

Reinforcement reduces the size–latency phenomenon: A cost–benefit evaluation of saccade triggering

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Saccadic latencies are known to change as a function of target eccentricity and size. Recently, it has been shown that latencies consistently change according to the amplitude of the step in proportion to the size of the target (Madelain, Krauzlis, & Wallman, 2005; Harwood, Madelain, Krauzlis, & Wallman, 2008; De Vries, Azadi, & Harwood, 2016). This effect, called the *size–latency phenomenon*, might be seen as a function of a cost–benefit relationship: Longer latencies might be explained by the lower benefit of making a saccade while the target mostly remains within the attentional field. Here, we probe this hypothesis by manipulating the cost–benefit relationship using a reinforcement procedure. Participants tracked a target stepping horizontally with varying amplitudes and sizes such that the step-to-size ratio was equal to either 0.3 or 1.5. We used a dynamic-reinforcement criterion in the blocked conditions. In the 0.3-ratio condition, any latency shorter than the criterion was reinforced. In the 1.5-ratio condition, any latency longer than the criterion was reinforced. During baseline, we observed the size–latency effect with large differences in latencies depending on the ratio in force (229 and 161 ms, respectively, for 0.3 and 1.5). After learning, distributions shifted toward the shorter or longer value (198 and 236 ms, respectively, for 0.3 and 1.5). On average, latencies decreased by 31 ms and increased by 75 ms according to the ongoing reinforcement contingencies. Our results indicate that reinforcement contingencies can considerably affect

saccadic-latency distributions, and support the idea of a cost–benefit evaluation of saccade triggering.

Introduction

Targets appearing in the visual field are usually followed by saccades with variable latencies averaging 150–200 ms that result in skewed reaction distributions (Sumner, 2011). Saccade latencies are affected by many factors, both complex and simple. Target eccentricity increases latencies at very small and large eccentricities (Wyman & Steinman, 1973; Kalesnykas & Hallett, 1994), and larger targets weakly increase latencies in some conditions (Boch, Fischer, & Ramsperger, 1984; Dick, Ostendorf, Kraft, & Ploner, 2004; Ploner, Ostendorf, & Dick, 2004) but not in others (Kowler & Blaser, 1995; McGowan, Kowler, Sharma, & Chubb, 1998). There is some evidence for interactions between eccentricity and size (Boch et al., 1984; Kalesnykas & Hallett, 1996; Dick et al., 2004), but because these findings have generally been small or mixed, they have previously not received great attention.

Recently, by concentrating on target step amplitudes that are fractions of the target size, researchers have shown that target eccentricity and size strongly and consistently interact (Madelain, Krauzlis, & Wallman, 2005; Harwood, Madelain, Krauzlis, & Wallman, 2008; De Vries, Azadi, & Harwood, 2016). In the Madelain et

Citation: Vullings, C., Harwood, M. R., & Madelain, L. (2019). Reinforcement reduces the size–latency phenomenon: A cost–benefit evaluation of saccade triggering. *Journal of Vision*, 19(4):16, 1–9, <https://doi.org/10.1167/19.4.16>.



al. (2005) experiments, observers were required to track two concentric rotating rings of different sizes. The two concentric rings were made up of several segments, and observers were instructed to attend to either the large or the small ring. The two rings would step together, and contingent on the step, the number of segments in the rings would briefly change. Observers had to regain fixation and report the number of segments of the attended ring after the step. It was found that saccades in response to the rings' step had noticeably different latencies depending on which ring was attended: Latencies in the attend-large condition were longer than in the attend-small condition by 135 ms on average. These variations were then further probed by Harwood et al. (2008), demonstrating a strong relation between the latency, size, and eccentricity of the target. While latencies vary considerably depending on both the absolute eccentricity and the ring size, evaluating latencies in terms of the amplitude of the step in proportion to the size of the target (step-to-size ratio) yields a consistent relation between the reaction time and the step-to-size ratio. It is noteworthy that this latency difference is not explained by the stimulus shape, as it was also observed with various stimuli such as vertical lines instead of rings. This effect causes large latency increases of up to 200 ms—a large figure when compared to other effects on saccadic reaction time (for detailed comparisons, see De Vries et al., 2016). Importantly, this effect was also found in simple saccade tasks and could not be easily attributed to established inhibitory mechanisms of saccade initiation (De Vries et al., 2016).

Harwood et al. (2008) proposed that this effect, termed the *size–latency phenomenon*, might be attributed to a cost–benefit relationship: The difference in latencies might be explained by the benefit of making a saccade while the target mostly remains within the attentional field. Because vision is impaired during saccade—a phenomenon known as *saccade suppression* (Matin, 1974; but see Castet & Masson, 2000; Balsdon, Schweitzer, Watson, & Rolfs, 2018)—one might consider that there is a cost to saccade (Harris & Wolpert, 2006). On the one hand, the cost of a particular size of saccade might be regarded as fixed within the context of controlled laboratory settings. On the other hand, the benefit of the saccade varies: If the step is large relative to the size of the object, the saccade strongly enhances the object's visual detailed perception, whereas if the step is small relative to the size of the object, the visual information remains mostly available without a saccade. To illustrate this argument, one might picture what would happen in trying to follow the displacement of an animal that has moved by 1 m: If it were a fly, the benefit of a saccade would be high, yielding regular latencies, whereas if it were an

elephant, the benefit would be lower, yielding longer latencies.

In this article, we aim to probe this hypothesis by controlling the cost–benefit relationship using a reinforcement procedure. More specifically, we manipulated the benefit of making saccades with either short or long latencies by controlling reinforcement contingencies, as it has been demonstrated that reinforcement may have a strong effect on saccade reaction times (Madelain, Champrenaut, & Chauvin, 2007; Vullings & Madelain, 2018). We diminished the size–latency phenomenon by reinforcing on the one hand shorter latencies for the ratio with typically long ones (i.e., ratio 0.3 yielding a median latency of 229 ms) and on the other hand longer latencies for the ratio with typically regular ones (i.e., ratio 1.5 yielding a median latency of 161 ms).

Methods

Participants

Six adults (three women, three men; 18–47 years old) participated in this study. They were unaware of the purpose of the study, except for two participants (S1 and S6, an undergraduate student and the last author), and had normal or corrected-to-normal vision. Participants were instructed to earn as many points as possible by following target displacements while aiming at the target center; no further explanation was given as to how to earn points. The instructions were given at the beginning of the reinforcement sessions with ratios 1.5 and 0.3 (see later) to assure that participants would focus on the task. Participants who were unaware of the study's purpose received 5 euros for participating, plus an additional sum depending on the points collected (2 cents per point); they received 50 euros on average at the end of the experiment. All experimental procedures received approval from the Ethical Committee in Behavioral Sciences of the University of Lille (Agreement 2017-5-S51) and conformed to the standards set by the Declaration of Helsinki. All participants gave informed written consent.

Apparatus

Stimuli were generated using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) for MATLAB (MathWorks, Natick, MA) and displayed on a video monitor (Iiyama HM204DT, 100 Hz, 22 in.). Participants were seated on an adjustable stool in a darkened, quiet room, facing the center of the computer screen at a viewing distance of 60 cm. To minimize

	Amplitude (°)	Diameter (°)
Ratio 1.5	1.5	1
	2.5	1.67
	6	4
	10.5	7
Ratio 0.3	1.2	4
	1.5	5
	2.1	7
	2.5	8.33

Table 1. Stimulus features for amplitude-to-diameter ratios 1.5 and 0.3.

measurement errors, the participant's head movements were restrained using a chin and forehead rest, so that the eyes in primary gaze position were directed toward the center of the screen. Viewing was binocular, but only the right eye position was digitized in both the vertical and horizontal axes. Eye movements were measured continuously with an infrared video-based eye-tracking system (EyeLink, SR Research Ltd., Ontario, Canada), sampled at 2000 Hz. Data were transferred, stored, and analyzed via programs written in MATLAB running on an Ubuntu Linux computer.

Stimuli were light-gray rings (luminance = 16 cd/m²), with various diameters (ranging from 1° to 8.33°), displayed on a dark-gray background (luminance = 1.78 cd/m²). The target randomly stepped from the screen center to the left or right with horizontal amplitudes ranging from 1.2° to 10.5°. The target diameter and target step were chosen such that the step-to-size ratio was either 0.3 or 1.5 (see Table 1 and Figure 1A).

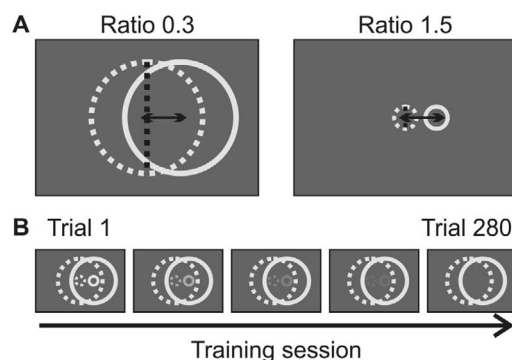


Figure 1. (A) Illustration of the stimuli used for ratios 0.3 and 1.5 in the case of a 2.5° step. The ring diameters are 8.33° and 1.67°, respectively, for ratios 0.3 and 1.5. (B) Illustration of the principle of the fading procedure used during the training phase. The fading procedure consisted of more steps than the five represented—i.e., 280 gradual gray-level steps in which the inner-ring luminance decreased from 16 cd/m² to 1.78 cd/m² (the background luminance).

Before each experimental session, we calibrated the eye tracker by having the participant fixate a set of 13 fixed locations distributed across the screen. Every 50 trials, participants looked at a target displayed on the center of the screen for a one-point calibration check.

Procedure

The experiment lasted 30 sessions of 320 trials each, divided between training, baseline, and reinforcement sessions. Three daily sessions were typically recorded, separated by 5-min breaks during which participants were free to move. The experiment lasted 10 consecutive weekdays (five days a week, from Monday to Friday). Regardless of the actual condition, participants were required to make saccades toward the horizontally stepping target.

Training

Participants were trained to make saccades without blinking, anticipating, or looking away from the target. Training sessions of 320 trials lasted until at least 75% of saccades were detected online (see Acquisition and data analysis). Because the probability of eliciting a saccade is reduced with a 0.3 step-to-size ratio (Harwood et al., 2008), participants were trained with a stimulus composed of two concentric rings simultaneously stepping and corresponding to the ratios 0.3 and 1.5 (e.g., for a 2.5° step, the sizes of the outer and inner rings would be 8.33° and 1.67°, respectively; see Figure 1B). The rings stepped randomly to the left or right. Throughout the session, the inner ring (corresponding to the ratio 1.5) faded out progressively such that only the outer ring (corresponding to the ratio 0.3) would remain. When the saccade was considered incorrect, a feedback was given consisting of a low-pitched beep (100 ms, 400 Hz) and a written comment (“No saccade” if the participant had blinked, anticipated, or not made a saccade; “Wrong distance” if the participant did not correctly aim at the target center).

Baseline

On average, four 320-trial baseline sessions were completed, in which participants were instructed to follow the target displacement. At the beginning of the trial, the participant fixated the target displayed at the center of the screen for a period varying between 750 and 1,250 ms. The target then stepped randomly toward the left or right, and the participant made a saccade. If the latency was less than 80 ms or greater than 500 ms, or if no saccade was detected, the target disappeared and the trial was discarded without repeat. Saccadic latency was defined as the interval of time elapsed between the target step and

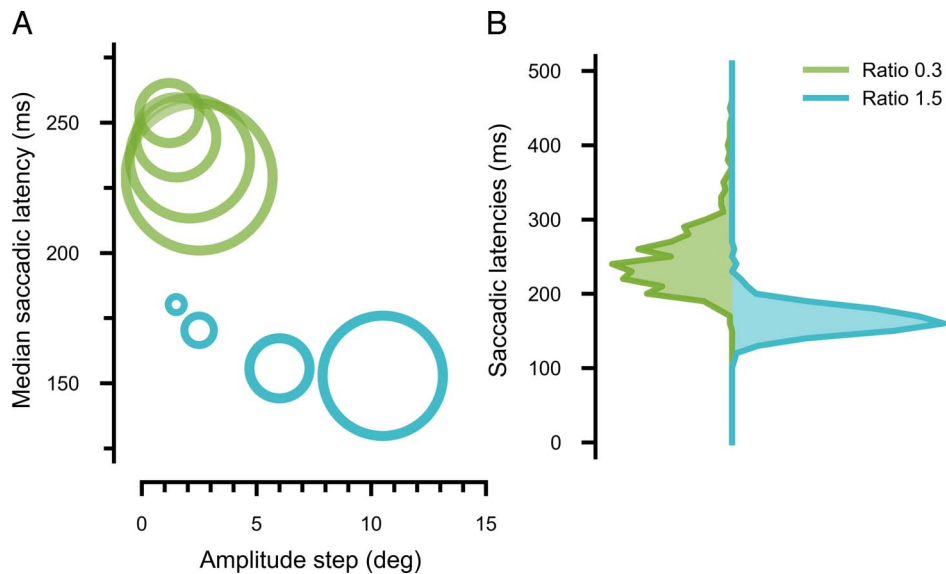


Figure 2. Illustration of the size–latency phenomenon during baseline for a representative participant. (A) Median saccadic latency as a function of the amplitude step. The size of the ring represents the diameter of the actual stimulus (from 1° to 8.33°). The green rings represent the stimuli used for ratio 0.3, and the blue ones for ratio 1.5 (the actual ring color was always light gray). (B) Frequency distributions of saccadic latencies for ratios 0.3 (leftward distribution, in green) and 1.5 (rightward distribution, in blue) measured during baseline. The size–latency phenomenon is illustrated by the longer latencies observed with ratio 0.3.

the saccade onset. A session was composed of eight alternating blocks of 40 consecutive trials with a step-to-size ratio of either 1.5 or 0.3.

Reinforcement sessions

On average, 23 reinforcement sessions of 320 trials were completed, separated into two counterbalanced experimental conditions: one using a step-to-size ratio of 1.5 and one using a ratio of 0.3. During reinforcement with ratio 1.5 (Rft 1.5), the 320 trials used exclusively target sizes and steps yielding a step-to-size ratio of 1.5 (see Table 1). We used a dynamically increasing criterion for reinforcement in order to increase saccadic latencies (see later). During the ratio-0.3 reinforcement condition (Rft 0.3), the 320 trials consisted of target sizes and steps yielding a step-to-size ratio of 0.3 (see Table 1) and we used a dynamically decreasing criterion for reinforcement to decrease saccadic latencies. In both conditions, the criterion was the median latency computed over a 50-trial moving window. In Rft 0.3, any latency below the criterion was reinforced. In Rft 1.5, any latency above the criterion was reinforced. The reinforcer consisted of a brief auditory feedback (100 ms, 500 Hz) and earning a point, which was exchanged for 2 cents at the end of the experiment. Every 50 reinforcement trials, the number of points earned was displayed on the monitor. The total number of 320-trial reinforcement sessions completed in each condition depended on the time needed to reach stable reaction-time distributions. Our stability criterion used the median and first and last quartiles of the saccadic-latency distributions for the last two sessions,

with the requirement that these statistics should not be different (98% confidence intervals of rejecting the null hypothesis) from those of the preceding three sessions.

Acquisition and data analysis

Eye movements were recorded and measured throughout each trial. For online saccade detection, we used the EyeLink online saccade detector to identify saccade onset and offset, using a 30°/s velocity and 8,000°/s² acceleration thresholds. Saccade parameters were retrieved on average with a 12-ms delay after saccade offset. For off-line analyses, a human observer first validated each saccade manually; saccades with amplitude gain (saccade amplitude/target amplitude) less than 0.5 or greater than 2 were discarded. On average, we kept 84.71% ($SD = 8.05$) of saccades per participant.

We used bootstrapping methods (resampling with replacement 100,000 times) to estimate all the individual statistical parameters and 98% confidence intervals (CIs; Efron, 1979). Statistics were compared using Fisher's exact test with 100,000 permutations. Differences across latency distributions were estimated using the Kolmogorov–Smirnov distance.

Results

Figure 2 illustrates the baseline size–latency phenomenon for one representative participant (S6),

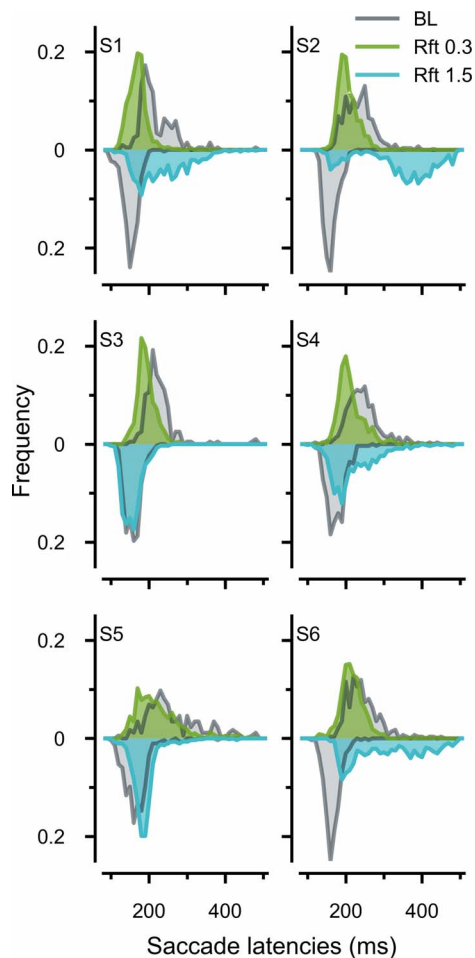


Figure 3. Frequency distributions of saccadic latencies for each participant in the last two sessions of the baseline and reinforcement conditions. The distributions for ratio 0.3 are plotted in the upper part of the graphs. Baseline latency distributions are plotted in light gray, latency distributions in reinforcement are plotted in green. The distributions for ratio 1.5 are plotted in the lower part of the graphs. Baseline latency distributions are plotted in light gray, latency distributions in reinforcement are plotted in blue.

showing that latencies were determined by the combined step-to-size ratio rather than by step amplitudes or target sizes alone. Large median differences between the ratios 0.3 and 1.5 (Figure 2A, green and blue—respectively, 237 and 164 ms) cannot be explained by differences in either amplitude steps or target sizes: Median latencies are clustered according to the step-to-size ratio used. Latency distributions merged across all ring sizes also show a remarkable segregation of latencies beyond the medians based on the step-to-size ratio (Figure 2B).

The size–latency phenomenon was replicated strongly in the baseline sessions of all participants. Baseline distributions from the last two sessions for each participant are plotted in light gray in Figure 3,

	Baseline (ms)	Reinforcement (ms)	Δ (ms)	KS	<i>p</i> value
Ratio 0.3					
S1	204	169	–35	0.63	<0.0001
S2	234	201	–33	0.41	<0.0001
S3	218	189	–29	0.49	<0.0001
S4	240	205	–35	0.4	<0.0001
S5	242	210	–32	0.29	<0.0001
S6	237	214	–23	0.3	<0.0001
Mean	229	198	–31		
Ratio 1.5					
S1	152	223	+71	0.73	<0.0001
S2	158	365	+207	0.84	<0.0001
S3	157	154	–3	0.1	0.0349
S4	173	204	+31	0.41	<0.0001
S5	164	185	+21	0.35	<0.0001
S6	164	286	+122	0.82	<0.0001
Mean	161	236	+75		

Table 2. Median latencies for ratios 0.3 and 1.5 in baseline and reinforcement for all participants, with the difference in median latencies and the Kolmogorov–Smirnov distance (KS). The last line shows the mean values and mean differences for each condition.

where the frequencies for the ratios 0.3 and 1.5 are represented upward and downward on the *y*-axis, respectively. First, we retrieved for all participants the size–latency effect, finding differences of 52, 76, 61, 67, 78, and 73 ms in median latencies (all values greater than the null-hypothesis 98% CIs) between ratios 0.3 and 1.5 for participants S1–S6, respectively. We used the Kolmogorov–Smirnov distance (KS) to individually assess the differences in distributions: When $KS = 1$, there is no overlap between the two cumulative curves; when $KS = 0$, the overlap is complete between the two saccadic-latency distributions. The latency differences between both ratios were all significant across participants ($KS = 0.86, 0.82, 0.86, 0.78, 0.78$, and 0.87 for participants S1–S6, respectively; all $ps < 0.0001$).

Our key result is how reinforcement shifts the distributions in opposite directions for each ratio (Figure 3; gray vs. green: 0.3 ratio; gray vs. blue: 1.5 ratio). Most interestingly, for ratio 0.3 the latency distributions strongly shifted toward shorter values when shorter latencies were reinforced in comparison to the baseline ones (mean latency decrease = 31 ms; all values greater than the null-hypothesis 98% CIs; mean $KS = 0.42$; all $ps < 0.0001$; see Table 2). When long latencies were favored for ratio 1.5, the distributions shifted toward longer values for 5 out of 6 participants (mean latency increase for these participants = +90 ms; see Table 2); S3 did not change at our significance level (latency difference = –3 ms value within the null-hypothesis 98% CI; $KS = 0.1$; $p = 0.0349$; see Table 2).

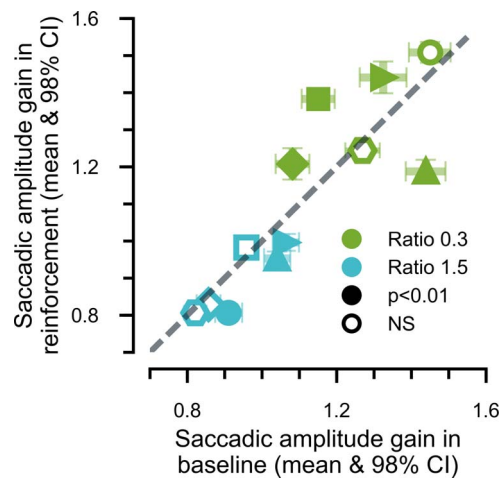


Figure 4. Mean saccadic-amplitude gain in the last two reinforcement sessions as a function of the mean saccadic-amplitude gain in the last two baseline sessions for ratios 0.3 (green) and 1.5 (blue) for each participant. Each data-point shape represents an individual participant. The bootstrap 98% confidence intervals are shown for both the baseline and reinforcement means. The dashed line represents the equality line.

It is noteworthy that the learning patterns across conditions and participants were idiosyncratic: Abrupt changes and progressive transitions were observed. Overall, reinforcing longer or shorter saccadic latencies strongly affected the distributions.

Furthermore, we checked whether the changes in saccadic latencies could be explained by changes in saccadic amplitudes between the baseline and reinforcement sessions. Figure 4 plots the saccadic-amplitude gain in reinforcement as a function of the saccadic-amplitude gain in baseline for both ratios and across participants. Although there is a difference in amplitude gain between ratios 0.3 and 1.5, we observed no consistent changes between baseline and reinforcement sessions which could explain the changes observed in latencies. Note that the overshooting in baseline and reinforcement sessions to the 0.3 ratio and undershooting to the 1.5 ratio are compatible with the range effect typically seen for smaller versus larger target steps, as seen in the consistent negative correlations between amplitude gain and target step: -0.59 , -0.41 , -0.51 , -0.42 , -0.48 , and -0.54 for participants S1–S6, respectively (all $ps < 0.0001$). Correlations between amplitude gain and target size were more limited and inconsistent: 0.27 , 0.20 , -0.10 , 0.09 , 0.09 , and 0.16 (all $ps < 0.0001$). Finally, we did not observe any consistent change in peak velocities across conditions and participants.

Discussion

In the current article, we aimed at experimentally probing whether the size–latency phenomenon (Madelain et al., 2005; Harwood et al., 2008; De Vries et al., 2016) could be explained by a cost–benefit relationship. First, the present study further reports the large and systematic difference in saccadic latencies depending on the step-to-size ratio (averaging 68 ms in our data). Second, saccadic-latency distributions considerably changed as a function of reinforcement contingencies, as we were able to reduce the size–latency phenomenon simply by reinforcing specific latencies.

One could postulate that the increase in latencies in the size–latency phenomenon could be explained by the increased object size, thereby leading to greater uncertainty about the exact location of an object’s center, as pointed out by De Vries et al. (2016). Indeed, perhaps our observed overshooting here of the target center in the ratio-0.3 condition is indicative of greater difficulty in targeting the center. However, as shown in Table 1, we used similar target diameters and steps for both ratios, which means that we cannot explain the latency differences by the sole use of one of these parameters. Therefore, the uncertainty about the exact location of an object’s center cannot be invoked to explain the increased latencies at ratio 0.3. The difference in amplitude gain between ratios 0.3 and 1.5 could be well accounted for by the range effect (Kapoula & Robinson, 1986), as shown by the strong correlations found between amplitude gain and the target step. Therefore, although latencies could not simply be explained by target size or eccentricity, the larger amplitude gains for ratio 0.3 were well accounted for by the typical overshoot of near targets.

Our proposed explanation for the size–latency phenomenon is functional. Indeed, it has been well established that saccades are an operant behavior, that is, a response that depends on its consequences (for a review, see Madelain, Paeye & Darcheville, 2011). Harwood et al. (2008) pointed out that delaying a saccade might be a way of prioritizing actions. While the benefit of executing a saccade is the enhancement of visual details at the target location, it also comes at a cost, as it leads to a temporary impairment of vision. Therefore, saccade triggering might be regarded as resulting from a trade-off between foveating an object of interest and temporarily sacrificing vision. For a small object in the far periphery, the benefit of making a saccade might outweigh the vision impairment, whereas for large objects close to fixation the benefit of making a saccade is limited. In this latter case, the cost might be high compared to the benefit, and delaying such saccades may be a way for the saccadic system to prioritize fixation over movement. Deliberately delaying saccades to larger, more proximal targets that can

be seen well defers the cost of visual disruption that occurs both during the saccade and immediately after (Honda, 1989; Binda, Cicchini, Burr, & Morrone, 2009). Importantly, delaying saccades reduces opportunity costs of a more critical target occurring after the system is committed to a nearby choice. Saccade execution has a point of no return around 60 ms before the saccade (e.g., Ludwig, Mildinhall, & Gilchrist, 2007); coupled with refractory periods between saccades (Carpenter, 1988), this creates a significant potential delay between committing to one saccadic choice and being able to refoveate a more valuable target. This has potential survival implications for key visual events.

Explaining saccadic latencies with this functional hypothesis echoes recent studies demonstrating that saccadic-latency distributions are strongly affected by reinforcement contingencies (Madelain et al., 2007; Vullings & Madelain, 2018). By directly manipulating the benefit of saccades using reinforcement, our results support the idea of a cost–benefit evaluation for saccade triggering. Showing that step-to-size ratio can be used to differentially reinforce saccade latencies is indeed an important step in testing whether a cost–benefit evaluation causes the size–latency phenomenon. A failure to find reinforcement specific to step-to-size ratio would have been a direct falsification of the cost–benefit hypothesis. Theories of optimal decision making have cost–benefit evaluations as a central decision-signal component alongside sensory evidence and prior probabilities (Gold & Shadlen, 2001). Our contention is that the size–latency phenomenon arises by modulating sensory evidence and prior choice probabilities by a cost–benefit evaluation of the likely visual benefit from the choice between moving to the eccentric target and deferring the cost of the saccade to acquire information about a target that is offset from the central fovea (Harwood et al., 2008). If a cost–benefit (fixate–move) balance is strongly modulated by relative eccentricity (step-to-size ratio), one would expect this central ratio factor to form a plausible reinforcer even to arbitrary nonvisual reward (e.g., money). Conversely, if instead the effect of ratio operates downstream from the central decision signal, for example as a simple delay of motor preparation in executing a movement to a less precisely defined target, it is unclear why one would then be able to differentially reinforce latencies according to ratio.

The key test of our hypothesis would be to manipulate the informational value of the movement, for example by making postsaccadic visibility of the target dependent on ratio. There is a rich possibility of spatiotemporal parameters that could be chosen as the reinforcer. Rather than speculating on a particular informational parameter, we chose to be conservative in our first step and chose arbitrary financial benefit. If

that had failed to be an effective reinforcer, the cost–benefit hypothesis would have been falsified.

Perhaps because we manipulated an arbitrary reinforcer instead of the visual benefit of saccades, we only greatly reduced the size–latency phenomenon; we did not eliminate it. Our arbitrary reinforcer might have conflicted with our hypothetical visual-perception cost–benefit.

Our financial reinforcer is probably less biologically relevant than the ones obtained in natural settings. Indeed, biological constraints are known to have profound influences on operant conditioning (e.g., Domjan & Galef, 1983). One could postulate that if we had used the postsaccadic ability to extract visual information as a consequence instead of a monetary reinforcer, we would have increased the changes in saccade latencies, as it has been shown that making the visual perception of a target contingent on latencies has a strong and rapid effect on latency distributions (e.g., Montagnini & Chelazzi, 2005). Similar analysis of the reduced effects of nonvisual reinforcers has been discussed before in the contexts of saccade-latency reinforcement (Madelain et al., 2007; Vullings & Madelain, 2018) and reinforcement-induced saccade-gain change (Madelain, Paeye, & Wallman, 2011; Meermeier et al., 2017). Future research should further investigate the effects of using the ability to see an object on saccadic latencies in the context of the size–latency phenomenon.

Delaying saccades as a way to prioritize fixation over movement is an idea that is compatible with other known behavioral phenomena, such as the gap and overlap effects (Saslow, 1967) and the delayed saccades to acquire information in specific preparations (e.g., Meermeier, Gremmler, & Lappe, 2016). At the neurophysiological level this prioritization is also well explained by the recently proposed equilibrium hypothesis (for a related discussion, see Krauzlis, Goffart, & Hafed, 2017). It is interesting, therefore, that the size–latency phenomenon might also parsimoniously explain some past monkey data in a gap paradigm.

Boch et al. (1984) investigated the effect of eccentricity, intensity, and target size on express saccadic latencies with monkeys. Their figure 5 (p. 227) shows what seems to be a rather complex relationship between the size, eccentricity, and latencies: It is hard to define a clear-cut trend. They tested four different eccentricities, and the last data points of the graph are quite interesting: When the target size is the largest (4°), the express saccade latencies are longer for the 1° step (at around 95 ms) and then the 2° step (at around 85 ms), and they finally tend toward an asymptote for the 4° and 8° steps (around 70–65 ms). One could not postulate that this effect is solely due to the target eccentricities, as shorter latencies have been found for the smallest step but with a smaller target size (around

80 ms for the 1° step with a 1° target size). If we transform these data with the step-to-size ratio, we observe the longest latencies for the smallest ratio (95 ms for ratio 0.25), then for the intermediate one (85 ms for ratio 0.5), with the shortest latencies for ratios above 1 (70 and 65 ms for ratios 1 and 2, respectively). Therefore, the difference in latencies obtained with the 1° step (e.g., 95 vs. 80 ms) could be explained by the step-to-size ratio (0.25 vs. 1). It is noteworthy that the size–latency phenomenon can be observed in other articles and species, but also with express saccades.

Conclusions

We found that the size–latency phenomenon, in which saccade latencies increase when the step-to-size ratio is small, is robust but can be strongly affected by reinforcement contingencies. These results are consistent with a hypothetical cost–benefit sensitivity used by the saccadic system to control saccade triggering. We proposed that delaying saccades might be viewed as a way to prioritize fixation over movement, an idea that is compatible with other known behavioral phenomena and neurophysiological models of saccade latencies. It may be crucial to further unravel the origins of the remarkable adaptability of saccadic reaction times to environmental constraints in order to better understand the underlying process of movement triggering.

Keywords: saccade, size–latency phenomenon, reinforcement

Acknowledgments

This research was supported by Agence Nationale de Recherche Grant ANR-13-APPR-008 (LM), National Science Foundation Grant NSF:1232654 (MRH), and a scholarship from the French Ministry of Research (CV).

Commercial relationships: none.

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References

- Balsdon, T., Schweitzer, R., Watson, T. L., & Rolfs, M. (2018). All is not lost: Post-saccadic contributions to the perceptual omission of intra-saccadic streaks. *Consciousness and Cognition*, *64*, 1–13, <https://doi.org/10.1016/j.concog.2018.05.004>.
- Binda, P., Cicchini, G. M., Burr, D. C., & Morrone, M. C. (2009). Spatiotemporal distortions of visual perception at the time of saccades. *The Journal of Neuroscience*, *29*(42), 13147–13157.
- Boch, R., Fischer, B., & Ramsperger, E. (1984). Express-saccades of the monkey: Reaction times versus intensity, size, duration and eccentricity of their targets. *Experimental Brain Research*, *55*, 223–231.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.
- Carpenter, R. H. S. (1988). *Movements of the eyes* (2nd ed.). London, UK: Pion.
- Castet, E., & Masson, G. S. (2000). Motion perception during saccadic eye movements. *Nature Neuroscience*, *3*(2), 177–183, <https://doi.org/10.1038/72124>.
- De Vries, J. P., Azadi, R., & Harwood, M. R. (2016). The saccadic size-latency phenomenon explored: Proximal target size is a determining factor in the saccade latency. *Vision Research*, *129*, 87–97, <https://doi.org/10.1016/j.visres.2016.09.006>.
- Dick, S., Ostendorf, F., Kraft, A., & Ploner, C. J. (2004). Saccades to spatially extended targets: The role of eccentricity. *NeuroReport*, *15*(3), 453–456.
- Domjan, M., & Galef, B. G. (1983). Biological constraints on instrumental and classical conditioning: Retrospect and prospect. *Animal Learning & Behavior*, *11*(2), 151–161.
- Efron, B. (1979). Bootstrap methods: Another look at the jackknife. *The Annals of Statistics*, *7*, 1–26.
- Gold, J. I., & Shadlen, M. N. (2001). Neural computations that underlie decisions about sensory stimuli. *Trends in Cognitive Sciences*, *5*(1), 10–16.
- Harris, C. M., & Wolpert, D. M. (2006). The main sequence of saccades optimizes speed-accuracy trade-off. *Biological Cybernetics*, *95*(1), 21–29, <https://doi.org/10.1007/s00422-006-0064-x>.
- 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, <https://doi.org/10.1152/jn.00589.2007>.
- Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics*, *45*(2), 162–174.
- Kalesnykas, R. P., & Hallett, P. E. (1994). Saccades and the latency of eye saccades. *Vision Research*, *34*(4), 517–531, [https://doi.org/10.1016/0042-6989\(94\)90165-1](https://doi.org/10.1016/0042-6989(94)90165-1).

- Kalesnykas, R. P., & Hallett, P. E. (1996). Fixation conditions, the foveola and saccadic latency. *Vision Research*, *36*(19), 3195–3203.
- Kapoula, Z., & Robinson, D. A. (1986). Saccadic undershoot is not inevitable: Saccades can be accurate. *Vision Research*, *26*(5), 735–743.
- Kowler, E., & Blaser, E. (1995). The accuracy and precision of saccades to small and large targets. *Vision Research*, *35*(12), 1741–1754.
- Krauzlis, R. J., Goffart, L., & Hafed, Z. M. (2017). Neuronal control of fixation and fixational eye movements. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1718):20160205.
- Ludwig, C. J., Mildinhall, J. W., & Gilchrist, I. D. (2007). A population coding account for systematic variation in saccadic dead time. *Journal of Neurophysiology*, *97*(1), 795–805.
- Madelain, L., Champrenaut, L., & Chauvin, A. (2007). Control of sensorimotor variability by consequences. *Journal of Neurophysiology*, *98*(4), 2255–2265, <https://doi.org/10.1152/jn.01286.2006>.
- Madelain, L., Krauzlis, R. J., & Wallman, J. (2005). Spatial deployment of attention influences both saccadic and pursuit tracking. *Vision Research*, *45*, 2685–2703, <https://doi.org/10.1016/j.visres.2005.05.009>.
- Madelain, L., Paeye, C., & Darcheville, J.-C. (2011). Operant control of human eye movements. *Behavioural Processes*, *87*(1), 142–148, <https://doi.org/10.1016/j.beproc.2011.02.009>.
- Madelain, L., Paeye, C., & Wallman, J. (2011). Modification of saccadic gain by reinforcement. *Journal of Neurophysiology*, *109*, 219–232, <https://doi.org/10.1152/jn.01094.2009>.
- Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin*, *81*(12), 899–917.
- McGowan, J. W., Kowler, E., Sharma, A., & Chubb, C. (1998). Saccadic localization of random dot targets. *Vision Research*, *38*(6), 895–909.
- Meermeier, A., Gremmler, S., & Lappe, M. (2016). The influence of image content on oculomotor plasticity. *Journal of Vision*, *16*(8):17, 1–12, <http://doi.org/10.1167/16.8.17>. [PubMed] [Article]
- Meermeier, A., Svenja, G., Richert, K., Eckermann, T., & Lappe, M. (2017). The reward of seeing: Different types of visual reward and their ability to modify oculomotor learning. *Journal of Vision*, *17*(12):11, 1–13, <http://doi.org/10.1167/17.12.11>. [PubMed] [Article]
- Montagnini, A., & Chelazzi, L. (2005). The urgency to look: Prompt saccades to the benefit of perception. *Vision Research*, *45*(27), 3391–3401, <https://doi.org/10.1016/j.visres.2005.07.013>.
- 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*(1), 237–242, <https://doi.org/10.1037/0735-7044.118.1.237>.
- 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*(8), 1024–1029.
- Sumner, P. (2011). Determinants of saccade latency. In S. P. Liversedge, I. D. Gilchrist, & S. Everling (Eds.), *The Oxford handbook of eye movements* (pp. 413–424). New York: Oxford University Press.
- Vullings, C., & Madelain, L. (2018). Control of saccadic latency in a dynamic environment: Allocation of saccades in time follows the matching law. *Journal of Neurophysiology*, *119*, 413–421, <https://doi.org/10.1152/jn.00634.2017>.
- Wyman, D., & Steinman, R. (1973). Latency characteristics of small saccades. *Vision Research*, *13*, 2173–2175.