Saccadic suppression during voluntary versus reactive saccades

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Saccades are fast eye movements that reorient gaze. They can be performed voluntarily—for example, when viewing a scene—but they can also be triggered in reaction to suddenly appearing targets. The generation of these voluntary and reactive saccades have been shown to involve partially different cortical pathways. However, saccades of either type confront the visual system with a major challenge from massive image motion on the retina. Despite the fact that the whole scene is swept across the retina, a saccade usually does not elicit a percept of motion. This saccadic omission has been linked to a transient decrease of visual sensitivity during the eye movement, a phenomenon called saccadic suppression. A passive origin of saccadic suppression based on temporal masking has been proposed as well as an active central process that inhibits visual processing during the saccade. The latter one would need to include an extraretinal signal, which is generated already during saccade preparation. Since saccade generation differs for voluntary and reactive saccades, timing and nature of this extraretinal signal as well as its impact on visual sensitivity might also differ. We measured detection thresholds for luminance stimuli that were flashed during voluntary and reactive saccades and during fixation. Detection thresholds were higher during voluntary than during reactive saccades such that suppression appeared stronger during voluntary saccades. Stronger suppression in voluntary saccades could arise from a stronger extraretinal signal that activates suppression or could indicate that a suppression underlying process itself partially differs between voluntary and reactive saccades.

Introduction

Voluntary saccades are made to gather information about the environment and explore the visual scene. These exploring eye movements are self-paced and usually directed at will to objects in the scene. Sudden changes in the visual field, in contrast, trigger reactive saccades that are provoked to bring the gaze as fast as possible to a new, potentially threatening or interesting target. The time spent on saccade preparation is short in reactive saccades. Latencies range from 150 to 200 ms (Smit, Van Gisbergen, & Cools, 1987). The preparation time of voluntary saccades during scanning of a scene is less easy to quantify, since the time of decision for making a saccade is not overtly observable. However, typical fixation durations during scene observation last several hundred milliseconds.

Although voluntary saccades are much more frequent in everyday life, investigations in the lab have often focused on reactive saccades because they can easily be elicited with reliable timing. Comparisons between reactive and voluntary saccades regarding their origin, purpose, and preparation time, however, showed differences in the underlying control networks of the brain. The voluntary saccade network is believed to include pathways from frontal cortex to superior colliculus and the brainstem (Rivaud, Müri, Gaymard, Vermersch, & Pierrot-Deseilligny, 1994; Müri & Nyffeler, 2008) while the reactive saccade network includes parietal pathways to the superior colliculus and the brainstem saccade generator (Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991; Gaymard, Lynch, Ploner, Condy, & Rivaud-Pechoux, 2003; Müri & Nyffeler, 2008). Furthermore, functional magnetic resonance imaging studies have shown that for the sensorimotor transformation for saccade generation the intraparietal sulcus oculomotor areas are more strongly involved during voluntary than during reactive saccades (Mort et al., 2003) while hMT + /V5 activation is weaker for voluntary saccades than reactive saccades (Schraa-Tam et al., 2009). Furthermore, several behavioral studies found that saccadic adaptation—that is, the modification of saccade amplitude after consistent errors at saccade end—is not transferred completely from one saccade type to the

other (Erkelens & Hulleman, 1993; Deubel, 1995; Fujita, Amagai, Minakawa, & Aoki, 2002; Hopp & Fuchs, 2004; Collins & Doré-Mazars, 2006; Zimmermann & Lappe, 2009). The brain areas active during adaptation of the two saccade types partially differ as well (Gerardin, Miquée, Urquizar, & Pélisson, 2012). Areas in the cerebellum and the frontal cortex were found to be active during adaptation of both saccade types, whereas activity in medial and posterior areas of intraparietal sulcus was related to voluntary saccade adaptation and activity in the temporo-parietal junction and hMT + /V5 was related to reactive saccade adaptation. Hence, voluntary and reactive saccades do not only serve different purposes in information gathering, they also involve partially different neurophysiological operations.

However, both types of saccades concur with certain challenges to visual perception. Object positions in retinal coordinates change across the saccade, and the movement itself creates massive retinal motion as the visual scene is swept across the retina. The latter should lead to the percept of blur but usually we are not aware of this blur during the eye movement. This lack of perception or omission is linked to a phenomenon called saccadic suppression—namely a decrease of visual sensitivity around saccades—which reduces the impact of the retinal motion during the saccade on the visual system (Campbell & Wurtz, 1978). Thresholds for the detection of flashed stimuli during saccades are raised 3-fold compared to those during fixation (Volkmann, 1962). Velocity thresholds for motion detection have also been found to be increased during saccades (Burr, Holt, Johnstone, & Ross, 1982) as well as detection thresholds for target displacement (Bridgeman, Hendry, & Stark, 1975). Saccadic suppression is stronger for luminance stimuli with low spatial frequencies than for stimuli with high spatial frequencies (Burr et al., 1982), while the detection threshold for equiluminant gratings modulated in color is not elevated during saccades (Burr, Morrone, & Ross, 1994). In the last decades two different origins of this drop in visual sensitivity have been discussed: a passive one in which mainly temporal masking and retinal processes account for the suppression and an active one in which a central process inhibits visual processing (Castet, 2009; Wurtz, 2008). Temporal masking is a well-studied effect (Breitmeyer, 1980). It describes that a briefly presented stimulus is suppressed when a temporally adjacent and spatially overlapping mask is presented either before or following the stimulus. During saccades, the pre- and postsaccadic image could work as a mask and hence decrease the visibility of the intrasaccadic blur (Castet, Jeanjean, & Masson, 2002). Another purely passive contribution to the phenomenon of saccadic suppression was proposed by Castet (2009). A brief drop in luminance of the whole visual field could arise from shearing forces during the saccade that lead to a brief decrease in retinal light absorption. This drop would decrease the visibility of simultaneously presented stimuli.

Contrarily, a central origin of saccadic suppression via an active process was proposed to act on the magnocellular pathway since suppression does not occur for chromatic equiluminant gratings, and also to act on a very early site since it seems to precede the site of contrast masking (Burr et al., 1994). On the other hand, Watson and Krekelberg (2009) showed that intrasaccadic stimuli that are not consciously perceived by the subjects can still influence the perception of postsaccadic presented stimuli using a shape contrast illusion. Neither a completely passive retinal origin of saccadic suppression nor an active origin at an early stage can account for this finding. However, every active central contribution to saccadic suppression would need to include an extraretinal signal that allows the process to act from the beginning of the eye movement on or even earlier than that since studies on the timing of saccadic suppression have shown that suppression starts 50 ms before saccade onset (Latour, 1962; Diamond, Ross, & Morrone, 2000; Berman & Wurtz, 2011). Such an extraretinal signal may originate from oculomotor structures that are active during saccade preparation and fed back to visual structures to modulate their sensitivity (Wurtz, 2008). This signal, or its effectiveness, could be different for voluntary and reactive saccades. First, because voluntary and reactive saccades involve partially different cortical structures, and, second, because different latencies of voluntary and reactive saccades allow different preparation or integration times for this signal.

Materials and methods

Subjects were students from the Institute of Psychology of the University of Münster. Participation in the experiment was recompensed with study points required for successful graduation. In total 18 students participated in our study (eight males) who were all naive to the purpose of the experiment. All subjects had normal or corrected-to-normal vision and gave their informed consent in written form. The experiment design was approved by the ethics committee of the Department of Psychology and Sport Science of the University of Münster.

Recording of eye movements and stimulus presentation

Eye movements were recorded with an Eyelink 1000 system (SR Research, Ontario, Canada) with a
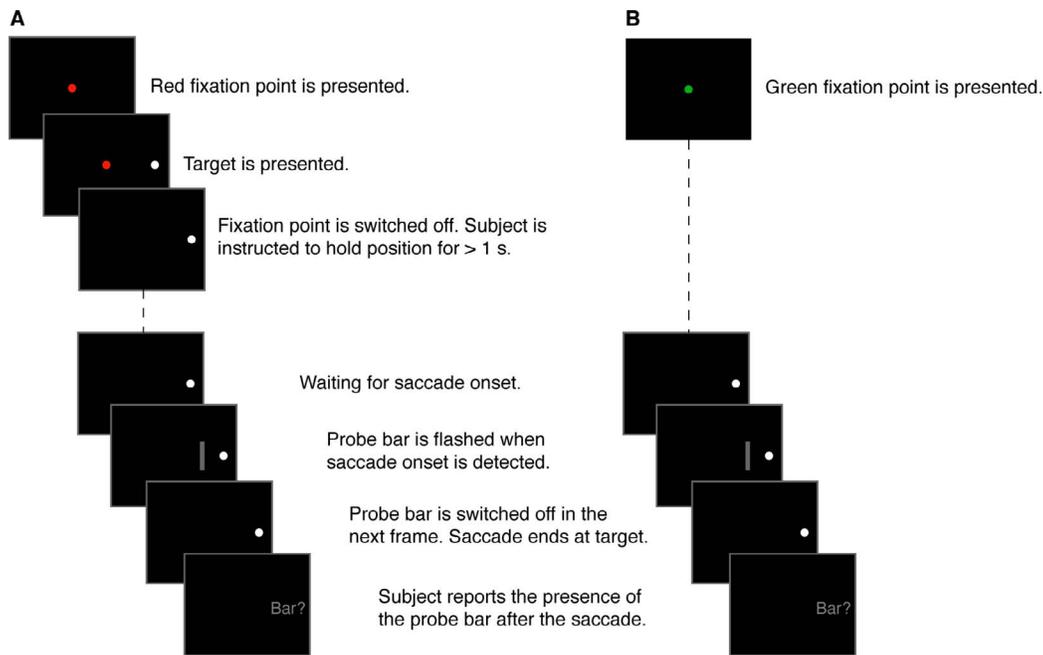
Figure 1. Trial layout for the voluntary (A) and the reactive (B) experimental conditions. The color of the fixation point told the subjects if the trial was a voluntary (red) or a reactive (green) trial. In voluntary saccades, the subjects held their gaze on the fixation point when the target was presented. When the fixation point was switched off subsequently, the subjects were instructed to keep their eyes on the fixation position for at least another second and then start the saccade to the target at any time they want. From then on, both trial types go on identically. As soon as a saccade is detected online, the probe bar is flashed in 80% of trials and the subjects report after the saccade if there had been a visible probe bar on that trial. In reactive trials, the subjects started a saccade as soon as the target was presented and the fixation point was switched off simultaneously.

frequency of 1000 Hz. Viewing was binocular while the right eye was recorded. The stimuli were presented on an Eizo FlexScan 22-in. monitor (Eizo, Hakusan, Japan) with a display resolution of 1152×864 pixel and a refresh rate of 75 Hz. The participants were seated with the head in a chin rest at a distance of 57 cm in front of the monitor in a completely dark room. A transparent foil covered the display and reduced the maximum luminance of the display from 54.1 cd/m^2 to 3.2 cd/m^2. Experimental control and data analysis was performed in Matlab (MathWorks, Natick, MA) with the Psychophysics Toolbox extension (Brainard, 1997; Kleiner et al., 2007).

Behavioral task

We investigated if the detection of flashed stimuli is suppressed to a different extent during the execution of voluntary versus reactive saccades. Subjects had to perform reactive and voluntary saccades and report whether they perceived a bar that was flashed during the eye movement. The probe bar was flashed with four different luminance values of 3.4, 7.1, 14.1, and 27.4 mcd/m^2 with equal probability. In addition, in 20% of trials no bar was flashed (luminance value zero). Subjects had no knowledge about the ratio of trials

with and without the probe bar. The size of the probe bar was $0.5° \times 1.4°$ visual angle, and it was presented at half the distance between the fixation point and the target of the saccade. Diameter and luminance of the saccade target was 0.5° and 1.1 cd/m^2. Every trial started with the presentation of a fixation point horizontally in the middle of the screen and vertically on eye level. The fixation point was either red or green. Diameter and luminance of the fixation point was 0.5° and 0.71 cd/m^2. The color of the fixation point told the subject if a reactive (green) or a voluntary (red) saccade would follow in the trial. For description of trial layout, see Figure 1.

In case of a green fixation point, and thus a reactive saccade, the fixation point was switched off after a randomized time between 0.7 and 1.0 s (Figure 1B). At the same time the target was presented 15° to the left or right of the fixation point on the same vertical position. As soon as the onset of the subject's reactive saccade was detected, the probe bar was flashed for one frame halfway between the fixation point and the target. Photodiode measurements showed that a stimulus presented for one frame persists less than 4 ms on the screen (Georg, Hamker, & Lappe, 2008). Online threshold for saccade detection was an eye velocity of 138°/s in horizontal direction. At the end of the saccade only the saccade target was visible. After 0.5 s the target

was switched off and the subject reported if a bar flashed during the previous saccade using the up arrow key for "yes" and down key for "no." After the subject responded with a key press, the screen went black and the next trial started after an interim time of 0.7 s.

In the case of a red fixation point, and thus a voluntary saccade trial, the saccade target was presented between 0.4 and 0.7 s after fixation point onset while the fixation point was still present (Figure 1A). Like in reactive saccade trials, the target was located 15° to the right or left of the fixation point. When the target was presented, the subjects had to hold gaze position on the fixation point. After a randomized time between 0.3 and 0.5 s subsequent to target onset the fixation point was switched off. The subjects then still had to hold their gaze position at the former place of the fixation point for at least one more second and could then start the saccade to the target at will and without any external trigger. In the case that the subject started the saccade too early, an acoustic signal was given and the subject returned his or her gaze back to the fixation position. The fixation point was switched back on if it had been switched off already and the trial went on in a normal manner, switching off the fixation point after a waiting time between 0.3 and 0.5 s. At the time when the start of a valid voluntary saccade was detected, the probe bar was flashed and the subject reported after the end of the saccade with a key press if he or she had perceived a flashed bar in that trial in the same manner as in the reactive saccade trials. The next trial started with the presentation of the fixation point after the interim time of 0.7 s.

In total, the session consisted of 300 trials—150 reactive saccade trials and 150 voluntary saccade trials. The 150 trials of one saccade type were divided into five groups of 30 trials each. Each group had a constant luminance value of the probe bar: 0 (no flash), 3.4, 7.1, 14.1, and 27.4 mcd/m^2. Of the 30 trials of one group, 15 saccades were directed to the left and 15 saccades were directed to the right. The sequence of the trials in one session was randomized. To familiarize the participants with the task, a short training preceded the data recording. This training session consisted of eight trials—four reactive saccade trials and four voluntary saccades. Each saccade type was performed twice to the right and twice to the left. Furthermore, we added a control condition in an independent session. In that session, no saccades were made during the trials. Instead, after presentation of the fixation point that was either red or green, a probe bar was flashed 7.5° to the right or left of the fixation point. Subsequent to the flashing of the bar, the subject was asked to use the up arrow key for "yes" and the down key for "no" if there had been a flashed bar in this trial. After the subject responded with a key press, the screen went black and the next trial started after an interim time of 0.7 s.

There were 80 trials in that session with 40 trials having a red fixation point and 40 trials having a green fixation point. The 40 trials were divided into four subgroups of 10 trials with each subgroup having one probe bar luminance: 0, 0.3, 2.2, and 7.1 mcd/m^2. This control experiment was performed directly before the training session without the subject leaving the dark room in between.

Data analysis

Subjects who failed to detect the probe bar on at least 50% of the trials even at the highest luminance value were excluded from the analysis. This applied to three subjects who failed to detect 50% of probe bars with the highest luminance in the main experiment and one subject who failed to do so in the control session. Thus 15 subjects were analyzed in the main experiment and 17 subjects were analyzed in the control session. Furthermore, trials in which the frame containing the probe bar did not end at least 10 ms before the end of the saccade were excluded from the analysis since the suppression ends at the end of the saccade. This proceeding assured that the probe bar vanished at least 12.7 ms before saccade because the probe bar in the center of the screen was presented in the middle of the 13.3-ms frame duration and the phosphor persistence of the monitor was less than 4 ms (Georg et al., 2008). The start and end of saccades were tagged in the offline analysis when eye velocity exceeded (started) or dropped below (ended) 30°/s and acceleration exceeded or fell below 8000°/s^2. Overall, 85.6% of trials in the reactive condition and 76.7% of trials in the voluntary condition could be used for analysis. In total 1,926 trials from the reactive condition and 1,727 trials from the voluntary condition were analyzed. Additionally, 1,360 trials were analyzed in the control condition, 680 with a red and 680 with a green fixation point.

Results

For the analysis of the main experiment we calculated for every subject the five rates of positive responses for the five different flash luminance values in the voluntary and the reactive condition, respectively. A repeated measures two-way analysis of variance was conducted to compare the effect of the variables probe bar luminance (five levels: 0, 3.4, 7.1, 14.1, and 27.4 mcd/m^2) and saccade type (two levels: voluntary and reactive) on the rate of positive responses of all 15 subjects. The effect of probe bar luminance was statistically significant, $F(4, 140) = 316.48$, $p < 0.001$, as
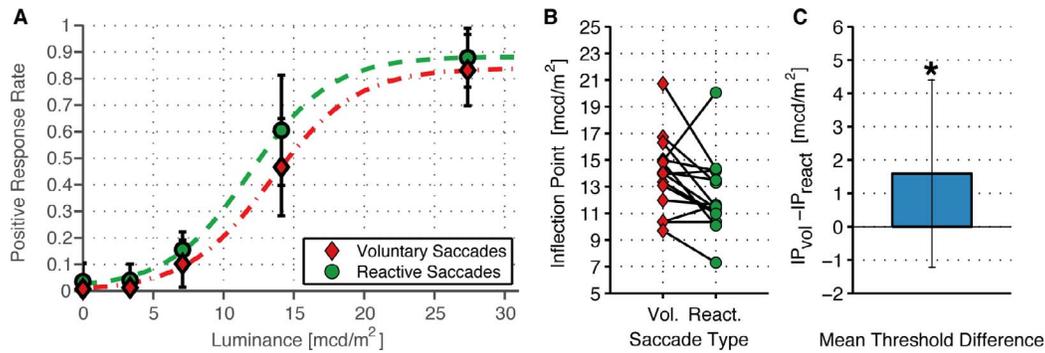
Figure 2. (A) Average detection rate over all 15 valid subjects plotted as a function of luminance of the probe bar for voluntary (red) and reactive saccades (green). Error bars indicate standard deviation. The data of each condition was fit with a psychometric function as described in the text. The fit parameter are $H_O = 0.84$, $L_O = 0$, $a_O = 13.4$ mcd/m^2, and $b_O = 3.0$ m^2/mcd for the voluntary condition ($R^2 = 0.9993$) and $H_R = 0.87$, $L_R = 0.01$, $a_R = 11.9$ mcd/m^2, and $b_R = 2.9$ m^2/mcd for the reactive condition ($R^2 = 0.9994$). (B) Inflection points (i.e., detection thresholds) during both conditions were calculated for each subject individually as the luminance values at inflection point of the fit functions to the subject's response rates in the voluntary and reactive conditions. Detection thresholds are plotted in red for the voluntary condition and green for the reactive condition. The two thresholds of each subject are connected with a black line. (C) The mean difference between detection thresholds during voluntary and reactive saccades is 1.6 mcd/m^2 (SD = 2.8).

was the effect of saccade type, $F(1, 140) = 10.14$, $p = 0.002$. These results indicate that probe bars with higher luminance values were detected with higher probability and that detection rates differed between voluntary and reactive saccades.

Figure 2 provides an overview of the experimental results showing the average results of all subjects. Figure 2A shows the average detection rate as a function of probe bar luminance in the voluntary condition (red) and the reactive condition (green) together with a fit to the data for each condition with a psychometric function DR_R and DR_O:

$$DR_{type}(lum) = L + \frac{H}{1 + e^{-(lum-a)/b}}$$

$$\text{with } H, L \in [0, 1] \text{ and } a, b \in R^{\geq 0}$$

Note that we did not force the fit to reach an upper asymptote H of 1 because probe bars were always flashed during saccade execution and thus could always be influenced by saccadic suppression. Furthermore, we accounted for potential different false alarm rates in the two conditions by choosing $L \in [0, 1]$.

The luminance value at the inflection point of the fit is defined as the detection threshold of the probe bar. For the grand average data of all subjects the detection thresholds are $T_{GA, V} = 13.4$ mcd/m^2 for the voluntary condition and $T_{GA, R} = 11.9$ mcd/m^2 for the reactive condition. Thus the probe bar is detected more easily during reactive saccades than during voluntary saccades and hence suppression appears less complete in reactive saccades. To test this effect for significance in the next step, we calculated the values of the two detection thresholds for every single subject. Therefore, for every individual subject the rate of positive

responses was plotted as a function of probe bar luminance for both the reactive and the voluntary conditions. The two data sets then were fit with two psychometric functions, DR_R and DR_O, to calculate the detection threshold of each subject individually for voluntary and reactive saccades, independently (see Figure 2B). The mean detection threshold of all subjects during voluntary saccades was $T_{M, V} = 14.0$ mcd/m^2 (SD = 2.8) and during reactive saccades $T_{M, R} = 12.4$ mcd/m^2 (SD = 2.8). Thus, the mean threshold difference between voluntary and reactive saccades over all subjects was 1.6 mcd/m^2 (SD = 2.8) and was significantly different from zero (one-sample t test, $p < 0.05$). The mean threshold difference is presented in Figure 2C. In the main experiment, we found weaker suppression during reactive saccades than during voluntary saccades.

Control experiment

To analyze the data of the control experiment we calculated the 17 valid subjects' rates of positive responses for the four different flash luminance values in the two conditions. In the control session in one condition the trials had a red fixation point, and in the other condition the fixation point was green. In Figure 3A the average rates from all subjects are plotted for both conditions as a function of probe bar luminance. A repeated measures two-way analysis of variance was conducted to compare the effect of the variable probe bar luminance (four levels: 0, 0.3, 2.2, and 7.1 mcd/m^2) and color of fixation point (two levels: red and green)
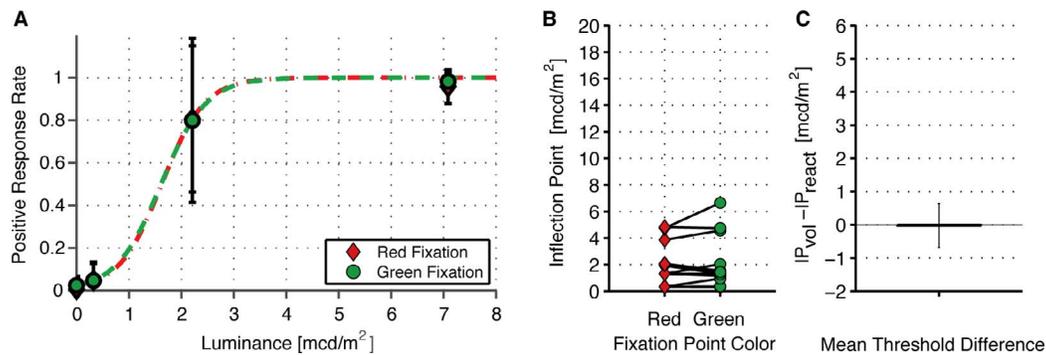
Figure 3. (A) Average detection rate plotted as a function of luminance of the probe bar during the control condition with red and green fixation points. Error bars indicate the standard deviation. (B) The detection thresholds of each subject for both conditions. (C) The mean difference between detection thresholds during fixation of a red and a green fixation point was not significantly different from zero.

on the rate of positive responses of all 17 valid subjects (number of replicates 17). The effect of probe bar luminance was statistically significant, $F(3, 128) = 232.58$, $p < 0.001$, while the effect of fixation point color was not significant, $F(1, 128) = 0.07$, $p = 0.79$. These results indicate that in the control condition probe bars with higher luminance values were detected with higher probability and that probe bars were perceived with an equal probability during fixation of the red or the green fixation point. Similar to the data from the main experimental session, we calculated the control data for the detection thresholds for the probe bar for all subjects individually in both conditions (Figure 3B). The mean threshold difference between the conditions red and green fixation points over all subjects is -0.002 µcd/m² (SD = 0.07) and is not different from zero (one-sample t test, $p = 0.88$). Thus, the different level of suppression found in our study during voluntary and reactive saccades does not originate from different colors of the fixation point.

Saccade metrics

Since the cortical pathways as well as preparation times differ between voluntary and reactive saccades, the metric properties of the saccades executed in our experiment might differ as well. Such differences could possibly influence the amount of suppression. In the following, we compare saccade metrics between voluntary and reactive saccades to make sure that the higher threshold of perception during voluntary saccades cannot originate from a difference in saccade execution. In the voluntary condition the evoked saccades had a mean amplitude of 13.0° (SD = 1.1°), and in the reactive condition the mean amplitude was 13.6° (SD = 0.8°). This difference was significant (two-tailed paired t test, $p < 0.01$). Since the voluntary saccades hence landed closer to the probe bar position,

it is unlikely that the difference in amplitude can account for a higher detection threshold in that condition.

The mean eye velocity profiles from both conditions can be found in Figure 4 together with the timing of bar onset relative to saccade start for all analyzed trials. Since the probe bar was presented in just one frame on the cathode ray tube (CRT) monitor, the bar was illuminated for less than 4 ms after the plotted frame
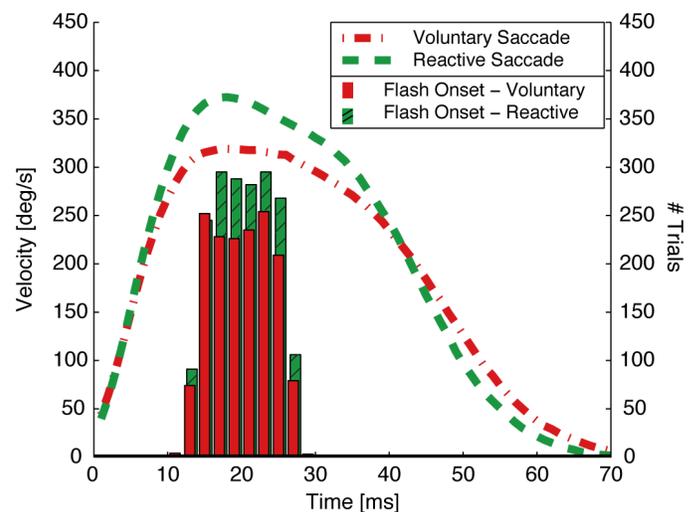
Figure 4. Mean eye velocity during the saccade in both conditions. The velocity profile from the voluntary condition is depicted as the dashed-dotted red line and the velocity profile from the reactive condition is depicted as the dashed green line. The embedded histogram shows the flash onset time relative to saccade start of all analyzed trials. The red bars show the timing of the probe bar in the voluntary condition and the green striped bars show the timing of the probe bar in the reactive condition. Since fewer trials were excluded in the reactive condition, the green bars include a higher number of data trials. Nonetheless, the probe bars are presented in both conditions when the mean eye velocity is above 250°/s.

onset time. Figure 4 shows that the probe bar was flashed at the time of highest eye velocities in both conditions and thus was switched off long before the suppression vanished at saccade end. However, the velocity profiles differed between the two conditions. The mean peak velocity was 379.4°/s (SD = 40.6°/s) in the voluntary condition and 426.9°/s (SD = 55.6°/s) in the reactive condition. These values also differed significantly (two-tailed paired t test, $p < 0.01$). Hence, eye velocity at the time of bar presentation was higher in the reactive condition. This results in potential stronger blur in the reactive condition at the time of probe bar presentation. Since saccadic suppression was actually weaker in that condition, it is implausible that the difference in eye velocity at bar presentation can account for the difference in suppression strength. The slower eye velocity in the voluntary saccades further-more led to a mean eye position across probe bar presentation of 7.0° (SD = 0.6°) in the voluntary saccades and a mean eye position across probe bar presentation of 7.6° (SD = 0.8°) in the reactive condition. Since the probe bar was presented at 7.5°, the bar was presented on average close to the fovea in both conditions.

A further difference between the two conditions was the time that was available for saccade preparation— that is, the time the target was visible before saccade start. In the voluntary condition the saccade started on average 1211 ms (SD = 81) after target presentation while in the reactive condition the saccade started on average 316 ms (SD = 79) after target presentation. The latter value may be considered high for typical reactive saccades, which normally occur around 180 ms after target onset. The increase probably originates from the experimental design. Since voluntary and reactive saccades were randomly intermixed, and participants had to hold fixation in the voluntary trials, participants may have occasionally held fixation in reactive trials, too. However, this would only lead to an underesti-mation of the difference in suppression between the two saccade types in our sample. The period of time in which the target is visible before the eye movement is started—that is, the time that is available for saccade preparation—is many times longer for voluntary saccades. This is a major difference between the two examined saccade types. It could influence the prepa-ration or integration of any efference copy signal generated during the saccade planning. Therefore, we analyzed the relationship between the detection rate and the saccade latency in both conditions. We sorted all trials by their saccade latency for each condition and divided the trials into blocks of 50 trials each. We then plotted the detection rate within these 50 trials against the mean latency of the block (Figure 5). If all trials from both conditions are considered, we find a significant negative correlation between detection rate
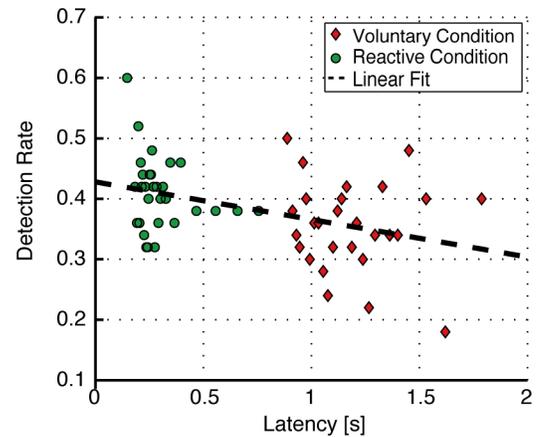
Figure 5. Correlation between detection rate and saccade latency. Each data point depicts the detection rate in a block of 50 trials, which are clustered for the saccade latency and the mean latency of the saccades in the block. Data from the reactive condition is plotted with green dots and data from the voluntary condition is plotted with red diamonds. The dashed black line is a linear fit to the data (DR = a ∗ x + b, a = −0.06, b = 0.43). We found a negative correlation between detection rate and latency (see text).

and saccade latency ($\rho = -0.41$, $p = 0.001$). Hence, the more preparation time is available for the saccade, the more distinct is the drop in visual sensitivity during the saccade. However, no significant correlation emerged in our data sample if only the trials from just one condition are considered separately (voluntary: $\rho = -0.12$, $p = 0.5$; reactive: $\rho = -0.24$, $p = 0.2$). Therefore, in our data sample the detection rate is not a function of latency within one condition. Noteworthy, however, is the fact that the block in the reactive condition with the smallest saccade latency of 169.1 ms (SD = 58.5) shows by far the best detection rate. This may indicate that the fastest reactive saccades have an even lower detection threshold than the average in our study. As mentioned above, this underestimation may be the consequence of our interleaved trial sequence, which leads to prolonged reaction times in the reactive condition. Again, however, this effect could only produce an underestimation of the difference in suppression between the two saccade types in our sample.

Discussion

We compared saccadic suppression between reactive and voluntary saccades. We found that detection thresholds for an intrasaccadic probe stimulus were higher during voluntary than during reactive saccades. Thus our results show that saccadic suppression is

stronger during voluntary saccades than during reactive saccades.

Different mechanisms contribute to saccadic suppression. Passive mechanisms emerge from the input to the retina during and after a saccade (Campbell & Wurtz, 1978; Castet, 2009). For instance, the image presented to the retina after the saccade can act as a mask that overwrites the blurred and grayed-out image that is experienced by the retina during the movement. Additionally to this backward masking, the prefixation image can mask the following blur on the retina during the saccade as well, functioning as a forward mask (Campbell & Wurtz, 1978; Corfield, Frosdick, & Campbell, 1978). These temporal masking effects are regarded to be the primary cause of threshold elevations during saccades in natural scenes (Volkmann, 1986; Wurtz, 2008). However, the difference in threshold elevation during reactive and voluntary saccades found in our study cannot be explained by passive masking processes. First, the retinal input after the saccade, the postsaccadic image, is identical in both conditions. Thus the threshold difference cannot be caused by backward masking. Second, in the voluntary saccade condition, the eye movement starts in complete darkness, while in the reactive condition, a fixation point is presented until shortly before the saccade. Hence, a stronger forward masking effect is to be expected in the reactive condition, which is inconsistent with our data. Hence, our study provides further evidence that saccadic suppression includes active mechanisms in addition to passive temporal masking.

Active suppression of the visual input during saccades needs an extraretinal signal that mediates the sensitivity during an eye movement. Since behavioral (Latour, 1962; Diamond et al., 2000) and electrophysiological (Ibbotson & Krekelberg, 2011) evidence showed suppression to start even before the actual eye movement, this extraretinal signal must be an efference copy of the oculomotor command that prepares or initiates the eye movement. Different threshold elevation for reactive and voluntary saccades could be explained by potential differences in origin, timing, or usage of this efference copy signal between voluntary and reactive saccades.

Differences in origin of the signal might emerge from different brain areas involved in the generation of voluntary and reactive saccades (Pierrot-Deseilligny et al., 1991; Rivaud et al., 1994; Gaymard et al., 2003; Mort et al., 2003; Müri & Nyffeler, 2008; Schraa-Tam et al., 2009; Pélisson, Alahyane, Panoiulleres, & Tilikete, 2010). Alternatively, if the efference copy for both saccade types is generated in the same brain structures the longer preparation time of voluntary compared to reactive saccades may lead to a better developed or stronger efference copy signal, which, in turn, would lead to stronger suppression. However, we found decreasing detection rates with increasing saccade latency but we only found a significant correlation between true detection rate and saccade latency for the complete data sample and not within one condition.

Saccades impose essentially two unrelated challenges for the visual system. The first concerns the self-induced retinal motion that accompanies the eye movement. An elevation of response threshold for retinal stimulation during the saccade reduces the impact of that stimulation. The second challenge is the displacement of the retinal projection of the visual scene during the saccade. Objects that are visible before and after the saccade have changed place on the retinal surface. This second type of challenge is commonly associated with saccadic suppression of displacement, an elevation in threshold for the discrimination of an object displacement across the saccade (Bridgeman et al., 1975). Recently, Zimmermann, Morrone, and Burr (2013) reported that saccadic suppression of displacement became weaker when saccade latencies became longer. Thus, while our study showed an increasing threshold for detection of intrasaccadic stimulation for voluntary saccades with a longer saccade preparation time, their study showed a decreasing threshold for detection of intrasaccadic displacement with increasing saccade preparation time. However, we believe that both findings support the same conclusion, namely that a longer preparation time leads to a better representation of the saccade and a stronger efference copy. Zimmermann et al. (2013) proposed that when a subject starts a saccade to an appearing target without delay (i.e., a reactive saccade) the target position is not sufficiently encoded in memory due to a lack of proper representation. This leads to stronger suppression of displacement because the postsaccadic position of the target cannot be compared to a reliable expected position from presaccadic memory. Similarly in our reactive saccades, the preparation of the efference copy signal may not be sufficiently developed and hence the suppression based on that signal is incomplete. In that sense, a reactive saccade may at the same time lead to insufficient suppression of stimuli presented during the saccade and to insufficient predictability of the location of objects after the saccade.

Acknowledgments

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