



The saccadic size-latency phenomenon explored: Proximal target size is a determining factor in the saccade latency



J.P. De Vries^{a,*}, R. Azadi^b, M.R. Harwood^{a,c}

^a Department of Biology, City College of New York, City University of New York, New York, NY, USA

^b Graduate Center for Vision Research, SUNY College of Optometry, New York, NY, USA

^c Department of Psychology, University of East London, London, UK

ARTICLE INFO

Article history:

Received 7 July 2016

Received in revised form 11 September 2016

Accepted 16 September 2016

Available online 11 November 2016

Keywords:

Eye movements

Saccade latency

Size-latency phenomenon

Motor control

Saccade adaptation

ABSTRACT

Saccade latencies are known to increase for targets presented close to fixation. Recently, it was shown that not only target eccentricity, but the size of a proximal saccade target also plays a crucial role: latencies increase rapidly with increasing target size. Interestingly, these latency increases are greater than those typically found for other supra-threshold manipulations of target properties. Here we evaluate to what extent this phenomenon is distinct from known delays in saccade initiation and whether the phenomenon is truly related to the size of a proximal target. In Experiment 1 we focus on the importance of the required amplitude. Employing a saccade adaptation paradigm we find that the required amplitude is not a determining factor. Focusing on the role of size, in Experiment 2, we find that while latency increases are strongest for targets elongated in the direction of the fovea, elongations perpendicular to this direction also lead to an increase in latencies. Finally, in Experiment 3 we verify that the latency increases are driven by the properties of the saccade target rather than visual input in general. Together these experiments provide converging evidence that the current phenomenon is both novel and a consequence of the relation between proximal target size and its eccentricity.

© 2016 Published by Elsevier Ltd.

1. Introduction

The limited resolution of the visual periphery and peripheral crowding requires observers to make saccadic eye movements to inspect objects of a scene in detail. While the typical latency of eye movements to a new visual stimulus is around 200 ms (in laboratory setups), it has been shown that this number rapidly increases for targets within 2° of the current fixation. This phenomenon was already revealed over four decades ago (Kalesnykas & Hallett, 1994; Wyman & Steinman, 1973). However, two recent studies have provided an important extension: Aside from the required saccade amplitude, proximal target size appears to also be a determining factor of the saccade latency (Harwood, Madelain, Krauzlis, & Wallman, 2008; Madelain, Krauzlis, & Wallman, 2005). In their experiments, observers were required to attend to, and track two concentric rings of different sizes. The two rings were made up of separate segments, allowing them to rotate, and observers had to either attend to the larger ring or the smaller ring. During the tracking, the rings would step and con-

tingent on the step the number of segments in the ring would briefly change. Observers had to regain fixation and report the number of segments after the step of the attended ring. It was found that saccades contingent on the step had drastically different latencies depending on which ring was attended: Latencies in the attend-to large condition were considerably longer than in the attend-to small condition (Madelain et al., 2005). Interestingly, Harwood et al., 2008, uncovered a striking relation between the latency, size and eccentricity of the target: While latencies vary considerably depending on both absolute eccentricity and ring size, evaluating latencies in terms of the amplitude of the step in proportion to the size of the target there appears to be a consistent response time according to this step-size ratio (See Fig. 1 for more information).

As latency differences in Madelain et al. and Harwood et al. typically exceed 100 ms and reach as high as 200 ms, the fluctuations associated with this *size-latency* phenomenon are considerable. While large latency increases have been found previously by lowering the contrast of a saccade target (e.g. Ludwig, Gilchrist, & McSorley, 2004), phenomena based on supra-threshold stimuli typically cause increases on a more limited scale. Inhibition of return, for instance, is typically associated with delays in saccade execution between 10 and 40 ms (see for an overview: Klein,

* Corresponding author.

E-mail address: vriesdejelmer@gmail.com (J.P. De Vries).

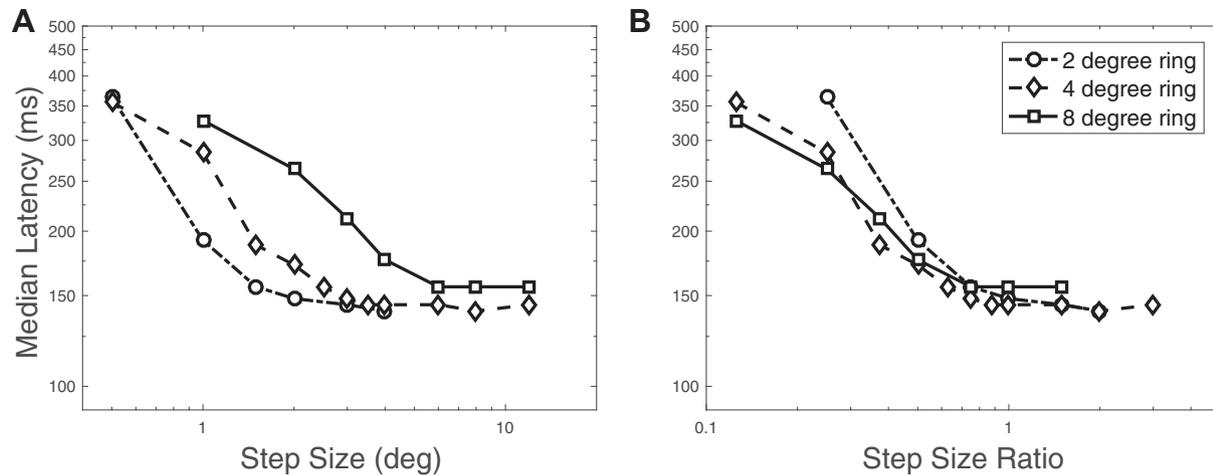


Fig. 1. Median latencies for stepping rings of 3 different sizes for a typical observer (data replotted from Harwood et al., 2008). Employing eight similar attentional paradigms Harwood et al. extensively varied the combination of target size and eccentricity. While latencies for targets at a set eccentricity vary as a function of size, expressing the saccade latency as a function of amplitude divided by ring size (step size ratio) results in highly similar curves for different ring sizes. For the plotted data, the observer had to fixate a ring and make a saccade as soon as it stepped. The ring was segmented, allowing it to rotate, and the number of breaks changed for 150 ms contingent on a step away from fixation. Observers had to report the transient number of breaks (2AFC) at the end of each trial. In A the median latencies are plotted as a function absolute step size for each ring diameter. In B the same data is plotted as a function of step size divided by the ring diameter. As can be seen median latencies are highly similar for all three-ring sizes when the step size is normalized by the stimulus size.

2000). Remote distractors that onset around the time of the target in the contralateral hemifield lead to a latency increase of around 20–30 ms in latencies (Walker, Kentridge, & Findlay, 1995; Weber & Fischer, 1994). This increase just exceeds 50 ms when the distractor is placed at fixation (Walker, Deubel, Schneider, & Findlay, 1997). A manipulation that has been shown to cause more considerable fluctuations in latencies is the gap effect. Here the removal of the fixation marker 200 ms prior to target onset decreases latencies considerably. However, while the initial findings surrounding the gap effect showed latency decreases up to 100 ms (Saslow, 1967; Weber, Aiple, Fischer, & Latanov, 1992) later findings reported much smaller effects (Reuter-Lorenz, Hughes, & Fendrich, 1991). It is likely that aside from the benefit of releasing inhibition at fixation, the offset serves as a warning signal for the upcoming stimulus (Fendrich, Demirel, & Danziger, 1999; Reuter-Lorenz, Oonk, Barnes, & Hughes, 1995). Hence, the great reduction in latencies appears to be a compound of two effects. Considering the relatively large latency differences associated with the current phenomenon it is a highly interesting candidate for advancing understanding of the sensorimotor decision process in general.

The current paper evaluates whether the *size-latency phenomenon* is distinct from previously reported phenomena in the literature and what the determining factors are. While the reported measure is the saccade latency, in both the papers by Madelain et al. and Harwood et al. the independent variable was encapsulated in an additional attentional task. Potentially, observers employing conscious strategies to cope with the attentional task could have caused the latency difference.¹ Therefore, it is important to verify the existence of the phenomenon in simple saccade tasks. Previous studies requiring only saccades towards spatially extended targets have either reported no size-effect on saccade latency (Kowler & Blaser, 1995; Mcgowan, Kowler, Sharma, & Chubb, 1998), or much weaker effects than found in the studies of Madelain et al. and Harwood et al. (Dick, Ostendorf, Kraft, & Ploner, 2004;

Ploner, Ostendorf, & Dick, 2004). However, as we have argued previously, these absent or weak effects (latency differences < 25 ms) were likely due to size-distance variations in the asymptotic short-latency region of Fig. 1 (e.g. 13 out of 15 of the size/eccentricity conditions in Ploner et al. (2004)). Finally, an indication that the current phenomenon extends to regular saccade preparation (i.e. without additional tasks) comes from latencies for two observers who performed the ring task, without any additional attentional task (Harwood et al., 2008, supplemental materials). The purpose of the current paper is to evaluate whether the findings are indeed generally applicable (i.e. hold for saccades even in simple tasks) and whether it is truly a novel phenomenon in the sense that it cannot be explained by established inhibitory mechanisms of saccade initiation.

Referring to the current phenomenon as the *size-latency phenomenon* suggests that the phenomenon mainly relies on target size. However, the strong latency increases found when reducing saccade amplitudes raise the question to what extent the current phenomenon is dependent on the required saccade amplitude. In Experiment 1 we focus on this question by employing a saccade adaptation paradigm. In two separate sessions, large proximal targets are either stepped backward or forward, upon saccade initiation. Previewing these results we find that despite strongly adapting amplitudes, latencies remain primarily unaffected. Given the strong reliance on visual target properties in Experiment 2 we evaluate whether it is correct to consider size as the determining factor; we evaluate how increasing target size in different directions affects latencies. As this again shows a strong reliance on visual input in general, in Experiment 3 we verify that the phenomenon relies on the properties of the saccade target and not visual input per se.

2. Experiment 1: required saccade amplitude

What is the role of the required saccade amplitude in the *size-latency phenomenon*? As mentioned above, several studies have already found that latencies increase for more proximal targets. While the *size-latency phenomenon* appears distinct from this, as it relies on target properties as well as eccentricity, it is unclear what the role of the required saccade amplitude is. Therefore, in

¹ For instance, when the small ring steps, the visual acuity of the target diminishes to the extent where an observer may require a saccade to complete the segment counting task. Conversely, when the large ring steps, the observer's fixation is still within the ring and the strategy may be to first complete the attentional task and to only prepare the saccade afterwards, hence delaying the execution of the saccade in the large ring condition.

this experiment we evaluate the role of the saccade amplitude and evaluate whether the latency increase is directly linked to the required amplitude or solely based on preparing a saccade to a proximal target. To this end, we employ a saccade adaptation paradigm. In saccade adaptation experiments, a consistent saccadic error caused by changing the target location during the saccade leads to an adaptation of the executed amplitude (McLaughlin, 1967). If the required saccade amplitude is a determining factor of latencies in the size-latency phenomenon we expect that saccade adaptation will also lead to an adaptation of saccade latencies. Thus saccade adaptation allows us to create a situation in which the required saccade amplitude is adapted without altering the pre-saccadic target appearance.

In line with the previous findings that amplitudes can affect latency (Kalesnykas & Hallett, 1994; Wyman & Steinman, 1973) the studies of Madelain et al. (2005) and Harwood et al. (2008) took into account a potential role of saccade amplitude. Madelain et al. showed that saccade amplitudes were principally determined by the size of the step and that the size of the target did not give systematic amplitude biases despite consistent effects on latency. Moreover, Harwood et al. performed a multiple regression analysis including amplitude and target eccentricity relative to its size. This revealed only 4.3 ms of the latency difference could be accounted for by amplitude. While this demonstrated that amplitude could not explain the latency deviations in these studies, the question whether the *required* amplitude is an intricate part of the size latency phenomenon is still open. For a single ring size at different target eccentricities both Madelain et al. and Harwood et al. find vastly different latencies: Latencies steeply decrease when the target eccentricity is larger than its own amplitude. Does the size-latency phenomenon rely purely on the eccentricity of the target or is there a role for the required amplitude?

The current experiment includes two separate sessions: In the *forward-step condition* the target appears close to fixation, but steps forward towards a more eccentric location upon saccade initiation. Conversely, in the *backwards-step condition* the target appears more eccentric, but steps backward to the location close to fixation upon saccade initiation. Thus initially target eccentricity is smaller in the forward-step, compared to the backward-step condition. Assuming successful adaptation, saccade amplitudes will be larger in the forward-step compared to the backward-step condition. Therefore, if the required saccade amplitude is a determining factor in latencies in the size-latency phenomenon we expect that latencies for adapted saccades will be longer in the backward-step compared to the forward-step condition. However, if it is only the target eccentricity that matters we expect that, despite the change in amplitudes, latencies should still be longer in the forward-step condition.

2.1. Methods

2.1.1. Observers

Ten observers (7 female) aged 23 through 40 (average: 30 years; sd: 4.6 years) participated in the experiment. Observers either worked or studied at the City College of New York. Staff participated on a voluntary basis while students were compensated in the form of a monetary reward. All observers were naive to the purpose of the experiment, except authors JV and RA. The methods of the study were approved by the local review board of the City College of New York. Prior to the experiment, observers were informed of their rights and informed consent was obtained in accordance with the guidelines of the Helsinki Declaration.

2.1.2. Stimulus and procedure

Each trial started with a small white fixation dot on a mid-grey background placed on the horizontal line on the vertical center of

the screen randomly within a range extending 3.9° to the right and 3.9° to the left of the horizontal center of the screen. After a stable fixation was detected the fixation dot was replaced with a large white ring (diameter: 9° ; thickness: 0.4°). A representation of the trial chronology can be found in Fig. 2. After a period ranging from 500 to 1500 ms the ring stepped to the right (either 3° : forward-step condition, or 6° : backward-step condition). Observers were instructed to re-fixate the center of the ring as quickly as possible. Approximately 400 ms after the initiation of their saccade the trial would come to an end. The next trial would start automatically after the observer re-fixated the fixation dot that would reappear after the trial ended. However, to ensure validity of the calibration every twenty trials a drift check was performed, at which point it was required to press space while fixating the central dot.

In adapting trials the ring would step 3° upon saccade detection (for detection parameters, see Apparatus and Eye Movement Analysis, below), either forward or backward, depending on the condition. Observers were made aware that regardless of any observed movements that their task was simply to fixate the center. Moreover, it was emphasized not to anticipate any subsequent movement. The adapting phase was followed by a post-adapting phase without intra-saccadic step, similar to baseline, in order to evaluate recovery from the adapted state.

Typically a considerable amount of time separates the different adaptation conditions to allow the system to fully de-adapt, but pilots demonstrated that adaptation and de-adaptation was rapid for our proximal targets. Therefore, we decided to run both conditions in close temporal contingency (a brief break, of 5 min or less, was included between conditions) in order to allow for a within-subject comparison of latencies between the conditions. To prevent an influence of condition order, session order was counter-balanced over the observers. A total of 220 trials were included in each session, divided over three phases: 70 baseline, 100 adapting and 50 post-adapting trials.

2.1.3. Apparatus and eye movement analysis

Stimuli were presented on a 22 in. Viewsonic (P220f) at a resolution of 1024×768 , at a frame rate of 120 Hz. Stimuli were generated using the Psychtoolbox (Brainard, 1997; Kleiner, Brainard, Pelli, et al., 2007; Pelli, 1997) on a Mac G5 and eye movement recording was managed using the EyeLink toolbox (Cornelissen, Peters, & Palmer, 2002). Movement of the eye was recorded using an SR-Research EyeLink 1000 system at a sampling frequency of 1000 Hz. The observer's head was placed in a chin-rest so that the eyes were at a distance of 57 cm from the screen. Images were viewed binocularly, but eye movements were recorded from the right eye only. A 13-point calibration procedure was executed prior to the forward step and backward step condition, individually.

Eye movement data were used both for online and off-line analysis. Online analysis was used to detect whether the eye had returned to the central fixation and to detect saccades for the timing of the step. This was established by detecting when the eye position returned to a position within 2.0° of the central fixation for at least 150 ms. A saccade was detected when one of two criteria was fulfilled; either the eye moved outside of an imaginary circle around the initial fixation of each trial with a radius of 1.6° or the velocity of the eye exceeded $79^\circ/s$. For offline saccade detection a velocity threshold of $20^\circ/s$ was used, after which start and endpoint of the saccade were approximated by searching back and forth until the velocity was two standard deviations higher than the velocity during fixation (as in Smeets & Hooge, 2003). Saccades with amplitudes smaller than 0.5° were removed from the analysis. When a small saccade was removed, the fixations before and after this saccade were added together. Fixations shorter than 25 ms were excluded from further analysis.

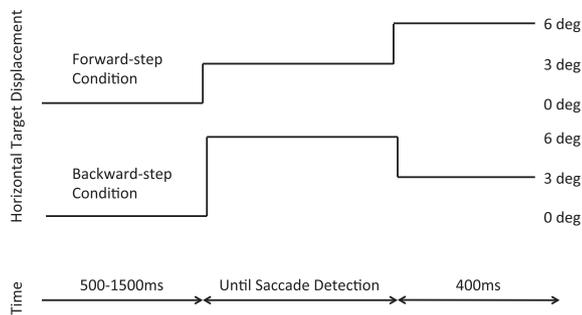


Fig. 2. Horizontal displacement of ring during an adaptation trial of Experiment 1. A 9-degree diameter ring started with its center on the horizontal line at the vertical center of the screen. After a delay of 500–1500 ms the ring would step to the right, either by 3° (forward-step condition), or by 6° (backward-step condition). In adaptation trials the ring would step again upon detection of the initial saccade, either 3° right (forward-step condition) or 3° left (backward-step condition). The ring would disappear 400 ms after saccade detection. Or after 1000 ms from trial onset if no saccade was detected.

Finally, to only include trials where the observer executed the correct behavior we applied 4 criteria on the basis of which we excluded trials from further analysis: Trials where the observer's initial fixation was not within 1.5° of the center of the initial ring (occurrence: 1.6%); trials where the saccade latency was either shorter than 90 ms or longer than 700 ms (2.4%); trials where the angular direction of the initial saccade deviated more than 60° from the central position of the stepped ring (3.8%); finally, to exclude saccades not aimed at the actual target we excluded saccades with amplitudes outside of the range from 1 to 9° (2.9%). The combination of these criteria led to an exclusion of 8.3% of the trials. Note that this percentage is smaller than the summation of the above percentages as more than one criterion could be violated on a single trial.

2.2. Results

2.2.1. Amplitude Adaptation

To evaluate the potential adaptation of latency, it is important that amplitudes adapted strongly in the direction of the step during the adaptation phase. To show the course of adaptation we plotted the amplitude of the initial saccade for each trial averaged over all observers, in the top row of Fig. 3 (in case an observer's trial was excluded, this observer's trial was not taken into account for the average of the specific trial). As the figure shows, the adaptation procedure rapidly altered saccadic amplitude during the adapting phase in both the forward-step (left) and backward-step session (right). While amplitudes do not have to adapt with the same gain as the intra-saccadic step size, ideally, for the current situation amplitudes in the forward-step condition exceed amplitudes in backward-step condition. As adaptation typically is not instantaneous (see for an overview: Hopp & Fuchs, 2004) we excluded the first 30 trials and used only the last 70 trials for evaluating the amplitude of the adapted saccade. In the left column of Fig. 4 we plotted the magnitude of adaptation for the forward step condition. For each phase the average of the median amplitudes per observer are displayed. To allow for further inspection of the data also individual observer data has been plotted as circles for each phase. Similarly, the right column of Fig. 4 contains the data for the backward step condition. Comparing the amplitudes from the baseline to the adapting phase there appears to be almost a reversal of amplitudes. As our main interest lies in the adapted phase we directly compare the adapted amplitude in the forward step condition to the backward step condition. A *t*-test shows that the adapted amplitudes in the forward step condition are significantly greater than the adapted amplitudes in the backward step

condition (mean difference: 1.3°, $t(9) = 2.93$, $p < 0.05$). Thus despite the fact that pre-saccadic amplitude of the ring is smaller in the forward-step condition than in the backward-step condition, the adapted saccade amplitude is larger in the forward-step condition. Therefore, the adaptation magnitude fits the intention of the manipulation well.

2.2.2. Latency Adaptation

Given that the amplitude manipulation was successful we focus on the potential change in latency to evaluate the role of the required amplitude. In the lower row of Fig. 3 we plotted the latency for each trial averaged over observers corresponding to the amplitudes in the upper row of the figure. There appears to be little change in latency with adaptation. Clearly, if the required amplitude determined latencies, one would expect latencies to be shorter in the forward-step condition than in the backward-step condition. Conversely, if the latencies were unaffected or only minimally affected we should find latencies to be shorter in the backward-step condition than in the forward-step condition. On the lower row of Fig. 4 we show the median latencies corresponding to the amplitudes on the upper row. Comparing the average latency over observers from the adaptation phase we find that the latencies in the forward-step condition are significantly longer than in the backward-step condition (mean difference: 34 ms, $t(9) = 3.31$, $p < 0.01$).

Critically, while amplitudes are significantly shorter in the backward-step condition, latencies are still significantly longer in the forward-step condition. This demonstrates that the required amplitude is not directly linked to the latency increase. However, it does not exclude the possibility that latencies do not adapt at all. If latencies would have adapted with amplitude adaptation, in the forward-step condition latencies should have decreased. Conversely, during adaption in the backward-step condition latencies should have increased. While the extent of the latency adaptation could be of a varying magnitude, for an estimate, one could use the latencies in the pre-adapt phase. Here we see that the difference in latencies prior to any adaptation averages 32.25 ms. However, inspection of the average latencies in the adaptation compared to the baseline phase reveals only minimal latency changes in the direction opposite to expectation (forward-step condition: 0.1 ms; backward-step condition –1.6 ms).

2.3. Discussion

The results suggest that the role of the required amplitude in the size-latency phenomenon is minimal at best: Despite clear adaptation in the saccade amplitudes, the latencies in the forward step condition are still significantly longer than in the backward step condition. One shortcoming of the critical statistical test is that it does not explicitly demonstrate that latencies do not adapt at all. However, as we expected latencies not to adapt, we wanted to avoid obtaining a null result. Therefore we considered that significantly longer latencies in light of a reversal of saccade amplitudes would be a strong indication that the role of the required saccade amplitude is minimal. While, the test does not allow us to conclude that latencies are completely unaffected by the required amplitude, it is clear that the pre-saccadic properties of the proximal target are a more crucial factor. Importantly, the average latency during adaptation barely deviates from the average latency pre-adaptation in both the forward-step, as well as the backward-step condition, providing further indication that latencies are not related to the required amplitude of the saccade.

With this, the current data extend on previous analyses showing that natural deviation in saccade amplitude for different target sizes could not explain saccade latency differences (Harwood et al., 2008; Madelain et al., 2005). The limited role of the required

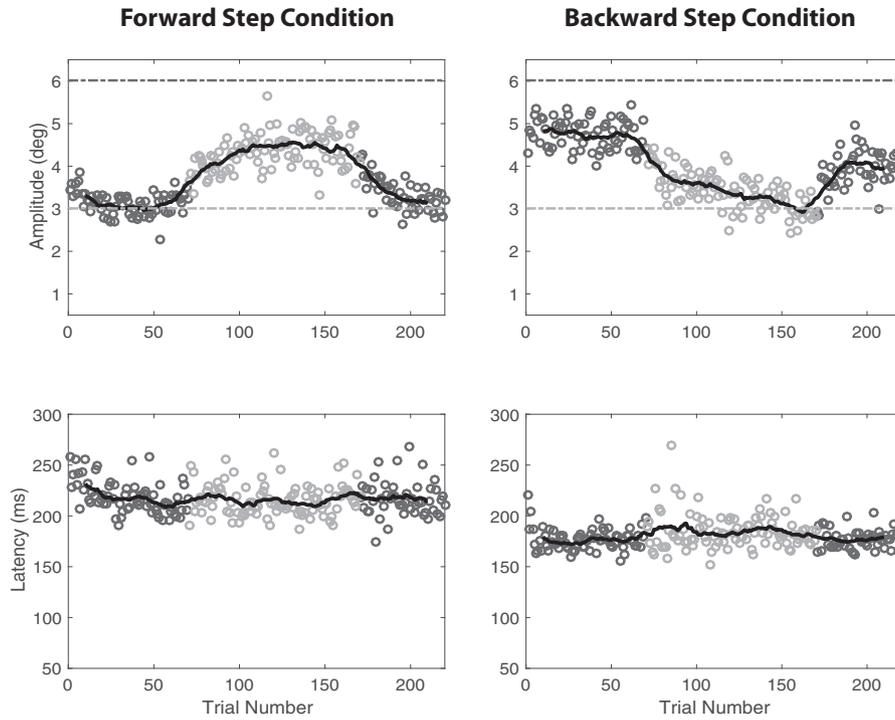


Fig. 3. Trial data averaged over observers, where each point represents the average of all observers in the specific trial. The left column shows the trials from the forward step condition and the right column shows the trials from the backward step condition. In the upper row, saccade amplitudes are plotted; baseline (trials 1–70) and post-adapting trials (171–220) are represented by dark circles and adapting trials (trials 71–170) are represented by light circles. The black line represents the moving average (window size of 20 trials). The darker dotted line represents the initial target displacement, while the lighter dotted line represents the displacement after the step. On the lower row the accompanying latencies are plotted.

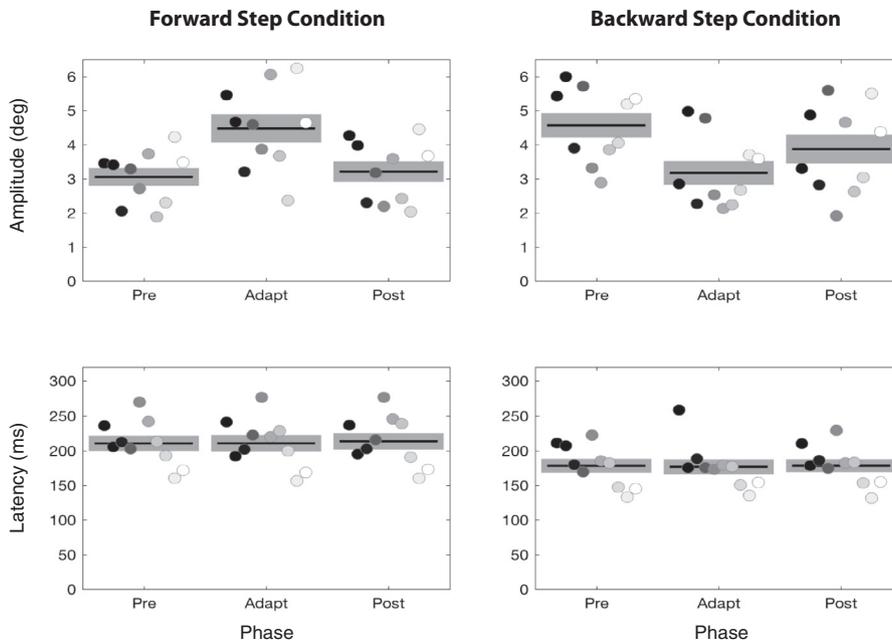


Fig. 4. Data averaged over observers. The left column shows the averages for the forward step condition, the right column the averages for the backward step condition. On the top row the median saccade amplitude is plotted for the baseline (Pre), adaptation (Adapt) and recovery (Post) phases. The black horizontal bar indicates the average over observers. Data for each individual observer is displayed by the circles stretching the width of the bar. The vertical deviation of the greyed area surrounding the bar indicates the standard error of the mean. In the lower row the median latency for each phase (including individual observers) is plotted in the same manner.

amplitude may indicate that previous interpretations of long latencies accompanying short saccade amplitudes are worth revisiting. For instance, in *Vlaskamp, Over, and Hoog (2005)* longer latencies in dense displays were speculated to be the result of oculomotor limitations. However, the average amplitudes accom-

panying these latencies exceeded the small amplitudes typically associated with increased latencies. Such latency increases may be the result of the same mechanisms as those underlying the size-latency phenomenon rather than a consequence of small saccade amplitudes per se.

While saccade adaptation may take up to a 100 trials to converge (e.g. Watanabe, Orgino, Nakamura, & Koizuka, 2003), in our experiment this appears to occur more rapidly. This raises the question to what extent the current adaptation relies on the same mechanisms as typical saccade adaptation. One could argue that rather than neuronal plasticity the current adaptation could be the result of strategic re-aiming. In this light it is important to note that observers were implored to make a speeded saccade toward the target and not anticipate the step in any way. Also, characteristic for saccade adaptation the gain decrease appears more complete in the backwards condition than in the forward condition (e.g. Deubel, Wolf, & Hauske, 1986). Importantly, it seems unlikely that we are dealing with strategic re-aiming, as in such a case we would expect that latencies in the forward step condition should at least be considerably decreased during adaptation. Nevertheless, we cannot say with certainty what underlies the current adaptation. In general, there is considerable debate on what underlies adaptation and, recently, it has become clear that adaptation does not rely on a single mechanism (e.g. Cotti, Panouilleres, Munoz, et al., 2009). Important to the current case is that we are only interested in saccade adaptation as a tool to manipulate required amplitudes while keeping the saccade target constant.

3. Experiment 2: shape versus size

We refer to the phenomenon as the size-latency phenomenon because in previous studies (Harwood et al., 2008; Madelain et al., 2005) it appears that increasing target size is what causes latency increases. However, Madelain et al. and Harwood et al. primarily rely on size changes of circular rings to increase target size. While increasing ring size does increase the area of the object, it also places the near edge of the ring closer to fixation or even beyond fixation in the direction opposite to the required saccade. With the shape overlapping more of the central area previously uncovered inhibitory mechanisms may be at play. For instance, the overlap of fixation may delay saccades in a phenomenon akin to the overlap effect as in (Saslow, 1967). However, at small eccentricities the visual input (resulting from the edges) may actually be further away from fixation compared to a more eccentric ring (see Fig. 5 for an example). However, aside from delays caused by visual input at fixation, irrelevant distractors in other locations are also known to delay saccade initiation (Walker et al., 1995, 1997). With such *remote distractors* causing the largest latency increase when placed directly opposite to the target direction (angle >150°; McSorley, McCloy, & Lyne, 2012) it is possible that edges extending in the direction opposite to the saccade destination may be an important factor driving the latency increase. As such it is still an open question how increasing size in the various direction away from the fovea affect latencies.

A notable exception to the ring experiments is Experiment 1B of Harwood et al. where observers were required to attend to two vertically separated lines and make a horizontal saccade towards their middle. When the lines stood further apart, latencies did increase. This is a good indication that increased size in directions away from fixation lead to increased latencies. However, the manipulation was not necessarily one of target size. The task in Experiment 1B consisted of attending to the two separate lines and judging their orientation while also making a saccade towards their combined center. As increasing the distance between the lines also increases the difficulty of the additional attentional task it does not allow us to unequivocally conclude that latencies for larger proximal objects are consistently increased.

In the current experiment no additional attentional requirements are present and target size is varied both on the axis extending from the fixation dot as well as orthogonal to it. In total four

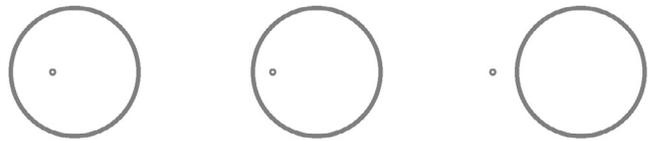


Fig. 5. Three examples of ring placement relative to fixation (the small dot). From left to right the ring is placed at a step/size ratio of 1/6, 2/6 and 4/6. The 2/6 compared to 4/6 ratio resembles the situation in Experiment 1. Here one can see the edges are closer to fixation in the 2/6 than in the 4/6. However, this difference is minimal. For the situation with the ring placed at a step-size ratio of 1/6 the left edge is further removed from fixation than when the ring placed at a ratio of 2/6.

primary conditions are included: The basic manipulation of a *large ring* and *small ring* condition is contrasted by the introduction of two ellipsoid conditions. Both ellipsoid conditions use an ellipsoid covering an equal amount of surface area as the large ring; however, in the *radial ellipse* condition the long side of the ellipse will coincide with the radial axis that travels through the fixation point and the center of the ellipse. In the *orthogonal ellipse* condition the long axis of the ellipse will coincide with the axis orthogonal to this radial axis. Together this makes for four primary conditions; to evaluate the typical proximity effect we also introduce three distance conditions.

3.1. Methods

3.1.1. Observers

Eight observers (4 females) participated in the experiment. The number of observers deviates from Experiment 1 as the number of observers was decided on for each experiment, individually. No observer data was excluded from any of the experiments. The reason fewer observers were included compared to Experiment 1 is that while we were unsure of the consistency of amplitude adaptation over observers, previous experiments on the size-latency phenomena demonstrated it to be highly consistent over observers. When the introduction of different shapes does not result in a similar consistency over observers it may be an indication that the subjective interpretation of the shape plays a role and a follow-up experiment will be required. All observers had normal or corrected to normal vision and ranged in age from 23 to 42 (mean: 31.6; sd: 6.0 years). Observers were sampled from the same pool as in Experiment 1. All except authors JV, RA and MH were naive to the purpose of the experiment.

3.1.2. Stimulus

All displays consisted of a single white annulus (be it circular or ellipsoid) presented on a mid-grey background. Depending on the condition the annulus was small and circular (diameter: 3.8°; small ring condition; Fig. 6, top-left), large and circular (diameter: 7.5°; large ring condition; Fig. 6, bottom-left), ellipsoid with the long side lying on the radial axis (short diameter: 3.8° long diameter: 15.1°; radial ellipse condition; Fig. 6, top-right) or ellipsoid with the long side lying on the orthogonal axis (short diameter: 3.8° long diameter: 15.1°; orthogonal ellipse condition; Fig. 6, bottom-right). Thickness of each annulus type was 0.25° and its center was always placed randomly on an imaginary circle around the fixation point with an eccentricity of 1.26, 2.51 or 5.03° (1/6, 2/6 or 4/6 of the diameter of the large ring).

3.1.3. Procedure

Observers were instructed to saccade towards the annulus as quickly as possible upon its appearance. While observers were instructed to keep in mind that this meant targeting the (perceived) center of the annulus, it was also emphasized that they should not sacrifice speed to do so. The annulus appeared after a

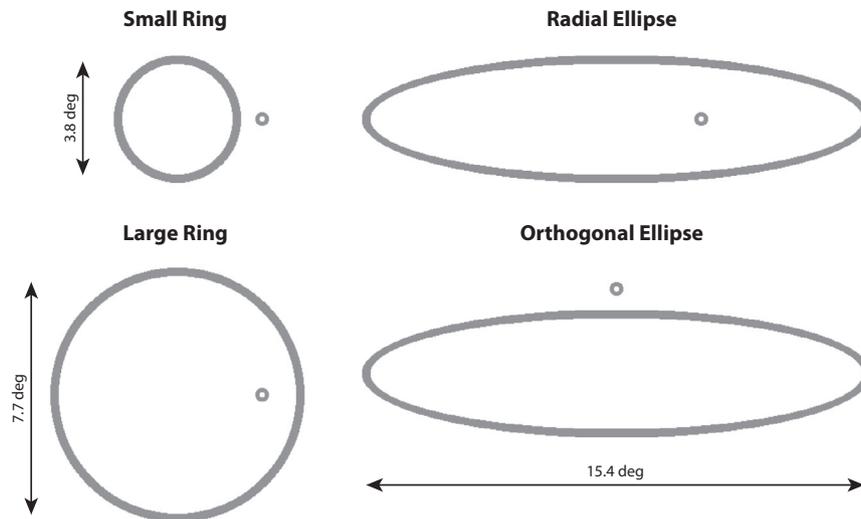


Fig. 6. Overview of the annuli used in Experiment 2. Colors are inverted compared to the actual experiment where annuli were white on a mid-grey background. All four types of possible annuli (left column: small and large ring; right column radial and orthogonal ellipse) are displayed relative to a fixation dot. In the experiment, however, the fixation dot would disappear upon the onset of the ring. The task was to make a speeded saccade towards the ring's center. In the current examples the fixation dot is presented to the right of the annulus's center except for all but the orthogonal ellipse (where the fixation dot appears directly above its center). In the experiment the center of the annulus could appear at any position on an imaginary circle with a radius of one of three eccentricities (1.26° , 2.51° , or 5.03°).

delay of 413–800 ms and trials were self-paced: once the observer recommenced fixation of the fixation dot the delay of the next trial would begin. The fixation dot disappeared upon annulus appearance. Each of the four main conditions comprised of 180 trials (60 trials for each different eccentricity) making for a total of 720 trials. All trial types were randomly mixed, however, to prevent fatigue from influencing the results, the 720 were split in 2 blocks and a short break was included between the blocks.

3.1.4. Apparatus and eye movement analysis

Parameters were mostly the same as in Experiment 1. Contrasting to Experiment 1 the screen refresh rate was 75 Hz and the resolution was set to 1600×1200 . Also the window for fixating the fixation dot was 1.3 rather than 2° . Nevertheless, offline analysis parameters were the same as in Experiment 1.

To exclude erroneous trials we again employ several criteria to ensure a saccade was indeed directed at the ring or ellipse. Starting point had to be within 1.5° of the fixation dot and latencies had to lie between a minimum of 90 and maximum of 700 ms. Depending on the annulus type it is well possible that amplitudes could be very different. To not exclude saccades that were indeed correctly aiming for the target, but slightly off the center, we employ a rather liberal distance criterion: A saccade had to land within 3° of the target's center. However, to ensure that it was directed to the target we combined the liberal distance criterion with a radial criterion stating that the saccade direction was not allowed to deviate more than 60 angular degrees from the direction of target's center. The combination of the above criteria led to an exclusion of 2.9% of the trials.

3.2. Results

Because latencies have been shown to rise with shorter eccentricities we first verify that amplitudes are similar for each condition. In Fig. 7A we plot the amplitudes of the saccades for each condition. Here we see that amplitudes for the radial ellipse are longest. If latencies for these ellipses are shorter this could be due to the increased amplitude, however, this does not lie within the expectation. To evaluate how the size changes affect latencies we plot latency as a function of eccentricity in Fig. 7B for each con-

dition, separately. A two-way repeated measures ANOVA with annulus type and eccentricity as factors and latency as a measure showed a significant main effect of the annulus type ($F(1.31, 9.18) = 83.04$, $p < 0.000005$; Greenhouse-Geisser correction applied due to violation of sphericity assumption) and a significant main effect of eccentricity ($F(1.14, 7.97) = 152.64$, $p < 0.000005$; Greenhouse-Geisser correction applied due to violation of sphericity assumption). Moreover, a significant interaction between annulus type and eccentricity was also found ($F(6, 42) = 13.27$, $p < 0.00001$). Pairwise comparisons (bonferroni corrected p values) clearly show that the time it takes to initiate a saccade towards the radial ellipsoid are longest (radial versus large ring, $p < 0.0005$; radial versus orthogonal ellipse, $p < 0.005$; radial ellipse versus small ring, $p < 0.00005$). This is followed by the saccades targeting the large ring (large versus orthogonal ring, $p < 0.05$; large versus small ring, $p < 0.00005$). Finally, the orthogonal ring elicited longer latency saccades than the small ring ($p < 0.0005$). Interestingly, here latencies were always shortest for the small ring, for each observer, at each eccentricity, individually.

Finally, in Fig. 7C we plot latencies as a function of radial ratio. Radial ratio is calculated by dividing the eccentricity of the annulus's center by the radial diameter (annulus diameter with respect to the radial axis extending through the fixation dot). In this plot we can see that while latencies for the radial ellipse were longer than those for the large ring as function of absolute eccentricity they were not as long as one would expect if the radial diameter were the only determining factor in the increasing latencies in the size-latency phenomenon.

3.3. Discussion Experiment 2

The results paint a dual picture. First, they provide evidence that increasing target size in any direction increases latencies. Importantly this happens without any direct need to use the full shape of the ellipse: Even though the orthogonal ellipse extends away from fixation observers were free to adopt strategies using only input closest to fixation. Nevertheless, for each of the eight observers median latencies were longer for this orthogonal ellipse than for the small ring at each eccentricity, individually. Conversely, for some observers the median latency for the orthogonal

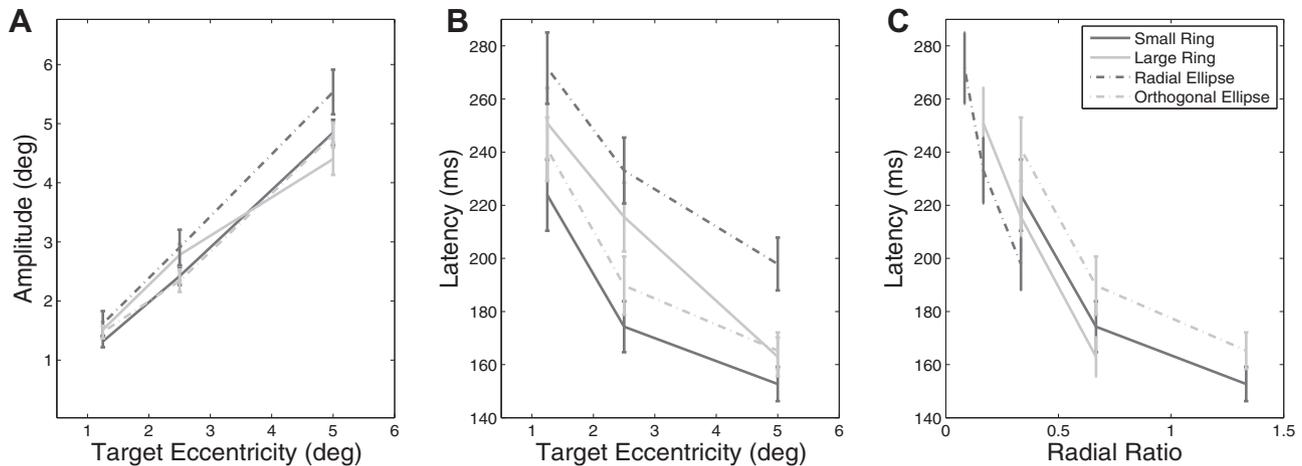


Fig. 7. Saccade characteristics for Experiment 2. A) Amplitudes as a function of target eccentricity per condition, averaged over observers. B) Median latencies as a function of target eccentricity per condition, averaged over observers. C) Same median latencies as in B but now as a function of *radial ratio*. Radial ratio is calculated by dividing the eccentricity of the annulus by the diameter of the annulus in the radial direction (the direction of the required saccade vector respective to the central fixation). Error bars represent standard error of the mean.

ellipse was longer than the latency for the large ring at the longest eccentricity. Second, we also find that latencies in the radial ellipse condition are longer than in the large ring condition even though the ellipse and the large ring encompass the same area size. Thus it appears that stretching an object in the direction of the fovea does lead to the greatest increase in latencies.

4. Experiment 3: general visual input or target appearance

Given that many models of saccade preparation incorporating inhibitory mechanisms are able to explain the fixational delay and the remote distractor effect (e.g. Trappenberg, Dorris, Munoz, & Klein, 2001; Wilimzig, Schneider, & Schöner, 2006) the question arises whether such models cannot simply explain the current results? Indeed it is well possible that the results from Experiment 1 and 2 can be described by models that inhibit saccade initiation based on activation of inhibitory mechanisms due to the presence of the visual input. However, such models would not predict the findings by Madelain et al. (2005) and Harwood et al. (2008) where both a small and a large target were presented simultaneously. In these previous two studies latency differences were the result of only the instruction to attend to either a large or small target, while visual parameters were held constant. This provides a strong indication that the size-latency phenomenon cannot be explained by the above-mentioned models. However, despite a similar latency effect, one may speculate that the current results are distinct from those in the Madelain and Harwood study as in those studies the additional attentional task might have caused the latency difference.

To verify that the current findings and those of Madelain et al. (2005) and Harwood et al. (2008) indeed pertain to the same phenomenon we run a two-alternative forced choice task: While keeping displays constant, observers have to saccade towards a previously designated ring: either the large one (*large ring condition*) or small one (*small ring condition*). In this manner visual stimulation is kept constant as in the previous studies, but no additional task is present.

4.1. Methods

Most of the methods overlap with those described in Experiment 2; below we only discuss differences.

4.1.1. Observers

Seven observers (4 females) aged 24 through 34 (average: 28.9 years; sd: 3.3 years) participated. Considering the simple nature of the task and the expected large and consistent latency difference only 7 observers were included in the final experiment. Observers JV and RA are both authors on this paper. Observers were sampled from the same pool as the previous experiments.

4.1.2. Stimulus and procedure

Each display consisted of two white rings, one small (diameter: 1.5°, thickness: 0.25°) and one large (diameter: 7.5°, thickness: 0.25°). See Fig. 8 for an example of a trial display. The first ring was drawn with its center at a random point on an imaginary circle (radius: 2.5°) centered on the fixation dot. The second ring was drawn on the same circle within an angular range extending from 90 to 270° clockwise from the center of the first ring. Therefore, minimal angular separation between the centers was 90° and maximum angular separation was 180° (directly opposite to the other ring).

Upon initiation of the trial (triggered in the same way as the previous experiments) after a delay of 507–1000 ms the fixation would disappear and the rings would appear. The instruction was to make a saccade towards the designated target. The designated target changed over blocks: Each observer completed 4 sequential blocks, alternating by the instruction to go to the large ring or the small ring. Whether the first block started with the instruction to go to the small ring or go to the large ring was alternated over observers. Each block consisted of 38 trials making for 76 trials per condition and a total of 152 trials. Note that throughout all the blocks the parameters of the stimulus generation were constant.

4.2. Results and discussion

The key question is whether latencies vary based on target condition. In Fig. 9A we plot median latencies averaged over observers. This quickly reveals a considerable difference (67 ms) between latencies for saccades towards the small ring compared to those aiming for the large ring. A *t*-test confirms a significant difference ($t(6) = 6.57$ $p < 0.001$). Moreover, in Fig. 9B we plot the latency distribution collapsed over observers. To account for potential differences in latencies between observers we have divided all individual latencies by the median latency of each observer in

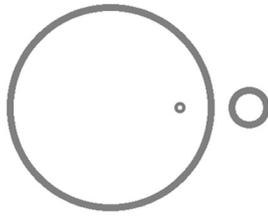


Fig. 8. Representation of a trial in Experiment 3 (colors are inverted colors; in the experiment the ring was white on a mid-grey background). The small and large ring were both present on each trial, and always appeared simultaneously upon the disappearance of the fixation dot. Depending on the current block observers either had to saccade towards the center of the small or the large ring, which always stood at an eccentricity of 2.5° from the fixation point (vectors varied in direction once again, see Methods). The small ring was 1.5° in diameter and the large ring 7.5°.

the small ring condition. This clearly demonstrates that despite using constant parameters to generate stimulus displays, the target instructed to the observer determined the latency of the saccade. While this does not negate the possibility that the presence of a large ring in general delays saccade initiation, the current experiment clearly demonstrates that the size-latency phenomenon exists besides the typical delays as a result of visual input inhibiting saccade initiation.

5. General discussion

In the current paper we set out to explore whether the saccade latency increases reported in Madelain et al. (2005) and Harwood et al. (2008) are best explained by the size of the saccade target, applicable to saccades in general and whether we are dealing with a truly novel phenomenon rather than an extension of already known saccade phenomena. Interestingly, in Experiment 1 we find the phenomenon is not directly coupled to the required amplitude, but target eccentricity appears the main determining factor. This clearly distinguishes the phenomenon from previous reports showing that short amplitudes cause an increase in latencies. Thus there is a strong reliance on the visual properties of the proximal

saccade target. To further evaluate the importance of the target size we manipulated the shape of the target while (except for the small ring condition) keeping surface area the same (Experiment 2). This revealed that while a target overlapping more of the observer’s central vision leads to the longest latencies, increasing target size in the orthogonal direction also prolongs the accompanying saccade latencies. While the previous studies already demonstrated that it is the properties of the specific saccade target and not the presence of stimulus elements per se that influence the latencies, the findings of Experiment 1 and 2 could potentially be explained by biologically inspired models incorporating inhibitory properties in the saccade map (e.g. Trappenberg et al., 2001; Wilimzig et al., 2006). Therefore, in Experiment 3 we verified that it is truly the size of the saccade target that drives the large latency difference, rather than visual input. As such, inhibitory responses to visual input cannot explain the phenomenon.

Importantly, the three experiments also emphasize that the findings from the studies by Madelain et al. (2005) and Harwood et al. (2008) are not limited to dual tasks where a demanding attentional task is added to the saccade task. In combination with these studies, the current results provide strong evidence that the size of a proximal target is crucial in determining saccade latencies. We should note that this does not refute the previously made claim that scaling of attention is the cause of the latency increase. However, it emphasizes that the size-latency phenomenon is likely to occur in a broad range of situations, beyond those where explicit attentional tasks are present. While the current experiments each have their own specific purpose, if we consider the individual tasks they stretch a considerable range: In Experiment 1 a saccade has to be made based on a stepping ring; in Experiment 2 a saccade has to be made towards a sudden onset and, finally, in Experiment 3 a saccade has to be made towards one of two available targets. In all of these tasks we find considerably effects of latency. As such, it is highly likely that in an observer’s interactions in daily life, saccades will be subjected to the size-latency phenomenon. Given the robustness of the phenomenon and the drastic latency increases the question arises what underlies this phenomenon. Below we discuss this question from three different perspectives with respect to mechanism, uncertainty and functionality.

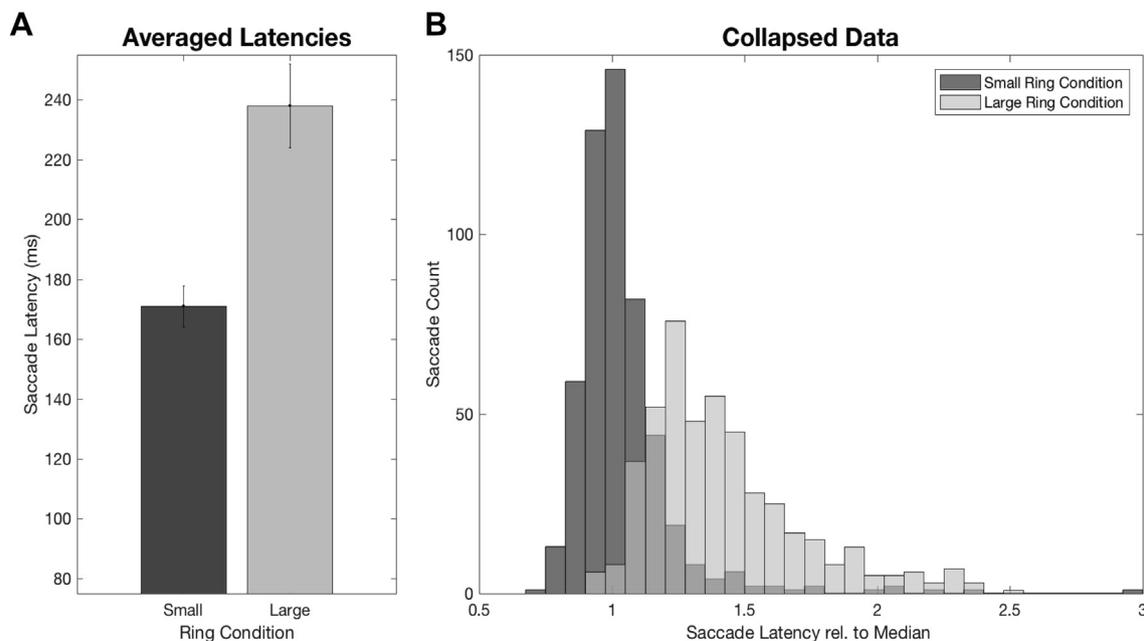


Fig. 9. Latencies from Experiment 3. A) Median latencies averaged over observers for the small ring and large ring condition. Error bars represent standard errors of the mean. B) Histogram of all saccade latencies collapsed over observers. Latencies have been normalized on the basis of median latencies in the small ring condition: For each observer the initial saccade latency of each trial is divided by the median latency in the small ring condition.

We can only speculate on the mechanism behind the size-latency phenomenon. However, the results from Experiment 2 clearly show that stretching an element in the direction of the observer's central vision and to the side opposite of the required saccade direction increases latencies strongest. This pattern is reminiscent of the fact that fixational neurons at the rostral pole of the superior colliculus have been found to inhibit saccade initiation (e.g. Munoz & Guitton, 1989). However, in behavioral studies, latency increases are typically a result of visual stimulation. Contrastingly, Experiment 3 demonstrates that the size-latency phenomenon is not driven by overall visual stimulation, but purely by the properties of the saccade target. Moreover, the visual stimulation associated with the rings used in the current experiments is produced only by its edges, which, for rings at the short eccentricities can be further removed from fixation than for rings farther from fixation (see also Fig. 5). Nevertheless, as motor preparation should result in a saccade to the ring's center, neurons with receptive fields inside the ring are likely also involved. Therefore, the physiological representation of the whole target overlapping the fovea is potentially an important factor in determining latencies. As such, it is likely that the dynamics of cells representing the central area around the rostral pole of the superior colliculus play an important role even if they are not directly stimulated by visual input. The high density of small receptive fields means that many of these cells could be involved in determining the landing-point of the upcoming saccade. While inhibitory neurons with receptive fields only at the fovea would not directly explain why larger rings extending away from the fovea also lead to such large increase latencies, there is evidence that these fixational neurons also respond to larger saccades (Munoz & Wurtz, 1995). Potentially, the programming of a saccade toward a target that is represented in the superior colliculus by neurons that are also active in the prevention of saccade initiation leads to delayed initiation beyond that of general non-target visual stimulation.

Alternatively, there is an ongoing discussion over whether the fixational zone at the rostral pole of the superior colliculus is truly functionally independent from its surroundings (for a discussion see: Hafed & Krauzlis, 2012; Sugiuchi, Izawa, Takahashi, et al., 2007). Based on measurements showing that neurons in the rostral pole of the superior colliculus increase their activity before and during microsaccades (Hafed, Goffart, & Krauzlis, 2009), it has been hypothesized that fixation is maintained through a balance in activation of neurons coding for microsaccades (Gandhi & Katnani, 2011; Hafed et al., 2009). Consequently, when programming a saccade to a large ring (overlapping fixation) involves cells that code for small saccades in opposite directions, this could potentially explain why a large ring extending in all directions from fixation results in the largest latency increase.

On a computational level it may be argued that increasing object size may lead to greater uncertainty about the exact location of an object's center. It is possible that the phenomenon can best be explained as a delay directly related to an increased time required in establishing the saccade target's center. If we assume that uncertainty of the center on the radial axis (the axis aligned with the saccade vector) is the strongest determining factor, this could explain the ordering of latencies for the four types of rings in Experiment 2. The small target is associated with the least uncertainty, followed by the orthogonal ellipse, the large ring and the radial ellipse, respectively. However, we should note that increasing latencies could be seen as a deviation from how uncertainty is typically dealt with in the saccadic system. That is, scanning at a faster pace is often prioritized over slowing saccades to ensure accuracy (Araujo, Kowler, & Pavel, 2001; Kowler & Pavel, 2013; Wu, Kwon, & Kowler, 2010). Rather if we turn to the many studies showing speeded saccades are often attracted by onsets or salient distractors (e.g. de Vries, Hooge, Wiering, & Verstraten, 2011;

Theeuwes, Kramer, Hahn, & Irwin, 1998; van Zoest & Donk, 2006) one could argue sacrificing accuracy for speed to be a feature of the system. From this point of view it can be considered atypical that uncertainty about a target's center would cause a large delay in saccade latencies. Nevertheless, this does not exclude the possibility that the uncertainty for large targets at short eccentricities has to be resolved to execute a saccade. Further research will have to demonstrate whether this explanation is indeed the best suited to describe the current phenomenon.

The question of why saccades towards larger objects should be delayed brings us to an explanation of the phenomenon on a functional level. As Harwood et al. (2008) points out it is possible that the delay may be a way of prioritizing actions. While the benefit of executing a saccade is that it enhances the ability to extract visual details from a newly fixated location, it also comes at a cost: the temporary loss of vision. Thus making a saccade is a trade-off between processing input at a lower resolution in the periphery and sacrificing temporary vision loss in order to process an object at a higher resolution at the fovea. While for a small object in the far periphery the benefits of making a saccade clearly outweigh the temporal vision loss associated with making a saccade, for large objects close to fixation the benefit of making a saccade is limited and thus the cost compared to the benefits are much higher. Delaying such saccades may be a way of the saccadic system to prioritize not only fixation over movement, but also one movement over another. Until now, little research has been performed on the possibility that latencies are related to a cost-benefit ratio of the execution of the saccade. Nevertheless, some reports of diminished saccade frequency in light of larger targets exist. For instance, in Wu et al. (2010), where sequences of saccades to multiple targets were required, it was found that when the distance to the target after the execution of primary saccades was smaller relative to the size of the target, the occurrence of secondary saccades decreased and accompanying latencies increased.

In conclusion the current paper demonstrates that the phenomenon in which latencies rise drastically with increasing saccade target size is well described as the size-latency phenomenon and, that this phenomenon, is distinct from previous reports on delays in saccade latency in literature. Therefore, the phenomenon provides an important addition to literature. On the one hand, the robustness of the phenomenon shows it is likely to apply to many eye movements made in daily life. On the other hand, the novelty is interesting from a fundamental perspective: The timing of saccades is still ill-understood and it is not yet known why the saccade latency lasts as long as it does (see for instance: Ludwig, Gilchrist, McSorley, & Baddeley, 2005). Understanding the nature of the size-latency phenomenon may be crucial to a better understanding of the events leading up to the execution of the saccade.

Grants

This research was supported by a National Science Foundation grant (1232654) to M.R. Harwood and a Fight For Sight grant (PD14003) awarded to J.P. de Vries.

References

- Araujo, C., Kowler, E., & Pavel, M. (2001). Eye movements during visual search: The costs of choosing the optimal path. *Vision Research*, 41, 3613–3625. [http://dx.doi.org/10.1016/S0042-6989\(01\)00196-1](http://dx.doi.org/10.1016/S0042-6989(01)00196-1).
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436. <http://dx.doi.org/10.1163/156856897X00357>.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The EyeLink Toolbox: Eye tracking with MATLAB and the psychophysics toolbox. *Behavior Research Methods, Instruments, and Computers*, 34, 613–617. <http://dx.doi.org/10.3758/BF03195489>.

- Cotti, J., Panouilleres, M., Munoz, D. P., et al. (2009). Adaptation of reactive and voluntary saccades: Different patterns of adaptation revealed in the antisaccade task. *Journal of Physiology*, 587, 127–138. <http://dx.doi.org/10.1113/jphysiol.2008.159459>.
- de Vries, J. P., Hooge, I. T., Wiering, M. A., & Verstraten, F. A. (2011). How longer saccade latencies lead to a competition for salience. *Psychological Science*, 22, 916–923. <http://dx.doi.org/10.1177/0956797611410572>.
- Deubel, H., Wolf, W., & Hauske, G. (1986). Adaptive gain control of saccadic eye movements. *Human Neurobiology*, 5, 245–253.
- Dick, S., Ostendorf, F., Kraft, A., & Ploner, C. J. (2004). Saccades to spatially extended targets: The role of eccentricity. *NeuroReport*, 15, 453–456.
- Fendrich, R., Demirel, S., & Danziger, S. (1999). The oculomotor gap effect without a foveal fixation point. *Vision Research*, 39, 833–841. [http://dx.doi.org/10.1016/S0042-6989\(98\)00164-3](http://dx.doi.org/10.1016/S0042-6989(98)00164-3).
- Gandhi, N. J., & Katnani, H. A. (2011). Motor functions of the superior colliculus. *Annual Review of Neuroscience*, 34, 205–231. <http://dx.doi.org/10.1146/annurev-neuro-061010-113728>.
- Hafed, Z. M., Goffart, L., & Krauzlis, R. J. (2009). A neural mechanism for microsaccade generation in the primate superior colliculus. *Science*, 323, 940–943. <http://dx.doi.org/10.1126/science.1166112>.
- Hafed, Z. M., & Krauzlis, R. J. (2012). Similarity of superior colliculus involvement in microsaccade and saccade generation. *Journal of Neurophysiology*, 107, 1904–1916. <http://dx.doi.org/10.1152/jn.01125.2011>.
- Harwood, M. R., Madelain, L., Krauzlis, R. J., & Wallman, J. (2008). The spatial scale of attention strongly modulates saccade latencies. *Journal of Neurophysiology*, 99, 1743–1757. <http://dx.doi.org/10.1152/jn.00589.2007>.
- Hopp, J. J., & Fuchs, A. F. (2004). The characteristics and neuronal substrate of saccadic eye movement plasticity. *Progress in Neurobiology*, 72, 27–53. <http://dx.doi.org/10.1016/j.pneurobio.2003.12.002>.
- Kalesnykas, R. P., & Hallett, P. E. (1994). Retinal eccentricity and the latency of eye saccades. *Vision Research*, 34, 517–531. [http://dx.doi.org/10.1016/0042-6989\(94\)90165-1](http://dx.doi.org/10.1016/0042-6989(94)90165-1).
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, 4, 138–147. [http://dx.doi.org/10.1016/S1364-6613\(00\)01452-2](http://dx.doi.org/10.1016/S1364-6613(00)01452-2).
- Kleiner, M., Brainard, D., Pelli, D., et al. (2007). What's new in Psychtoolbox-3. *Perception*, 36, 1.
- Kowler, E., & Blaser, E. (1995). The accuracy and precision of saccades to small and large targets. *Vision Research*, 35, 1741–1754.
- Kowler, E., & Pavel, M. (2013). Strategies of saccadic planning. In C. Chubb, B. Doshier, Z.-L. Lu, & R. Shiffrin (Eds.), *Human information processing: Vision, memory, and attention* (pp. 133–147). American Psychological Association.
- Ludwig, C. J. H., Gilchrist, I. D., & McSorley, E. (2004). The influence of spatial frequency and contrast on saccade latencies. *Vision Research*, 44, 2597–2604. <http://dx.doi.org/10.1016/j.visres.2004.05.022>.
- Ludwig, C. J. H., Gilchrist, I. D., McSorley, E., & Baddeley, R. J. (2005). The temporal impulse response underlying saccadic decisions. *Journal of Neuroscience*, 25, 9907–9912. <http://dx.doi.org/10.1523/JNEUROSCI.2197-05.2005>.
- Madelain, L., Krauzlis, R. J., & Wallman, J. (2005). Spatial deployment of attention influences both saccadic and pursuit tracking. *Vision Research*, 45, 2685–2703. <http://dx.doi.org/10.1016/j.visres.2005.05.009>.
- Mcgowan, J. W., Kowler, E., Sharma, A., & Chubb, C. (1998). Saccadic localization of random dot targets. *Vision Research*, 38, 895–909.
- McLaughlin, S. C. (1967). Parametric adjustment in saccadic eye movements. *Perception Psychophysics*, 2, 359–362. <http://dx.doi.org/10.3758/BF03210071>.
- McSorley, E., McCloy, R., & Lyne, C. (2012). The spatial impact of visual distractors on saccade latency. *Vision Research*, 60, 61–72. <http://dx.doi.org/10.1016/j.visres.2012.03.007>.
- Munoz, D. P., & Guitton, D. (1989). Fixation and orientation control by the tectoreticulo-spinal system in the cat whose head is unrestrained. *Revue Neurologique (Paris)*, 145, 567–579.
- Munoz, D. P., & Wurtz, R. H. (1995). Saccade-related activity in monkey superior colliculus. I. Characteristics of burst and buildup cells. *Journal of Neurophysiology*, 73, 2313–2333.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442.
- Ploner, C. J., Ostendorf, F., & Dick, S. (2004). Target size modulates saccadic eye movements in humans. *Behavioral Neuroscience*, 118, 237–242. <http://dx.doi.org/10.1037/0735-7044.118.1.237>.
- Reuter-Lorenz, P. A., Hughes, H. C., & Fendrich, R. (1991). The reduction of saccadic latency by prior offset of the fixation point: An analysis of the gap effect. *Percept Psychophysics*, 49, 167–175. <http://dx.doi.org/10.3758/BF03205036>.
- Reuter-Lorenz, P. A., Oonk, H. M., Barnes, L. L., & Hughes, H. C. (1995). Effects of warning signals and fixation point offsets on the latencies of pro- versus antisaccades: Implications for an interpretation of the gap effect. *Experimental Brain Research*, 103, 287–293. <http://dx.doi.org/10.1007/BF00231715>.
- Saslow, M. G. (1967). Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *Journal of the Optical Society of America*, 57, 1024–1029. <http://dx.doi.org/10.1364/JOSA.57.001030>.
- Smeets, J. B. J., & Hooge, I. T. C. (2003). Nature of variability in saccades. *Journal of Neurophysiology*, 90, 12–20. <http://dx.doi.org/10.1152/jn.01075.2002>.
- Sugiuchi, Y., Izawa, Y., Takahashi, M., et al. (2007). Controversy on “fixation zone” of the superior colliculus. *Neuro-Ophthalmology*, 31, 147–155. <http://dx.doi.org/10.1080/01658100701647688>.
- Theeuwes, J., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: Capture of the eyes by new objects. *Psychological Science*, 9, 379–385.
- Trappenberg, T. P., Dorris, M. C., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience*, 13, 256–271. <http://dx.doi.org/10.1162/089892901564306>.
- van Zoest, W., & Donk, M. (2006). Saccadic target selection as a function of time. *Spatial Vision*, 19, 61–76.
- Vlaskamp, B. N. S., Over, E. A. B., & Hooge, I. T. C. (2005). Saccadic search performance: The effect of element spacing. *Experimental Brain Research*, 167(2), 246–259. <http://dx.doi.org/10.1007/s00221-005-0032-z>.
- Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). Effect of remote distractors on saccade programming: Evidence for an extended fixation zone. *Journal of Neurophysiology*, 78, 1108–1119.
- Walker, R., Kentridge, R. W., & Findlay, J. M. (1995). Independent contributions of the orienting of attention, fixation offset and bilateral stimulation on human saccadic latencies. *Experimental Brain Research*, 103, 294–310. <http://dx.doi.org/10.1007/BF00231716>.
- Watanabe, S., Orgino, S., Nakamura, T., & Koizuka, I. (2003). Saccadic adaptation in the horizontal and vertical directions in normal subjects. *Auris, Nasus, Larynx*, 30, 41–45.
- Weber, H., Aiple, F., Fischer, B., & Latanov, A. (1992). Dead zone for express saccades. *Experimental Brain Research*, 89, 214–222. <http://dx.doi.org/10.1007/BF00229018>.
- Weber, H., & Fischer, B. (1994). Differential effects of non-target stimuli on the occurrence of express saccades in man. *Vision Research*, 34, 1883–1891. [http://dx.doi.org/10.1016/0042-6989\(94\)90312-3](http://dx.doi.org/10.1016/0042-6989(94)90312-3).
- Wilimzig, C., Schneider, S., & Schöner, G. (2006). The time course of saccadic decision making: Dynamic field theory. *Neural Networks*, 19, 1059–1074. <http://dx.doi.org/10.1016/j.neunet.2006.03.003>.
- Wu, C. C., Kwon, O. S., & Kowler, E. (2010). Fitts's law and speed/accuracy trade-offs during sequences of saccades: Implications for strategies of saccadic planning. *Vision Research*, 50, 2142–2157. <http://dx.doi.org/10.1016/j.visres.2010.08.008>.
- Wyman, D., & Steinman, R. (1973). Latency characteristics of small saccades. *Vision Research*, 13, 2173–2175.