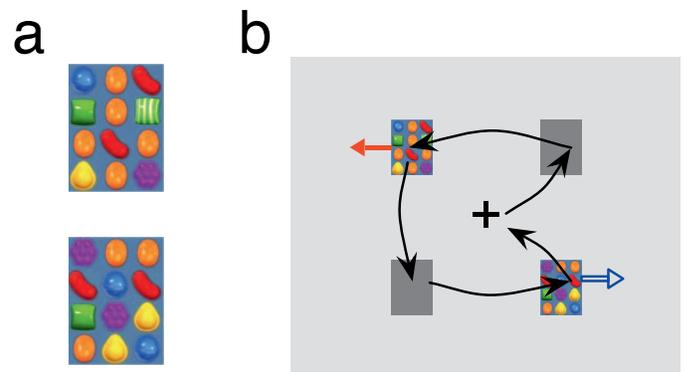


Figure 1. (a) Example for a high-value (top) and low-value (bottom) stimuli we created, modeled after the game Candy Crush. The high-value stimulus allows for a rewarding move, the low-value stimulus does not. (b) Scanning path for one example trial (counterclockwise, high value in the upper left corner). On detection of saccade onset, the stimulus pattern stepped into the direction of the saccade inducing a forward step of 4° . In the depicted trial, the step for the high-value target to the left is red (filled arrow), and for the low-value target, the arrow is blue (open arrow, saccade to the right).

of Psychology and Sport Sciences of the University of Muenster. Participants received monetary compensation of 12 Euro for their participation.

Stimuli

For one stimulus image ($3^\circ \times 4^\circ$), 12 candies were arranged in a 3×4 pattern, in which a highly rewarding move was either possible or not (see Figure 1). Candies were in color and presented on a medium blue rectangle, which was constructed to resemble the background color of the Candy Crush game. A total of 108 different candy arrays were constructed, with 54 high-value and 54 low-value arrangements. An additional 108 different noise images (1 pixel random noise in grayscale) were constructed as masks. Each image had its own masking image. The stimuli in the experiment were presented peripherally and were quickly masked after the saccade, which raises the question of whether the difference between high- and low-rewarding stimuli could be deduced in the experiment. Therefore, before commencing with the experiment, we ran a screening study with two raters who each completed 162 trials. The screening setup matched the experimental setup, with the only difference being that the high-value target appeared randomly either after the second saccade or after the fourth saccade. After each trial, the rater had to indicate, using two arrow keys, the position at which the high-value target had been shown (second saccade = arrow up, fourth saccade = arrow down). The trials were separated into three blocks, with each block containing all stimuli. Both raters completed the screening with more than

90% correct, Rater 1 = 91.93% (2.81) correct, Rater 2 = 91.32% (2.77) correct, indicating that recognition of the targets was possible under the conditions of the experiment.

In addition to the above-described initial screening, we asked subjects in the debriefing whether they recognized that the experiment displayed stimuli with different values in Candy Crush. Many subjects reported that one position always contained a high-value image while the other position did not. This indicated that, although the images were not present in the context of the game itself, our subjects still recognized their game value.

We applied the same masking to the Candy Crush stimuli as in Meermeier et al. (2016). In that study we found that the influence of target content is most pronounced when subjects only see a brief glimpse of the target. An interval of 200 ms is just enough time to make a saccade to first target positions (approx. 55 ms), and for an average latency of corrective saccades (approx. 150 ms). In this way, only parafoveal perception of the target was possible for Candy Crush images.

Apparatus

Participants were seated in a dimly lit room in front of an Eizo FlexScan F930 monitor (Eizo, Hakusan, Japan) that presented a visual field of $40^\circ \times 30^\circ$. The display resolution was 1152×864 pixels at a refresh rate of 75 Hz. To stabilize head position, the participants placed their heads on a chin rest located 57 cm from the screen. For experimental code as well as for the stimulus presentation, we used MATLAB (Mathworks, Natick, MA) with the Psychophysics toolbox extensions (Brainard, 1997). Eye movements were monitored by the EyeLink 1000 system (SR Research, Ontario, Canada), which sampled gaze positions with a frequency of 1000 Hz.

The calibration was performed with EyeLink software at the beginning of each recording session using a nine-point calibration grid.

Behavioral task

At the beginning of each trial, four images appeared in a square pattern in front of a gray background with a horizontal and vertical distance of 12° between their midpoints. The center of the square displayed a black fixation cross ($2.3^\circ \times 2.3^\circ$). During the main experiment, the candy images were presented on the upper left side and the lower right side, so that two of four rectangles presented colored candy icons and the other two were homogenous dark gray rectangles. The candy images were used as targets of the two horizontal saccades, thus being the second or the fourth saccade in

the scanning path. Depending on the experimental condition, the high-reward image was presented either on the upper left or the lower right side. The scanning direction was either clockwise or counterclockwise, but always started and ended at the fixation cross. Thus, the experiment consisted of four distinct manifestations of the task, resulting in two for clockwise and two for counterclockwise scanning directions, which were counterbalanced across the subjects.

Induction of adaptation

After fixation at the central fixation cross for 300 ms, a small red arrow of 1.5° appeared centrally for 200 ms, indicating the direction of the first saccade. During the first trial, the scanpath was highlighted with red lines for 5 s. Participants scanned the targets at their own pace, following the path back to the fixation cross. Subjects' gaze had to stay within a 3° window of each stimulus for at least 100 ms for the experiment to continue, ensuring valid completion of the task. This was controlled online via position and velocity criteria on the eye data. If the criteria were not fulfilled, the data were discarded and the trial was later repeated; this occurred in 6% of all adaptation trials. On the horizontal saccades, the whole pattern stepped 4° into the direction of the saccade, thereby inducing a lengthening of saccadic amplitude. If a participant successfully completed a trial in the right order, the fixation cross in the center of the display turned red for 700 ms. Subsequently, a new trial started after 1.5 s.

Procedure

Before the eye tracking task started, subjects had to show their gaming device to the experimenter, and fill out a short questionnaire about how long and often they play the video game. Subjects then had a 3 min time interval to play Candy Crush to bring the game and its rules to mind. The eye tracking experiment consisted of 30 baseline trials in which no target step occurred, followed by 200 adaptation trials in which the whole stimulus arrangement stepped in saccade direction during the two horizontal saccades to the Candy Crush images. Viewing was binocular but only the left eye was recorded.

Data analysis

From the recorded eye movements, we selected as primary saccades the horizontal saccades that take the fovea from the homogenous gray rectangle to the Candy Crush images. We excluded those primary saccades in which fixation criteria were not met. We also discarded primary saccades that were not in the expected direction or whose amplitude was shorter than

7° or larger than 20° (i.e., about 60% and 160% of the original target distance). Saccades with a deviation of 3° or more from the starting point were also excluded. Based on these exclusion conditions, 7.11% of all trials were excluded from data analysis. We calculated amplitude change (AC) according to Equation 1.

$$AC = (A_{\text{all}} - A_{\text{pre}}) / A_{\text{pre}} \times 100 \quad (1)$$

We also computed saccadic peak velocities and latencies to investigate possible effects of rewarding target images onto saccade characteristics. We conducted a repeated measures ANOVA including within-subject factors reward (high/low) and session (first/second). Since we wanted to investigate the selective influence of different stimuli, we applied Bayesian analysis to those results that did not show a significant main effect in the ANOVA. Bayesian analysis allows direct comparison of evidence for the presence of a difference with evidence for its absence (Wagenmakers, Lodewyckx, Kuriyal, & Grasman, 2010). In order to compute valid Bayes factors it is crucial to choose a prior that is suitable for the experiment. As we are dealing with saccade amplitudes (i.e., naturalistic data), a normal distribution seemed a sensible choice. The prior distribution was centered at 0, since we wanted to investigate possible deviations from the null hypothesis (i.e., that there is no difference between conditions). To estimate the width of the prior distribution we used the data from the previous experiments (Meermeier et al., 2016; Meermeier et al., 2017). The standard deviation of single subjects' differences in the amount of achieved adaptation was 5.75 and 5.97. This analysis suggests a value of 6 as a most likely prior width. Since amounts of saccadic adaptation can be highly variable between subjects, we calculated all Bayes factors additionally for standard deviations of 4 as a lower and 10 as an upper bound. All experimental code was written in Matlab (2014b; Mathworks). Analysis of data was conducted in MATLAB, Bayes factors were computed with the brms package in RStudio (Bürkner, 2016).

Results and discussion

To determine the strength of adaptation we calculated the change in saccade amplitude during late adaptation. The mean amplitude change in late adaptation towards high value targets was 13.40% (6.33) and not significantly different from the change toward low value targets 13.67% (6.99), $F(1, 26) = 0.117$, $p = 0.74$, (see Figure 2). There were no significant interactions or main effects for either session.

The ANOVA did not reveal any differences between the high- and low-reward stimuli, suggesting that saccadic adaptation was the same for both images. However, because of the way standard hypothesis

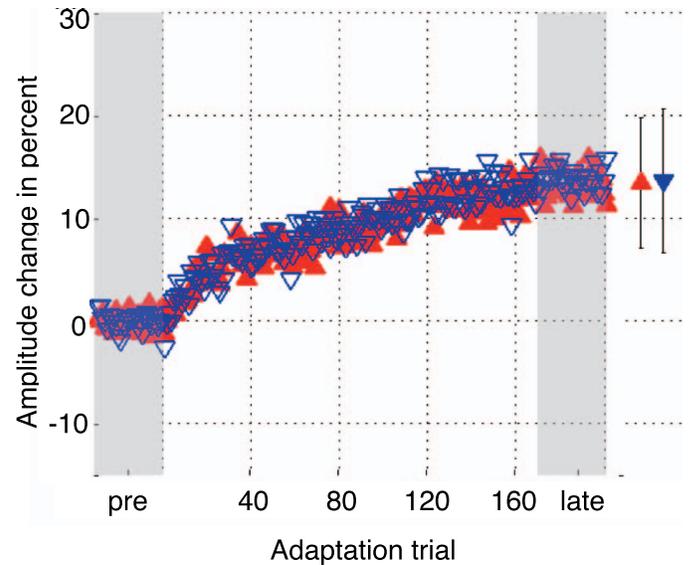


Figure 2. Grand averages of series of saccadic amplitudes in amplitude change (AC). Red filled triangles represent saccades toward high-value targets; blue open triangles depict saccades toward low-value targets. Gray background depicts the pre- and late-adaptation trials in which the stimuli remain stationary. Group average in late adaptation is shown on the right. Red upward pointing triangles represent saccades towards high-value stimuli, and the blue downward pointing triangles represent saccades toward low-value stimuli. Bars indicate standard deviation.

testing is conducted the failure to find a significant effect in the ANOVA cannot be interpreted as evidence that the two conditions are likely the same. To determine whether the two stimuli indeed induced the same amount of saccadic adaptation we computed the Bayes factor as the evidence ratio for the same model. Bayesian testing revealed evidence for the null hypothesis, $\text{Bayes Factor}_{01} = 5.49$ (3.73, 9.08), which means that it is about five times more likely that the groups have truly the same mean (0) as that they have not (1). We conclude that the reward meaning of learned stimuli from a video game has no effect on the amount of saccadic adaptation.

To investigate the possible effect of reward value onto saccade characteristics, we also calculated saccade latencies and peak velocities. Saccade latencies towards high value images were 321.41 ms (76.31), toward low value images they were 312.58 ms (66.97), $F(1, 26) = 2.845$, $p = 0.10$, $\eta_p^2 = 0.095$. There was a trend influence of session, $F(1, 26) = 3.516$, $p = 0.07$, $\eta_p^2 = 0.115$, since latencies in the first session tended to be longer than in the second session (mean difference = 26.62 ms, $SE = 14.20$ ms, $t(27) = 1.875$, $p = 0.07$).

Saccade peak velocities towards high value targets were on average 515.67°/s (66.47) and lower than towards low value targets peak velocities 521.44°/s (64.84). To calculate the ANOVA for saccade peak

velocities, we took the inverse of the data ($1/\text{velocity}$), to meet the criterion of normal residuals. There was no significant main effect nor interaction for value or side.

Taken together, Experiment 1 did not show any effect of acquired meaning onto saccade plasticity nor saccade characteristics. Bayesian testing showed that it is about five times more likely that there is no difference in the amounts of adaptation toward high-value Candy Crush images versus low-value Candy Crush images than that there is a difference in the amounts of adaptation. Learned reward pairings for Candy Crush images, therefore, do not seem to function as reinforcers for saccadic adaptation, unlike the images of humans in Meermeier et al. (2016).

Experiment 2

Experiment 2 tested a different kind of acquired meaning of visual stimuli, namely the formation of written words from characters. The meaning of certain combinations of characters is acquired during learning to read. Thus, in terms of visual images, words could qualify as secondary (i.e., acquired) reinforcers during reading. If the literal meaning boosts the reinforcing qualities of a stimulus, words should induce a higher amount of oculomotor learning in comparison to jumbled character strings.

Methods

Apparatus

The apparatus was the same as in Experiment 1.

Participants

Twenty subjects participated in the experiment (average age = 23.7; $SD = 5.99$) years; two men, 18 women). All gave informed consent, and all were able to read.

Stimuli

The meaningful words were 160 German five-letter words related to objects of nature, while the 160 meaningless character strings contained five characters, which could be either a consonant or one of the special characters %, ?, &, or \$. Furthermore, the meaningless character strings were presented upside down to decrease readability (Figure 3a). Images of words and images of character strings measured a horizontal extent of 2.5° , with 0.5° per letter.

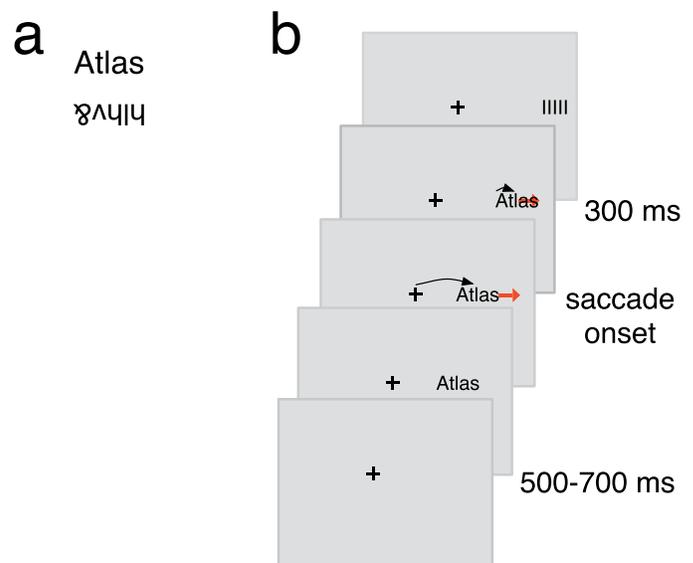


Figure 3. (a) Examples of words (top) and character strings (bottom). (b) Events during one example adaptation trial in which the word is presented as target of the rightward saccade. On detection of saccade onset, the high-value target on the left is stepped by 4° into the saccade direction, thereby producing a consistent post-saccadic error. The red arrow marks the intrasaccadic step. Black arrows depict typical eye movements.

Behavioral task

One session consisted of 320 trials. Every trial started with a fixation point in the center of the screen. A word or character string was then presented at a distance of 11° to the closest character, either to the left or to the right, and the subject started a reactive saccade to the target. For one-half of the participants, the words were always presented on the right and the character strings were always presented on the left. The directions were exchanged for the other half of the participants.

Adaptation procedure

In the preadaptation trials, the target remained visible after the saccade for 700 ms. It was then switched off and a new trial started with the onset of the central fixation point after another 700 ms. The subjects were instructed to return their gaze back to the central fixation point as soon as the target was switched off. After the preadaptation phase, the adaptation phase started, which consisted of 280 adaptation trials, 140 trials for each direction. The target in those trials was shifted 4° away from the fixation point as soon as the saccade onset was detected online. Analogous to Meermeier et al. (2016), the targets were only presented briefly, for 300 ms, and then masked with a character string containing five times the letter l (“ell”; see Figure 3b). Viewing was binocular but only the left eye was recorded.

Data analysis

We excluded trials with amplitudes smaller than 50% of the primed saccade amplitude (5.5°) and those that were larger than 150% (16.5°). Furthermore, we excluded trials with latencies shorter than 100 ms or longer than 400 ms. Overall, 3.73% of all trials were excluded.

The sessions started with 40 preadaptation trials, 20 trials of each condition. These trials were used to calculate a mean preadaptation amplitude in each condition for every subject. The last 40 trials of the adaptation phase contained 20 trials of each condition. These trials were used to calculate the mean end-of-adaptation saccade amplitude in each condition for every subject. We analyzed the amplitude change (AC) as in Experiment 1 (see Equation 1). We computed paired samples t tests and also Bayesian testing to investigate the main finding of amplitude change.

Results and discussion

In the pre trials, average saccade amplitude toward words was 11.75° (0.49) and toward character strings, it was 11.59° (0.63). Thus, the gaze landed on the second letter of the five-letter word, which is consistent with typical fixation patterns for five-letter words (Nazir, Ben-Boutayab, Decoppet, Deutsch, & Frost, 2004).

Figure 4 shows the development of saccade amplitudes during the adaptation phase. The grand average of saccade amplitudes of all subjects in the adaptation phase is plotted for the two conditions separately.

The mean amplitude change in the word condition was 12.53% (7.42) and not significantly different from that in the character string condition 13.11% (7.97), paired t test, $t(19) = -0.302$, $p = 0.77$. Bayesian testing revealed some evidence for the null hypothesis, Bayes Factor₀₁ = 3.21 (2.22, 5.16).

Latencies were on average 162.14 ms (16.48) for saccades toward words, and significantly shorter than latencies of saccades towards nonwords, which were 168.73 ms (16.49), paired t test, $t(19) = -2.302$, $p = 0.03$. Thus, latencies for reactive saccades to words were shorter than to nonwords.

Peak velocities for saccades towards words were on average $493.98^\circ/\text{s}$ (83.14) and $496.89^\circ/\text{s}$ (78.04) for meaningless character strings, paired t test, $t(19) = -0.987$, $p = 0.34$.

The results indicate that meaningful words as saccade targets did not induce stronger adaptation compared to meaningless character strings. The Bayes factor shows moderate evidence for the null hypothesis that the amounts of adaptation for words and meaningless character strings are the same. Thus, we did not see a modulation of amplitude adaptation by

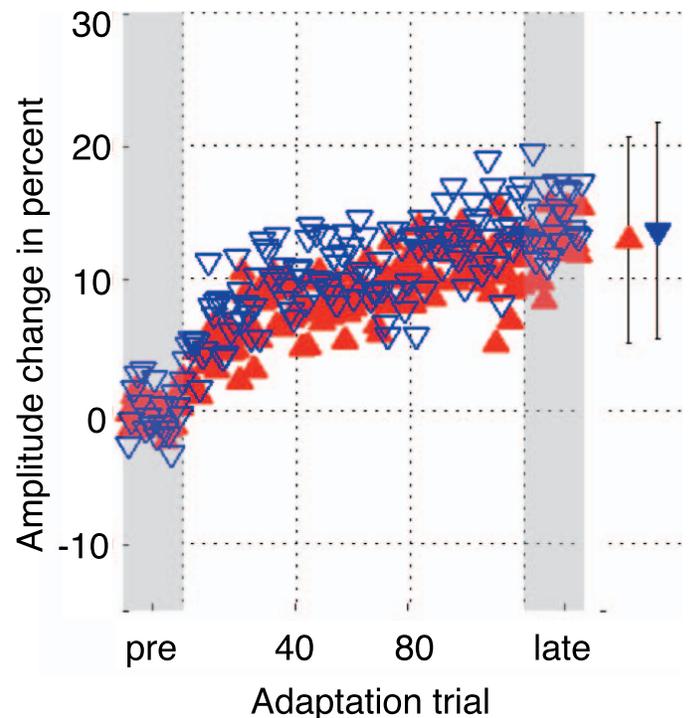


Figure 4. Grand averages of amplitude change during saccadic adaptation. Red upward-pointing triangles represent saccades toward word targets, and blue downward-pointing triangles depict saccades toward meaningless strings of characters. Gray background depicts the pre- and late-adaptation trials. Group averages in late adaptation are shown on the right. Bars indicate standard deviation.

the factor readability or literate meaning. We conclude that learned literate meaning differs from the meaning that the picture of a human figure conveys. Literate meaning alone is not enough to lead to an increased amount of oculomotor learning.

Interestingly, saccadic reaction times were shorter for word stimuli. Such a reduction in latency can be interpreted as a form of saccadic facilitation, as an increase in saccadic readiness (Collins, 2012). Collins observed this increased saccadic readiness for saccades that could successfully reach the target. The reward of seeing a target in comparison to not seeing it could have similar effects onto saccadic latencies as seeing words in comparison to jumbled characters. However, this increase in saccadic readiness does not trigger an increased amount of oculomotor learning. As a consequence, we assume that there might be two independent mechanisms that are responsible for latency reduction and a difference in saccadic adaptation.

The word superiority effect describes the phenomenon that words are perceived as taller than size-matching nonwords (New, Dore-Mazars, Cavezian, Pallier, & Barra, 2016). Saccadic adaptation can be induced by an increase in target length during a

between-objects saccade (Bosco, Lappe, & Fattore, 2015). Lavergne, Vergilino-Perez, Collins, & Dore-Mazars (2010) found that within-object saccades adapt if the length of a character string is changed midflight. Importantly, our stimuli changed horizontal position but not horizontal extent midflight. Furthermore, our saccade amplitudes toward words and meaningless character strings did not differ before adaptation. Readability and the word superiority effect might increase perceived vertical extent and might contribute to the reduction in latency.

Experiment 3

Experiments 1 and 2 showed no difference of saccadic adaptation for learned meaning in video game stimuli or words. Experiment 3 used stimuli similar to those of Meermeier et al. (2016). It shows a difference in saccadic adaptation to meaningful images versus noise images and establishes the robustness of the difference with regard to a number of experimental parameters. First, this experiment used reactive saccades, like Experiment 2 of the present study, while Meermeier et al. (2016) used scanning saccades. Higher order saccades, such as scanning saccades, are thought to involve other cortical processing than reactive saccades. Understanding target content requires cortical processing. Furthermore, scanning saccades are much more relevant with regard to looking at interesting targets. In every day life, they are particularly prone to go to regions most interesting. In reactive saccades, a target suddenly appears while the fixation point is extinguished. Such a situation is very rare outside the lab. It would be interesting to see whether the influence of human figures as target content can also influence reactive saccade adaptation even though they have less correspondence to real-life situations. Second, unlike Meermeier et al. (2016) this experiment did not mask the stimuli after the saccade but simply displayed them for a brief duration. Third, the present experiment used both male and female participants, unlike Meermeier et al. (2016) who used mostly female participants. This allowed us to see whether our findings generalize to both genders.

Participants

Twenty-two subjects (14 men, eight women) participated in a saccadic outward adaptation task of reactive saccades. All subjects had normal or corrected-to-normal visual acuity. On average subjects were aged 27.4 (8.5) years. All subjects gave informed consent.

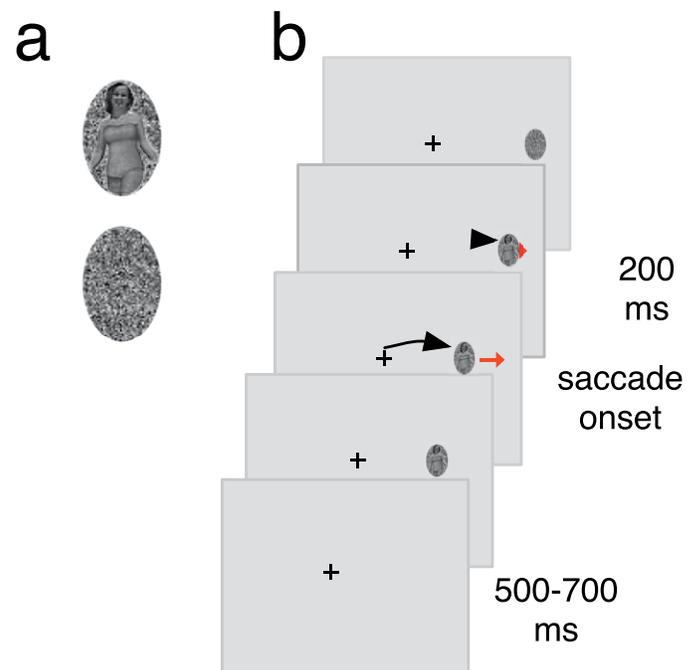


Figure 5. (a) Example images of human figure (top) and noise stimulus (bottom). (b) Events during one example adaptation trial with the human image on the right side. The red arrow marks the intrasaccadic step and the black arrows depict typical eye movements. The images were obtained from the Florida Memory collection of the State Library & Archives of Florida (<https://www.floridamemory.com/>).

Stimuli

Stimuli were grayscale pictures of human females, including head and upper body. Meaningless pictures of noise served as control condition. Stimuli were oval in shape and measured 2.4° in maximal width and 3.2° in maximal height (see Figure 5a). There were 140 different human pictures and 140 different noise images.

Behavioral task

Subjects started with fixating a red fixation dot (0.5×0.5 deg) for 700 to 1200 ms. Then, on either the right or the left side at 11° horizontal eccentricity a target appeared while simultaneously, the fixation dot disappeared. Subjects made reactive saccades toward the targets. The targets were only displayed for 200 ms after saccade onset, and then extinguished. After an intertrial interval of 500 ms, the experiment proceeded.

Adaptation procedure

Saccades were detected by a spatial threshold of 3° . Upon detection of saccadic onset during an adaptation trial, the targets stepped 4° into the direction of the saccade, hereby introducing consistent postsaccadic

error (see Figure 5b). In one adaptation session, a human picture was always displayed on one side and on the other side, there was always a noise pattern. In the second session, the human and noise pattern were reversed. Whether subjects started with human images on the right or on the left side was counterbalanced across participants. Subjects participated in two sessions of reactive outward adaptation measurement. Sessions were separated by at least 24 hours but preferably longer, resulting in an average of 4.7 interim days (range 1–18). In this way, the amount of adaptation for image and noise stimulus was measured within one subject and session, which is important to avoid day-by-day variation in saccadic amplitude. There were 10 baseline trials during which there was no shift of the target images, followed by 130 adaptation trials into both directions.

Data analysis

We analyzed primary saccade amplitudes during which saccadic adaptation took place. The last 10 adaptation trials served as an estimate of the amount of saccadic adaptation. As in Experiment 1, we calculated amplitude change (in percent). We excluded trials that resulted in amplitudes smaller than 50% of the primed saccade amplitude (5.5°) and those that were larger than 150% (16.5°). Furthermore, we excluded trials with latencies shorter than 100 ms or longer than 400 ms. Overall, 2.28% of all trials were excluded. We computed repeated measures ANOVAS and implied Bayesian testing for the analysis of amplitude change (AC).

Results and discussion

A repeated measures ANOVA, including within-subject factors content (image/noise), side (leftward/rightward), and the between-subjects factor gender, revealed that the amount of adaptation was higher for saccades toward human images 11.97% (6.64) than toward noise, 7.37% (5.53), $F(20, 1) = 24.136$, $p \leq 0.001$, $\eta_p^2 = 0.54$ (see Figure 6).

There were no main effects or interactions for side or gender. The results of this experiment show an increased amount of adaptation toward images of human figures in comparison to noise. Since there were no gender effects in this more balanced sample, this finding can be generalized to both male and female participants.

Saccadic latencies toward images were shorter 150.52 ms (19.09 ms) than toward noise patterns 158.88 (20.87) ms, $F(1, 20) = 15.01$, $p \leq 0.001$, $\eta_p^2 = 0.417$. There were no main effects or interactions for side or gender. Similar to Experiment 2, the significantly

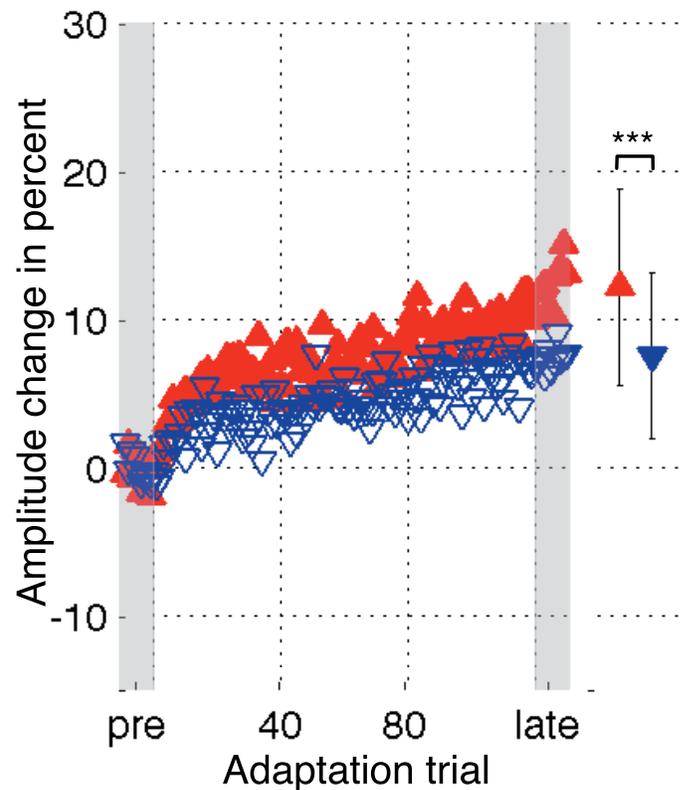


Figure 6. Grand averages of amplitude change during saccadic adaptation. Red upward-pointing triangles represent saccades toward human images and blue downward-pointing triangles depict saccades toward noise stimuli. The gray background illustrates the pre- and late-adaptation trials. The group average in late adaptation is shown on the right. Bars indicate standard deviation.

shorter latencies might hint at an increased saccadic readiness.

Saccadic peak velocities toward images $506.90^\circ/s$ (73.85) were not different from peak velocities toward noise patterns $505.89^\circ/s$ (70.56), $F(1, 20) = 0.057$, $p = 0.81$. There were no main effects or interactions for side or gender. Peak velocities did not differ for image content of human versus noise.

General discussion

We studied the influence of image content on the strength of saccadic adaptation to meaningful images. While most studies on saccadic adaptation were performed with simple point targets, the present study and two previous ones (Meermeier et al., 2016; Meermeier et al., 2017) showed that adaptation strength depends on image content. Experiment 3 of the present study and the experiments in Meermeier et al. (2016) showed that adaptation of saccades to images

of humans is stronger than to noise images. The results of Meermeier et al. (2017) showed that adaptation of saccades to such images is even stronger when each trial presents a novel image than when the same image is shown repeatedly, suggesting that novelty of image content is also processed in saccadic adaptation. Experiments 1 and 2 of the present study, however, showed that saccades to meaningful character strings (i.e., words) and saccades to high-value images from the video game *Candy Crush* did not produce stronger adaptation than saccades to the respective meaningless or low-value counterparts. Bayes factor analysis confirmed that, in these cases, equal adaptation strength was more likely than a difference in adaptation strength. The lack of difference in these two conditions provides important novel information about the boundaries of the influence of image content on saccadic adaptation. In the following section, we will first discuss findings on saccade latencies and peak velocities, two established markers of target value in saccade performance, and then discuss the implications of our findings on amplitude adaptation.

We found decreased saccade latencies in the reactive saccades toward words in comparison to nonwords (Experiment 2) and to images of human figures in comparison to noise (Experiment 3). A decrease in latency is a robust finding for rewarded targets (Madelain, Champrenaut, & Chauvin, 2007; Milstein & Dorris, 2007; Milstein & Dorris, 2011; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002). Successful foveation of targets can induce the same effect, indicating that the successful foveation of a target can be perceived as a rewarding and reinforcing event to the oculomotor plant (Collins, 2012). A perceptual task in comparison to a control task can also result in reduced saccade latencies (Bieg, Bresciani, Bühlhoff, & Chuang, 2012; Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005; Wolf & Schütz, 2017). Reduced saccade latencies indicate a facilitation of the rewarded or task relevant saccade, which has been described as saccadic readiness. Experiment 2 thus provides evidence for a facilitation for words in comparison to meaningless character strings. This finding is also proof of the subject's adequate processing of the stimuli. Likewise, the difference in latency of saccades to images versus saccades to noise patterns in Experiment 3 confirmed the influence of content on saccade performance. Experiment 1 differed from this pattern since there was no difference in latency between the two experimental conditions. However, unlike Experiments 2 and 3, Experiment 1 used a sequential scanning saccade task in which subjects could dwell on one target before they make the saccade to the next in the sequence. In this case, latencies are difficult to determine and confounded with fixation durations. Consistent with this, the latency difference that we observed in the reactive

saccades of Experiment 3 of the present study was not observable in the study of Meermeier et al. (2016), which used the same stimuli but a scanning saccade task.

Saccade peak velocities were not different in all of the experiments in the present study. This seems to be at odds with the findings in the literature, which showed increased peak velocities for saccades towards faces (Xu-Wilson, Zee, & Shadmehr, 2009) and rewarded targets (Chen, Chen, Zhout, & Mustain, 2014; Chen, Hung, Quinet, & Kosek, 2013). However, the difference may be explained by intricacies of the adaptation paradigm. The systematic increase of saccade amplitude in the adaptation phase is associated with a change the peak velocity (Bahill, Clark, & Stark, 1975; Carpenter, 1988). In turn, substantially more variation is introduced into the system by the adaptation, which might reduce the chances of finding differences in saccadic peak velocities.

With respect to amplitude adaptation, Experiment 3 showed that the stronger adaptation to images than to noise also occurs for reactive saccades but the stimuli in Experiments 1 and 2 did not produce any difference in adaptation. What does the lack of difference in adaptation strength in Experiments 1 and 2 tell us about the mechanisms of saccadic adaptation and the role of image content in eye movements? First, it is possible that the comparison between an image and a meaningless noise pattern provides a stronger difference than the comparison between two visually similar images that differ only in meaning (high vs. low value, or words vs. nonwords). Although this is an intuitive explanation, it does not seem to be the whole story. In Meermeier et al. (2017), we investigated the effect of novelty in the adaptation paradigm. In a scanning outward adaptation task, the same image of a human figure was always presented in one position, whereas in the other position, a new picture of a human figure was presented in every trial. We observed an increased amount of adaptation toward the position at which the novel stimulus appeared in comparison to the position with the repeating stimulus. Hence, in that case, an image versus image comparison was able to induce an increased amount of saccadic adaptation.

Our study relates to studies of attentional or information-seeking processes contributing to the strength of saccadic adaptation. There is evidence that saccadic adaptation can be influenced by the attentional load of the task (Gerardin, Nicolas, Farné, & Péliçon, 2015). An increased amount of saccadic adaptation could be mediated by an increased amount of attention given to the human stimuli. Other studies stress the role of information gain for oculomotor learning (Paeye, Schütz, & Gegenfurtner, 2016; Schütz, Kerzel, & Souto, 2014). These studies show that other high order processes can impact the general ability of

saccadic adaptation. Attentional load and information seeking are mostly studied in the context of tasks (e.g., discrimination tasks). Our studies pose no such task framework but are only concerned with the image content as a picture.

The stimuli used in Experiment 1 have acquired an association with either high or low reward in the context of a video game. In the context of our experiment they did not predict any reward. Perhaps a difference in saccadic adaptation would appear if the stimuli were put in the context of the game and subjects were to act on them in a game-related manner. Such an effect, however, would seem more related to the influence of task on saccadic adaptation (Schütz et al., 2014; Schütz & Souto, 2015) than on the value presented by the image itself.

The social nature of the images in Experiment 3 in comparison to nonsocial images in the other experiments may also contribute to a stronger reinforcing signal. Social stimuli are unique in their significance for survival, which is why they might trigger a more automatic processing than nonsocial stimuli (Greene, Mooshagian, Kaplan, Zaidel, & Iacoboni, 2009). Orientation to social stimuli in a scene is well documented (Bindemann et al., 2007; Downing et al., 2004; Downing et al., 2001; End & Gamer, 2017; Hershler & Hochstein, 2005; Ro et al., 2007; Rothkopf et al., 2007) and occurs from a very young age on (de Schonen et al., 1989; Johnson et al., 1991). Therefore, the social content of our images may constitute a form of primary reinforcement to the visual system. Primary reinforcers are reinforcers that are not learned but unconditioned and inherent or intrinsic to the system.

In this view, the stimuli used in Experiment 1 and Experiment 2 should be considered secondary reinforcers as their meaning regarding value in the Candy Crush game, or literally in the word/nonword comparison, is clearly learned. The observation that the meaning of these stimuli does not influence adaptation strength suggests that only primary but not secondary reinforcement affects saccadic adaptation.

Reinforcement learning of saccade amplitude modifications has also been shown in situations where no target is visible after the saccade and, instead, an auditory signal related to saccade accuracy served as reinforcer (Madelain et al., 2011b). Such auditory reinforcement was also effective when the target was visible but shifted such that it was not informative of saccade accuracy (Madelain et al., 2011b; Paeye & Madelain, 2011). Clearly, such tones could not be considered primary reinforcers. Hence, these studies demonstrated that also nonprimary reinforcers can induce saccadic adaptation. However, our experiments differ from those studies, since we ask which of two stimuli induces more saccadic adaptation rather than whether or not either stimulus induces saccadic

adaptation at all. Thus, in our study subjects always experienced spatial errors as the whole target pattern stepped during the saccade. The reinforcing qualities of the stimuli thus modulated the process of saccadic adaptation that was primarily based on spatial error. Our conclusion, however, is similar to the one of Madelain et al. (2011a). Saccadic adaptation is not only triggered by spatial errors, but also by reception of a rewarding stimulus at saccade end.

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

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