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Saccadic latencies depend on functional relations with the environment

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Cécile VULLINGS

THESE
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Pr. Laurent MADELAIN

Composition du Jury :
Pr. Thérèse COLLINS, Université Paris-Descartes (Examinateur)
Dr. Casimir LUDWIG, University of Bristol (Examinateur)
Dr. Armando MACHADO, Universidade do Minho (Rapporteur)
Pr. Laurent MADELAIN, Université de Lille (Directeur)
Dr. Anna MONTAGNINI, Institut de Neurosciences de la Timone (Rapporteur)

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ABSTRACT

Conventional decision models, based on the saccadic system as a sensorimotor model, typically view reaction time as a byproduct of decisional processes, reflecting the time needed to make a decision. However, research has shown that saccadic latencies are twice as long as the decision time and that the organization of the environment affects saccade latencies. This thesis dissertation provides an alternative view of saccadic reaction times (SRTs) by showing that saccade latency distribution can be altered by their own consequences. We defend that saccadic latency depends on functional relations with its environment.

This thesis conducted a functional analysis of saccadic latencies. The first study probed whether it is possible to choose one's latencies depending on the reinforcement contingencies in force, in order to assess the extent of temporal control with saccades. The allocation of short and long latencies matched the relative reinforcement obtained, demonstrating a fine control of SRTs. The second study further investigated the effect of beneficial consequences on SRTs, using the size-latency phenomenon. The reinforcement procedure was effective in manipulating the benefit of shorter SRTs and reducing the size-latency phenomenon. The third experiment demonstrated how antecedent stimuli come to control specific reaction times through operant learning. Reinforcement contingencies induced discriminative control of latencies between different stimuli. Finally, the last experiment explored the involvement of classical learning processes in stimulus control of saccade latencies. This pilot study highlighted the influence of the environment and learning history in the temporal control of saccades.

Our results emphasize the exquisite plasticity of the saccadic system, and extend it to the temporal control of saccades. This thesis shows that a general learning process, based on the functional consequences of saccades, can parsimoniously explain changes in saccadic latency. Demonstrating that latency is an operant dimension of saccades, the organization of the environment controls the temporal organization of saccades.

Keywords: latency, saccade, temporal control, decision, operant learning, classical conditioning

RÉSUMÉ

Les modèles de décision conventionnels, basés sur l'utilisation du système saccadique comme modèle sensorimoteur, considèrent typiquement les temps de réaction comme un sous-produit des processus décisionnels, reflétant le temps nécessaire pour prendre une décision. Cependant, des recherches ont montré que les latences saccadiques sont deux fois plus longues que le temps de décision, ainsi que l'organisation de l'environnement affecte les latences saccadiques. Cette thèse propose une interprétation alternative des temps de réaction saccadiques (SRTs) en montrant que les distributions de latences saccadiques peuvent être altérées par leurs propres conséquences. Nous défendons l'hypothèse que les latences saccadiques dépendent de relations fonctionnelles avec leur environnement.

Cette thèse a réalisé une analyse fonctionnelle des latences saccadiques. La première étude a évalué s'il était possible de choisir ses propres latences en fonction des contingences de renforcement en cours, dans le but d'explorer l'étendue du contrôle temporel des saccades. L'allocation des latences courtes et longues correspondait au renforcement relativement obtenu, démontrant un contrôle fin des SRTs. La seconde étude a évalué de manière plus approfondie l'effet de conséquences bénéfiques sur les SRTs, en utilisant le phénomène de taille-latence. La procédure de renforcement a été efficace pour manipuler le bénéfice de SRTs plus courts et pour réduire le phénomène de taille-latence. La troisième étude a démontré comment les stimuli antécédents en viennent à contrôler des temps de réaction spécifiques à l'aide d'un apprentissage opérant. Les contingences de renforcement ont induit un contrôle discriminatif des latences entre des stimuli différents. Enfin, la dernière expérience a exploré l'implication des processus d'apprentissage classique dans le contrôle par le stimulus des latences saccadiques. Cette étude pilote met en évidence l'influence de l'environnement et de l'historique d'apprentissage dans le contrôle temporel des saccades.

Nos résultats soulignent l'incroyable plasticité du système saccadique, et l'étend au contrôle temporel des saccades. Cette thèse montre qu'un processus général d'apprentissage, basé sur les conséquences fonctionnelles des saccades, peut expliquer de manière parcimonieuse les changements dans les latences saccadiques. Démontrant que la latence est une dimension opérante des saccades, l'organisation de l'environnement contrôle l'organisation temporelle des saccades.

Mots-clés : latence, saccade, contrôle temporel, décision, apprentissage opérant, conditionnement classique

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ABBREVIATIONS

AFC: Alternative Forced Choice
AMD: Age-related Macular Degeneration
AO: Abolishing Operation
CI: Confidence Interval
COD: Change-Over Delay
CR: Conditional Response
CRF: Continuous Reinforcement
CS: Conditional Stimulus
DRL: Differential Reinforcement of Low-rate
EO: Establishing Operation
ERP: Event-Related Potential
FEF: Frontal Eye Field
FI: Fixed Interval
FR: Fixed Ratio
IRT: Inter-Response Time
KS: Kolmogorov-Smirnov
LATER: Linear Approach to Thresholds with Ergodic Rate
MRT: Manual Reaction Time
NS: Neutral Stimulus
OKR: Opto-Kinetic Reflex
RI: Random Interval
SC: Superior Colliculus
SD: Standard Deviation
SOA: Stimulus-Onset-Asynchrony
SRT: Saccadic Reaction Time
UR: Unconditional Response
US: Unconditional Stimulus
VOR: Vestibulo-Ocular Reflex

PREFACE

How does the environment control the temporal organization of behaviors? This is the broader question this thesis tries to address. Because the world we live in is dynamic and continuously changing, most organisms need to learn to regulate their behavior in time, whether it is to find food, light or information, or to avoid predators. One must decide when to behave as much as where to.

The present work, using the saccadic system as a sensorimotor model, demonstrates that one learns and uses the temporal properties of one's environment to interact with it. The first part of this dissertation will present how saccade latencies are typically used to quantitatively study the decision-making processes involved in this interaction (chapter 1). We will see that if the conventional decision models regard saccadic reaction times as a byproduct resulting from accumulation of visual information, this is not the case according to the behavior analysis theory. Our main hypothesis is that saccadic latencies depend on their functional relationship with the environment. The second part of this thesis will therefore review theoretical and empirical data supporting the functional analysis of oculomotor control and saccadic latencies (chapter 2).

Our interpretation regarding a functional control of saccadic latencies will be supported by the experimental contribution of this thesis. Using classical techniques of reinforcement, we have conducted a functional analysis of reaction times through four experimental studies, supporting the alteration and control of saccade latencies by reinforcement contingencies. The first study probes the possibility of choosing one's latencies in experimental conditions favoring defined reaction times (chapter 3). This research, assessing the extent of control over latencies, goes against classical interpretation of reaction times postulating that it is not possible to produce a bimodal distribution of short and long latencies in a given experimental condition. The second study aims at demonstrating the essential effect of beneficial consequences on saccadic reaction times (chapter 4). This research enabled to alter a strong effect caused by an antecedent stimulus thanks to the use of reinforcement contingencies. Finally, the third and fourth studies investigate how antecedent stimuli come to control saccadic latencies through instrumental (chapter 5) and classical (chapter 6) conditioning. Stimulus control over specific latencies was observed and maintained, even when the reinforcement contingencies were withdrawn.

Since the manipulations of the antecedents and consequences of eye movements have been effective in changing the temporal properties of saccades, these four studies demonstrate the functional role of these consequences in oculomotor learning. More specifically, saccadic latencies appear to be dependent on their functional relationships (chapter 7). Thus, these studies suggest that this learning is based on the same principles as those governing other operant behaviors. This thesis shows that the organization of the environment constrains the temporal, and not only the spatial, allocation of behaviors.

Concepts & Theoretical Framework

Chapter 1:

Saccadic eye movements and decision

This chapter will succinctly address some main characteristics of the saccadic system. In a first part, we will briefly review the human vision, then we will focus on one type of eye movements in particular, the saccades, and their involvement in the decision field.

1.1. Vision: a selective review

1.1.1. The visual field and visual perception

A large majority of animal species, around 95%, have eyes (Land & Nilsson, 2012), revealing the evolutionist advantage of having eyes in many environments. For more than half a billion years, the ocular system has been differentially shaped through natural selection and not all animal eyes are identical (Krauzlis, 2008; Land & Nilsson, 2012). Human and other primate eyes are characterized by a cornea and a lens that concentrate and project rays of light to a layer of photosensitive cells located at the bottom of the eye: the retina (Land & Nilsson, 2012). The retina is then responsible for translating the differences in the wavelengths of light (i.e., colors), the contrast and the luminance into a biological signal, which is transmitted to the visual cortex by the optic nerve and the neuronal pathways.

The binocular human visual field extends to about 220° horizontally and 135° vertically (Snowden, Thompson, & Troscianko, 2012). However, the level of perceived details is not homogeneous along the visual field: the ability to discriminate a single isolated letter falls in a linear manner from 100% at 3° from fixation to 50% at 10° (Gilchrist, 2011). It is noteworthy that, if the target letter is flanked by two other letters, the performance is already impaired at 1° with just 80% and it drops to 35% at 3° (Bouma, 1970). The quality of visual information depends on where it is projected on the retina. About 94% of the photosensitive cells of the eye are rods and about 6% are cones. The rods do not require a lot of light to work but only provide a blurred and drab image of our environment; they are responsible for low spatial acuity. Human eyes are equipped with cones for a more detailed and clear vision. There are three varieties of cones: those sensitive to short (i.e., blue), medium (i.e., green), and long (i.e., red) wavelengths. They are very effective at providing a clear picture but require higher light levels to work; they are responsible for high spatial acuity. This is the reason why one loses one's ability to see colors when it is dark: in this instance the rods, requiring lower light levels, are mainly used to record the visual information, which then produces a gray scale image. The cones are mostly concentrated in the fovea, providing a clear and bright retinal image of the environment in this region. The portion of the visual field processed by the fovea (i.e., high density of cones), called the foveal visual field, is an area with a slightly irregular shape with a diameter of about 1-2°. This full color area represents the width of your thumb when you stretch your arm in front of you, with your thumb up. Throughout the rest of the visual field (i.e., the peripheral visual field), the image we perceive is blurred, and as a result, it is more difficult to interpret and discriminate in detail.

In addition to having a very limited visual field, our eyes are rather slow at recording changes in the visual environment, compared to the refresh rates of recent computer screens. Indeed, the light sensors in the eyes, the photoreceptors, need to be stimulated continuously for about 20ms in order to give a decent response (Land & Nilsson, 2012). The ability to encode an image depends both on its complexity and the light intensity. The eye works as a camera: a picture taken in a poorly lit room will be blurred and non accurate as opposed to one taken outside in the daylight. The eye also needs time for an image to disappear from the retina, which again depends on the intensity of the light. This phenomenon is called visual persistence and can last up to 100ms (Bowen, Pola, & Matin, 1974). Because of these mechanisms, the visual perception is very variable and research has shown that one can get the gist of complex visual scene within 150ms (e.g., also termed superstitious behaviors Rayner, Smith, Malcolm, & Henderson, 2009), even if the stimulus duration lasts around 10ms (Bachmann & Allik, 1976; Hegdé, 2008). In these experimental settings, although the behavioral response is only seen 150ms after the stimulus onset, the average event-related potential (ERP) responses show that the stimulus is quickly categorized, within 75-80ms (VanRullen & Thorpe, 2001). In the instance of more simple stimuli, the visual processing is even quicker: the visual information required for reading can be gathered in 50-70ms (Ishida & Ikeda, 1989; Rayner, Inhoff, Morrison, Slowiaczek, & Bertera, 1981). The aforementioned studies focused on how the visual cortex encodes the visual input from a single fixation, however because the visual field is wider and the point of best visual acuity (the fovea) is quite small, one has to orient one's eyes to explore one's visual environment.

1.1.2. Eye movements

Although the fovea represents a small part of the visual field (less than 1%), the visual information it encodes represents around 10% of what is sent to the visual cortex through the optical nerve (van Essen & Anderson, 1995), as the peripheral vision has a low acuity and is rather specialized for detecting movements and contrasts. Thus, the origin of eye movements comes from the necessity to place a visual target on the fovea in order to see the stimulus with details (Walls, 1962). Indeed, there are two ways to scan our visual surroundings: either moving our head and body, or moving our eyes. The former is the perfect option when one has to see what is happening behind oneself. However, the latter is more efficient when the face is oriented toward the portion of the environment to be explored –which is usually the case in the daily coordination between vision and motor tasks. The human eyeball can have three different movements thanks to six oculomotor muscles: the superior rectus and the inferior rectus –responsible for movements in the horizontal axis, the lateral rectus and medial rectus –responsible for the vertical axis, and the superior oblique and inferior oblique –responsible for the torsional movements. The eye movements have two main functions that are to 1) place the information of interest on the fovea (Walls, 1962), and 2) stabilize the retinal image on the fovea (Dubois & Collewijn, 1979). The evolution has shaped several eye movements (Krauzlis, 2008); some are reflexes and correspond to the second function such as the vestibulo-ocular reflex (VOR) and the opto-kinetic reflex (OKR), while others are voluntary and related to the first function such as the smooth pursuit or saccade.

The VOR and OKR are both reflexes that aim at stabilizing the retinal image on the fovea (Figure 1). If the eyes were immobile in their eyeballs, the smallest movement in our body or the environment would produce a blurred image. Indeed, the photoreceptors would not be stimulated with the same visual image for at least 20ms and a degraded vision would result from it. To prevent this situation, the eyes need to move as a function of the head movement or the stimulus displacements. The VOR deals with head movement thanks to the vestibular system, which is sensitive to rotations and accelerations. Each rotation of the head is automatically compensated by an eye movement in the opposite direction with the same speed and a latency shorter than 12ms (Hess, 2011); as a result, the image of the environment remains at the same location on the retina. This reflex is the reason why one can shake one's head and still read a word. The OKR completes the former reflex in that it also serves visual stability. The function of the OKR is to follow the environment when it is slowly moving, whether it is entirely or a large portion of the visual field. This reflex is the reason why one can still read while moving a book in a sinusoidal fashion at a slow speed.

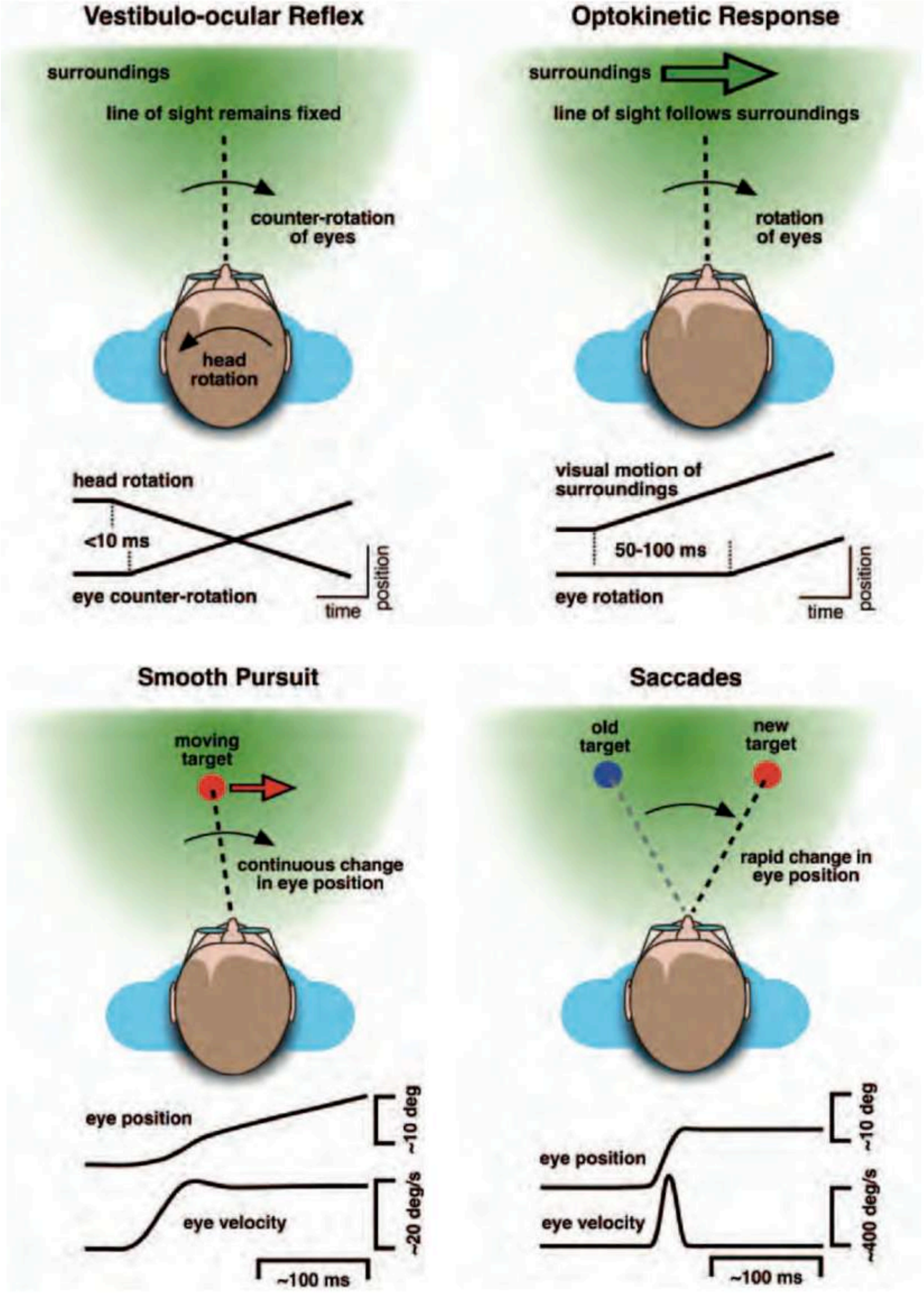

Figure 1: From Krauzlis (2008). The upper panel represents eye movements that stabilize gaze. The vestibulo-ocular reflex keeps the line of sight fixed in the world by counter-rotating the eyes during movements of the head. Here, the eyes rotate rightward at a short latency after the beginning of the leftward head movement. The optokinetic response stabilizes the line of sight with respect to the moving visual surround, but does so after a longer latency. The lower panel represents eye movements that shift gaze. Smooth pursuit continuously changes the line of sight to minimize blurring of the target's retinal image. These movements are characterized by smooth and continuous changes in eye position involving low eye velocities. Saccades shift the line of sight to place the retinal image of visual targets onto the fovea. They are characterized by rapid changes in eye position involving very high eye velocities.

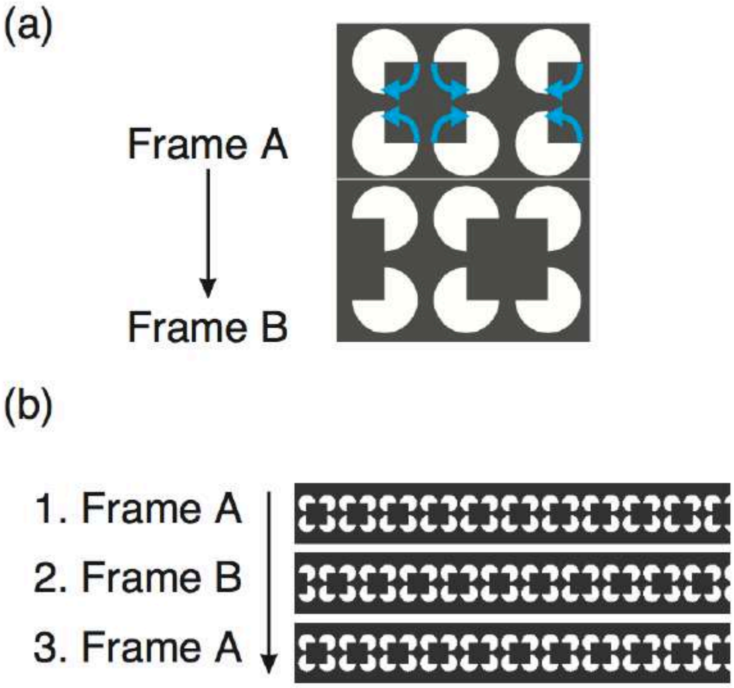

Figure 2: From Madelain & Krauzlis (2003b). (a) Illustration of the visual stimuli used to induce the apparent motion of an illusory square. The transition from frame A to frame B is accomplished by rotating the circular inducers by ±90°, as illustrated by the blue arrows. (b) The alternation of frames A and B induces bi-directional apparent motion of the illusory contours.

Smooth pursuit is an eye movement that resembles tremendously the OKR, as it happens when the eyes are following a slowly moving object (e.g., a bird in the sky; Figure 1). Smooth pursuit uses an object as a reference and tries to maintain its retinal image in the foveal vision by matching the target speed up to 90°/s and has a latency around 100-130ms (Barnes, 2011). This voluntary eye movement provides crucial support for vision by minimizing motion blur that would otherwise impair visual perception. This response is voluntary in that one can choose to follow or ignore the moving target. However, it is difficult to initiate ocular pursuit without a moving object (yet, it has been done through extensive training using auditory reinforcement; Madelain & Krauzlis, 2003a). Interestingly, smooth pursuit can be guided by not only the physical motion of a moving object but also by the perceived motion (Spering & Montagnini, 2011). Madelain and Krauzlis (2003b) used an illusory stimulus consisting of juxtaposed and rotating Kanizsa squares (Figure 2) which produced an apparent horizontal motion of the squares and observed that participants were able to smoothly track the illusory motion in the absence of a physical movement. Therefore, it would seem that smooth pursuit might not be initiated because of the displacement of the retinal object but by its functional perceptual consequences (Madelain, Paeye, & Darcheville, 2011). Finally, if the object moves too quickly, the eye makes catch-up saccades.

Saccades enable a quick exploration of the environment, as they are discrete rapid eye movements between two fixations that relocates the fovea in an abrupt way. The eyeball is quite mobile and making frequent (up to 3 saccades per second) and fast (tens of milliseconds) movements holds a relatively low metabolic cost, which is strongly balanced by the minimization of inter-fixation time and the maximization of the amount of fixated locations (and therefore information gathered). Although saccadic eye movements are often triggered by visual stimuli within 150-250ms, they do not exclusively require a visual stimulus and can be guided by other modalities (e.g., auditory stimulus; Zambarbieri, Schmid, Magenes, & Prablanc, 1982) or directed toward an imagined or remembered targets (White, Sparks, & Stanford, 1994). Saccades typically occur in series, with a saccade-fixation strategy alternating almost-ballistic saccadic eye movements and fixations (during which the eye is kept at the same location thanks to three types of small fixational eye movements: microsaccade, tremor and drift); this sequence is called a scanpath (Noton & Stark, 1971; Yarbus, 1967; see Figure 3). This strategy enables to gather useful visual information during the fixation and –because visual acuity decreases drastically away from the current gaze direction, saccades are used to relocate the eyes to regions of interest (determined during the fixation, through peripheral vision). A saccadic sampling of the environment appears to be an effective way for the coordination of vision and motor tasks as this eye-movement system has been observed with head movements for birds (Wallman & Letelier, 1993) or patients without the ability to move their eyes (Gilchrist, Brown, Findlay, & Clarke, 1998; Gilchrist, Brown, &

Findlay, 1997), even during daily naturalistic tasks (Land, Furneaux, & Gilchrist, 2002). Since the visual environment contains several possible targets, the saccadic target selection is regarded as an interaction between the visual properties of the stimulus and the goal of the observer (Gilchrist, 2011), which will be discussed further in this thesis (see I.1.2.4. A common sensorimotor model: saccadic decision-making).

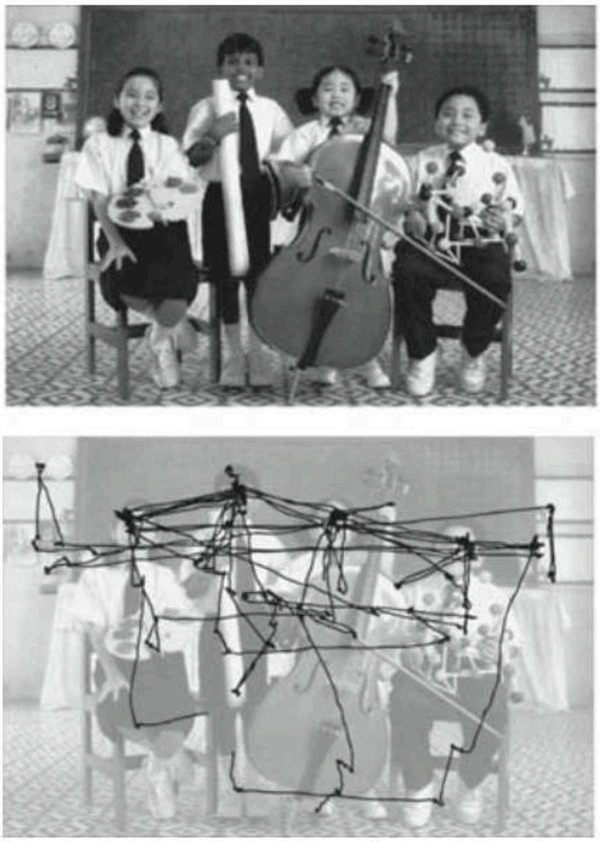

Figure 3: From Martinez-Conde & Macknik (2011). An observer views a picture (top) while eye positions are monitored (bottom). The eyes jump, seem to fixate or rest momentarily, producing a small dot on the race, then jump to a new region of interest. The large jumps in eye position illustrate saccades.

1.2. Saccadic eye movements

1.2.1. Characteristics of saccades: amplitude, duration, peak velocity, latency

During a saccade, the gaze moves from one stationary position to another in a short bout, by going through a quick acceleration and a rapid deceleration, with a high peak in velocity

(Figure 4). This eye displacement is often quantified using four characteristics: the amplitude of the displacement (sometimes represented by the gain, i.e., the ratio of the saccade amplitude divided by the target step amplitude), the duration of the displacement, the peak velocity (i.e., the highest velocity), and the latency (i.e., the time elapsed between the target onset and the saccade onset). Saccadic eye movements are rather stereotypical and tend to have relatively fixed relationships between its parameters across individuals. For instance, the saccade, illustrated in Figure 4, was triggered 129ms after an 8° target step with a duration of 44ms, and within that period, reached a peak velocity of 278°/s. The peak velocity of a saccade is closely related to the amplitude and there is a similar close linear relationship between the amplitude and the duration of saccade (Figure 5) called the "main sequence" (Bahill, Clark, & Stark, 1975), which has been elegantly explained by a computational model assuming a trade-off between the accuracy and the duration of the saccade (Harris & Wolpert, 2006).

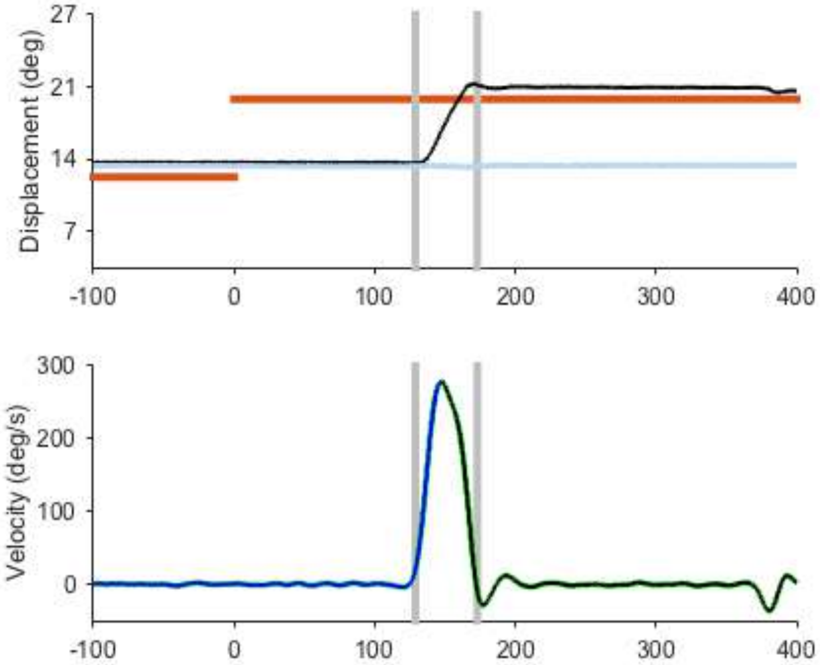

Figure 4: An example saccade of the eye moving 8° to the right. The upper panel represents the horizontal displacement in degrees of the target and the eye. The red lines show the step of the target; the black and blue lines show the horizontal and vertical displacement of the gaze, respectively. The lower panel represents the horizontal velocity of the eye. The gray lines frame the saccadic eye movement.

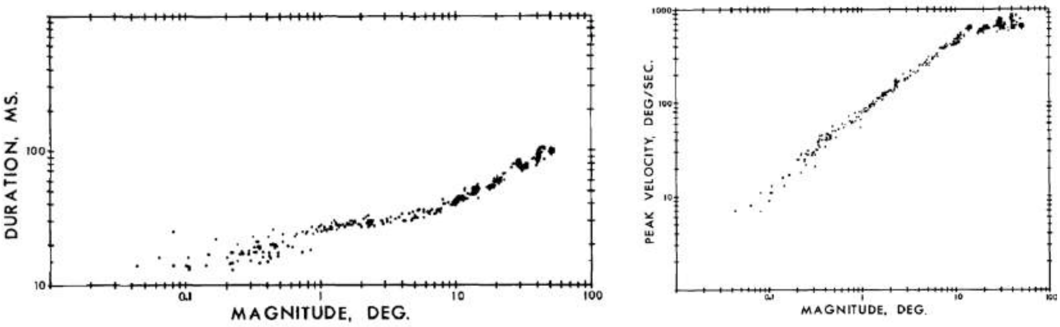

Figure 5: From Bahill et al. (1975). On the left panel, the duration versus magnitude of human saccadic eye movements. On the right panel, the peak velocity versus magnitude of human saccadic eye movements.

Because the gaze moves with a high velocity (up to 500°/s), the vision is impaired and individuals are almost blind during the eye flight, a phenomenon known as saccadic suppression (Matin, 1974; but see Balsdon, Schweitzer, Watson, & Rolfs, 2018; Castet & Masson, 2000). This phenomenon, associated with the loss of vision acuity in the peripheral vision, enables a large range of studies to use gaze-contingent paradigm where the display depends on the eye movements or to change some information in the display during the eye flight without the participant noticing it. From all of these saccadic dimensions, the latency (also known as reaction time) is maybe the most widely used variable. For a given target step, the duration, velocity and amplitude tend to be almost fixed whereas the latency is very variable at a trial-by-trial level. Depending on factors that will be discussed below, the latency can range from less than 100ms to 1000ms (Gilchrist, 2011). The saccadic latency distribution has a distinctive form: it is skewed, with a long tail for longer latency saccades (Figure 6). Also, the distribution is usually unimodal, but it is possible to observe another mode for shorter latencies, which have been termed express saccades (Fischer et al., 1993). Most studies, whether it is for saccade or manual reaction times, use the mean latency to describe the central tendency of reaction times and the standard deviation to illustrate the variability (Whelan, 2008). However, these statistics are not the most appropriate for capturing and describing the behaviors, as the saccadic latency distribution is not Gaussian. In this thesis work, because we will conduct our analysis on large number of trials (Miller, 1988), we will use the median and quartiles of the distributions in addition to show the shapes of the distributions.

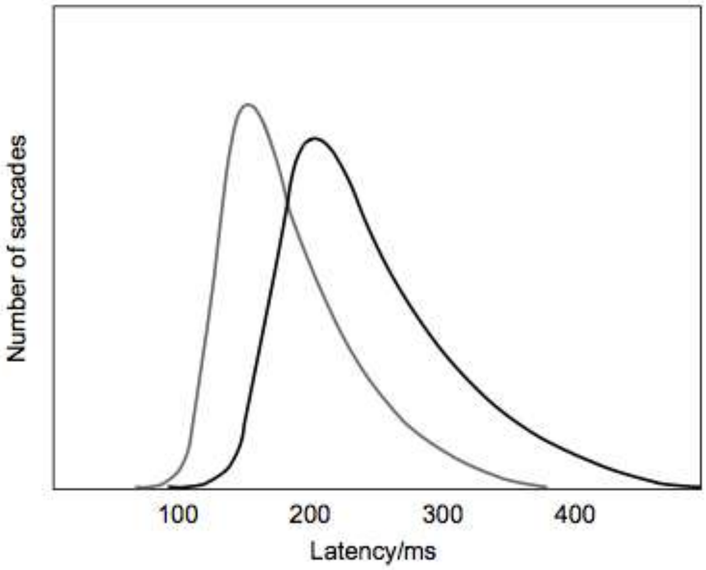

Figure 6: From Sumner (2011). The typical distribution of saccadic latencies. The two distributions represent a practiced (in gray) and a novice (in black) participants making saccades to simple onset targets. The illustrated distributions differ in their means and variances, but not in shape (skew). Latency distributions with this kind of shape seem to be a fundamental property of most animal response systems.

1.2.2. Determinants of saccade latency: a non-exhaustive review

Because of the variability of saccadic latency distributions, many papers have focused on and investigated the factors that can affect the reaction times. These factors have often been categorized as either bottom-up factors, that is to say effects caused by the properties of the stimuli or its context, or top-down factors, such as goal-oriented saccades or expectation. This section provides a non-exhaustive review of the existing literature on this dichotomy.

Bottom-up factors have been extensively studied for decades, as they constitute a window for understanding how the visual processes work. One of the first factors that have been highlighted is the stimulus intensity. Wheeless, Cohen, and Boynton (1967) conducted a pioneer study manipulating the luminance of the target and its contrast with the background.

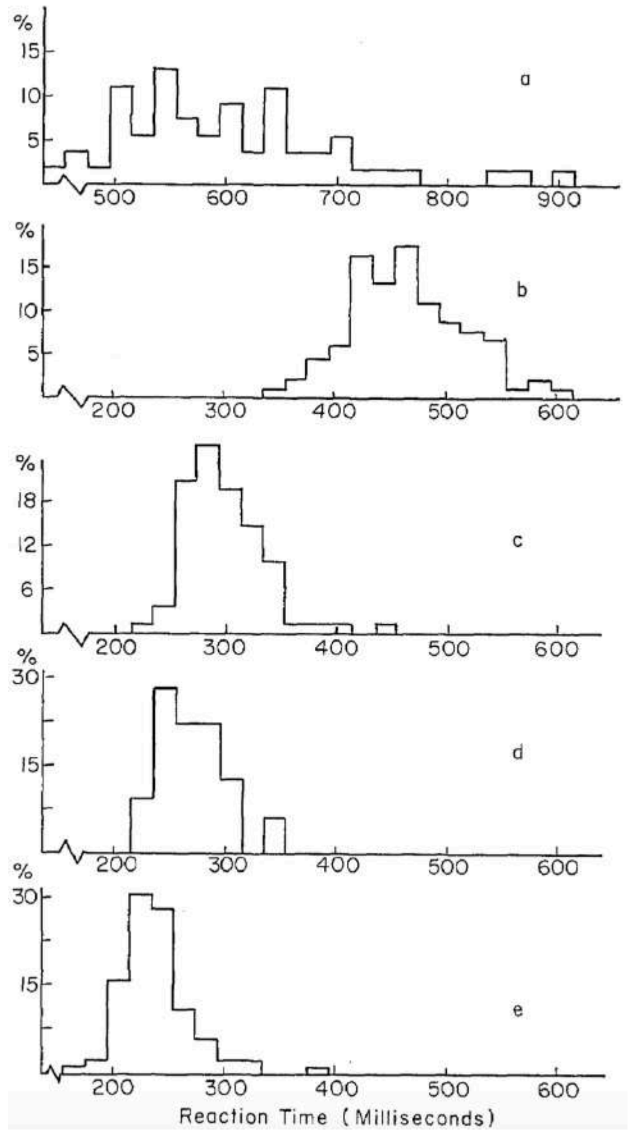

Figure 7: From Wheeless et al. (1967). Histograms of percent occurrence of eye-movement reaction times. (a) Target luminance 1.5 log units below foveal threshold; (b) 1.0 log units below; (c) at foveal threshold; (d) 1.0 log units above; (e) 2.0 log units above. Note that histogram (a) is represented in an abscissa that is shifted to the left with respect to the other four plots.

After determining the foveal threshold (i.e., the minimum amount of luminance increment on a uniform background that can be detected by the individual during fixation), participants had to follow the target step of stimuli with varying luminance in either a high-contrast condition, in which the projection screen was not illuminated, or a low-contrast condition, in which the screen was illuminated with the same luminance as the target. The saccadic latency distributions changed drastically as a function of the luminance: the average reaction time increased up to 600ms for the lowest luminance and decreased down to 250ms with the highest luminance (Figure 7), an outcome that was observed regardless of the contrast condition. Their results were replicated by several studies with humans (e.g., Bell, Meredith, Van Opstal, & Munoz, 2006; Carpenter, 2004; Kalesnykas & Hallett, 1994; Ludwig, Gilchrist, & McSorley, 2004), monkeys (e.g., Boch, Fischer, & Ramsperger, 1984; Marino, Levy, & Munoz, 2015; Marino & Munoz, 2009) and express saccades (e.g., Boch et al., 1984; Marino et al., 2015). Interestingly, Ludwig et al. (2004) observed that the spatial frequency of Gabor patch targets also had an inversely proportional impact on reaction times. The suggested explanation for the decrease in latency as a function of luminance is that stimulus intensity reduces the processing time along the visual pathway (Barbur, Wolf, & Lennie, 1998; Boch et al., 1984).

Another issue emerged around the same time as stimulus intensity about the effect of stimulus temporal organization on saccadic latencies, and more precisely, the impact of a stimulus-onset-asynchrony (SOA). There are two kinds of SOA, either negative or positive. A negative SOA happens when the fixation stimulus is extinguished before the target stimulus onset and causes a gap effect. A positive SOA consists in the target stimulus appearing while the fixation stimulus remains on the screen, causing an overlap effect. Note that the classical step paradigm used to study saccadic latencies has a null SOA, where the fixation stimulus offset happens at the exact same time as the target stimulus onset. Saslow (1967) was the first to use what has been called subsequently the gap and overlap paradigms. He tested sixteen asynchronies from a negative SOA of 400ms to a positive SOA of 350ms with random amplitude and direction steps (4° or 8° and left or right). In comparison to the typical synchrony between the fixation-offset and target-onset (i.e., SOA = 0; step paradigm), triggering saccadic latency around 200ms, the author observed an increase in latency to about 250ms during the overlap and decreased to about 150ms during the gap (Figure 8).

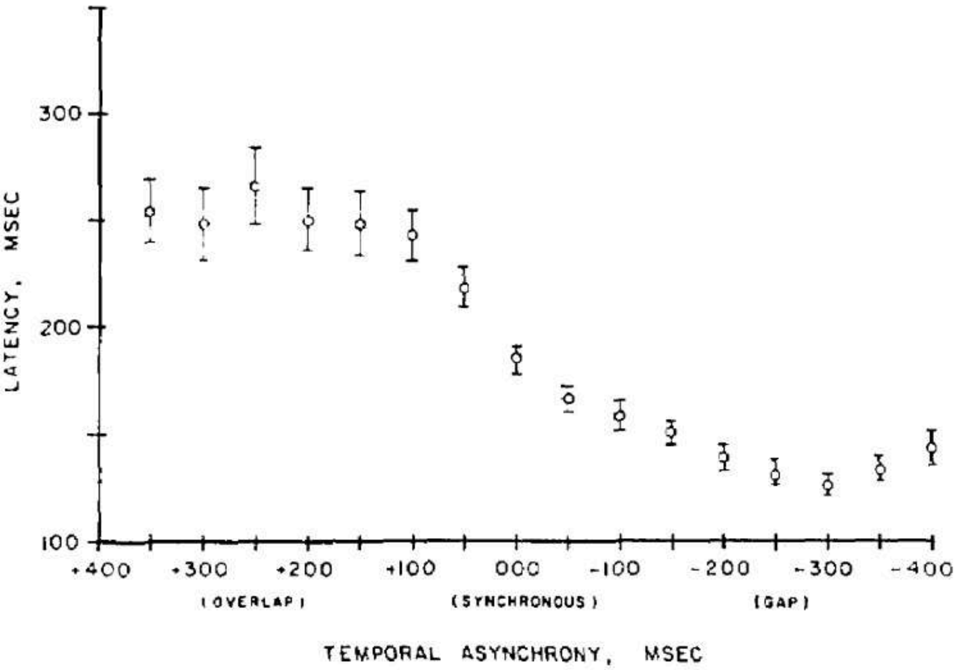

Figure 8: From Saslow (1967). Mean effects plus or minus two standard errors for one participant, 100 observations per mean (locations pooled).

The impact of the gap seemed to be gradual as the SOA got longer whereas the overlap effect seemed to reach an asymptote after 100ms; it was recently confirmed that this asymptote is reached around 140ms by a parametrically series of experiments manipulating the durations, energy and transient changes in stimuli (Vencato, Harwood, & Madelain, 2017). The gap paradigm also enables the occurrence of a second population of reaction times, the express saccades with latencies around 70-100ms (e.g., Boch et al., 1984; Fischer & Boch, 1983; Fischer & Ramsperger, 1984; Fischer et al., 1993), notably if the SOA is longer than 180ms. These effects are however variable across studies, though almost always found. For instance, Boch and Fischer (1986) observed eventually short latencies for the overlap SOA, with the production of reaction times around 300-500ms during the first training sessions. Kalesnykas and Hallett (1987) replicated the gap and overlap effects but one of their participants had longer latencies for the gap paradigm than the overlap paradigm and similar latencies between the overlap and step paradigm.

Several studies have demonstrated a peak in reaction times close to the fovea (see as illustrated in Figure 9; e.g., Boch et al., 1984; Kalesnykas & Hallett, 1994), a phenomenon already observed by Wyman and Steinman (1973) for small saccades. Opposing results have been raised in the literature on the impact of target eccentricities on saccadic reaction time. For instance, Kalesnykas and Hallett (1994) or Crawford and Muller (1992) observed a minimal effect of target eccentricities beyond 2° and a peak of about 100ms around the fovea (Figure 9). On the contrary, Boch et al. (1984) obtained an effect of target eccentricities until 8° for express saccades with monkeys while observing in addition an effect of the target size. Indeed, for the same target step (e.g., 1°), the saccadic latency was shorter (e.g., 70ms) for a small target (e.g., 1°) than for a bigger one (e.g., 95ms for 4° target size). The effect of target size has also been reported by Ploner, Ostendorf, and Dick (2004) who manipulated three sizes (i.e., 1°, 5° and 10°) for a target stepping randomly at various eccentricities (i.e., 5°; 7.5°; 10°; 12.5°; 15°) and obtained longer latencies for bigger stimulus. Madelain, Krauzlis, and Wallman (2005) observed the same phenomenon: when their participants attended to the large part of the stimulus (i.e., 8°), their saccadic latencies were longer (by 135ms) than when they attended to the smaller part of the stimulus (i.e., 0.8°) for the same target step. This large difference in latencies depending on the size of the attended part of the stimulus was later evaluated in terms of the amplitude of the step in proportion to the size of the target (De Vries, Azadi, & Harwood, 2016; Harwood, Madelain, Krauzlis, & Wallman, 2008). The latency distributions consistently changed according to this step-size ratio, regardless of the independent target size or target eccentricities. When the ratio was superior to 1, regular saccade latencies were observed, whereas when it was inferior to 1, they observed longer latencies (even for small target size).

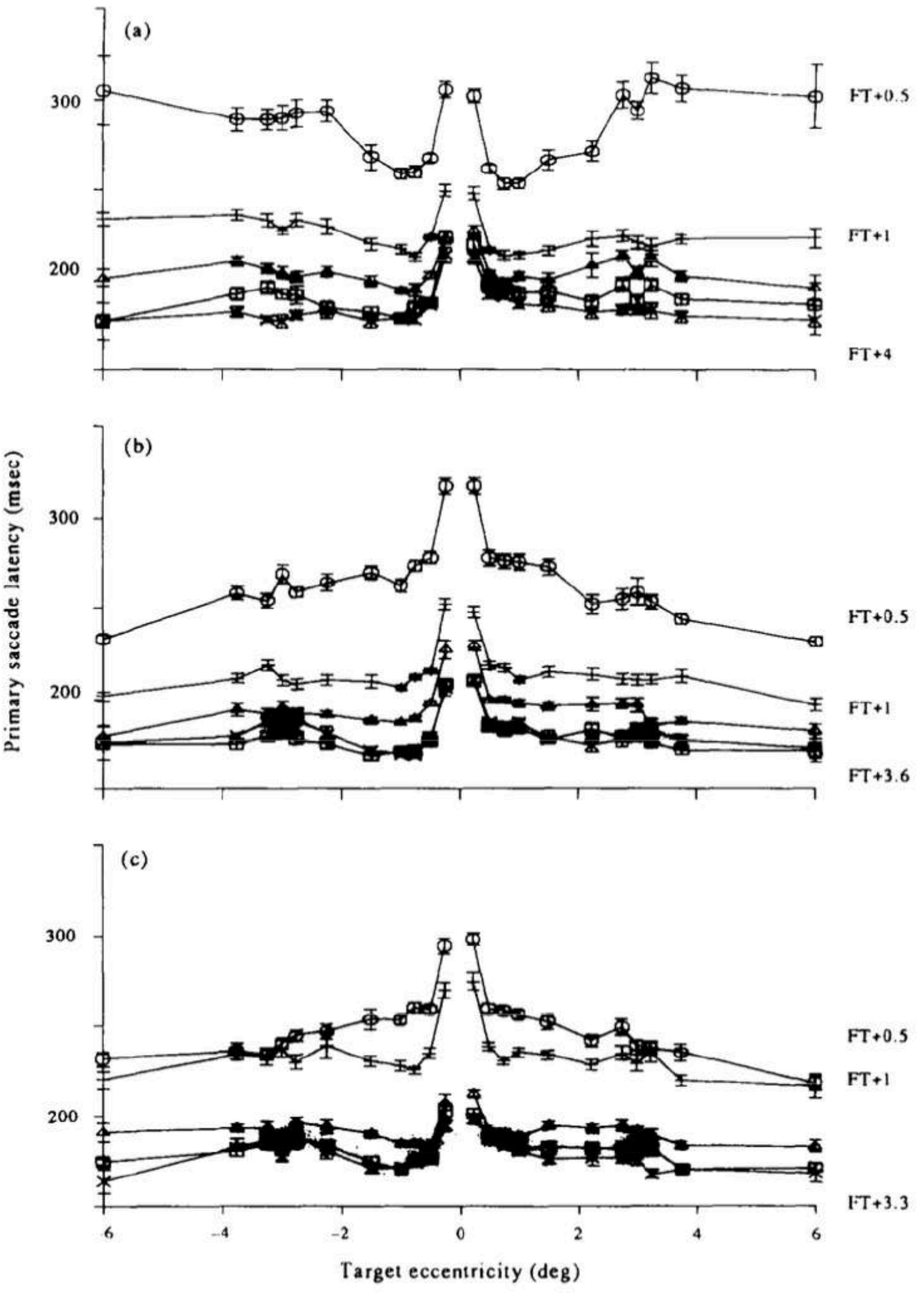

Figure 9: From Kalesnykas & Hallett (1994). Latencies of primary saccades as a function of retinal eccentricity, target intensity and color for one participant. The three panels (a-c) from top to bottom are for 670, 565, and 501nm targets.

For instance, the above-mentioned latency difference obtained by Boch et al. (1984) with express saccades could be explained by a step-size ratio of 1 for the shortest latencies versus a ratio of 0.25 for the longest. Interestingly, this effect was only found for saccadic latencies and not for manual reaction times (Harwood et al., 2008). The current hypothesis behind this phenomenon, called the size-latency effect, is a cost-benefit evaluation of saccadic latencies (for a more detailed discussion, see II.2.2.2. Reinterpreting the conventional determinants of saccade latency as antecedent stimulus).

Finally, the last factor that will be briefly reviewed in this thesis regarding bottom-up factors is the effect of multiple stimuli. A classic way of describing the effect of distractors on saccade latencies is to use Hick's law (Hick, 1952; Hyman, 1953), stating that latencies will increase logarithmically as a function of the number of response alternatives. Several papers have supported this effect of distractors on latency (e.g., Lee, Keller, & Heinen, 2005; Schiller & Kendall, 2004; Walker, Deubel, Schneider, & Findlay, 1997; Walker, Kentridge, & Findlay, 1995), which would illustrate a lateral inhibition between competing stimuli, increasing the period of time for the saccade to be triggered (Bompas & Sumner, 2009; Leach & Carpenter, 2001; Trappenberg, Dorris, Munoz, & Klein, 2001). However, the resulting impact on latencies appears to be more variable as some studies demonstrated no effect of the distractors or the opposite outcome depending on the timing, the distance or the direction of the distractors (e.g., Khan, Munoz, Takahashi, Blohm, & McPeek, 2016; Kveraga, Boucher, & Hughes, 2002; Lawrence & Gardella, 2009; Lawrence, St John, Abrams, & Snyder, 2008; Walker et al., 1997). Because of the amount of opposing outcomes (Bompas & Sumner, 2009) and the ability to reverse the effects, Lawrence and Weaver (2011) suggested that these results might not only be due to stimulus-based factors but also to higher-order factors.

The literature on top-down factors is as much –if not more– developed as the previous one and will be reviewed briefly as well; some topics will not be addressed in this thesis and some –especially regarding reward– will be discussed in chapter 2. The spatial or temporal expectation of the target onset is known to have a considerable effect on saccadic reaction times. The two kinds of expectation have an independent and differential impact on latencies. Michard, Têtard, and Lévy-Schoen (1974) independently manipulated the temporal uncertainty (i.e., either the participant controlled the stimulus onset by a button press or the inter-trial intervals were selected from a Poisson distribution) and the spatial uncertainty (i.e., probability of 1, 0.5 or 0.25). The authors observed that the temporal uncertainty had a strongest effect on latencies with increase of more than 50% (about 100ms) whereas the spatial uncertainty increased the reaction times by on average 12% (about 10-50ms). These effects of spatial expectation have been replicated by several studies, with the same range of latency decrease when the target location is predictable (see as illustrated in Figure 10 representing the reciprobit plots of latency for three target appearance probabilities; Anderson & Carpenter, 2006; Carpenter, 2004; Carpenter & Williams, 1995). Interestingly, Marino and Munoz (2009) who manipulated the effect of target luminance and target predictability on saccadic latencies in a step and gap paradigms with monkeys did not retrieve the effect of spatial expectation (i.e., there was a slightly decreasing trend during the step paradigm for less predictable target and during the gap paradigm, the mean latency increased for a predictability of 25% but decreased to the shortest latencies for the predictability of 12.5%). Tightly related to the expectation factor, a lot of studies have investigated the effect of cueing and warning signals on latencies. Unsurprisingly, when there is a warning stimulus onset, change or offset, saccadic reaction times are decreased (Ross & Ross, 1980, 1981). The explicit cueing of the future location of the target has also been effective in decreasing the latencies (Hoffman & Subramaniam, 1995; Van der Stigchel, Meeter, & Theeuwes, 2007; Walker et al., 1995) but most interestingly, the facilitation of saccadic latencies still appears when the spatial cues are subliminal (Mulckhuyse & Theeuwes, 2010). After investigating this effect with a paradigm of saccadic adaptation (in which the stimulus target is moved during the eye flight, causing an increase/decrease of the saccadic amplitude after learning), Khan, Heinen and McPeek (2010) suggested that the rational behind this facilitation was not in fact related to the spatial cue but to the saccade goal.

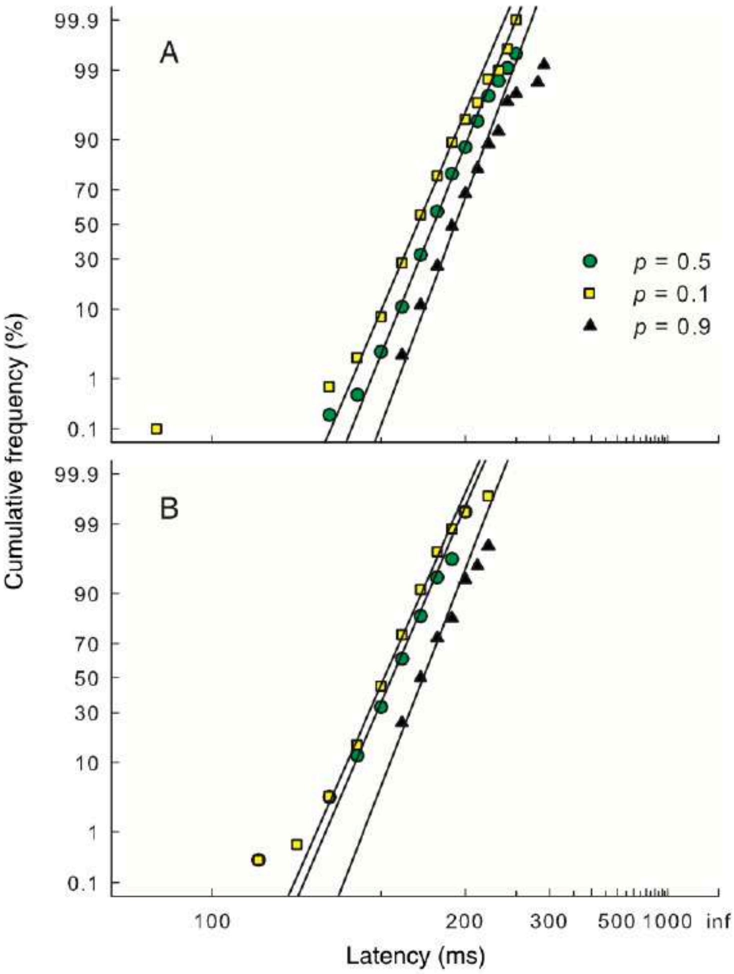

Figure 10: From Anderson & Carpenter (2006). Reciprobit plots of latency for three target appearance probabilities. Straits lines are maximum likelihood fits (Kolmogorov-Smirnov, p = 0.85 and 0.93 for Observers A and B, respectively) constrained to have a common intercept when latency is infinite, which is the characteristic pattern that occurs when an observer's prior probability shifts.

The urgency is another factor that have a drastic effect on saccadic latencies. Reddi and Carpenter (2000) conducted an experiment in which they instructed their participants to be either as fast or accurate as possible when the probabilities of appearance on either side of the screen were identical. First of all, the authors observed that the saccades were strongly accurate (up to 96.3%) when instructed to, but at the expense of reaction times (median latency around 450-700ms; Figure 11). Conversely, when participants were instructed to be as fast as possible, the saccadic latency distributions shifted toward shorter values (median latency around 350-400ms) while the accuracy dropped down to 61.8%. From these results, the authors surmise that a speed-accuracy tradeoff could explain how individuals could produce shorter reaction times. A puzzling issue in this study is why individuals had longer latencies than what is typically retrieved in classic settings (i.e., median latency of 200ms in a step paradigm versus median latency of 350-700ms here).

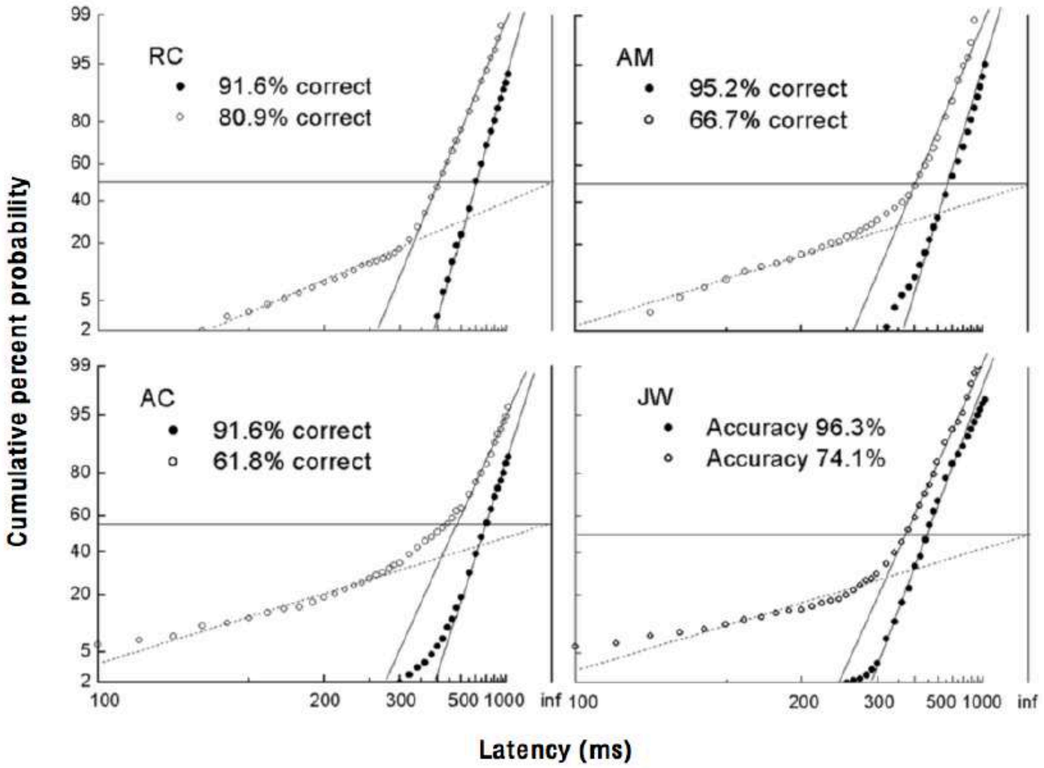

Figure 11: From Reddi & Carpenter (2000). Effect of urgency instructions on the distribution of saccadic latency. Reciprobit plots are shown for four representative participants given instructions to respond either as accurately as possible (filled circles) or as fast as possible (open circle). The actual percentages of correct responses under the two conditions are shown in the boxes. Most saccades follow a recinormal distribution, generating a linear cumulative distribution. However, particularly under the urgency condition, there is an obvious population of anticipatory responses generally lying on a different straight line (dashed) from that of the main population, with a swallower slope. The solid lines represent a best fit to the main population subject to the constraint of a common infinite-time intercept, demonstrating the expected swiveling of the distribution about a fixed intercept with the infinite-time axis.

Two other studies investigated the effect of urgency on saccadic reaction times (SRTs) but they did not report any significant change in the saccade accuracy. Trottier and Pratt (2005) instructed their participants to rapidly acquire visual information either in a condition in which they had simply to look at a peripheral target (“look”) or a condition in which they had to complete a post-saccadic visual discrimination (“look-obtain”). The instruction produced shorter latencies, and individuals had even shorter reaction times in the “look-obtain” condition. Most interestingly, when the authors introduced gap and overlap trials in their experiment, they observed that individuals were able to have identical latencies in the “overlap look-obtain” than in the “gap look” whereas there is typically a difference of 100ms between a gap and overlap paradigms. The urgency to look also works when there is no explicit instruction. Montagnini and Chelazzi (2005) designed a discrimination task in which the target stimulus (white capital letter E or F) was visible at the post-saccadic location for a brief fixed period of time (based on the individual time taken to program and execute the saccade), constraining a perceptual urgency. The authors observed a drastic median latency reduction of 15% in addition to an increase of on average 10% for the peak velocity without any accuracy trading.

These last two studies are compatible with the ones investigating the effect of informative targets on saccadic reaction times. Indeed, Bray and Carpenter (2015) conducted an experiment in which the first saccade enabled to collect reliable information regarding the next target location. Participants were told that the color was a consistent predictor of the future target position for only one of the side of the screen (Figure 12). After 200 trials, they observed a consistent decrease of about 13ms when the first saccade was made toward a reliable target and the same SRT reduction for the second saccade to the known location (which is compatible with the work of Michard et al. (1974), demonstrating that spatial certainty causes a decrease of only tens milliseconds in latencies). Interestingly, when asked, the participants were not able to report which side was the reliable one. In line with the pioneers works of Wyckoff (1952) stating that acquisition of information is reinforcing, it seems that obtaining information might select shorter latencies and be reinforcing for the oculomotor control. This view could provide one explanation for the phenomenon of inhibition of return in which saccadic latencies are longer (by 8 to 15ms) when individuals have previously fixated the target location (Vaughan, 1984). Indeed, the previously fixated target would not be informative anymore and the visual system could therefore present some sort of procrastination to look at it.

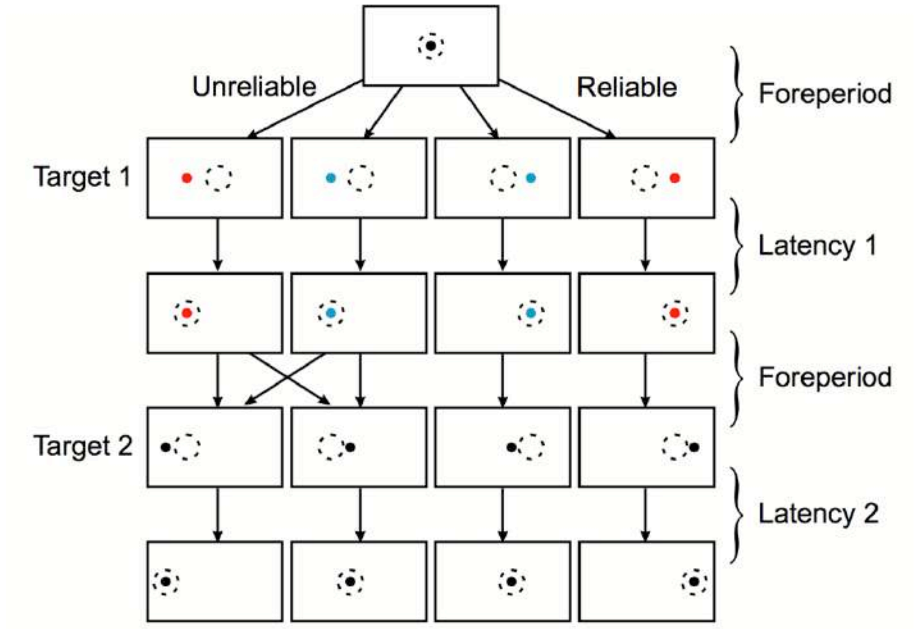

Figure 12: From Bray & Carpenter (2015). Diagram of the protocol. After a random foreperiod, a central black fixation target (top) was extinguished and one of four possible targets was presented, and randomly either red or blue. On the reliable side, the color of this target reliably predicted the position of a second target, displayed after a saccade was made to the first one; on the unreliable side, the color was completely uninformative. The dotted circle represents gaze position.

1.2.3. The neural basis of saccades: what are the neuronal reasons for saccadic latencies to be so long?

Saccadic eye movements involve both sensory functions and motor skills and therefore require a sensory-motor interaction: the visual stimulation will be transformed into a motor command to produce a saccade toward that stimulus. Several areas responsible for sensory, attentional, intentional, mnemonic and motor processes are involved in the production of saccades. This section does not aim at reviewing all of these processes, but rather at evoking three of them –the frontal eye field, the superior colliculus and the reticular formation– in order to depict what and how underlying processes cause the latency of a saccade.

The triggering of voluntary saccades is essentially based on a network of frontal areas. The frontal eye field (FEF) in the prefrontal cortex is known to disengage fixations and is involved in saccade triggering for exploration of the visual environment (Johnston & Everling, 2011; Pierrot-Deseilligny, Rivaux, Gaymard, Müri, & Vermersch, 1995), since its lesion is associated with an increase of saccadic latencies (Rivaud, Müri, Gaymard, Vermersch, & Pierrot-Deseilligny, 1994; Schiller, Sandell, & Maunsell, 1987). The FEF enables the production of voluntary saccades via projections to the superior colliculus, which will integrate visual information, as well as other sensory information and turn them into a driving command. These areas also project to basal ganglia, which is a key structure in controlling the production of voluntary movements (Hikosaka, Takikawa, & Kawagoe, 2000). The basal ganglia control the production of saccades by maintaining a tonic inhibition of the superior colliculus and they contribute to the initiation of saccades by removing this inhibition. The superior colliculus (SC) plays a central role in the sensorimotor integration associated with the production of saccades (King, 2004) because it receives afferences from sensory and sensorimotor areas and projects on pre-motor and motor structures of the brainstem circuitry. It is part of the final common route to reactive saccades and voluntary saccades for the production of rapid eye movements. The lesion of the SC will not prevent saccade production but induces a latency increase and accuracy impairment (Hanes & Wurtz, 2001; Schiller et al., 1987). Finally, the saccadic generator allowing the production of horizontal saccades is localized at the level of the reticular formation of the brainstem. The reticular formation is a set of interconnected nuclei that are located throughout the brainstem whose functions are modulatory and premotor. It generates an activation that is transmitted to the motor neurons of the oculomotor nuclei whose role is to activate the extraocular agonist muscles and inhibit the antagonists to produce a saccade in a given direction.

The production of saccades is based on a dense and well-described neural network. The main outline is that the onset of voluntary saccades involves the frontal cortex, while the sensorimotor integration takes place at the level of the superior colliculus, which thereafter sends information about the amplitude and direction of the saccades to the saccadic generator (see Scudder, Kaneko, & Fuchs, 2002 for a synthesis on saccade production). A large literature has investigated the minimal neural delay for saccade production. The minimal efferent limit delay –"the execution delay"– appears to be around 20ms for the eye muscles (Robinson, 1972; Robinson & Fuchs, 1969; Sparks & Jay, 1986; Sparks, 1978; Sumner, 2011; White & Munoz, 2011). The minimal afferent limit delay –"the sensory integration delay"– seems to be more variable and controversial across studies. Fischer and Ramsperger (1984) conducted a control study of express saccades in a gap paradigm to probe whether the 50ms latency peak they observed was due to visually guided saccades or anticipations. They simply instructed participants to make saccades with the same size and direction as during their experimental condition as soon as the fixation point was extinguished while there was no target onset. The saccadic latency distribution of this control condition was unimodal with a peak around 50ms, demonstrating that the former saccades were not visually guided. They concluded from their data that the first visually guided saccades had latencies around 75ms. Subtracting the average execution delay, the minimal afferent limit seemed to be about 50ms (White & Munoz, 2011). This result has been supported by Stein and Meredith (1990) who demonstrated that the sensory processing of an auditory stimulus was about 10-30ms while it could take 55-125ms for a visual stimulus in the periphery. Incidentally, the sensory integration in the SC has so far been used as the main explanation for the gap effect (Saslow, 1967) that produces shorter latencies. The early removal of the fixation point has been associated with a decrease in fixation-related activity of the SC which would facilitate the premotor processing and produce express saccades (Dorris & Munoz, 1995; Munoz & Wurtz, 1992, 1993; Reuter-Lorenz, Hughes, & Fendrich, 1991). This proposition will be discussed later in the thesis, as it has been shown that it is possible to observe express saccades without the early removal of the fixation point in classic step paradigm, and even overlap paradigm (Bibi & Edelman, 2009; Trottier & Pratt, 2005).

Because saccadic latencies are longer than the neuronal delays associated with the underlying sensorimotor processes, they are usually thought of as a composite of the time to process the visual stimulus, the decision process and the final motor execution. Especially, it is classically assumed that reaction times enable a quantification of decision processes (Glimcher, 2003; Schall, 2001).

1.2.4. A common sensorimotor model: saccadic decision-making

Saccadic eye movements are commonly used to study motor control since the collected data may be applicable to other motor responses. They appear to be an attractive sensorimotor model for studying behaviors, as they are a non-costly response for which it is possible to collect hundreds or thousands of data per subject. Indeed, Carpenter (1994) argued that the oculomotor system provides a microcosm of the brain with both sensory input and motor output that can be precisely manipulated and measured with exceptional accuracy thanks to eye-tracking equipment. The literature on decision has been focusing on saccadic decision-making and more precisely saccadic latencies because it is considered as an elegant window on decision processes (Glimcher, 2003). Indeed, we have previously discussed the neuronal substrate responsible for saccadic latencies, which cannot fully account for the time interval between the target onset and the saccade onset. The sensory and execution delays are considered as a “dead time”, also named a “non-decisional delay”, as they will always happen for a saccade and be relatively fixed for a given stimulation. Many researchers are interested in understanding why regular saccadic latencies are at least twice as long as the non-decisional delay (Ludwig, 2009). Thereby, saccadic reaction times have become one of the main behavioral measures to quantitatively study decision processes as they are regarded as a composite of the time of the visual integration, the decision and the motor command, reflecting the decision-making processes.

Most decision models, such as the LATER model (Linear Approach to Thresholds with Ergodic Rate; Carpenter & Williams, 1995; Tatler, Brockmole, & Carpenter, 2017) or the diffusion models (Ratcliff & Rouder, 1998; Ratcliff, Smith, Brown, & McKoon, 2016), are based on the assumption of some noisy accumulation of information over time to decision criterion (see Gold & Shadlen, 2007 for a review). Figure 13 illustrates the instance of the LATER model: following a change in the stimulus (in red), the decision signal (in blue) begins to accumulate sensory information starting from the initial point S_0 at a constant rate r (between trials, the rate varies in a Gaussian manner with mean μ and variance σ^2) until it reaches a decision threshold S_T. The critical parameters here are 1) the rate at which one accumulates information (mean and variance) depending on the stimulus strength (i.e., bottom-up factors), and 2) the threshold representing the urgency (i.e., top-down factors). To examine the changes in saccade programming due to changes in SRT distributions, the reciprobit transformation consists in transforming the latency distribution by its reciprocal (leading to a Gaussian-shaped distribution) and plotting it in a probit scale, which results in a straight line. There are three distinctive changes in the reciprobit distributions due to change in the saccade triggering mechanism (Figure 14). Changes in the threshold (e.g., urgency, prior probability) alter the slope, such that the line swivels around the infinite-time intercept (Figure 14, top panel), changes in the mean rate of accumulation (e.g., stimulus intensity, SOA) result in a parallel shift of the line (Figure 14, middle panel), and changes in the variance of the rate alter the slope with no change in median latency (Figure 14, bottom panel). Note that the reciprobit transformation can only be realized in the case of a unimodal distribution. A critical feature of these models is that saccadic latency is supposed to reveal the time needed to reach a decision regarding the target location. Thence, lowering the information threshold drives shorter latencies but at the expense of accuracy in a conventional speed-accuracy tradeoff (Reddi & Carpenter, 2000). Therefore, one would have a precise control over where to move the eyes but not when –the temporal dimension holding a limited role.

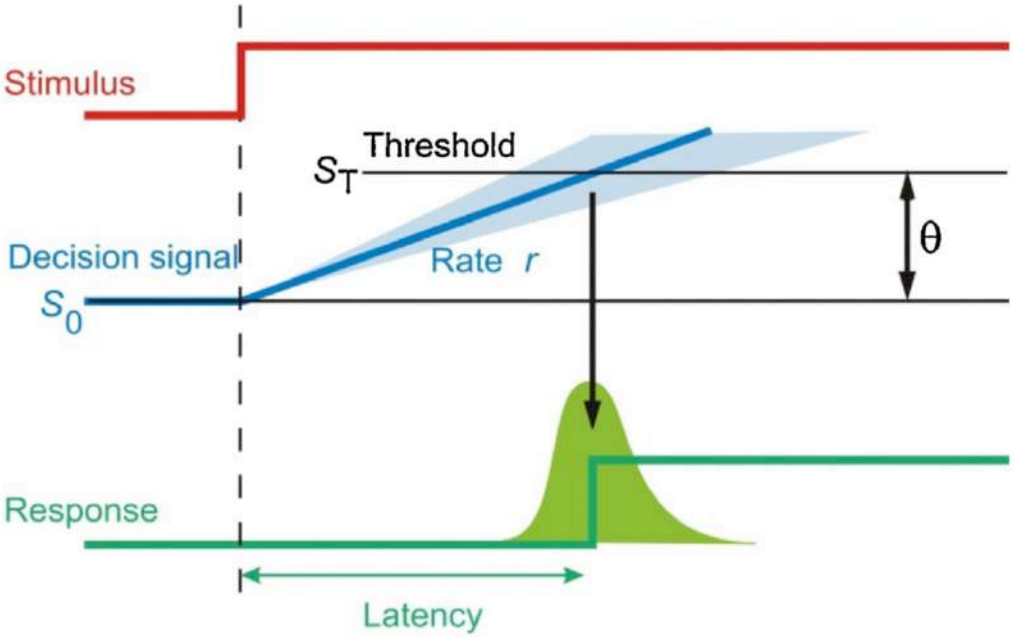

Figure 13: From Noorani & Carpenter (2016). The LATER model. A decision signal whose initial value is S_0 begins to rise in response to the stimulus at a constant rate r until it reaches a threshold at $S_T = S_0 + \theta$, when it triggers the response. On different trials, r varies in a Gaussian manner with mean μ and variance σ^2; as a result the latency distribution (green) is skewed.

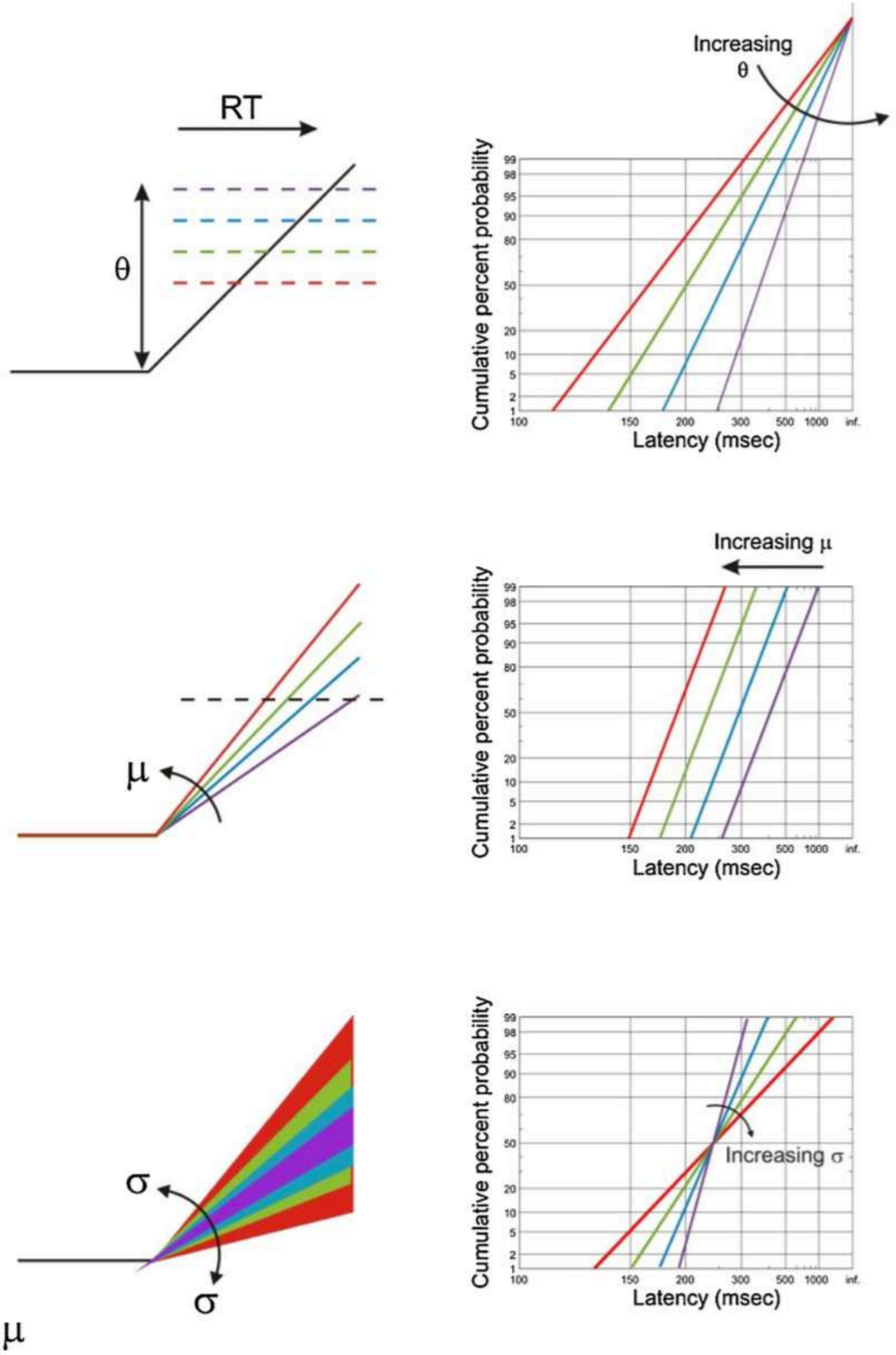

Figure 14: From Noorani & Carpenter (2016). Relation between parameters of the LATER model and parameters of the reciprobit plot. Top: variation in the threshold θ swivels the plot about the infinite intercept; middle: variation in the mean rate of rise μ leads to horizontal, self-parallel translation of the reciprobit plot; bottom: alterations in the variance σ^2 generate a change in the slope of the plot with no change in median latency.

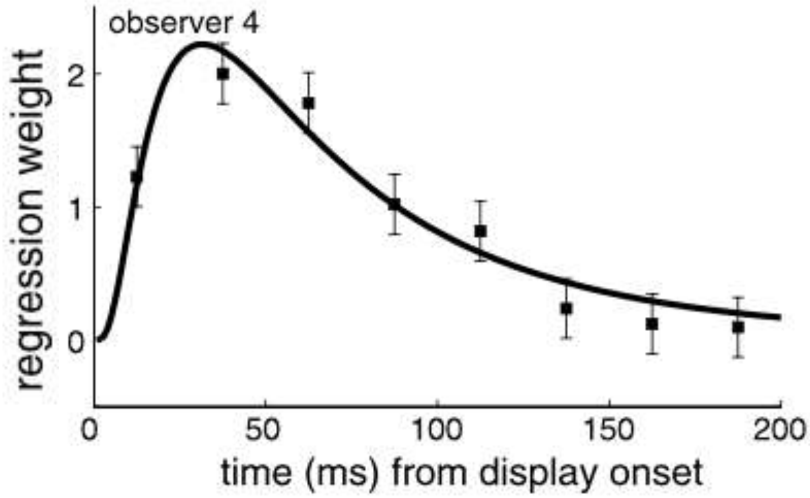

Figure 15: From Ludwig et al. (2005). Logistic regression weights as a function of time after display onset for a representative participant. Error bars are the standard error. The solid line is best-fitting log-Gaussian function.

Departing from the idea of a long-lasting information accumulation, Ludwig (2005, 2009) proposed that saccadic decisions might be time-limited and driven by the sensory information present within the first 100ms. A first experiment consisted in identifying the temporal impulse response of the decision mechanism (Ludwig et al., 2005) by relating the visual noise to the saccadic decision using a reverse correlation (see Caspi, Beutter, & Eckstein, 2004 for a detailed description of the data analysis method). Two stimuli with a fluctuating luminance (i.e., every 25ms) were presented to observers, who were instructed to saccade toward the brighter stimulus while no feedback was given. Median saccade latencies ranged from 298ms to 320ms. The authors observed that the first 25-75ms after display onset drove the decision most strongly (Figure 15) and concluded that the decision time averages 100ms. Knowing that the non-decision delay is around 60-100ms and the execution delay about 20-30ms (Sumner, 2011), there were still about 100ms in the saccadic latencies that were not accounted for, contrary to the classical integration-to-threshold point of view. Interestingly, their second experiment demonstrated that observers were not using this integration-to-threshold strategy. They manipulated the availability of information in two conditions: “same-different” for which the visual information was identical for the first 100ms then changed, and “different-same”, which was the reverse. Note that participants were not urged to respond quickly; there was enough time during a trial (i.e., 500ms) for observers to gather the information in the “same-different” condition (i.e., available from 100ms to 500ms with respect to display onset). The proportion of correct saccades was around 80% for the latter but dropped at almost 50% for the “same-different” condition, while the saccadic latency did not increase (which would be predicted by the conventional accumulation models: waiting to accumulate enough information to make a decision, thence longer latencies). One can then wonder why should saccadic latencies be longer than 100ms. The next part of this thesis will suggest and develop another interpretation of saccade triggering and SRTs, based on learning and the impact of reinforcement contingencies.

Chapter 2:

The plasticity of the saccadic system and the effects of reinforcement: saccade as an operant response

Behavior analysis defines learning and the development of behaviors as a lasting change in behavior, depending on its interaction with the environment (Baer & Rosales-Ruiz, 2003; Skinner, 1953). A three-term contingency describes the relations between a behavior and its environment (i.e., antecedents and consequences). The central factor in this interaction is the functional consequences of the behavior that will control its selection, occurrence and long-lasting retention. In other words, the behavior, named an operant or instrumental, is controlled by its own consequences (Skinner, 1963). When it is controlled by reinforcement contingencies (that is to say the relations between behaviors, their antecedents and their consequences), it is said that behavior has been reinforced. Behavior analysis postulates that learning comes from a parsimonious mechanism similar to natural selection (Skinner, 1981), in that the future probability of a behavior occurrence will be higher if it has been followed by consequences that are beneficial for the organism and be lower if there was no consequence or an aversive one. A posteriori, these beneficial consequences are called reinforcers only if they increase the future probability of occurrences (Skinner, 1953). Therefore, according to the behavior analysis theory, it is because in the past certain responses have been followed by beneficial consequences for the organism that their probability of occurence increases. The antecedents in the contingency are the environmental stimuli present before the behavior occurrence. Through learning, they come to signal the availability of reinforcement and are termed discriminative stimuli. Behavior analysis consists in systematically manipulating the antecedents and consequences of the environment, in order to experimentally ascertain the functional relationships with the behavior.

Departing from a classical evaluation of the SRTs based on information accumulation, we rather propose in this thesis that saccadic latencies derive from a functional relation with the environment. We will demonstrate this proposition by conducting a functional analysis – which consists in focusing on the behavior and manipulating the antecedents and consequences– using the classical techniques of behavior analysis. Importantly, the experimental analysis of behavior focuses on the analysis of observable behaviors and refuses to draw inferences about internal mechanisms that control the behavior. Thus, we will analyze saccadic eye movements and their reaction times from the viewpoint of behavior analysis by focusing on the observable behavior, and will not discuss the role of neural structures (albeit we do not refute their involvement). The experimental analysis of behavior can shed a different light on the control of SRTs insofar as it focuses on the selection of the behavior, the control of its occurrence and its retention by their own functional consequences.

We will see that if the classical decision models consider SRTs as resulting from information accumulation –that is as a byproduct ensuing from mechanical processes, this is not the case for behavior analysis. According to this theory, saccadic reaction times can be controlled and reinforced by the environment. Several studies have demonstrated the effect of reinforcement on the spatial allocation of saccades and a few on their temporal allocation; they will be reviewed in the current chapter. In other words, we regard saccade as an operant response and consider its spatial and temporal dimensions as equally affected by reinforcement. The experimental contribution of this thesis will evaluate the extent of the control of SRTs by reinforcement contingencies with different issues: choice in SRTs, manipulation of benefit, discriminative control and pavlovian processes. Should the manipulations of the consequences of eye movements be effective in changing the properties of saccades, it would attest to the functional role of these consequences in oculomotor learning. Saccadic latencies, besides saccades, would be based on the same principles as those governing other operant behaviors. Furthermore, it would imply that it is possible to learn to organize and control one's behavior in time as precisely as it is in space.

Many papers in vision sciences use the term "reward" or even "reinforcement". It appears they do not always fully master the general learning principles and mechanisms implied and, unfortunately, sometimes miss the behavioral reasons behind the observed results. Yet, these studies complete the past works demonstrating that voluntary eye movements are operant behaviors (Madelain, Paeye, & Darcheville, 2011) and highlight the exquisite plasticity of the saccadic system. The next section will present the theoretical and empirical elements allowing to regard saccades and the control of saccadic latencies from the angle of behavior analysis.

2.1. Effect of reinforcement on spatial allocation of saccades

2.1.1. Target selection according to behavior analysis

Pioneers works of Schroeder and Holland (1968a, 1968b, 1969) and Schroeder (1969a, 1969b) showed that the occurrence of gross saccadic eye movements with humans (i.e., allocating the gaze between defined wide areas) could be reinforced by the production of a stimulus using a multiple reinforcement schedule (which consists of alternating independent reinforcement schedules that are individually signaled by a specific antecedent stimulus) and placed under stimulus control in simple discrimination. Stimulus control happens when the antecedent stimulus comes to control the behavior through previous learning. In their 1968's experiment, the participants were seated in front of a screen and had to detect and press a button to indicate changes in the orientation of pointers located in four dials. Their results showed that the frequency of eye movements between quadrants followed the reinforcement schedules, in which reinforcement was contingent on either a low rate of saccades (i.e., DRL, differential reinforcement of low rate), a fixed amount of saccades (i.e., FR, fixed ratio) or on the first response after a fixed elapsed interval of time (i.e., FI, fixed interval). The authors concluded that the frequency of saccades does depend on the programmed rate of stimulus appearance and they observed similar patterns of responses to what is classically observed in these three reinforcement schedules (Ferster & Skinner, 1957). Identical outcomes had been observed by Berger (1968) with monkeys. These early works emphasized the operant nature of saccades whilst drawing a parallel with the concept of observing behavior, a class of responses that result in the exposition to discriminative stimuli (e.g., opening the mail box to check for mail, entering the PIN at an ATM, turning around). Since the primary function of saccades is to improve the visual perception of a target, this functional comparison seems appropriate. Most interestingly, the saccade would prove to possess the same operant nature and be subject to the same behavioral laws as any other instrumental response (Dube et al., 2006; Tomanari et al., 2007). Since then, the effects of reinforcement on several properties of eye movements have been experimentally explored on both monkeys and humans and have focused on finer eye movements in the course of past decades. While Schroeder and Holland’s experiments investigated gross saccadic eye movements (i.e., gaze location between four areas), research is now able to tackle the precise location of gaze (around about 0.25-0.5°) and to manipulate it using reinforcement. For instance, Chukoskie, Snider, Mozer, Krauzlis, & Sejnowski (2013) designed a gaze-contingent experiment aiming at reinforcing eye movements towards a specific location on a blank screen. The targeted location was invisible and unknown; on each trial, the observers had to explore the display to discover it within 20s. The location of the target was fixed for the duration of a session, however its spatial spread varied on each trial. When the participants remained steady for 50ms on the targeted location, a tone was delivered as a reinforcer and the trial was ended.

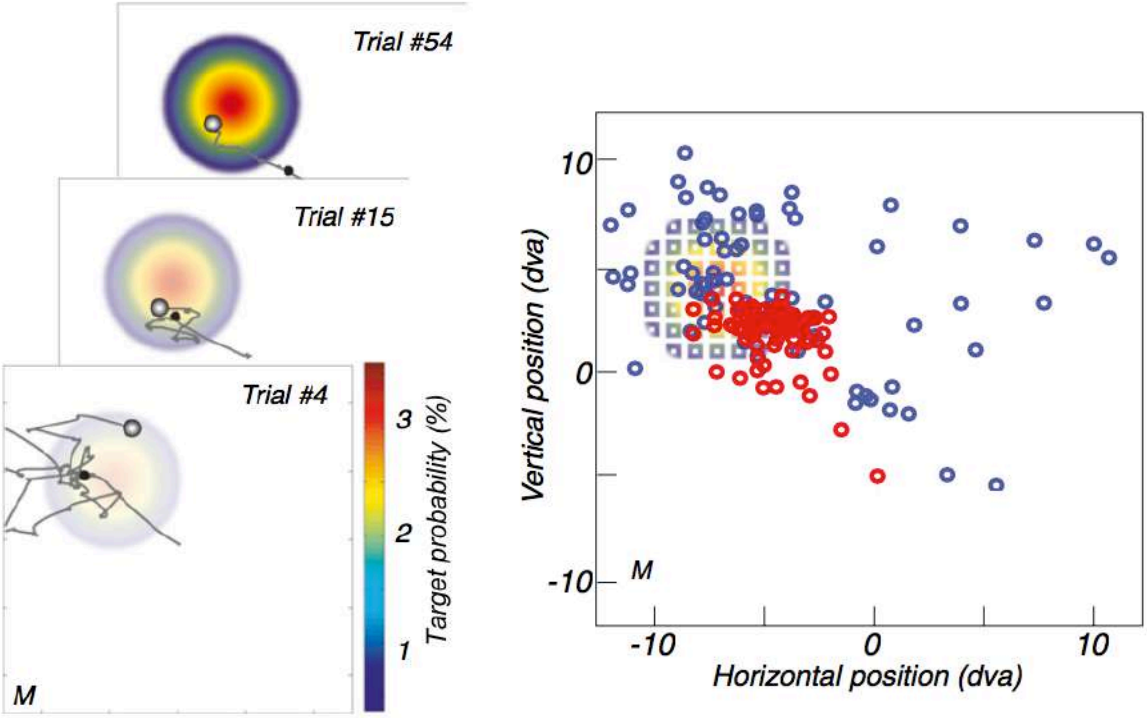

Figure 16: From Chukoskie et al. (2013). On the left, a representation of the screen is superimposed with the hidden target distribution that is learned over the session as well as sample eye traces from three trials for a representative participant. The first fixation of each trial is marked with a black circle. The final and reinforced fixation is marked by a shaded grayscale circle. On the right, the region of the screen sampled with fixation shrinks from the entire screen on early trials (blue circles; 87 fixations over the first five trials) to a region that approximates the size and position of the Gaussian-integer distributed target locations (squares, color proportional to the probability as given on the left) on later trials (red circles; 85 fixations from trials 32-39).

As illustrated in Figure 16, observers quickly and precisely learned to adapt their eye movements throughout a session. The use of an external stimulus (i.e., a tone) was efficient to select the oculomotor behaviors. The influence of saccadic consequences on target selection and the precise orientation of saccades has also been investigated by Stritzke, Trommershäuser and Gegenfurtner (2009) and Schütz, Trommershauser and Gegenfurtner (2012). In their experiments, the target and the juxtaposed distractor were associated with points (i.e., +100, exchangeable with money at the end) and a penalty (i.e., -500 points), respectively. They observed that most saccades landed accurately on the target (2° in diameter) and away from the area resulting in penalties.

The plasticity of the saccadic system has also been probed with clinical populations. Indeed, Janssen and Verghese (2015, 2016) demonstrated that it is possible to train efficient eye movements during visual search in individuals with a scotoma (i.e., either an artificial one or patients with age-related macular degeneration). A scotoma, which is a pathological blindspot, causes vision loss around the fovea and results in impaired vision and erratic eye movements. Because patients with AMD (age-related macular degeneration) might miss information present in their visual field, they need to learn new strategies to explore their environment. The authors used a discrimination task in which participants had to judge whether two stimuli (one being initially invisible without any eye movement) were identical or different, under time pressure. They observed that adults with healthy vision and individuals with AMD could quickly learn to move their eyes toward an informative target area that was initially hidden (by an artificial gaze-contingent scotoma or a genuine one). These studies support the reinforcing effects of visual information and the ability to perform a task for saccades –a stance that is increasingly growing in the vision field with human and non-human primates (e.g., Daddaoua, Lopes, & Gottlieb, 2016; Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014; Hayhoe & Matthis, 2018).

Another phenomenon has largely interested the community investigating target selection: the oculomotor and attentional capture of the eyes (see Failing & Theeuwes, 2018 for a recent review). When searching for a specific target, if a salient distractor that is currently irrelevant for the task appears, it will disrupt the eye movement by either causing longer SRT (e.g., Theeuwes, 1992; Yantis & Jonides, 1990) or attracting a saccade toward its location (Figure 17; e.g., Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Theeuwes, Kramer, Hahn, & Irwin, 1998; Yantis & Egeth, 1999).

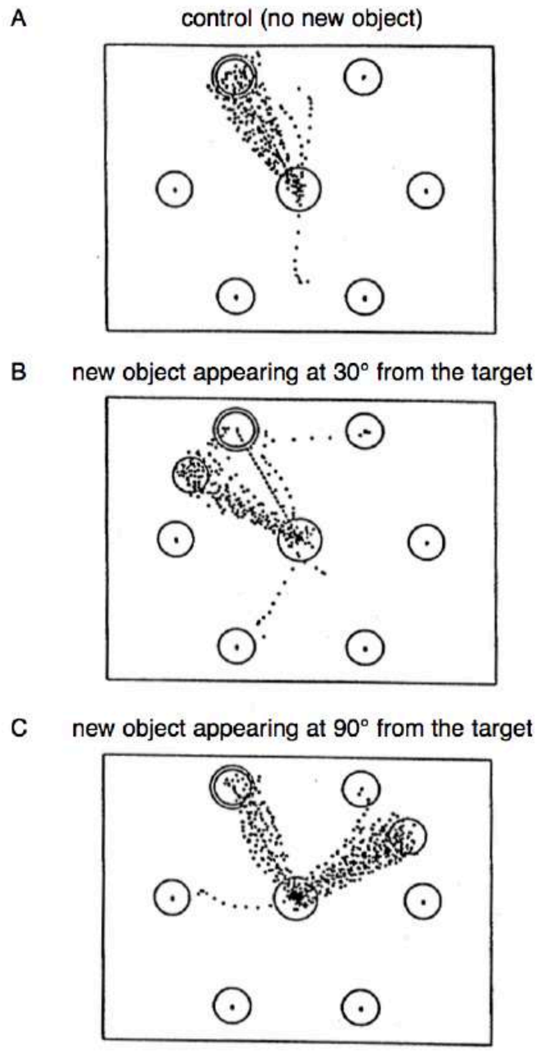

Figure 17: From Theeuwes et al. (1998). Initial tracks that the eyes took as they left the fixation point until the first fixation near one of the colored circles. Eye position was digitized at 250Hz. Thus, the points in the figure represent data points acquired every 4ms during the initial eye movement. Eye movement behavior of an observer is shown for the control condition (A), in which no new object was presented, and for the two onset conditions: when a new object was presented close to the singleton target (at 30° of arc, corresponding to a distance of 6.4° of visual angle) (B), and when a new object was presented farther away from the singleton target (at 90° or arc, corresponding to a distance of 19.4° of visual angle) (C). The results are collapsed and normalized with respect to the position of the target singleton (marked here with a double circle) and the position of the new object.

However, one key characteristic of these experiments is that the distractor has usually been associated with reinforcement (e.g., money) in a previous task. Interestingly, the fact that a stimulus signaling the availability of reinforcers attracts the saccade is reminiscent of sign-tracking or auto-shaping, that is the classic observation that animals tend to approach and contact discriminative stimuli (i.e., a stimulus signaling the reinforcement contingency in force). Auto-shaping has been studied by Brown and Jenkins (1968) with pigeons; the authors observed that it was sufficient to repetitively pair the lightening of a key and food without any operant constraint for the pigeon to begin to peck on the key. Similarly, Burns and Domjan (2000) designed a sign-tracking experiment in which a wood block (i.e., the conditional stimulus, CS), that was presented at one end of an eight foot long chamber, consistently preceded the release of a female copulation partner (i.e., the unconditional stimulus, US) at the opposite end. Despite the distance and the fact that male quails could see the CS from the end where the female was released, the birds systematically approached the CS. Paradoxically, by approaching the CS, the birds moved away from the reinforcer to come that was the female and had to go through the whole cage to join the female once it was released. Interestingly, the effect of eye capture disappears when the distractor is presented on more than half of the trials (Geyer, Müller, & Krummenacher, 2008), demonstrating a habituation for the oculomotor capture and an extinction for the attentional effect. A habituation effect is a well-known characteristic of elicited behavior that is manifest in nearly all species and situations, and is illustrated by a decline in responding that occurs with repeated presentation of a stimulus (Beck & Rankin, 1997). If the oculomotor capture is subject to alteration through habituation, it suggests that it is in fact an elicited behavior. Indeed, according to an evolutionist point of view, the saccadic system has been shaped through thousands of years to detect abrupt changes in the environment and the peripheral vision is sensitive to sudden target onsets or displacements that could be predators in the natural environment (or a fast car in our modern environment for instance). This stance is also supported by the fact that individuals detect faster the location of potential threats (Bannerman, Milders, de Gelder, & Sahraie, 2009) or that the effect of a distractor onset is drastically decreased when participants are warned about their intermittent appearances (Tudge & Schubert, 2016). On the other hand, the decline of the attentional capture suggests that there is an extinction happening, as the previously reinforced stimulus (i.e., a conditional stimulus, CS) is repeatedly presented without the reinforcement (see Bouton, 2004 for a review on processes in extinction). The impact of the conditional effect of the previously reinforced stimulus has even been recently highlighted in the latest paper of Theeuwes, in which the attentional capture is modulated according to the monetary gain associated with three different CS (Preciado & Theeuwes, in press).

It is noteworthy that reinforcement affects saccadic eye movements in other manners than attentional capture. Sugrue, Corrado and Newsome (2004) conducted an in-depth experiment probing the allocation of saccades in a concurrent schedule of reinforcement (i.e., two reinforcement programs operating independently and simultaneously on target selection). Monkeys were placed in a dynamic environment where they had to choose between two targets associated with independent interval reinforcement programs such that the relative reinforcement rates were 8/1, 6/1, 3/1 or 1/1 (Figure 18A). A schedule of interval reinforcement consists in reinforcing the first correct response after a defined interval of time has elapsed since the last reinforcer. The ratio 8/1 meant that over a period of time, the monkey could earn 8 reinforcers in one alternative and 1 in the other one. Importantly, the reinforcement contingencies for both alternatives changed regularly and randomly (i.e., every 100-200 trials), without any signals. The authors observed that the response proportions for the two alternatives followed the matching law (Baum, 1979; Herrnstein, 1961), i.e., matched the relative obtained reinforcement rates (Figure 18B). In addition, the transition between the non-signaled changed were abrupt (Figure 18C). This experiment replicated, with saccadic allocation in monkeys, results already obtained with lever press in rats (Gallistel, Mark, King, & Latham, 2001; Mark & Gallistel, 1994) and key pecking in pigeons (Davison & Baum, 2000, 2003; Dreyfus, 1991; Mazur, 1995). Therefore, animals familiar with the dynamic of an environment can match their behaviors to reinforcement contingencies, discriminate the unsignaled changes and adapt to them.

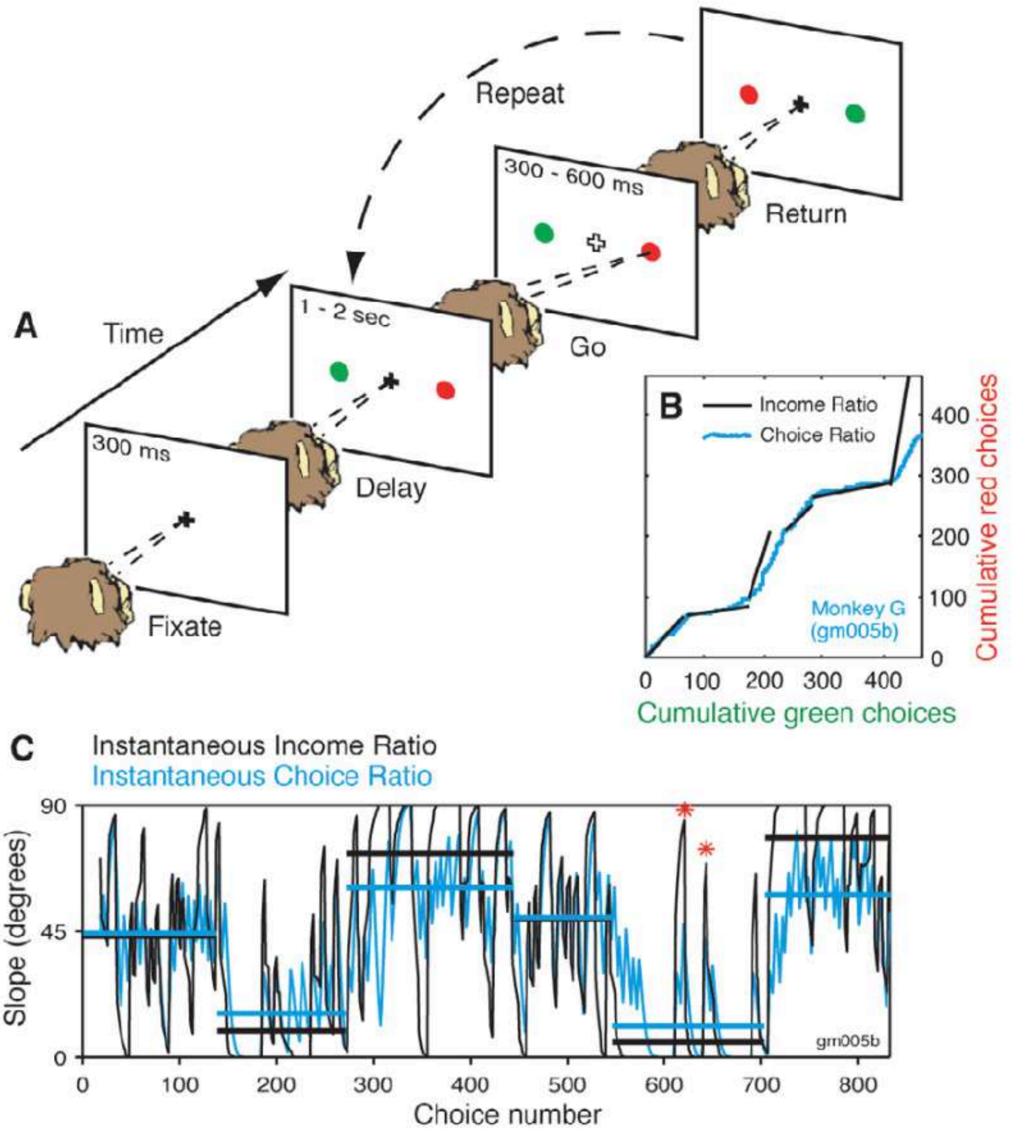

Figure 18: From Sugrue et al. (2004). Matching saccadic behavior in a dynamic task with monkeys. A) The sequence of events of an oculomotor matching task: (i) Fixate. To begin a run of trials, the animal must fixate the central cross. (ii) Delay. Saccade targets appear (randomized spatially by color) in opposite hemifields while the animal maintains fixation. (iii) GO. Dimming of the fixation cross cues a saccadic response and hold. (iv) Return. Brightening of the fixation cross cues return, target colors are then re-randomized, and the delay period of the next trial begins. Reinforcer is delivered at the time of the response, if at all. Overall maximum reinforcement rate is set at 0.15 reinforcers/s. Relative reinforcement rates changed in blocks (~100 to 200 trials) without warning; ratios of reinforcement rates were chosen unpredictably from the set {8:1, 6:1, 3:1, 1:1}. B) Dynamic matching behavior. Representative behavior of one monkey during a single session. Continuous blue curve shows cumulative choices of the red and green targets. Black lines show average ratio of incomes (red:green) within each block (here, 1:1, 1:3, 3:1, 1:1, 1:6, and 6:1). Matching predicts that the blue and black curves are parallel. C) Slope space. Same dada as in B), plotted to allow visualization of ongoing covariation in local ratios of income and choice. The x-axis shows session time (in choices). The y-axis shows running estimates of the ratios of income (black) or choice (blue). Ratios were computed after smoothing the series of reinforcers or choices with a causal half-Gaussian kernel (SD of six choices) and are expressed as slopes (arctangent or ratio). Thick horizontal black and blue lines indicate average income and choice ratios within each block. Red asterisks highlight example regions where the choice ratio obviously tracks local noise in the experiences ratio of incomes.

2.1.2. The modulation of saccadic amplitude as an illustration of saccadic plasticity

The spatial allocation of saccades concerns the direction of the displacement but also the accuracy and its precision, which are quantified through the saccadic amplitude. Usually, saccades are hypometrics (i.e., undershooting the target) with some saccadic endpoint variability. Classically, this variation is viewed as the outcome of neural noise occurring during sensorimotor processing (Faisal, Selen, & Wolpert, 2009; van Beers, 2007). However, in behavior analysis theory, variability is regarded as an operant essential to learning that might be placed under the control of reinforcement (e.g., Neuringer, 2002; Page & Neuringer, 1985). To further support the plasticity of the saccadic system, Paeye and Madelain (2011) probed the extent of control one can have over saccadic amplitude variability. Participants were required to make saccades toward a target horizontally stepping with an amplitude ranging from 9.5° to 14.2° while their saccadic amplitude gain was recorded. The gain is defined as the ratio between the saccadic amplitude and the target displacement; when the eye lands exactly on the target, the gain is equal to one; if the eye undershoots, the gain is inferior to 1 and if the eye overshoots, the gain is superior to 1. The saccadic gain is used to normalize saccadic amplitude when using several target amplitudes, which would otherwise prevent a direct comparison. During baseline, the saccadic gain was on average equal to 1 with some variability (standard deviation, i.e., SD, around 0.05) for all participants (Figure 19C-D). During learning, the authors induced high levels of variability while keeping constant the median gain by reinforcing the least frequent amplitudes with the contingent presentation of an auditory stimulus. Importantly, the post-saccadic target position was stabilized on the fovea so that the only variable inducing the changes in variability would be the tone (this was done by extinguishing the target during the eye flight and displaying it at the eye location after the saccade). Figure 19A and Figure 19B represent the saccadic gain distribution for one participant and illustrate well the large variability that was induced by the contingent presentation of an auditory stimulus on specific saccadic amplitude variations and disappeared once repetition was reinforced (recovery).

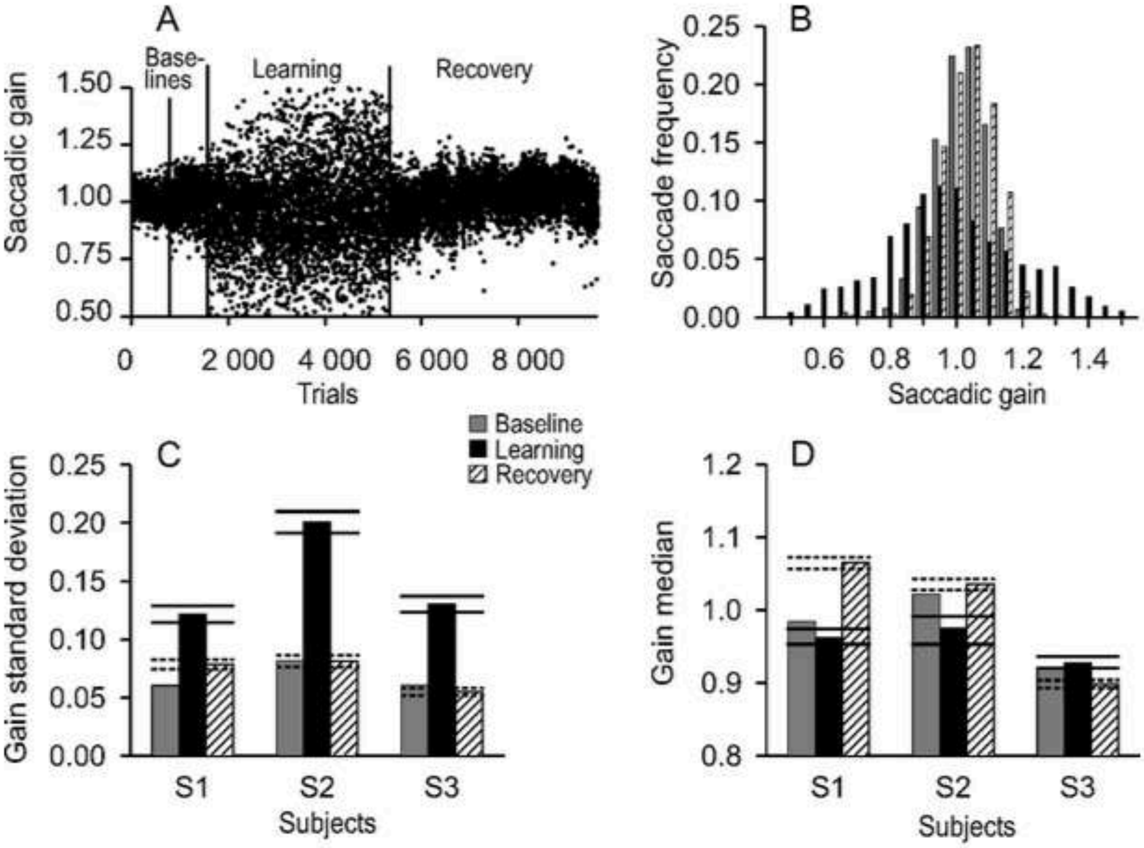

Figure 19: From Paeye & Madelain (2011). A) Saccadic gain in each experimental condition, each data point corresponding to one trial for a representative participant. B) Individual frequency distributions of saccadic gains for the stabilized baseline (800 saccades – gray), for the learning trials (last 800 saccades – black) and for the recovery trials (last 800 saccades – hatched). With the same representative participant. C) Saccadic gain standard deviations for the last four sessions (800 trials) of stabilized baseline (gray), learning (black) and recovery (hatched). 95th bootstrap percentile confidence intervals over the learning and recovery conditions, solid and dashed lines, respectively. D) Corresponding median gains. Bar colors and lines as in panel B.

Most interestingly, these high levels of variability can also be induced in more ecological tasks, such as visual search tasks. Paeye and Madelain (2014) and Paeye, Schütz, and Gegenfurtner (2016) replicated the latter results with a gaze-contingent paradigm in which finding the target was used as a reinforcer in a visual search task. They both observed that the contingent presentation of the target on specific amplitudes was sufficient to reliably change this saccadic dimension, without the use of an external reinforcer such as money or a tone. Because the function of saccades is to obtain clear visual information, the fact of using visual reinforcement may be more ecological and relevant for the saccadic system.

The main phenomenon commonly used to study the plasticity of the saccadic system is saccadic adaptation (Herman, Blangero, Madelain, Khan, & Harwood, 2013). During their ballistic execution, saccades cannot be controlled because they are too rapid. Therefore, motor corrections have to be done after the movement by trial and error: saccade accuracy is then maintained by changes in saccadic gain. Experimentally, saccadic adaptation is studied by introducing an unnoticed target step during the saccade execution, in a double-step paradigm (Becker & Jürgens, 1979; McLaughlin, 1967), resulting in a discrepancy between the eye position and the post-saccadic target position. At first, a corrective saccade (i.e., a second saccade that brings the eye closer to the target) occurs to foveate the target. If this movement error is repeated across trials, the amplitude of the initial saccade will progressively change (either increase or decrease as a function of the induced error), so that it will land on the post-saccadic target position over some hundreds of trials (e.g., Straube & Deubel, 1995). A classic interpretation of this phenomenon is that it is due to a recalibration of the saccadic system based either on the post-saccadic retinal error (i.e., the distance between the target and the fovea; Optican & Robinson, 1980) or the prediction error (Bahcall & Kowler, 2000). However, several studies have demonstrated that this plasticity is not simply due to the visual position error but to a functional relationship between the behavior and its consequence. Madelain, Harwood, Herman, and Wallman (2010) demonstrated that saccadic adaptation (either decreased or increased gain) occurred even if a conflicting distractor was appearing at the post-saccadic location, resulting in no retinal error but a goal error. Therefore, the saccadic system was able to selectively adapt its gain to the relevant visual stimulus and ignore the competing ones; a conclusion that was later confirmed using complex natural image scenes in which the eyes ignored the background and selected only the target displacement (Madelain, Herman, & Harwood, 2013). To demonstrate that it is the reinforcing effect of target selection that induces the saccadic changes, Madelain, Paeye, and Wallman (2011) designed a novel paradigm to induce saccadic adaptation without double-step stimuli. They manipulated the functional consequences of saccadic amplitude with two types of reinforcers: visual and auditory. The procedure consisted in extinguishing the target when the saccade was initiated and to deliver reinforcement (either a tone signaling monetary gain or a visual target located at the eye location) depending on the saccade amplitude. Both type of reinforcers yielded a consistent decrease in saccadic gain (Figure 20), similar to what is classically retrieved in a double-step paradigm (Rahmouni & Madelain, 2015).

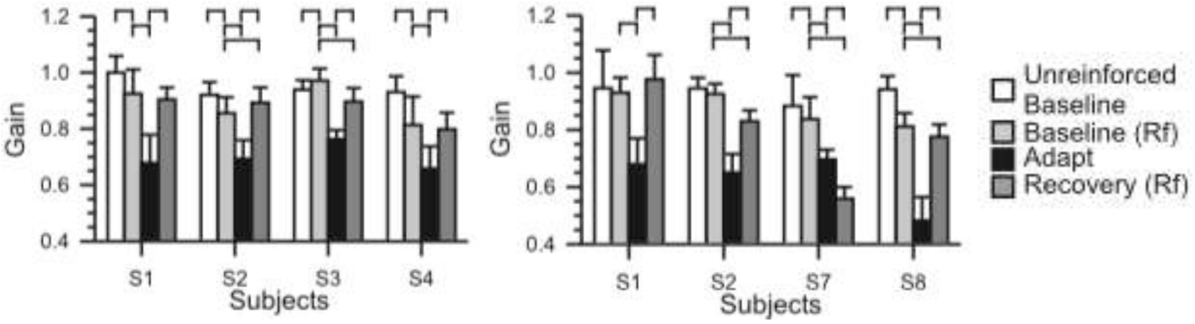

Figure 20: From Madelain, Paeye, & Wallman (2011). Mean and SD saccadic gain for each subject in target view reinforcement (on the left) and in auditory reinforcement with target view after every saccade (on the right).

Further establishing the effect of reinforcement on motor learning, Kojima and Soetedjo (2017) observed that when they provided a reinforcer after the corrective saccade for one saccade direction and not the other one in a double-step paradigm with monkeys, the saccadic adaptation on the reinforced side was much faster. Less explicitly, Meermeier, Gremmler and Lappe (2016) used visual reinforcement on saccadic adaptation. In a double-step paradigm, participants made saccade toward stimuli that could be either noise patches or pictures of women (Figure 21A). At saccade onset, the stimuli stepped at 4° from their initial location and could be masked by a different noise patch in three different conditions (Figure 21B): immediately at saccade onset (Im), 200ms after saccade onset (Inter) or they were always visible (Never). In the Inter condition, given that the average saccade duration was 55ms, the target could hardly be seen at the beginning of the learning because of the corrective saccade occurrence. However, with the change in the saccadic gain over trials, the participant had more time available to see the target. Similar to what was observed in the urgency task of Montagnini and Chelazzi (2005), the time constraint on the availability of visual information created an establishing operation (EO, i.e., any environmental variable that increases the reinforcing effectiveness of some stimulus, such as hunger when using food for reinforcement; Michael, 1982, 1983), which altered the effectiveness of the visual stimulus as a reinforcer. Thus, results showed that the learning was faster with women stimuli in the Inter condition than in the two other conditions, as for seeing the target before it was masked effectively selected the progressive change in saccadic adaptation. Additionally, the EO could also explain why a novel stimulus is more effective than a repetitive one in reinforcing faster saccadic adaptation (Meermeier, Gremmler, & Lappe, 2017). Indeed, the constant use of the same stimulus as a reinforcer can induce a satiety for that stimulus, which will therefore not act as a reinforcer anymore (this is true for food but also for several stimulus: for instance, seeing one's favorite movie once versus seeing it several times in a row). The repetitive use of the same stimulus created on the one hand an abolishing operation (AO, i.e., any environmental variable that decreases the reinforcing effectiveness of some stimulus; Michael, 1982, 1983), which altered the effectiveness of the repetitive visual stimulus as a reinforcer and, on the other hand, an EO for the novel stimulus.

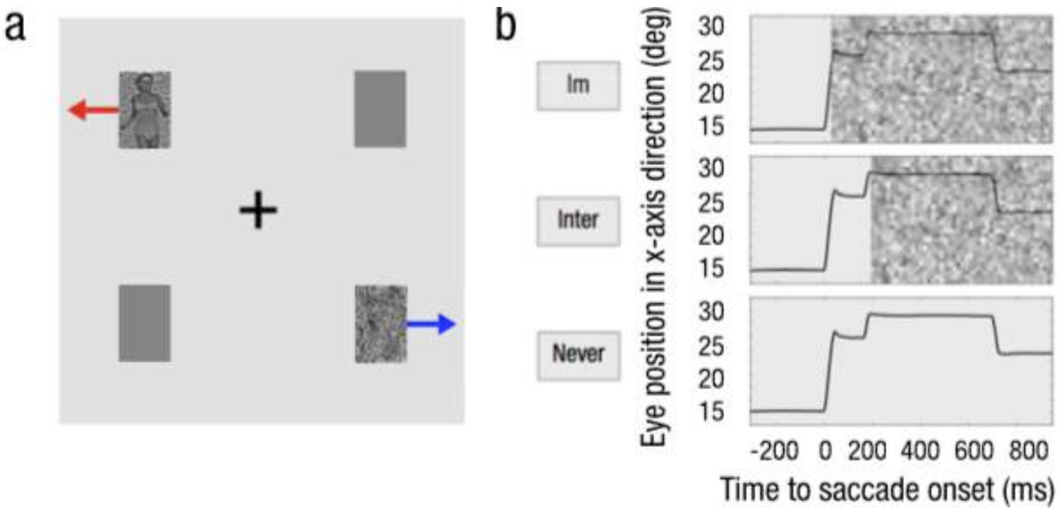

Figure 21: From Meermeier et al. (2016). A) Illustration of the stimulus arrangement in an example trial. The meaningful image is on the left; the noise stimulus is on the right side. Upon detection of a saccade toward the top left corner, all stimuli stepped 4° to the left (red arrow). Upon detection of a saccade toward the bottom right corner, stimuli shifted towards the right (blue arrow). B) Timing of the mask onset for the three masking conditions in reference to the eye position trace of a rightward scanning saccade and corrective saccade. In immediate masking (Im), the mask appears at saccade onset. In intermediate masking (Inter), the mask appears 200ms after saccade onset.

Recently, Rahmouni, Montagnini and Madelain (2017) conducted an experiment without a position error (since the target was extinguished at the saccade onset without reappearing at its offset) or explicit extraneous reinforcer (e.g., money or tone) to confirm the reinforcement interpretation of saccadic adaptation. After looking at a fixation point displayed on a background covered with irrelevant symbols, participants had to make a saccade toward a target. At saccade onset, the target was extinguished for the remainder of the trial. The post-saccadic background depended on the actual amplitude gain of the saccade. If the gain was within the criterion (either increasing or decreasing depending on the experimental condition), the background was covered with one of the four targets (E, 5, 3 or 2) for 60ms. Otherwise, the background was filled with one of the four irrelevant items (Figure 22). At the end of the trial, participants performed a visual discrimination in a four-alternative forced choice (4-AFC) task in which they had to select the target stimulus displayed on the background. By design, the task was feasible only if the saccadic gain had reached the criterion. Results demonstrated that this gaze-contingent paradigm was drastically effective in modulating saccadic amplitudes in the absence of post-saccadic position error signals. This study supported the fact that the motor learning happening during saccadic adaptation is selected by the functional consequences, i.e., here, the ability to perform a visual discrimination task. Overall, the experiments presented here demonstrate that it is the reinforcing consequence of target selection (i.e., landing near the target) that selects the saccadic gain and induces a discriminative control of this behavior over trials.

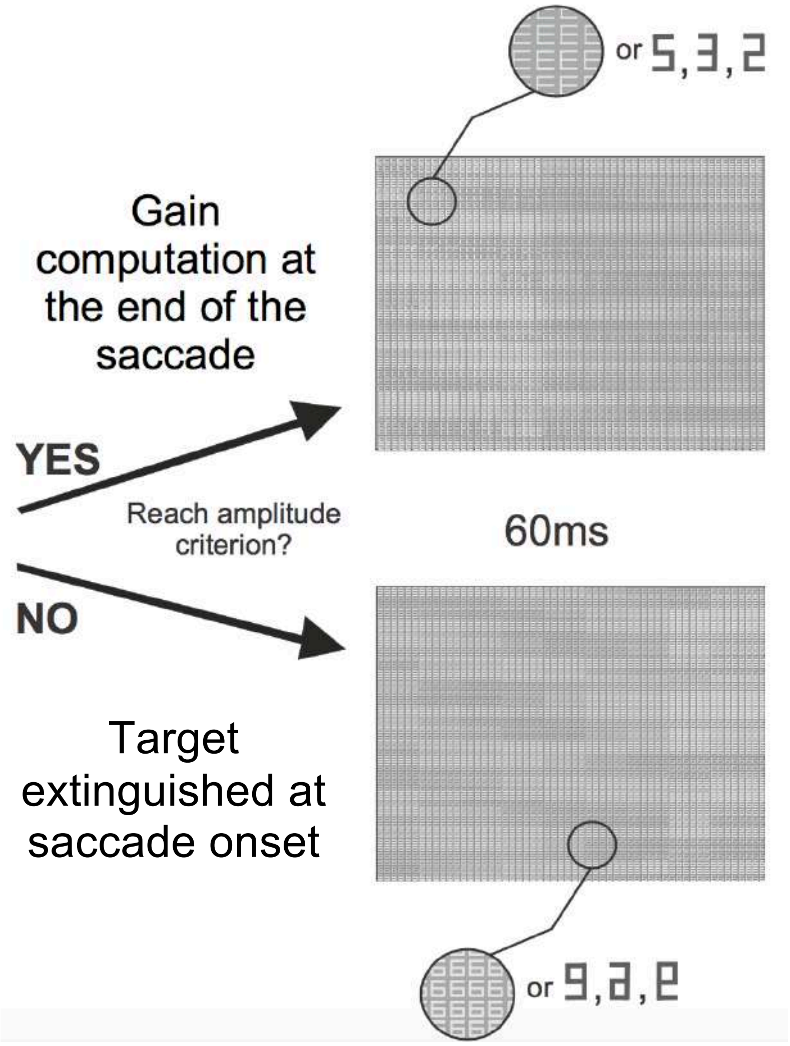

Figure 22: From the poster of Rahmouni, Montagnini, & Madelain (2017). Illustration of the gaze-contingent paradigm. The background display was covered by irrelevant items before the saccade. The participant fixated a fixation point and had to saccade toward a target onset. During the saccade, the target was extinguished and the items displayed on the post-saccadic background depended on the actual saccadic gain. The background was covered with one of the four targets (E, 5, 3 or 2) for 60ms if the gain was within the amplitude criterion or with one of the four irrelevant items if the amplitude did not reach the criterion. Then, the participant had to report in a 4-AFC the target that was displayed on the background.

2.1.3. The discriminative control of saccadic adaptation: differential saccadic responses can be placed under stimulus control

Discriminative control of saccadic adaptation has been investigated for decades to understand the mechanism of maintenance of saccade accuracy in response to new sensorimotor contingencies and determine what antecedent stimuli can control this motor learning. So far, it has been assumed that some cues can control differential saccadic adaptation, but not all. For instance, Azadi and Harwood (2014) conducted several experiments in different contexts to probe which antecedents could differentially control saccadic adaptation. During their task (Figure 23A), participants had to look at a fixation ring while a target was circularly moving around the fixation point. At the fixation offset, they had to make a saccade in the direction of the target in order to intercept it. During motor learning, the target jumped either inward or outward at saccade onset in order to induce differential amplitude decrease or increase, respectively. Three different contexts were used in the double-step paradigm to investigate discriminative control over differential saccadic adaptation (Figure 23B): 1) the direction of the moving target (gain-increase for clockwise and gain-decrease for counterclockwise), 2) the velocities of the moving target (gain-increase for high velocity and gain-decrease for low velocity), and 3) the color and shape of the moving target (gain-increase for green square and gain-decrease for red circle). Differential saccadic adaptation as a function of the discriminative stimuli was only observed when using the target motion, i.e., directions and velocities; no motor learning was obtained when the color and shape were manipulated. Azadi and Harwood's results replicate the ones found by Bahcall and Kowler (2000) and Deubel (1995) who did not observe any context-specific adaptation for target shape and color. Recently, Cecala, Smalianchuk, Khanna, Smith, and Gandhi (2015) provided further data to support the conclusion that target visual features cannot control differential saccadic adaptation. On the contrary, visual hemifield (Alahyane & Pélisson, 2004), depth in vergence (Chaturvedi & Van Gisbergen, 1997), head position (Shelhamer & Clendaniel, 2002), or gravity (Shelhamer & Clendaniel, 2003) can induce a discriminative control of saccadic adaptation.

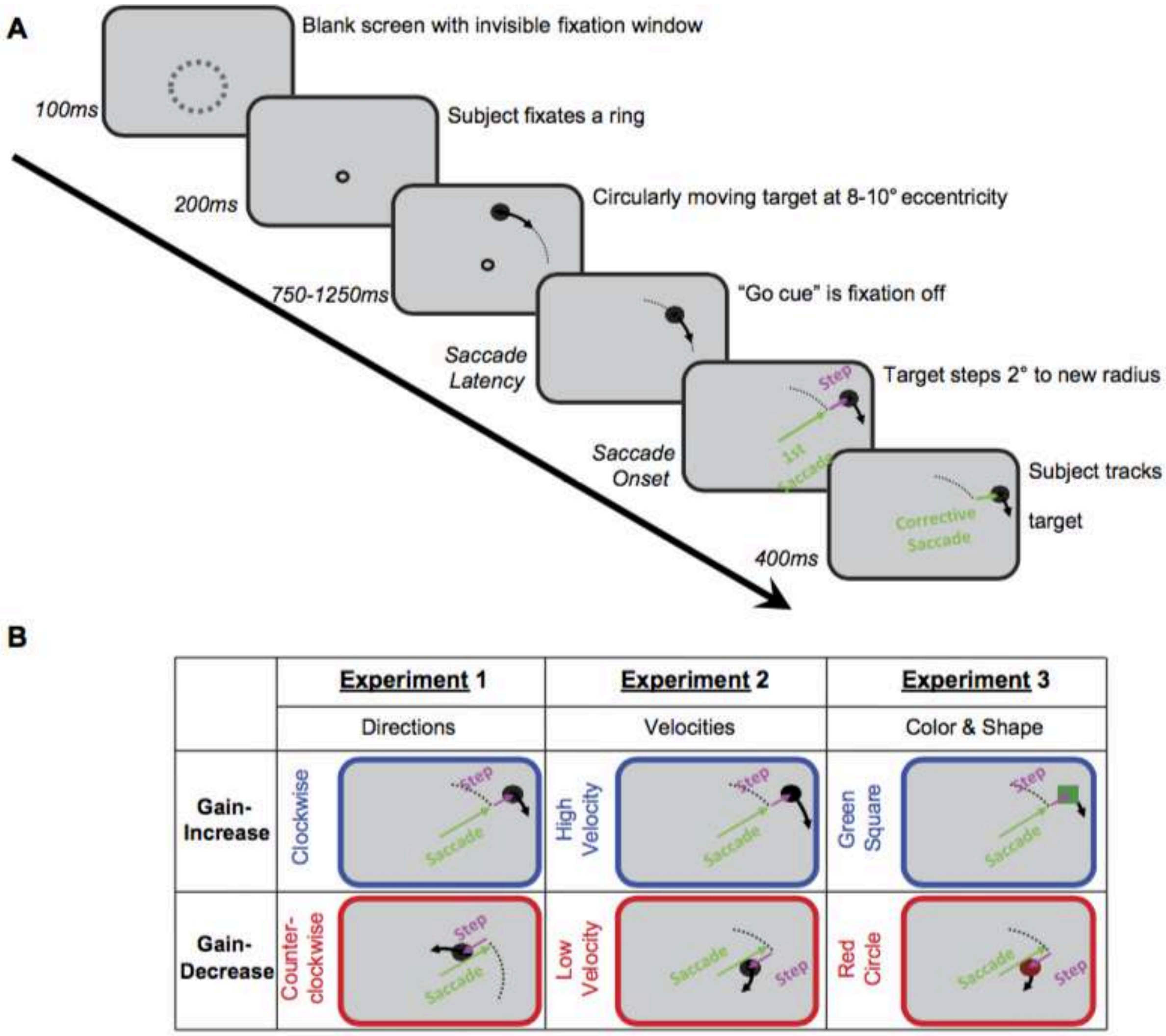

Figure 23: From Azadi & Harwood (2014). Experimental design. A) Schematic of a trial in adapting phases. The ring with dashed line in the first schematic screen shows the invisible boundary that subjects need to fixate inside of for 100ms for the black fixation ring to appear. After 200ms further fixation the moving target appears; the black arrow shows its movement direction. Fixation off, used as "Go cue", at a random time between 750 and 1250ms. The target stepped 2° on saccade onset (pre- and post-adapting phases did not contain this target step). Subjects usually made corrective saccades and finally pursued the target for 400ms until it disappeared. B) Examples of the 3 presaccadic contexts and their target steps on saccade onset. Experiment 1: direction was used as context; targets stepped outward in clockwise and inward in counterclockwise moving directions. Experiment 2: velocity was used as context; high velocity targets stepped outward and low velocity targets stepped inward. Experiment 3: shape and color were used as context; moving green squares stepped outward and moving red circles stepped inward. In all 3 experiments, the reverse conditions (the other combinations of step direction and contexts) were counterbalanced across subjects.

Rahmouni, Jozefowiez and Madelain (2016) suggested that the rationale behind these varying outcomes was the biological relevance of the context for the saccadic system; the target features triggered the same motor response whereas the other contexts, such as target directions, rested upon different activations of extraocular muscles. Indeed, biological constraints are known to have profound influences on operant conditioning (e.g., Domjan & Galef, 1983). Thence, the authors designed a novel double-step paradigm in which they added a distractor to force the selection of target features (Figure 24A). At saccade onset, the target was extinguished as in typical double-step paradigm and jumped upward or downward while a distractor appeared at the opposite location. Importantly, the color of the target was consistently reliable regarding the second target step in the experimental condition (e.g., on Figure 24A, the red disk always stepped upward and the green disk downward). In the control condition, when there was only the target, there was no differential saccadic adaptation between target colors. However, when a relevant distractor was introduced, the target colors differentially controlled the saccadic adaptation. The authors replicated the effect on motor learning with both colored and colorless shapes (i.e., triangle or cercle). Interestingly, when they conducted a conflict condition, with varying colors and shapes, the effect disappeared (except for one participant). In this condition, only the shape of the target was consistent with the post-saccadic possition (i.e., the circle would always step upward and the circle downward); the color of the target was not correlated with the post-saccadic position (Figure 24B). With this manipulation, the distractor does not induce target feature relevance anymore as it causes a conflict between two features of the initial target. On the contrary, it provokes a competition between the two discriminative stimuli blocking the learning of the relation between target shape and the post-saccadic position. This conflict is close to the overshadowing phenomenon, in which a more salient component of a compound stimulus is said to overshadow conditioning to the less salient component (Mackintosh, 1976; Pavlov, 1927).

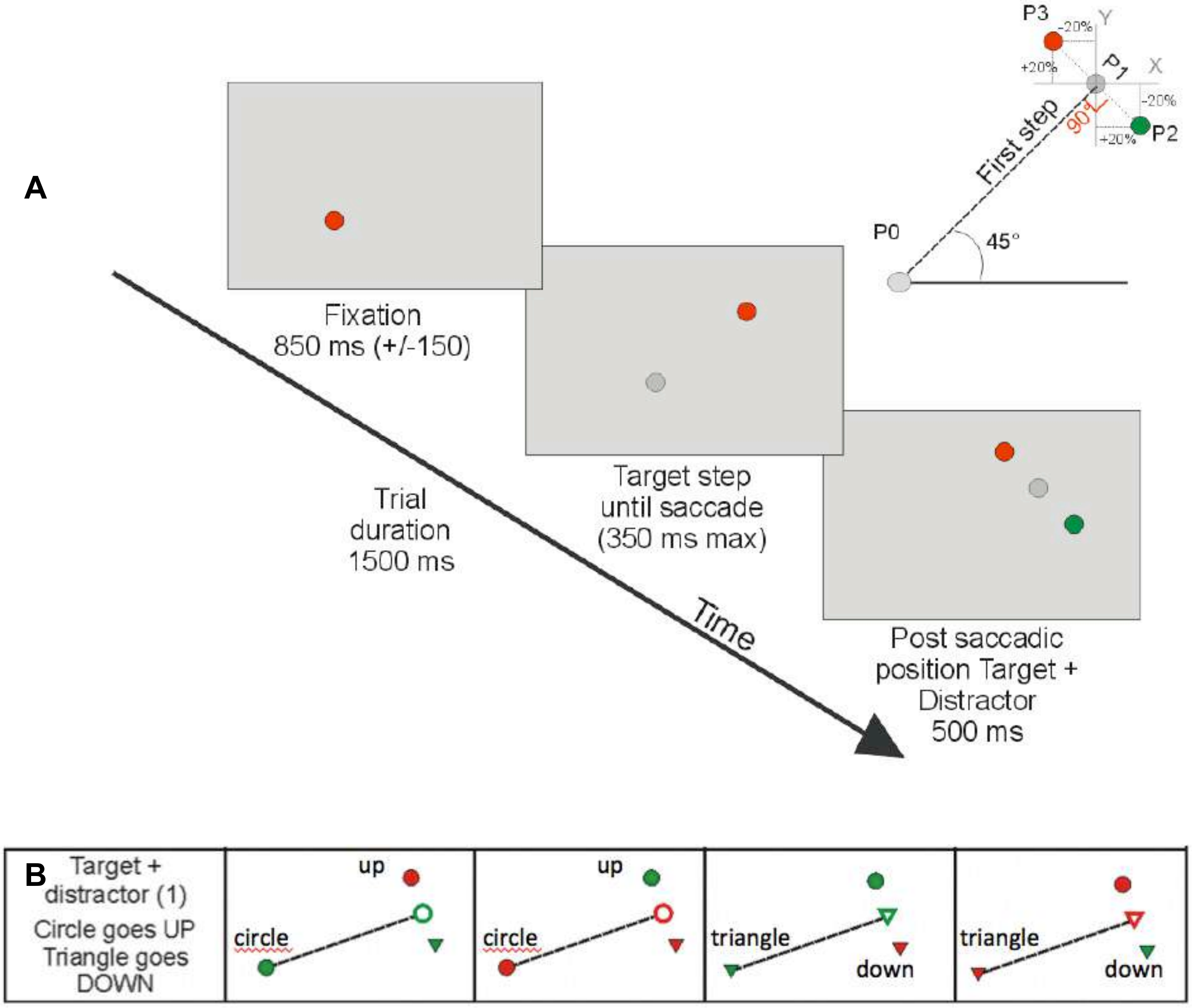

Figure 24: From the poster of Madelain, Jozefowiez, & Rahmouni (2015). A) Illustration of the double-step paradigm with a distractor, appearing at the opposite location of the second target step. The authors used the angle of the saccade instead of the usual saccade amplitude. The color here is the discriminative stimulus for the differential saccadic adaptation: red and green target were supposed to control angle-increase and angle-decrease, respectively. B) Illustration of the procedure in the conflict condition. Only the shape of the target is consistent with the post-saccadic position while the color of the target became the one of the distractor (without being consistent regarding the step direction).

This thesis section has reviewed the studies demonstrating that where to one moves one's eyes is controlled by reinforcement contingencies, whether this motor learning stems from instrumental or classical conditioning. The question that ensues from this spatial plasticity of the saccadic system is whether the same outcomes can be retrieved with another dimension of saccades: to wit, the saccadic reaction times. This question is highly relevant given that they are typically used to understand and quantify decision processes.

2.2. Effect of reinforcement on temporal allocation of saccades

Although the emphasis has been mainly put on spatial adaptation and target selection so far, some studies have exclusively investigated the temporal adaptation of saccades to the environment. Reinforcement is assumed to be one of the main factors guiding plasticity and perceptual learning (Roelfsema, van Ooyen, & Watanabe, 2010) and the temporal learning discussed in this section is incidentally thought to be at play outside the laboratory with sportsmen (Ceyte, Lion, Caudron, Perrin, & Gauchard, 2017; Di Russo, Pitzalis, & Spinelli, 2003; Khanal, 2015; Land & Mcleod, 2000; Zhang & Watanabe, 2005) or video-gamers (Chisholm & Kingstone, 2015; Mack & Ilg, 2014).

2.2.1. Using reinforcement on saccades incidentally impacts the temporal dimension of saccades

The first experiments highlighting the direct effects of reinforcement on the temporal dimension of saccades were mainly with monkeys as it is customary to use primary reinforcers (such as food or juice) to keep them involved in the experimental task while studying the neural circuits underlying these behavioral tasks. For instance, Lauwereyns, Watanabe, Coe, and Hikosaka (2002) studied the neurons involved in a spatially selective response bias depending on the expected gain. The behavioral task was quite simple; monkeys were required to make a saccade toward a target, which could appear leftward or rightward with respect to the center of the screen. They gave an auditory feedback when the monkey looked at the target, in addition to a systematic drop of water only for one saccade direction (Figure 25A). The reinforcement contingency changed automatically every 20 trials with a reversal in reinforced screen side. Saccadic latency distribution shifted toward shorter values and its spread was smaller for the reinforced location than the non-reinforced one (Figure 25B). The transitions during the reversal were maybe one of the most interesting features of the experiment, suggesting that saccadic latency could be an operant dimension of saccades. Indeed, when the saccade direction began to be reinforced, the saccadic reaction times drastically decreased by ~100ms immediately after experiencing one trial with the new contingency and barely varied (Figure 25C). However, when the reinforcement contingency switched between target positions, the increase in SRT was much slower –reaching a peak at the fifth trial– and the variation in latency increased (between 280ms and 350ms). These changes in saccade latency are typical of what happens in instrumental conditioning. On the one hand, the contingent presentation of the drop of water reinforced saccadic latencies and selected short values. On the other hand, the progressive increase of SRTs is typical of what happens in an extinction procedure. Extinction of an operant response consists in the non-presentation of the functional consequences, i.e., the reinforcer that was previously contingent on the behavior. This procedure is used to decrease and eventually suppress the behavior occurrence (note that the behavior in question here is the saccadic reaction time, not the saccade itself) but is also known to induce two side effects. The first one is a retention of the behavior for a short bout, often associated with a burst in responses; this is what was observed since the SRT did not increase by ~100ms after one trial. The second effect is to induce behavioral variability (Neuringer, Kornell, & Olufs, 2001) that is viewed as an evolutionist advantage as it increases the probability of emitting a behavior that might be selected by the environment; this is also what was observed during the non-reinforced trials.

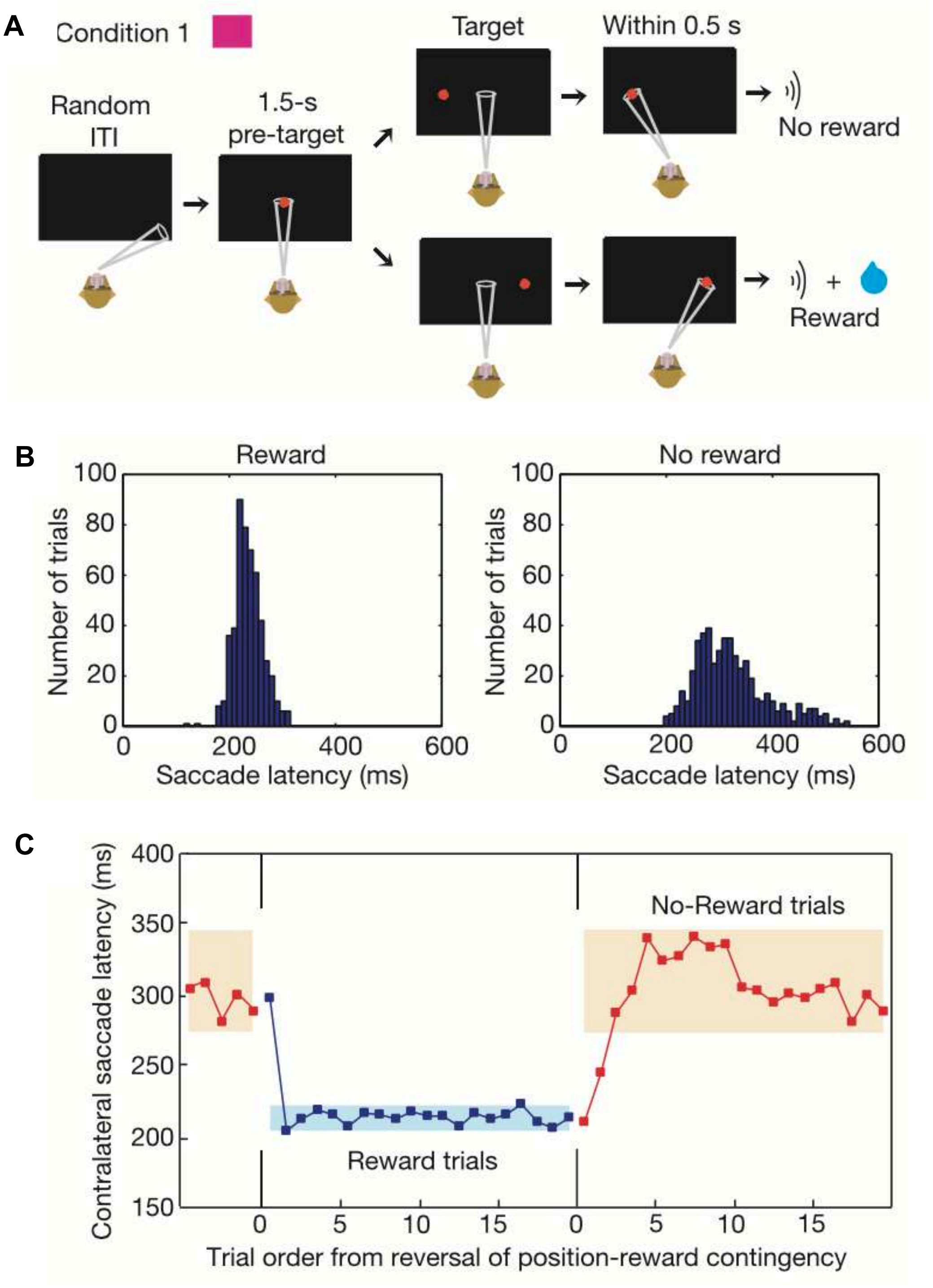

Figure 25: From Lauwereyns et al. (2002). Experimental design of the biased task. A) Sequence of events in condition 1, in which only correct rightward saccades are reinforced. B) Density function of saccade latency in reinforced trials versus non-reinforced trials (data from monkey 1, rightward saccades). C) Adaptation of behavior to a reversal of the reinforced-position contingency. Latency for contralateral saccades as a function of trial order from reversal of reinforced-position contingency. Blue data indicate reinforced trials; red data indicate non-reinforced trials. Colored backgrounds indicate the areas ± 2 SD from the mean in trials 6-20 (light blue, reinforced trials; light orange, non-reinforced trials).

In addition, the differential responding in SRTs between saccade directions suggests that the saccadic latencies were placed under discriminative control (i.e., location of the target). The discriminative control of saccadic latencies has been recently supported by Kojima and Soetedjo (2017): in addition to observing a differential learning rate of saccadic adaptation, they obtained shorter latencies for the only side of the screen that was reinforced.

The incidental effect of reinforcement on saccadic reaction times was also retrieved by Takikawa, Kawagoe, Itoh, Nakahara and Hikosaka (2002) in a biased memory-guided saccade task with four locations and by Watanabe, Lauwereyns and Hikosaka (2003) in a biased visually-guided saccade task. While monkeys fixated the center of the screen, a cue would briefly appear at one of the four possible target locations and, at the fixation point offset, they were required to saccade to the memorized location. The target reappeared 400ms after fixation offset and if the eye was within 3° around it, they received an auditory feedback. Out of the four locations, only one was reinforced with a drop of water simultaneously with the tone. The authors observed that when the saccade was reinforced, the SRT was shorter (on average by 25ms), the peak velocity was drastically higher (by ~150°/s) and the error rate was lower (near 2%) while there was no change in saccadic amplitude. These results, together with those of Ikeda and Hikosaka (2007), therefore suggest that it is possible to obtain shorter latencies without any change in saccadic amplitude, which is contradictory to the conventional speed-accuracy trade-off. Interestingly, Nakamura and Hikosaka (2006), later retrieved by Milstein and Dorris (2007) with humans, reported that the magnitude of reinforcement also modulated saccadic latencies, as they observed shorter SRTs for the saccade direction associated with large reinforcer gain (i.e., 0.4 mL of water/juice) than for the one associated with small reinforcer gain (i.e., 0.05 mL). Several studies have demonstrated that monetary gain can have a reinforcing effect on saccadic latencies with humans as well. For instance, Liston and Stone (2008) conducted a biased 2-AFC perceptual task, in which observers were required to look at the brightest of two stimuli and received auditory reinforcement when their choice was correct (exchangeable for money at the end of the experiment). The reinforcement schedule was however not equal between the two stimulus locations: for a given position, the probability of reinforcement was 10%, 50% or 90% (i.e., relative reinforcement rate of 1/9, 1/1 or 9/1) depending on the actual condition. In addition to observing a biased saccade direction for stimulus position with the larger reinforcement rate (which incidentally suggests that one can bias perceptual visual decision using reinforcement as it is feasible for time perception; Cambraia, Vasconcelos, Jozefowiez, & Machado, 2018; Morgan, Killeen, & Fetterman, 1993), the authors also observed shorter reaction times with no change in saccadic amplitudes. Dunne, Ellison and Smith (2015) investigated the effect of intermittent reinforcement on saccades. In their experiment, observers received points (i.e., the reinforcer) only for one saccade direction with a variable ratio schedule requiring on average 1.67 response for reinforcement delivery (i.e., out of the 300 reinforced-direction trials, 60% were actually reinforced). Results showed that even with an intermittent reinforcement schedule, shorter SRTs were selected for the reinforced direction (Figure 26). Interestingly, this outcome maintained for three blocks (i.e., 180 trials) when reinforcement was withdrawn (from block 13) before recovering to the same mean SRT as during baseline. It is noteworthy to point out that the modulation of saccade latencies with reinforcement has also been observed with arbitrary reinforcers, such as points (Chen, Mihalas, Niebur, & Stuphorn, 2013; Dunne et al., 2015), or with information (Bray & Carpenter, 2015; Daddaoua et al., 2016). Some experiments pointed out that human faces could act as a reinforcer on reaction times and peak velocities compared to neutral stimulus or noise patches (Meermeier, Gremmler, Richert, Eckermann, & Lappe, 2017; Rothkirch, Ostendorf, Sax, & Sterzer, 2013; Xu-Wilson, Zee, & Shadmehr, 2009), yet the effects were quite small (differences in latency around 8ms) and could not always be replicated. Collins (2012) demonstrated that visual information could also be reinforcing for saccade latencies. Observers received a visual feedback (i.e., seeing the target) for one saccade direction and no visual feedback (i.e., the target was extinguished) for the other one, which reduced the saccade latency by 35ms when the feedback probability was 1 for that saccade direction. However, when the contingency was withdrawn (i.e., the probability of the target offset was identical on the left and right sides), saccadic latencies were similar between saccade directions. This experiment highlighted the effects of the ability to see a post-saccadic target as a reinforcer.

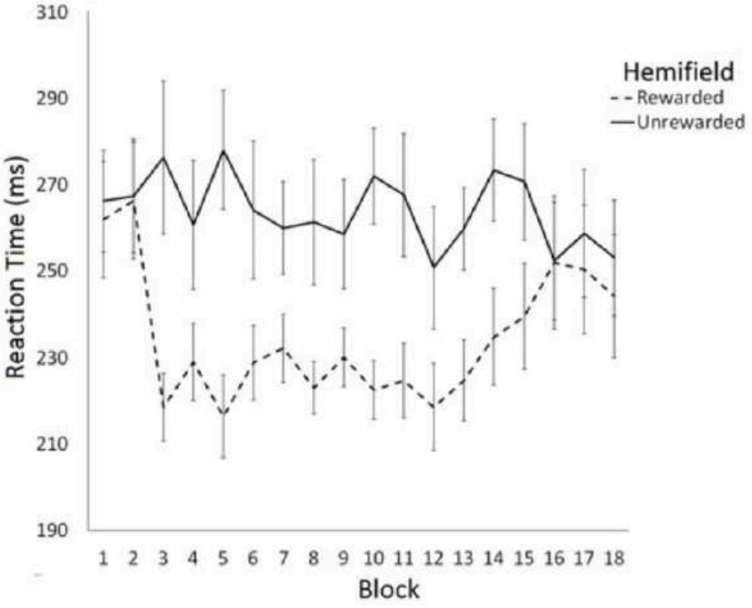

Figure 26: From Dunne et al. (2015). Latency of saccades to the reinforced and non-reinforced hemifields across baseline (blocks 1-2), conditioning (blocks 3-12) and test (blocks 13-18). Error bars show ±1 standard error of the mean.

2.2.2. Reinterpreting the conventional determinants of saccade latency as antecedent stimulus

We have previously reviewed in chapter 1 that cues and warning typically facilitates saccade, ensuing shorter reaction times for target selection. They have been categorized as top-down factors since they seem to be under the control of the individual. However, Mulckhuyse and Theeuwes (2010) recently investigated the effect of subliminal cues on saccades. Observers had to saccade toward a target that could appear either to the left or right of the fixation point; before target onset, a stimulus displayed for 16ms cued the side on which the target would appear. Importantly, participants were not able to report the orientation of the cue, indicating that it was subliminal. The authors observed that cueing the target location caused slightly shorter saccadic latencies (i.e., on average 311ms) than when the cue was invalid (i.e., 321ms) or neutral (i.e., 317ms). Two conclusions can be drawn here. First, the effect on saccadic latency without reinforcement is, albeit significant, quite small. Second, because subliminal cues were used, the typical explanation of a conscious control of SRTs cannot be used. It is noteworthy that behavioral selection does not need awareness to happen.

A challenging phenomenon in the literature remains the occurrence of express saccades, that is saccades with extremely short latencies. So far, the express saccades are mainly explained by the fact that the early removal of a fixation point (gap paradigm) enables a decrease in fixation-related activity of the superior colliculus and therefore facilitates the sensory integration for the target stimulus (Dorris & Munoz, 1995; Munoz & Wurtz, 1992, 1993; Reuter-Lorenz et al., 1991). Although this hypothesis is sensible, some experiments have shown that it cannot be the sole reason. Iwasaki (1990) conducted an experiment to compare the effect of a gap paradigm with a step paradigm (i.e., no SOA between fixation offset and target onset) on saccadic reaction time (SRT) and manual reaction time (MRT). He replicated the well-known gap effect on SRTs and observed express saccade latencies with a peak around 100ms (Figure 27). However, the MRT distribution for the naïve participant was unaltered and there was a shift of ~30ms for the other participant, who was the author. The classical interpretation of express saccades is that the gap facilitates the sensory integration of the target stimulus; there is no remit for saccade decision or saccade execution, which also add time to latencies. Therefore, according to this stance, the gap paradigm should induce a latency shift regardless of the motor behavior, which was not observed in this experiment. In addition, the naïve participant also presented some express saccades during the step paradigm when there was no early fixation offset. A more recent experiment of Bibi and Edelman (2009) demonstrated that it is possible for humans naïve to oculomotor experiments to make express saccades in a step paradigm with a brief training. With a biofeedback, observers moved from making saccades around 160ms to producing latencies around 110-120ms in 288 trials. Most interestingly, Jóhannesson, Edelman, Sigurþórsson and Kristjánsson (2018) conducted a study to investigate the extent of effects of saccade training on express saccades. Their experiment consisted in training solely the dominant eye with a gap paradigm and probing in a step paradigm whether there was a retention of the saccadic latencies in the dominant eye and a transfer of express saccades to the untrained eye. After training, results showed that mean SRTs for the dominant eye decreased by 50ms and the proportion of saccade express doubled in probe trials. Surprisingly, the SRTs for the untrained eye had the exact same modulation in probe trials. A plausible rationale behind these results would be that the gap in this training acted as an unconditional stimulus (US) eliciting an unconditional response (UR), which is the shorter SRTs; and that after repeatedly pairing saccade onset (i.e., NS, neutral stimulus) with the US, it became a conditional stimulus (CS) able to elicit a conditional response (CR) similar to the UR. This classical learning (Pavlov, 1927) would account both for the outcomes in the probe trials with the dominant and untrained eyes. Stimulus control learned through classical conditioning could in addition explain why individuals are faster to locate fearful facial expressions and body postures (Bannerman et al., 2009).

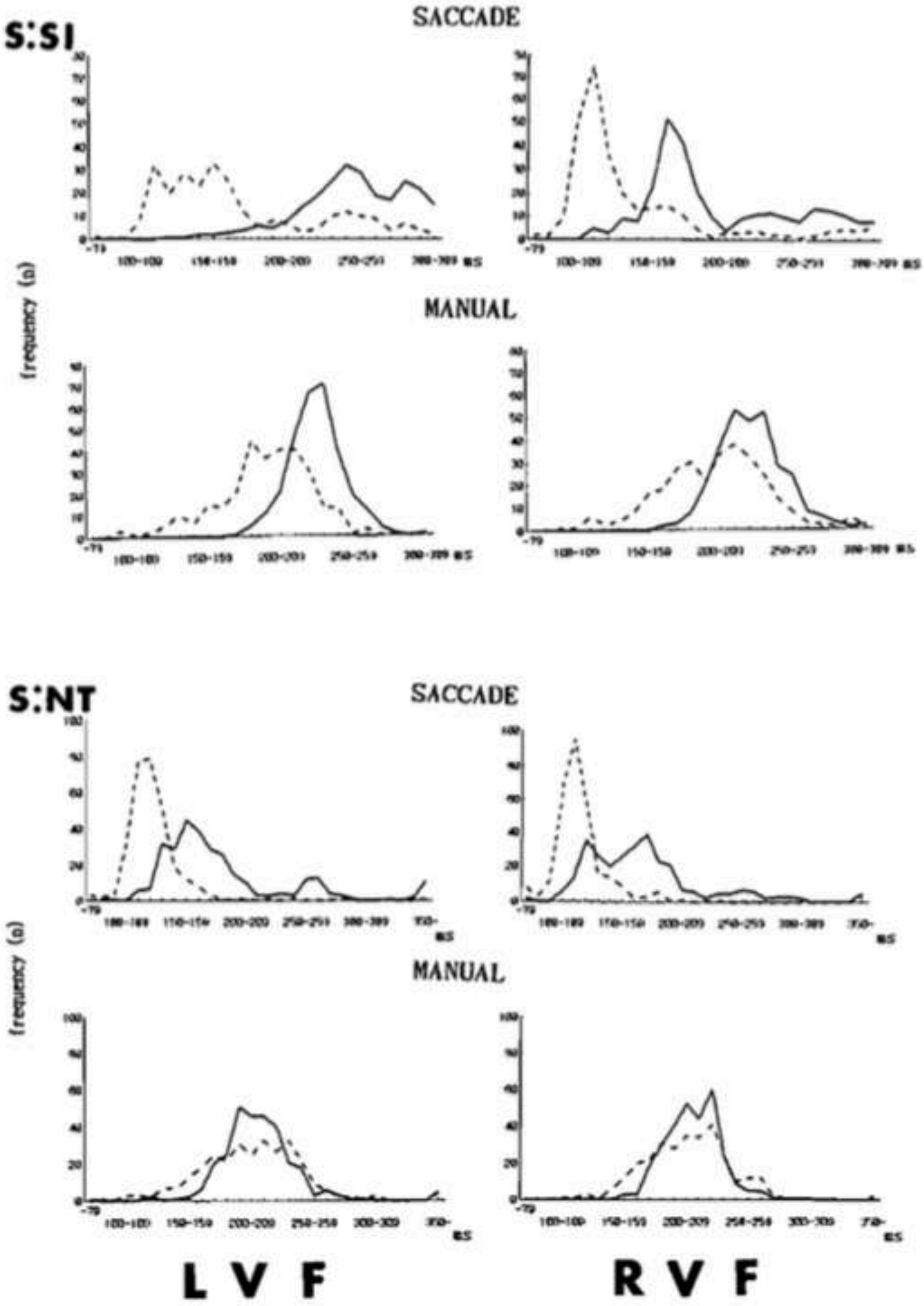

Figure 27: From Iwasaki (1990). Distributions of manual and saccadic reaction times. Each distribution was based on 300 trials. RTs were classified into 10ms bins. Solid lines were for step conditions and broken lines for gap conditions. LVF: left visual field, RVF: right visual field. S:SI and S:NT represent the two participants: the author and a naïve participant, respectively.

Finally, the size-latency phenomenon observed by Madelain et al. (2005), Harwood et al. (2008) and De Vries et al. (2016) demonstrated that the proportion between the amplitude step and the target size could evaluate and describe increased SRTs. For instance, for a given amplitude step of 1.5°, a 1° diameter ring represents a step-size ratio of 1.5, and a 5° diameter ring represents a step-size ratio of 0.3 (Figure 28A). When an observer attends to the small target, the proportion of new area is large (i.e., ≥ 1, there is no overlap between the fixation and target stimuli) whereas when attending to the large target, the proportion of new area is small (i.e., < 1, there is some overlap). When saccadic latencies, which varied according to target size and amplitude step (Figure 28B), are plotted as a function of this step-size, all data points collapse along a consistent curve (Figure 28C). Saccadic latencies increase when the ratio is inferior to 1 and tend towards an asymptote when the ratio ≥ 1. It is noteworthy that for a given amplitude step or target size, the authors observed both regular and long latencies. The difference in latencies observed between the two ratios might be explained by the cost versus benefit of deferring a saccade. On the one hand, the cost of making a saccade is possibly fixed, particularly in the case of laboratory settings, and related to the saccadic suppression during the eye flight, the energy deployed in the motor behavior (Binda & Morrone, 2018) or the commitment costs since choosing to gaze to a target implies not gazing at all other possible targets. On the other hand, the benefit is variable. If the step is large relative to the size of the object (e.g., a fly moving by 1m), the visual information in the foveal field has changed; the benefit of a saccade is high and causes regular latencies. If the step is small relative to the size of the object (e.g., en elephant moving by 1m), the visual information has not changed much in the foveal field; the benefit of a saccade is low and causes long latencies. Therefore, our hypothesis behind this phenomenon is that latencies are function of an implicit cost-benefit relationship: the step-size ratio acts as a discriminative stimulus signaling the availability of reinforcement (new visual information).

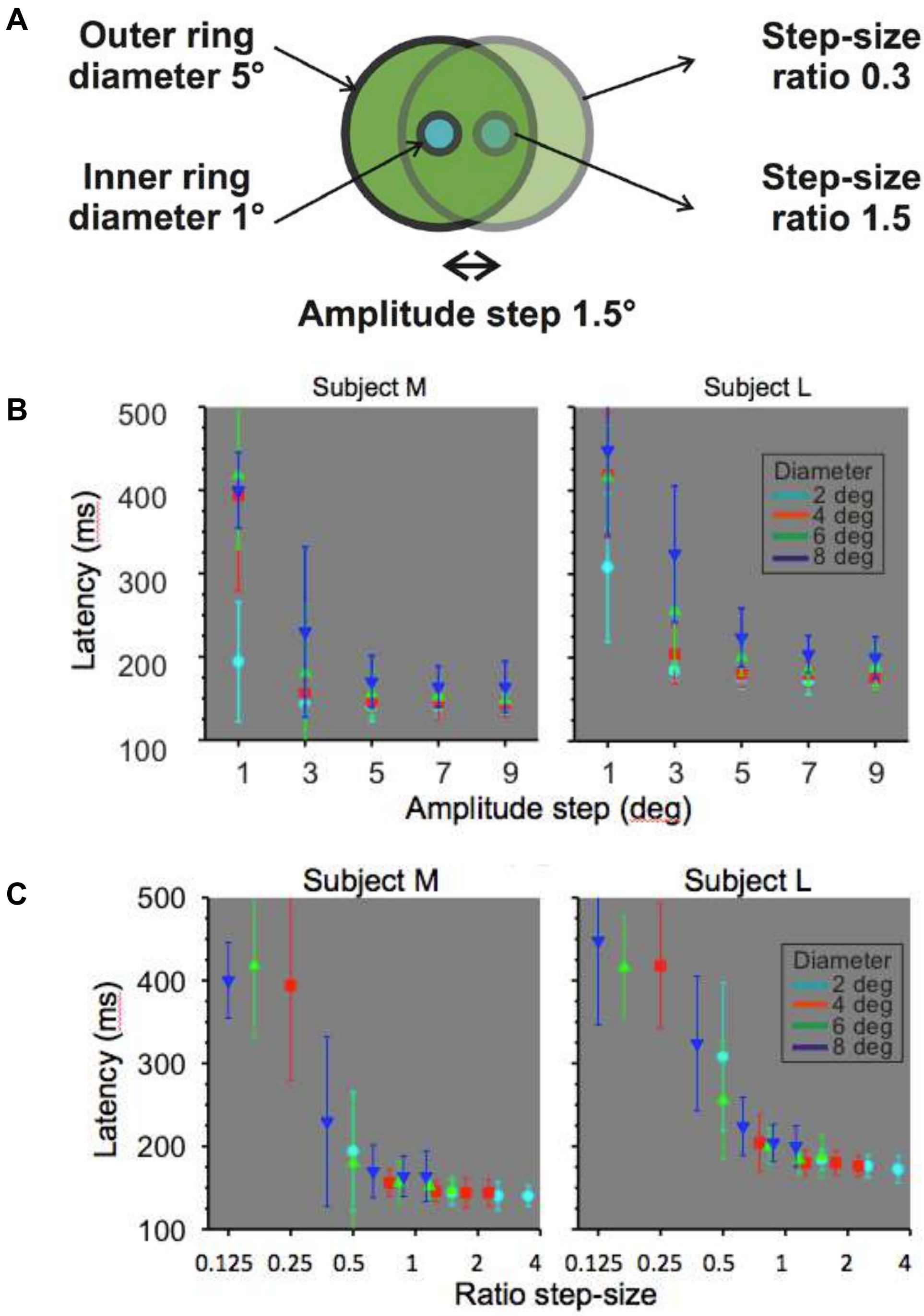

Figure 28: A) Illustration of step-size ratios of 0.3 (in green) and 1.5 (in blue) for an amplitude step of 1.5°. If an observer attends to the inner ring (1° of diameter), the ratio will be larger than 1 (some overlap between the fixation and target stimuli); the proportion of new area is small. If an observer attends to the outer ring (5° of diameter), the ratio will be smaller than 1 (no overlap between the fixation and target stimuli); the proportion of new area is large. B) Data reproduction from Harwood et al. (2008). Saccadic latencies for the different target diameters plotted as a function of amplitude step for two participants. C) Data reproduction from Harwood et al. (2008). Saccadic latencies plotted as a function of the step-size ratio.

2.2.3. Direct effect of reinforcement contingencies on saccadic latencies

The studies reviewed so far did not use reinforcement contingent on saccade latencies per se, but rather on saccade occurrence in general. However, a few research have focused on establishing the reinforcement contingency requirement on the reaction times. The study of Montagnini and Chelazzi (2005), previously discussed for the impact of urgency on saccades, is the perfect example of the effects of temporal requirement on saccades. Observers first completed a control condition in which they had to look at a target as soon as it appears on screen, randomly between the left and right side of the screen (Figure 29A). The saccadic latency distribution in this condition (Figure 29B and Figure 29D) was used to establish individual latency requirements. During the experimental task, a visual discrimination had to be made at the post-saccadic position (Figure 29A). The stimulus to discriminate could either be a capital E or F, which appeared at the target position after a critical delay following target onset. This critical delay was individually set as a function of the median latency and duration of saccades in the control task. Since the average saccadic duration was 59ms and the average median latency 151ms during the control task, the average critical delay for letter onset was 210ms across participants. The letter remained on screen for only one refresh rate, which approximated 13ms. Therefore, for a participant to be able to complete the 2-AFC discrimination task, his eyes had to be on target position before letter onset, which meant having a saccadic latency inferior to the control median latency (i.e., on average 151ms). Thus, the reinforcement in this experiment was a natural and functional consequence for the saccadic system: being able to discriminate an object. The alteration of saccadic latencies with the addition of this discrimination task was critical (Figure 29C and Figure 29E), the median latency decreased by 32ms (which represented a 15.6% latency reduction with respect to the control median latency) with no systematic change in saccadic gain.

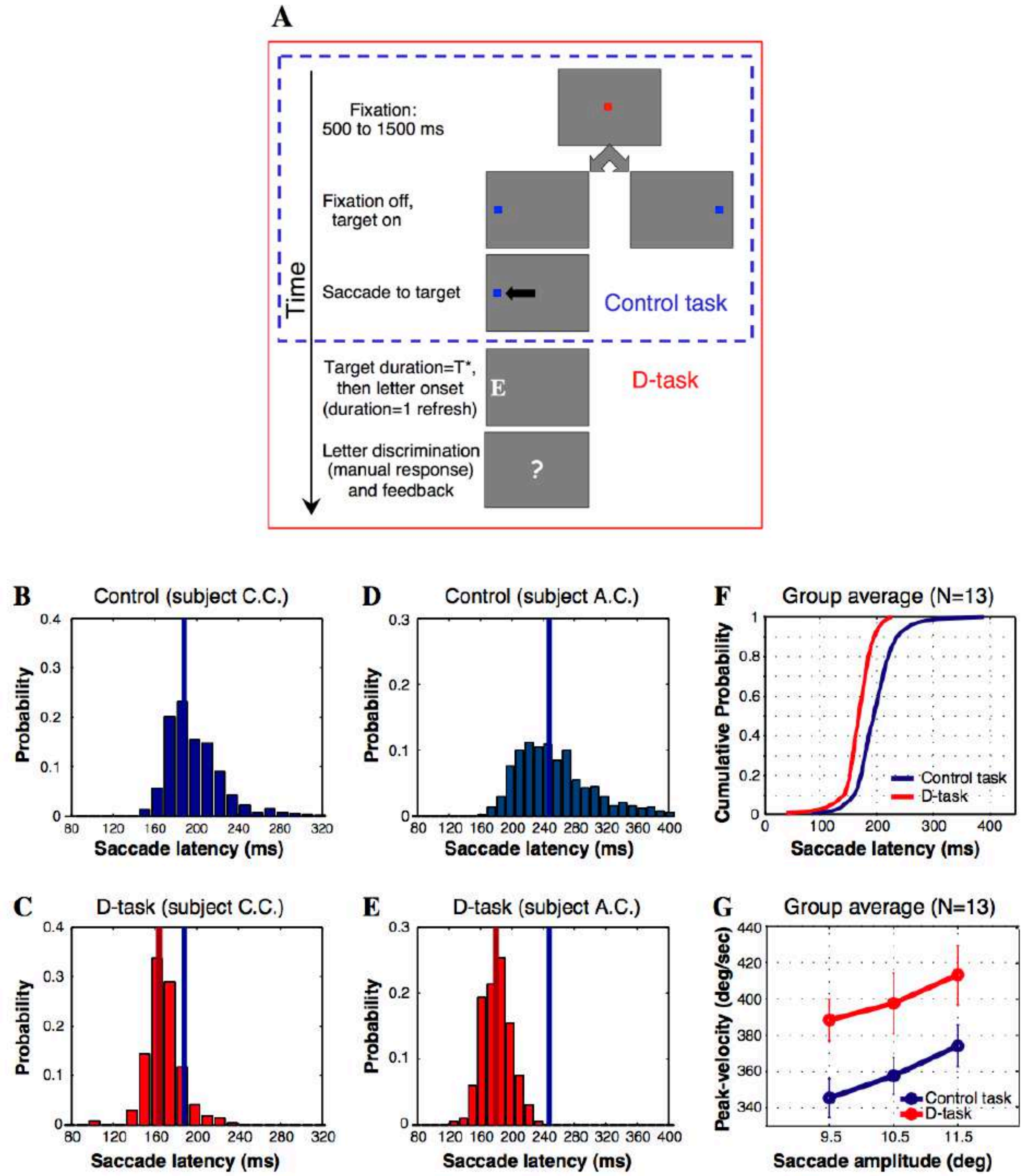

Figure 29: From Montagnini and Chelazzi (2005). The effects of perceptual urgency on saccadic latency and peak velocity. (A) We compared eye movements generated in a standard stimulus-elicited saccade task (Control task, schematically described within the blue dashed contour) with those generated when the observer is under time pressure to perform a speeded letter discrimination task at the location of the saccade goal (D-task red solid contour). The saccadic latency distribution histograms for two example observers are shown both in the Control (B and D), and the D-task (C and E). The blue vertical line in (B-E) represents the median latency computed in the Control condition, whereas the red vertical line in (C and E) represents the median latency in the D-task condition. (F) Group average cumulative distribution of saccadic latencies in the Control (blue) and D-task (red) condition. A vincentization procedure (Ratcliff, 1979) was applied to homogeneously sample the latency distribution from different subjects. (G) Mean saccadic peak velocity computed for three 1-deg-wide amplitude bins and averaged across subjects, in the Control and D-task conditions.

It is noteworthy that this significant latency decrease was not induced thanks to instruction as it was in Reddi and Carpenter (2000)'s experiment. Rather, the dynamics of the environment came to select the temporal dimension of saccades. Additionally, latency variance greatly decreased by at least 30% and the peak velocity increased by 35°/s. These results challenged a few concepts. They were indeed contradictory to the supposedly rigid relation of proportionality linking saccadic peak velocity and saccadic amplitude, that is the main sequence (Bahill et al., 1975), which predicts larger saccade amplitude for higher peak velocities (Figure 5, p25). Secondly, the authors tried to apply the LATER model (Reddi & Carpenter, 2000), which predicts that an urgency situation will imply a change in the threshold θ of the decision criterion (Figure 14, p43). Yet, they observed that their perceptual urgency manipulation affected the mean rate μ of visual information accumulation, rather than a lowering of the criterion θ for the decision signal. Overall, the model could not account well for the actual data and did not fully describe the effects of their urgency manipulation on saccadic latencies. Trottier and Pratt (2005) obtained similar results on saccadic latencies when they added a discrimination task to their experiment. Surprisingly, the addition of the discrimination task was even sufficient to decrease the long latencies obtained in an overlap paradigm to what was obtained in a control gap paradigm (which represents a typical decrease of 100ms).

Madelain, Champrenaut and Chauvin (2007) designed an experiment in which the response requirement was upon saccadic latencies. Similar to previous experiments, observers had to saccade as fast as possible toward the brightest stimulus in a 2-AFC task. Yet, three differential consequences could occur depending on saccade characteristics: 1) the fixation cross was displayed again if the participant looked at the distractor, 2) a gray square appeared around the fixation cross if the participant looked at the target but with a non-required latency (the color differed if it was too short or too long), and 3) the fixation cross was displayed again and a tone was delivered (when the auditory stimulus was delivered three times out of five trials, a point war earned) if the participant looked at the target with the required latency. After collecting the baseline individual saccadic latency distribution, the participant went through four experimental conditions that used a variation of a percentile procedure (Machado, 1989), which is commonly used to reinforce variability. The study aimed at investigating whether it was possible to independently manipulate the median and spread of the latency distributions: either by reinforcing different levels of variability with the same median latency (i.e., baseline median and low/high variability) or different latency shift with the same variability (i.e., short/long median latency and low variability). Results disputed the conventionally proposed mechanical relationship between the mean and variance of latencies (Wagenmakers & Brown, 2007; Wagenmakers, Grasman, & Molenaar, 2005), in that the distribution changed according to the reinforcement contingencies (Figure 30). Saccadic latencies were as flexible as saccadic amplitudes; they could be shorter or longer with low variability or having a fixed median latency with more or less variability depending on the reinforcement requirements. Interestingly, they found no effect on saccadic peak velocities. Opposite to the current view of the effect of reward on saccade vigor (defined as a higher peak velocity for a given amplitude; e.g., Choi, Vaswani, & Shadmehr, 2014; Reppert, Lempert, Glimcher, & Shadmehr, 2015; Shadmehr, Orban de Xivry, Xu-Wilson, & Shih, 2010; Xu-Wilson, Zee, & Shadmehr, 2009), the present study might stress the necessity to have reinforcement contingencies on peak velocity in order to modulate it (e.g., in Montagnini and Chelazzi's experiment, higher peak velocities were also selected as they enabled better chance at discriminating the target, whereas in Madelain and collaborators, they were not consistently followed by a functional consequence). Incidentally, Manohar, Finzi, Drew, & Husain (2017) obtained higher peak velocities for contingent rather than non-contingent reinforcement, which demonstrated that it is not the fact of receiving a reward that increases velocity but the contingencies that select the velocity through reinforcer delivery. This statement is also supported by a recent study from Wolf and Schütz (2017) in which the saccade latencies were negatively correlated with the probability that the target was task-relevant (i.e., the regression had a slope of -13.3ms and explained 99% of variance).

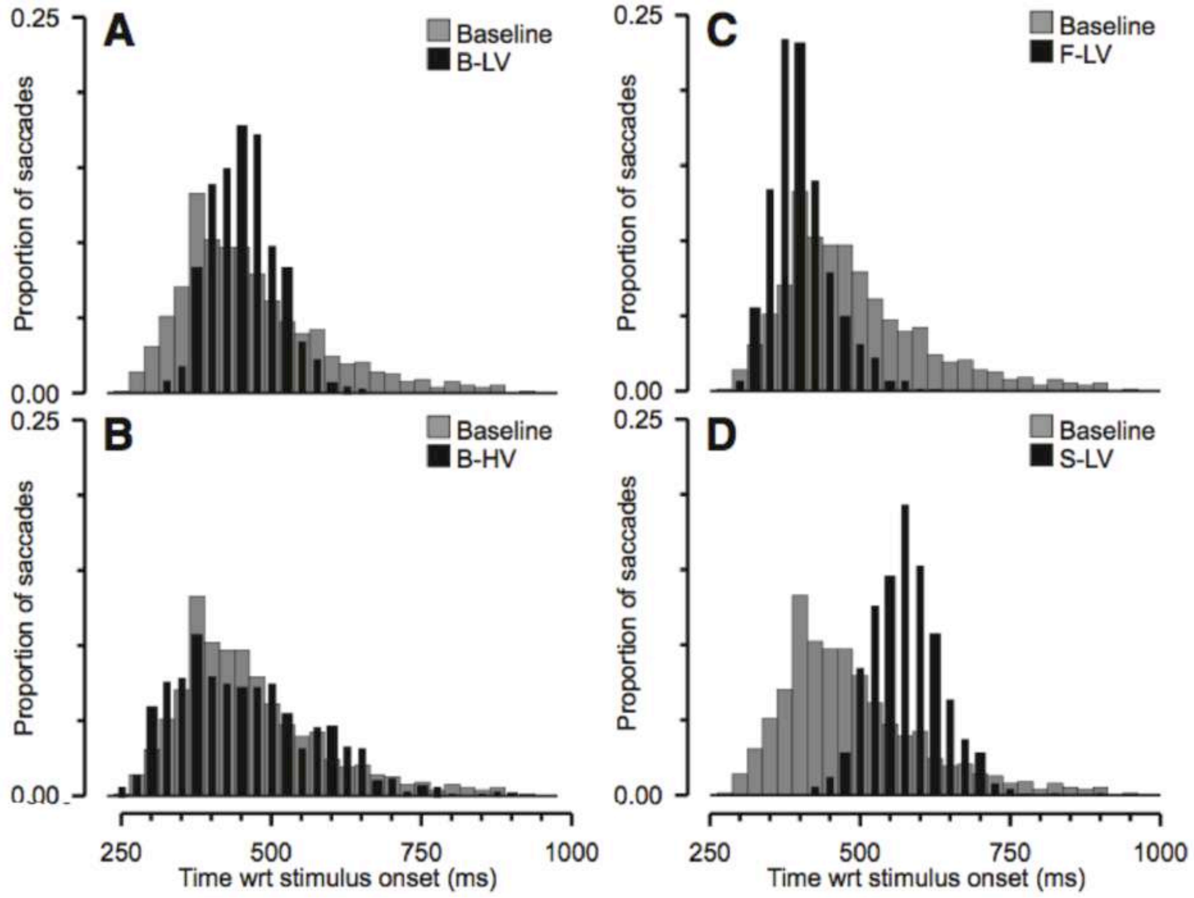

Figure 30: From Madelain et al. (2007). Frequency distribution of saccade latencies for the baseline (in gray) and the four experimental conditions (in black) for a representative participant: A) baseline median, low variability (B-LV); B) baseline median, high variability (B-HV); C) short median, low variability (F-LV); D) long median, low variability (S-LV).

The effects of reinforcement contingencies on saccadic latencies were also replicated with manual reaction times. Therefore, reaction time distributions (whether they are saccadic or manual) appear to be strongly affected by reinforcement contingencies and the variability of these latencies can be modified, reflecting their operant nature (Page & Neuringer, 1985). In other words, it is possible to change the probability of a subclass of latencies from a latency repertoire by controlling the relationship between a range of latencies and the reinforcer. In the same way that a complex organism is subject to an evolution by natural selection (Darwin, 1859), this study raises the question of the plasticity of the saccadic system, which proves to be affected by the reinforcement contingencies (Madelain, Paeye, & Darcheville, 2011). More precisely, just like it had been possible to target only the spatial dimension of saccades, it is possible to design experiments with operant requirements on the temporal dimension of saccades, namely the latencies. Overall, the aforementioned studies support the idea that saccade is controlled by a general learning mechanism that relies on the behavioral outcome of saccades in relation to the environment.

General question

Resources are not evenly distributed but instead are localized, and to successfully interact with their environment animals must engage in foraging activities that result in finding food or a potential mate, but also avoiding predators or aversive stimuli. Importantly these requirements also apply to stimuli signaling the availability of resources: information is localized as well. This is particularly true for visual information and the necessity to orient toward stimuli provides strong evolutionary pressures that have shaped the eye movement systems of animals depending on the visual neural structures and behavioral needs of each species (Land, 2011; Krauzlis, 2008). In primates, an additional requirement arises from the presence of a restricted high photoreceptor-density region of the retina, the fovea, and a corresponding increased functional acuity: we use saccades to shift gaze and fixation in combination to gather information when exploring our environment. A critical feature of our environment is that it is dynamic and constantly changing: visual information is therefore also localized in time and because the fraction of our visual surroundings perceived at any given moment is limited we must decide *when* as much as *where* to look, a fact that has been mostly overlooked so far. That visual information-foraging activity is most certainly dependent on both the spatial and temporal structure of our environment is indeed striking. To borrow an image from Hoppe and Rothkopf (2016), consider a person exploring the visual environment before crossing a busy street: the observer's behavior will be driven by environmental regularities to select informative spatial locations such as the street itself and ignore others such as the sky or the buildings. Because pedestrians, bicycles and cars are obstacles with different temporal properties, the observer might also use these regularities to sequentially allocate their limited visual resources over time. One may therefore postulate that we learn and use the temporal properties of our environments to shift gaze toward potentially informative locations at the right time. In other words, the temporal organization of our environment should constrain the temporal allocation of saccades.

Although SRTs are typically viewed as a byproduct of decisional processes, saccadic latency distributions might be manipulated in the laboratory using for instance a biofeedback (Bibi & Edelman, 2009), temporal constraints of the environment (Montagnini & Chelazzi, 2005; Trottier & Pratt, 2005) or reinforcement schedules (Madelain et al., 2007), revealing how the organization of the environment affects saccade latencies. The study from Madelain et al. (2007) investigated the direct effect of dedicated reinforcement contingencies on the dispersion of saccade latency distribution. They obtained shorter or longer latencies based on reinforcement requirements and demonstrated that it is possible to disentangle the median latency and the spread of the distribution, which challenged the conventional approach of SRTs. Most interestingly, this research also showed that saccade latencies might prove to be as plastic as saccade amplitude. Indeed, the amplitude of saccades has been extensively manipulated using reinforcement contingencies (e.g., Madelain, Paeye, & Wallman, 2011; Paeye & Madelain, 2011, 2014; Rahmouni et al., 2016, 2017) and appears to be an operant dimension of saccades (Madelain, Paeye, & Darcheville, 2011). This dissertation aims at testing the plasticity of the saccadic system and at investigating the extent of temporal control with saccades. More specifically, we defend the main hypothesis that saccadic latency depends on functional relationships.

To demonstrate that SRTs are dependent on their functional consequences, the experimental contribution of this thesis is divided in four studies based on a functional analysis of saccadic latencies. The first study will probe whether it is possible to choose specific latencies, in order to identify how sensitive one is at controlling one's latencies depending on the reinforcement contingencies in force. If SRTs are controlled by reinforcement, the allocation of short and long latencies should match the relative obtained reinforcement (Herrnstein, 1961).

Because we evaluate saccadic latencies as a function of their functional consequences, the second study will use the size-latency phenomenon known to induce longer latencies (De Vries et al., 2016; Harwood et al., 2008; Madelain et al., 2005) and aim at probing whether it is possible to alter it by manipulating the benefit of shorter reaction times with reinforcement. If SRTs actually depend on their beneficial consequences, then the saccadic latency distribution should shift toward shorter values.

Furthermore, a third study will verify whether it is possible to establish discriminative control over saccadic latencies, as it has already been demonstrated with saccadic amplitude (Azadi & Harwood, 2014). This experiment analyses the antecedent element of the three-term contingency and aims at understanding how antecedent stimuli come to control specific reaction times. If a general learning mechanism explains SRTs, then it should be possible to induce a discriminative control of latencies between different stimuli using reinforcement.

Finally, some experiments raise the possibility for saccade latencies to be controlled through classical conditioning (e.g., Daddaoua et al., 2016; Jóhannesson et al., 2018; Theeuwes et al., 1999). The fourth research in this thesis is a pilot study to evaluate whether it is possible to establish stimulus control through associative learning. If we observe a differential responding in SRTs depending on the stimuli, this research would be a first step in the study of associative learning with saccade latencies and the understanding of how the environment and learning history control reaction times.

Study 1: Control of saccadic latency in a dynamic environment: allocation of saccades in time follows the matching law

Chapter 3:

Choice of saccadic latency

ABSTRACT

When exploring the visual environment, one uses saccades to shift gaze and fixation to gather spatially and temporally localized information. We propose that the temporal structure of our environment should constrain the temporal allocation of saccades. In this study, we probed the possibility of learning to control saccadic latencies in a choice paradigm. Six participants made saccades within 80-300ms following a target horizontally stepping by 10deg between two fixed locations. For each participant we constructed two classes of latencies, "short" and "long", using the first and last quartiles of the individual baseline distribution (e.g., [80;152]ms and [185;300]ms respectively). Then, we concurrently reinforced each class in three blocked conditions across about 60 experimental sessions per participant, using different reinforcement probabilities such that the relative ratio of reinforcement rates for "short" versus "long" latencies was either 9/1, 1/9, or 1/1. Latency distributions followed the reinforcement conditions: distributions shifted toward the shorter or longer values or became strongly bimodal. Moreover, the relative rates of short over long latencies matched the relative rates of reinforcers earned for the corresponding latencies (slope up to 0.95), which reveals the ability to choose when to saccade. Our results reveal that learned contingencies considerably affect the allocation of saccades in time and are in line with recent studies on the temporal adjustment of behavior to dynamic environments. This study provides strong evidence for fine operant control of saccadic latency, supporting the hypothesis of a cost-benefit control of saccade latencies.

VALORIZATION

This study, adapted here for the thesis, has been published in 2018 in the *Journal of Neurophysiology* (a link toward the corresponding article has been attached in Appendix 1) and has been presented as three posters (to the national and international conferences *Forum annuel du Groupement De Recherche Vision* in December 2015, *Vision Sciences Society* in May 2016 and *European Conference on Visual Perception* in August 2016), as one talk (to the national conference *Forum annuel du Groupement De Recherche Vision* in November 2016) and as two talks in symposiums (to the international conferences *Association for Behavior Analysis International* in November 2017 and May 2018).

I. CONTEXT

Saccades may be regarded as an information-foraging behavior mostly concerned with the spatial localization of objects, yet our world is dynamic and the temporal regularities of the environment should also affect saccade decisions. To probe the hypothesis that saccadic latency depends on a functional relationship, we first have investigated whether it was possible for humans to learn to choose their saccadic latencies depending on the reinforcement contingencies. Three experimental conditions manipulated the beneficial consequences of short and long latencies to evaluate the extent of control over saccadic reaction times. This study assesses the existence of a cost-benefit-based policy that takes into account the learned properties of the environmental contingencies for controlling saccade triggering.

To investigate the adaptation of SRTs to the temporal properties of the environmental contingencies, we designed a task with four critical features. First, alternating between two fixed target locations isolated the temporal aspects of saccades from spatial selection and visual information other than target step. Second, we used the actual individual latencies to define “short” and “long” SRTs, to avoid imposing arbitrary constraints on SRT distributions. Third, we designed a temporal-choice task to probe the extent of control over SRTs, allowing us to quantify the allocation of latencies in response to the temporal structure of the reinforcement contingencies. Finally, we reinforced specific latencies to probe whether the law of effect could apply to SRTs.

In the event of a matching between the allocation of saccade latencies and the allocation of reinforcement, it would mean that the reinforcement contingencies consistently control SRTs and suggest that observers can learn to alter the triggering of saccadic eye movements in response to new environmental contingencies.

II. METHODS

2.1. Participants

Six adults (2 men and 4 women, mean age = 26.7 years, age range: 18-45 years) participated in this study. They were naïve as to the purpose of the study, except for two participants (i.e., the authors, S1 and S2, who experienced several pilot procedures prior to the actual experiment), and had normal or corrected-to-normal vision. Participants were informed that the experiment was about short and long reaction times and instructed to earn as many points as possible; no further explanation was given as to how to earn points. When the experimental conditions changed, the same instruction was given again. Naïve participants received 30 euros for participating, plus an additional sum depending on the points collected (one point equals 2cts); they received 94 euros on average at the end of the experiment. They were informed that they could earn up to 120 points per session, with a monetary bonus of 1 euro for each session in which their score exceeded 100. All experimental procedures received approval from the Ethical Committee in behavioral sciences of the University of Lille (Agreement n°2015-1-S34) and conformed to the standards set by the Declaration of Helsinki. All participants gave informed written consent.

2.2. Apparatus

Stimuli were generated using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997) for Matlab® and displayed on a video monitor (Iiyama HM204DT, 100 Hz, 22”). Participants were seated on an adjustable stool in a darkened quiet room, facing the center of the computer screen at a viewing distance of 60cm. To minimize measurement errors, the participant's head movements were restrained using a chin and forehead rest, so that the eyes in the primary gaze position were directed toward the center of the screen. Viewing was binocular, but only the right eye position was recorded and 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.), sampled at 2000Hz. Data were transferred, stored, and analyzed via programs written in Matlab® running on an Ubuntu Linux computer.

Stimuli were light gray disks (luminance = 15.99 cd/m^2), diameter 0.5°, displayed on a dark gray background (luminance = 1.78 cd/m^2). The target position alternated between two fixed locations on the screen separated by 10 degrees horizontally around the center of the monitor.

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

2.3. Procedure

The experiment lasted on average 60 400-trial sessions divided among familiarization, baseline and reinforcement sessions. Two participants also did four latency-training sessions between baseline and reinforcement (see below). Three daily sessions were typically recorded, separated by 5-min breaks during which participants were free to move. On average, the experiment lasted 20 consecutive days (five days a week, from Monday to Friday). Regardless of the actual condition, participants were asked to make saccades toward the horizontally stepping target.

Familiarization. Participants who had no previous experience in oculomotor experiments were trained to make saccades without blinking, anticipating, or looking away from the target. The 100-trial familiarization sessions lasted until at least 90% of saccades were correctly detected online (see Acquisition and data analysis) and were identical to baseline (see below) except for the number of trials.

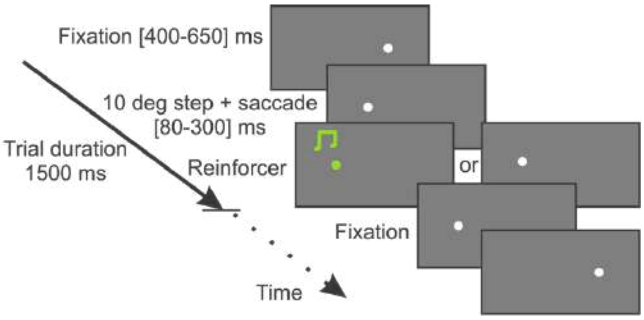

Figure 31: Experimental design of an ongoing trial during reinforcement conditions.

Baseline. Seven 400-trial baseline sessions were completed in which participants made saccades toward the target horizontally stepping between the two fixed positions (Figure 31). At the beginning of the trial, the participant looked at the target for an unpredictable period varying between 400 and 650ms (sampled from a uniform distribution). The target then stepped horizontally by 10 degrees to the other position. The participant made a saccade with a latency that had to range from 80 to 300ms. If the latency was outside this range or if no saccade was detected, the target disappeared for the remainder of the trial (i.e. the screen remained blank) and the trial was discarded for off-line analysis. The poststep period depended on the time elapsed since the beginning of the trial, so that each trial lasted 1500ms; there was no additional intertrial interval. The target position became the fixation position for the next trial. If the target had been extinguished in the previous trial, the target was turned on at the fixation position at the beginning of the trial. It should be noted that because the fixation period duration was randomized the timing of the target step was never predictable.

Saccadic latency was defined as the interval of time elapsed between the target step and the saccade onset.

After completion of the baseline, we constructed two individual latency classes – “short” and “long” saccadic latencies– using the first and last quartiles, respectively, of baseline latency distributions for each participant (Figure 32). These class boundaries were fixed for the remainder of the experiment. Latencies between 80ms and the first quartile were categorized as short latencies (i.e., the shortest 25% of all baseline SRTs; e.g., 80-152ms for S2), and latencies between the last quartile and 300ms were categorized as long latencies (i.e., the longest 25% of all baseline SRTs; e.g., 185-300ms for S2). The first and last quartiles were 164 and 214ms, 152 and 185ms, 157 and 185ms, 171 and 207ms, 140 and 169ms, 119 and 169ms for participants S1 to S6, respectively.

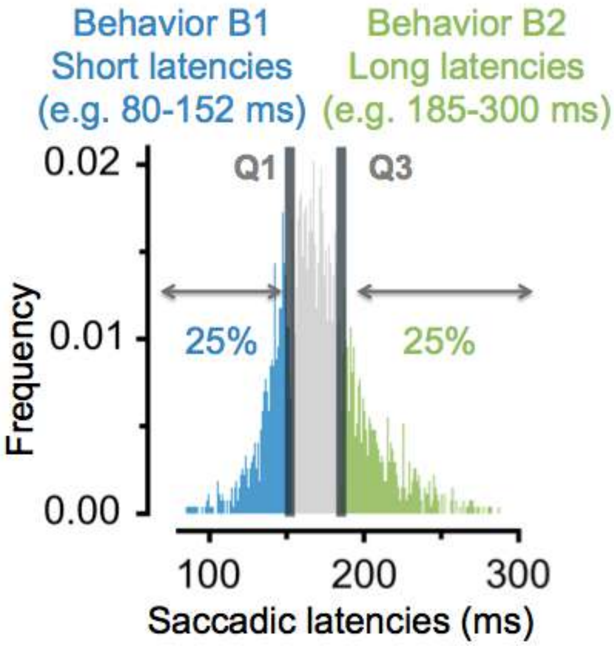

Figure 32: Construction of the two individual latency classes, the « short » and « long » latencies, using the first and last quartiles of baseline distribution for each participant (here, S2). Latencies between 80ms and the first quartile were categorized as short latencies and latencies between the last quartile and 300ms were categorized as long latencies.

Reinforcement sessions. In all of our reinforcement conditions, “short” and “long” latencies were independently reinforced on a concurrent random interval (RI) reinforcement schedule in which the relative probabilities of reinforcing “short” and “long” latencies were manipulated. The availability of reinforcement is time-controlled using interval schedules: they require a defined elapse of time since the last reinforcer before a response produces reinforcement. Once the interval of time is elapsed, reinforcement is delivered contingent on the first correct response. The RI schedule uses probabilities for assigning reinforcement randomly in time with exponentially distributed inter-reinforcement intervals (Millenson, 1963). Importantly, a reinforcer, once available, remains available until collected.

A concurrent reinforcement schedule is used to study choice between two alternatives by having two reinforcement contingencies operating independently and simultaneously for two responses. Typically, with interval schedules in a concurrent paradigm participants do not respond exclusively in one alternative but rather distribute their choices between the two options because the probability of being reinforced increases with time (Ferster & Skinner, 1957).

The reinforcer consisted of having the target turn green for the remainder of the trial (luminance = 5.3 cd/m^2), a brief auditory feedback tone (100ms, 500Hz), and earning a point that was exchanged for 2cts collected at the end of the experiment. The total number of 400-trial reinforcement sessions completed in each condition depended on the time needed to reach stable reaction time distributions. Our stability criterion used the proportion of trials with short vs. long latencies for the last three sessions with the requirement that these proportions should not be different by more than 1.5 standard deviations of the proportion from the mean proportion of the preceding seven sessions.

Schedule manipulations. Each class of latencies had a probability of being reinforced, and we manipulated the relative frequency of reinforcer availability between the two simultaneous concurrent alternatives such that the ratio of reinforcement rates for short vs. long latencies was either 1/1, 9/1, or 1/9. Across conditions, the overall programmed reinforcement rate was always 12 reinforcers per minute (note that because our trial duration was fixed at 1.5s this reinforcement rate may be discretized in reinforcement probability per trial). In the 1/1 ratio, both classes of latencies were reinforced with the same probability; a RI schedule with an interval of 10s on average was used for both short and long latencies. In the 9/1 ratio, reinforcers were more often available for short latencies than for long ones (average intervals for short latencies equaled 5.56s vs. 50s for long latencies). In the 1/9 ratio, the opposite was true. A changeover delay was used so that a reinforcer, once available, could not be collected with the first response in an alternative after a switch between alternatives. For instance, if a reinforcer for short latencies was available, the participant had to saccade twice in a row with short latencies for the reinforcement to be delivered; if they were to systematically switch between long and short latencies they would never obtain a reinforcer. This penalty is typically used to eliminate alternation and compel choice (Herrnstein, 1961).

Training. To probe whether latency discrimination training affects SRT control, we introduced a 4-session training phase following the baseline sessions for the two last participants (S5 and S6). For one participant, in the first session we instructed that short saccadic latencies would be reinforced and we used a continuous reinforcement schedule (i.e., CRF, the target turned yellow for every latency within the criteria). The second session was identical but reinforced long latencies. In the third session, only short latencies were intermittently reinforced (average intervals for the reinforcer availability equaled 5.56s). The fourth session was similar but long latencies were reinforced. The order between short and long latencies reinforcement sessions was counterbalanced across the two participants.

2.4. 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 saccades onset and offset, using a 30°/s velocity and $8000°/s^2$ acceleration thresholds. Saccade parameters were retrieved on average with a 12-ms delay after saccade offset. For offline analyses, saccades with amplitude gain lower than 0.5 or duration longer than 100ms were automatically excluded. A human observer then validated each saccade manually. On average, we kept 97.89%, 93.26%, 95.86%, 98.04%, 95.57% and 89.74% of saccades for participants S1 to S6, respectively. We observed very few anticipatory saccades (i.e., saccades with a latency shorter than 80ms) across the experiment (0.03%, 0.44%, 0.57%, 0.22%, 0.34% and 1.26%, for participants S1 to S6, respectively).

We used bootstrapping methods (resampling with replacement 100 000 times) to estimate all the individual statistical parameters and 98% confidence intervals (CIs; Efron, 1979). All means and medians were compared using Fisher's exact test: the confidence intervals of the null hypothesis were computed using 100 000 permutations.

III. RESULTS

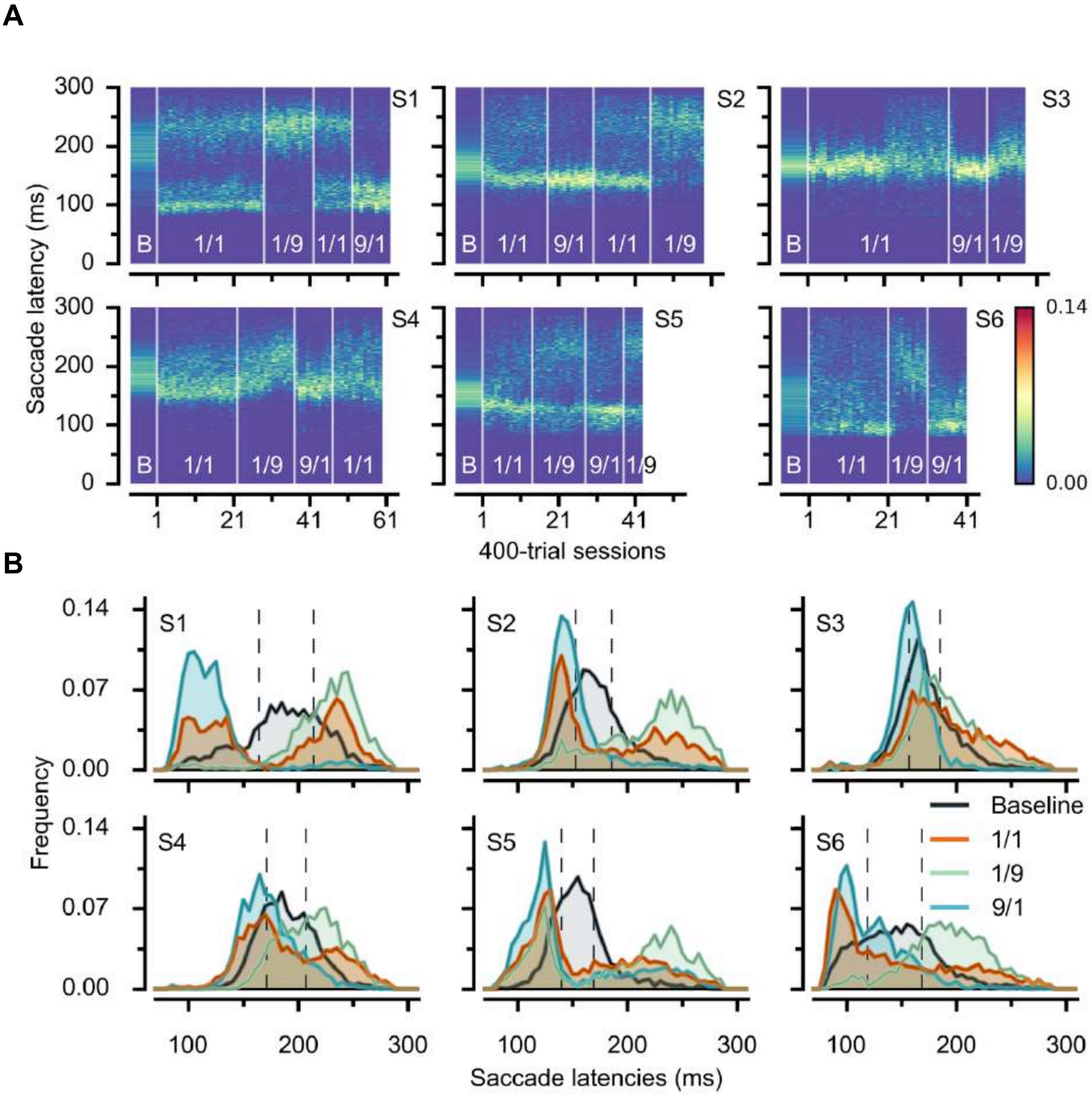

Figure 33: A) Saccade latency frequencies across all conditions (B, baseline; 1/1, 1/9, and 9/1, the three reinforcement conditions) for all participants in each session. Baseline sessions were combined in a single distribution. Color indicates the frequency of SRTs. B) Frequency distributions of saccadic latencies for baseline and ratio 1/1, 1/9, and 9/1 experimental conditions for all participants in the last 5 sessions of each condition. Vertical dashed lines plot the first and last individual quartiles of baseline distribution, used to construct the two individual classes of latencies. Latencies below the first quartile were categorized as « short » latencies, and those above the last quartile were categorized as « long » latencies.

Figure 33A plots the saccadic latency distributions for all sessions for all participants; each column of pixels represents one 400-trial session, and the color of the pixel in a given row indicates the frequency of SRTs in that time bin. Importantly, the distributions changed across experimental conditions: in the 1/9 condition in which long latencies were more likely to be reinforced more long SRTs are observed, whereas in the 9/1 condition the opposite is true. Moreover, distributions were much more spread in the 1/1 condition; bimodal distributions can even be observed in some participants (e.g., S1 or S5). It is noteworthy that transitions between conditions were idiosyncratic: progressive transitions were observed for some participants in specific cases (S4, S5 and S6), while other participants tended to show more abrupt transitions (S1, S2 and S3; see Figure 34 for an instance of abrupt transitions for S2). However, these transition patterns were not systematically observed for a given subject.

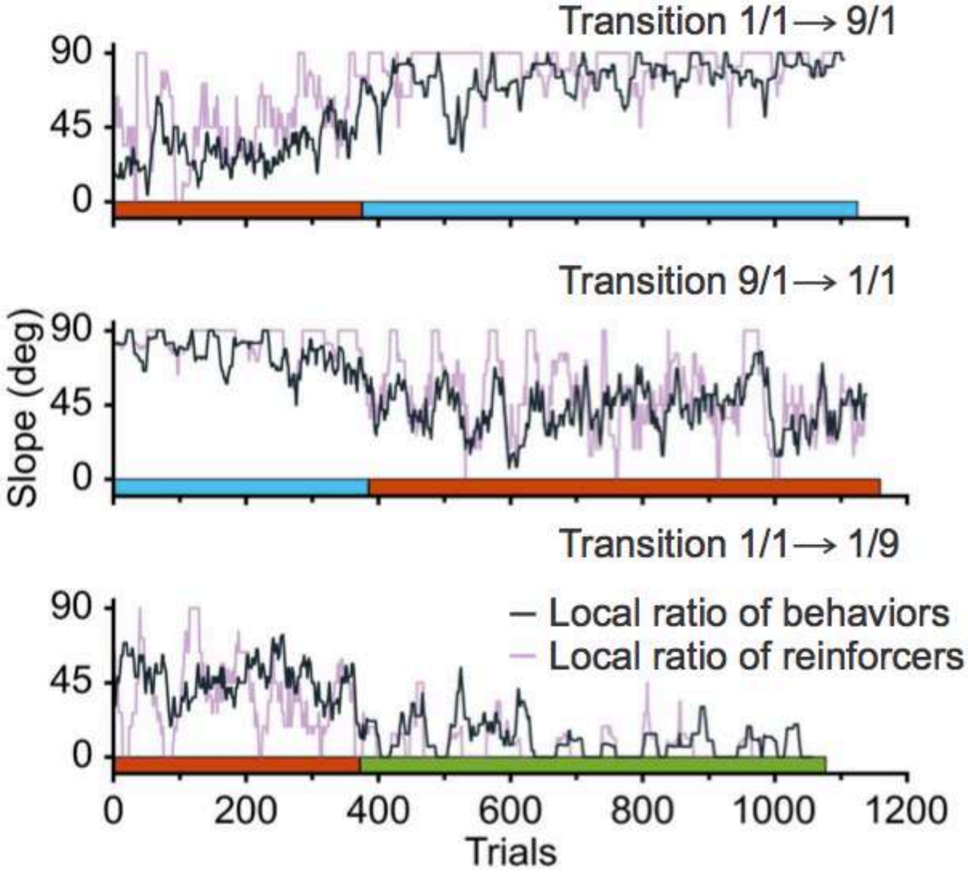

Figure 34: The transitions between experimental conditions for participant S2. The three panels represent the transition between the 1/1 (in red) and the 9/1 (in blue) conditions, the transition between the 9/1 and 1/1 conditions and the transition between 1/1 and 1/9 (in green) conditions. The plot represents the slopes in degrees of the local ratio of behaviors (in black) and the local ratio of reinforcers (in purple) as a function of trials. In the same fashion as Sugrue et al. (2004), the local ratio of behaviors was computed with a 20-trial moving window using the inverse tangent of the ratio of short latencies versus long latencies, and the local ratio of reinforcers was computed using the inverse tangent of the ratio of reinforcers obtained for short latencies versus those obtained for long latencies.

We now further describe these data considering the steady state (i.e., the last five sessions of each experimental condition). Figure 33B plots the SRT distributions for the steady state. In comparison to baseline, the distributions strongly drifted toward shorter values when short latencies were more often reinforced (i.e., 9/1 ratio). When long latencies were favored (i.e., 1/9 ratio), the distributions shifted toward longer values. In addition, for several participants (S1, S2, S4, and S5), we obtained a bimodal distribution when both short and long latencies were under identical reinforcement schedules (i.e., 1/1 ratio). We observed a large amount of very short latencies (between 80 and 110ms) for three participants (S1, S5, and S6).

To quantify the changes in the distributions, we computed the respective proportions of long and short latencies with respect to all latencies for each experimental condition in the steady-state sessions (Figure 35). The gray dashed lines show the baseline proportions for short and long latencies (25% each, by construction): data points falling away from these lines indicate a change in the proportion of short or long SRTs with respect to baseline levels. In the 9/1 ratio condition, instead of the baseline 25%, the distributions averaged 62.30% (SD = 16.69) of short latencies and 11.34 % (SD = 8.98) of long latencies. Conversely, in the 1/9 ratio condition, the distributions averaged 11.85% (SD = 11.46) of short latencies and 65.75% (SD = 11.14) of long latencies. Finally, in the 1/1 ratio condition, the average proportions were 39.88% (SD = 12. 43) for short latencies and 39.91% (SD = 6.59) for long latencies. For all participants, we observed significant differences with respect to baseline values: in all three conditions, all the points were different from baseline levels and 25% was never within the confidence intervals. This adjustment to reinforcement contingencies was also apparent in the proportions of intermediate-latency saccades (the central 50% of baseline distributions, i.e., latencies comprised between the first and last quartiles, which were never reinforced; e.g., 153-184ms for S2). Those proportions considerably decreased for the non-naïve participants S1 and S2 (13% and 17% on average across conditions, respectively). For naïve participants these proportions were 41%, 33%, 6% and 28% for participants S3 to S6, respectively. Interestingly, these proportions were lowest for S5 and S6 who received an additional latency-discrimination training phase. This is apparent when comparing the distributions on Figure 33B (e.g., S4 vs. S5).

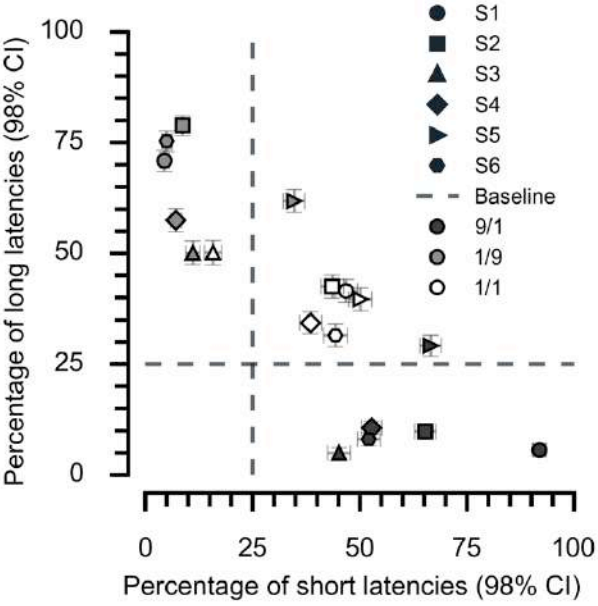

Figure 35: Percentage of long latencies as a function of percentage of short latencies (with respect to all latencies) for each of the last five sessions of the three reinforcement conditions for all participants. The bootstrap 98% confidence intervals are shown for both the short and long latency percentages.

To estimate how choices of saccadic latencies depended on the actual reinforcement conditions, we used the *matching law* (Baum, 1974; Herrnstein, 1961), which states that the relative rate of choices made to an option matches the relative rate of reinforcers earned from that option. This law describes the behavior allocation across reinforcement conditions: the frequency of a behavior occurrence depends on its own reinforcement schedule and on reinforcement frequencies from other activities performed by the individual. Expressed logarithmically, the equation, as proposed by Baum (1974) to account for deviation from strict matching, is:

$$\log\left(\frac{B1}{B2}\right) = s \times \log\left(\frac{R1}{R2}\right) + \log b$$

B1 and B2 represent the number of responses made for each alternative, and R1 and R2 correspond to the number of reinforcers respectively obtained for those options; "s" is a measure of the sensitivity of behavior to changes in the relative rate of reinforcement; "log b" is called bias, as it measures a constant proportional preference for one alternative over the other.

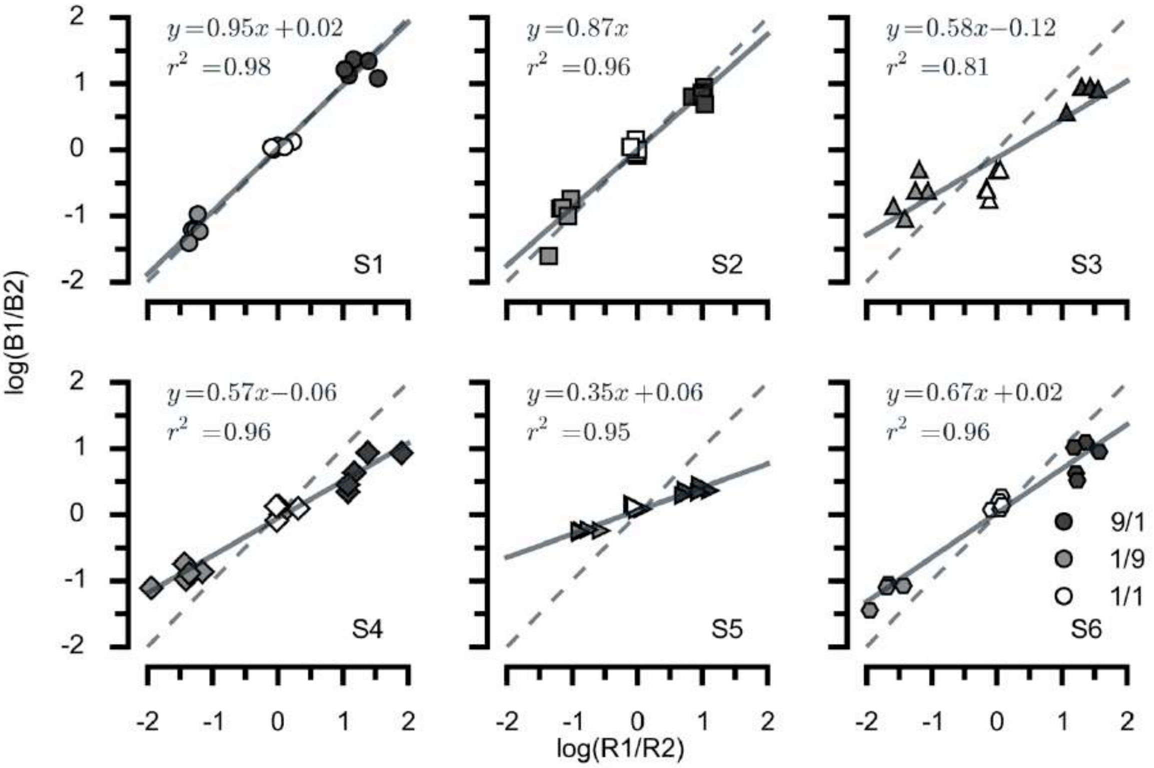

Figure 36: Relative rates of short and long latencies (log unit) as a function of relative rates of obtained reinforcers for short and long latencies (log unit) for the last five sessions of the three reinforcement conditions for all participants. B1 and B2 represent the total number of trials with short and long latencies, respectively; R1 and R2 represent the total number of reinforcers obtained for these two classes of latencies, respectively. Each point plots the log relative rate of latencies for one session. Solid lines were fitted to the data with the method of least squares. The equations of the regression lines are shown at top for each participant. The sensitivities (i.e., slopes of the linear fits) ranged from 0.35 to 0.95, and the log bias (i.e., intercept) ranged from -0.12 to 0.06. Dashed lines show the locus of perfect matching (s = 1.0).

Figure 36 illustrates the individual data for all participants, fitted by the method of least squares (solid line). The relative rates of latencies approximately matched the relative rates of reinforcement, albeit not perfectly (s = 1 in case of perfect matching), as measured by the sensitivity of latency choice to changes in reinforcement ratios, which was 0.95, 0.87, 0.58, 0.57, 0.35, and 0.67 for participants S1 to S6 respectively. The two non-naïve participants (S1 and S2) showed almost a perfect matching while sensitivity was lower for S3, S4 and S6. This range of deviation is classically observed and has been termed undermatching (see Baum, 1979 for a review). The bias remained small, indicating a lack of preference for one of the latency classes (log b values were 0.02, 0, -0.12, -0.06, 0.06, and 0.02 for participants S1 to S6, respectively). Observations were overall well fitted by the linear regression computed over 15 points (r^2 values were 0.98, 0.96, 0.81, 0.96, 0.95, and 0.96 for participants S1 to S6, respectively). Interestingly, we observed the lowest slope (s = 0.35) for S5 even though she had the lowest overall proportion of intermediate-latency saccades (6%) and the highest reinforcement rate across conditions compared to the other naïve participants (8.90 reinforcers/min for S5 vs. 6.35, 7.40, and 7.95 reinforcers/min for S3, S4, and S6, respectively). One explanation for the large undermatching in S5 would be that the change-over delay (COD) was not costly enough (see Baum, 1974 for a review) and resembles what has been found in the literature on matching eye movements without the use of a COD (Figure 37). It is noteworthy that this participant received the additional training phase.

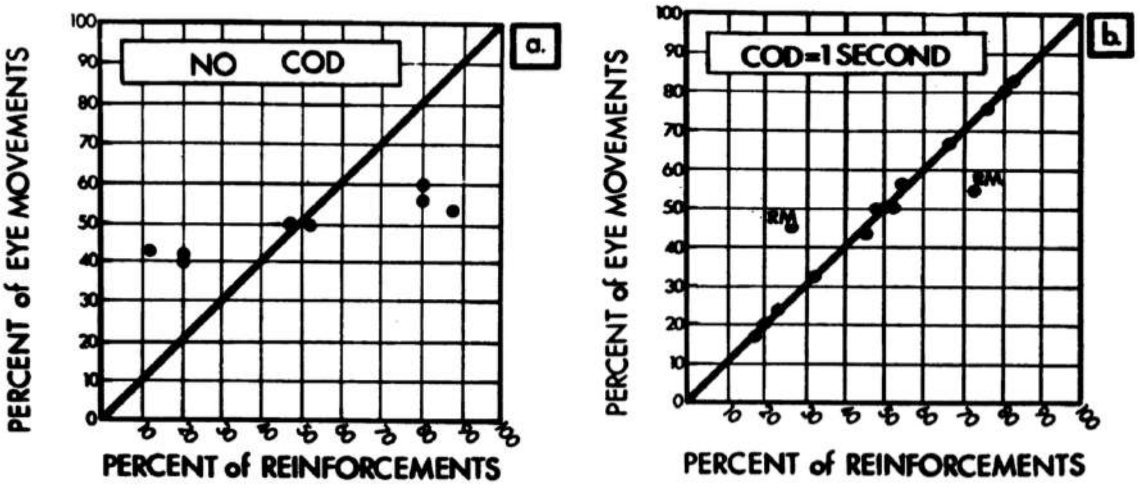

Figure 37: From Schroeder & Holland (1969). Relative eye-movement rate as a function of relative reinforcement rate for no COD (a) and a COD of one second (b) for the same participant.

A common criticism to the matching law is that it describes behavior as a function of the obtained and not the programmed reinforcement; thence, it has been categorized by some as a tautology (Killeen, 1972; Rachlin, 1971). Therefore, we wanted to check the dynamics of behaviors and obtained reinforcers with regard to the programmed reinforcement. Figure 38 plots the normalized cumulative long trials as a function of the normalized cumulative short trials for latencies (on the left) and obtained reinforcers (on the right). Should the latencies and obtained reinforcers followed the programmed reinforcement, the section for the 1/1 condition (in red) was expected to increase with a 45deg slope, the one for the 1/9 condition (in green) with a near 90deg slope and the one for the 9/1 condition (in blue) with a flat slope. As shown in Figure 38, the curves for both latencies and obtained reinforcers increased in the expected way for all participants and followed the programmed reinforcement.

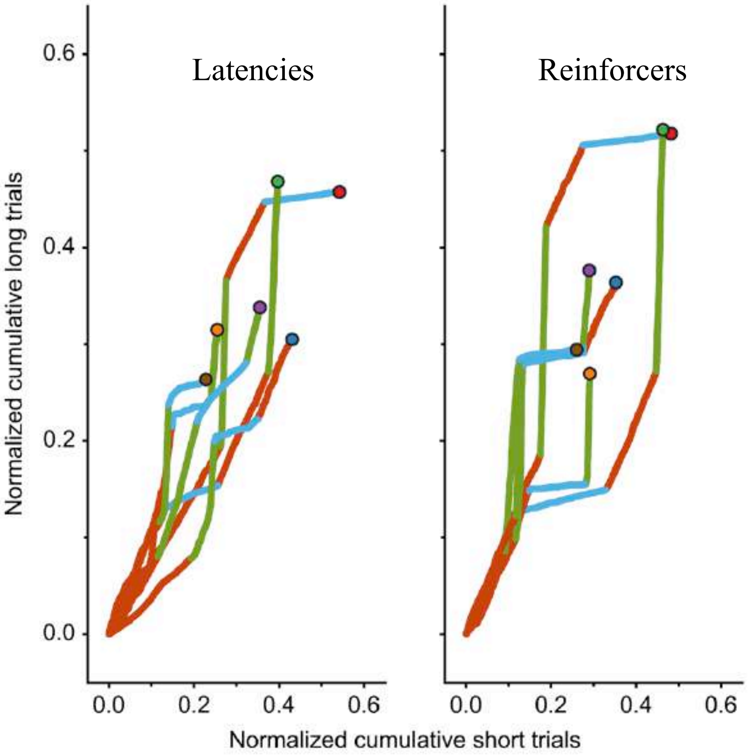

Figure 38: Normalized cumulative long trials as a function of the normalized cumulative short trials for latencies (on the left) and obtained reinforcers (on the right). Each curve represents one participant; the red, green and blue sections represent the 1/1, 1/9, and 9/1 conditions, respectively.

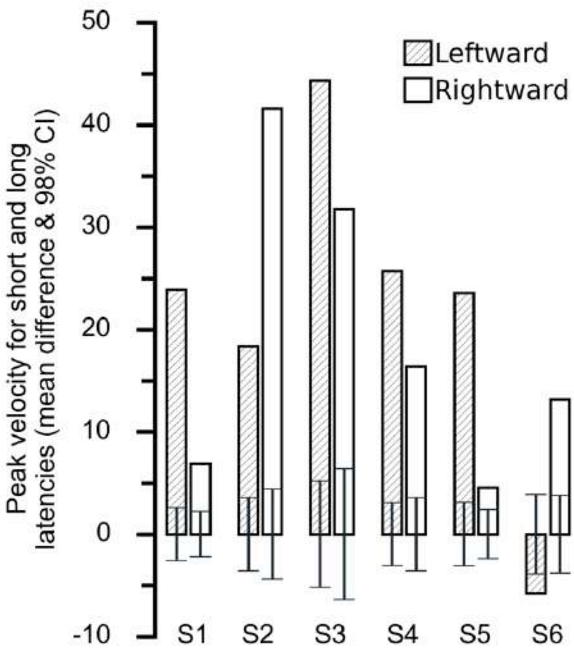

Figure 39: Differences of the means in saccadic peak velocity between the short and long latency trials across the last five sessions of the three reinforcement conditions (15 sessions in total) for leftward and rightward saccades for each participant. The corresponding 98% confidence intervals of the null hypothesis (i.e., the two groups of trials have identical probability distribution) are shown. All mean differences are outside the null hypothesis confidence intervals.

Finally, we asked whether the variations in latencies we have observed were accompanied by systematic changes in other saccade metrics. One could postulate that these variations were correlated with changes in the accuracy of the saccade such that amplitudes might change with latencies. To assess this relation we first probed whether there was any difference in amplitudes and peak velocities as a function of saccade direction, as left-right asymmetries have been reported (e.g., Collewijn, Erkelens, & Steinman, 1988; Vergilino-Perez et al., 2012). All participants made saccades with slightly shorter amplitudes toward the left (mean amplitude difference ranged from -0.07 to -0.46deg; all values greater than the null hypothesis 98% CIs) and had faster peak velocities toward the right (mean peak velocity difference ranged from -39.99 to -70.28deg/s; all values greater than the null hypothesis 98% CIs). We found no systematic change in amplitude between short- and long-latency saccades, regardless of saccade directions. However, as shown in Figure 39, the peak velocities were systematically faster for short-latency saccades (except for S6): the mean difference in peak velocities between short and long classes was 20.35deg/s (ranging from -5.79 to 44.29deg/s; all values greater than the null hypothesis 98% CIs). Surprisingly, participant S6 had slightly faster peak velocities for long latencies for leftward saccades but not for rightward ones.

IV. DISCUSSION

The present study is the first one to specifically manipulate SRTs in a latency-choice paradigm using reinforcement contingencies. SRT distributions considerably changed and choices between short and long latencies strongly matched reinforcement contingencies, revealing a fine control of SRTs. Factors such as visual saliency or reward expectancy (see Sumner, 2011) cannot account for the observed changes in SRT distributions. We discuss these findings in the context of previous studies on the temporal organization of behavior below.

4.1. SRTs and the matching law

Participants matched their SRT relative rates to the obtained reinforcer relative rates across all reinforcement contingencies (with the exception of S5 who showed weak matching at best; see Figure 4). This matching reveals proper choice adjustment: our study falls within a long history of research on matching behavior, i.e., the tendency of participants to match their relative choices to the relative incomes derived from them (reviewed in Davison & McCarthy, 2016; McDowell, 2013). Matching has been found in a variety of species, behaviors and reinforcers (see Baum, 1979; de Villiers & Herrnstein, 1976 for reviews) such that it has been proposed that it constitutes an innate policy (Gallistel, 2005). From an evolutionary perspective, matching reveals an effective foraging strategy, as it results in an equilibrium in which returns from two competing behaviors are equalized (Sugrue et al., 2004). The systematic matching relation we observed reveals that our participants adjusted their SRTs according to the reinforcement contingencies in force: they learned to choose when to saccade with short or long latency in our temporal foraging task. To our best knowledge, our study is the first one to establish that SRT allocation follows the same rule as the one found for other choice situations, revealing a common policy of the saccadic system for spatial (Sugrue et al., 2004) and temporal foraging.

4.2. SRTs and reinforcement

That SRT allocations followed the matching law provides further evidence that saccades are instrumental behavior (Madelain, Paeye, & Darcheville, 2011), i.e., are controlled by their functional consequences (Skinner, 1981), in line with previous studies on saccade latencies (e.g., Ikeda & Hikosaka, 2007; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Madelain, Champrenaut, & Chauvin, 2007; Montagnini & Chelazzi, 2005; Nakamura & Hikosaka, 2006; Watanabe, Lauwereyns, & Hikosaka, 2003), saccade peak velocities (e.g., Montagnini & Chelazzi, 2005; Reppert, Lempert, Glimcher, & Shadmehr, 2015; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002), saccade amplitudes (e.g., Madelain, Paeye, & Wallman, 2008; Paeye & Madelain, 2011, 2014) or target choice (Sugrue et al., 2004). Our results further establish that saccades follow the law of effect, which states that behaviors are shaped by their consequences: SRT allocation changed when functional consequences changed, revealing that the temporal structure of the environmental contingencies affects the temporal structure of behaviors. Future research should further examine these findings with a more ecological paradigm as well as probe its retention with the removal of reinforcement.

Because our study implied a learning procedure requiring a large number of reinforced trials to observe steady-state SRT allocations, we suggest that this sensitivity of the saccadic system to environmental contingencies relies on the accumulation of learning across time. Whether this learning concerns the temporal properties of the reinforcement contingencies, the temporal control of saccades, or both remains an open question at this stage.

It is noteworthy that this fine control of SRTs raises the issue of perceiving our own reaction times. In our paradigm, one can distinguish three candidate sources of uncertainty: the ongoing contingency (Gallistel, Mark, King, & Latham, 2001; Killeen & Smith, 1984), the perception of time (Wearden, 2016), and the SRT production (Sumner, 2011). Indeed, the actual contingency was unsignaled: participants were not explicitly told what the short or long latency classes were, nor did they have feedback on their actual latency. Thus, when a participant received a reinforcer they could view the behavior and the consequence as either related (contingent) or not (non-contingent). Our SRT distributions changed, implying that the credit assignment problem (Staddon, 2001) must have been solved, i.e., causes and effects were connected. Therefore, despite the uncertainties and noise regarding the motor execution, their own latency perception, and the reinforcement contingency, participants were surprisingly good at adjusting their relative rate of latencies to the relative rate of reinforcement.

4.3. SRTs are not a function of reward expectancy

One might interpret our results regarding SRTs as a function of reward expectancy. Indeed, predicted reward outcome is known to influence saccadic eye movements, with mean SRT being shorter in rewarded condition (e.g., Dunne, Ellison, & Smith, 2015; Glaser et al., 2016; Takikawa et al., 2002; Watanabe et al., 2003). Reward expectancy is also thought to have an effect on saccade vigor, i.e., a saccade velocity greater than the expected velocity given its amplitude (e.g., Reppert et al., 2015). Interestingly, Glaser et al. (2016) observed a negative correlation between vigor and latency. Thus, it is commonplace to associate reward expectation, short latencies, and saccade vigor. However, in our study, we cannot conclude that the observed changes in latencies are simply a function of reward expectancy. First, reward expectancy and shorter latencies were disentangled, since in our 1/9 condition reinforcement rate –and probably reward expectancy– was higher for long latencies, driving a higher proportion of long latencies. Second, higher peak velocities were observed for short latencies regardless of reinforcement expectancy (see Figure 39). Therefore, even if we have found, as others, greater vigor associated with shorter latencies, both vigor and shorter latencies are independent from reward expectancy.

4.4. Effects of a dynamic environment on saccades

To our knowledge, the article by Hoppe and Rothkopf (2016) reports the only previous study on the learning of temporal eye movement strategies in a dynamic task. They demonstrated that humans could efficiently learn to adapt the time spent within a particular region to temporal regularities depending on the target spatial location on the screen. Their study differed from our own in that: 1) we measured SRTs instead of the time spent in a specific region, 2) we used a concurrent paradigm with simultaneous alternatives, 3) we used shorter temporalities (between 80 and 300ms in our experiments vs. 150 to 1500ms) and 4) those temporal events were produced by the participant in the absence of external cues other than the target step. While these authors evidenced the effects of event durations on fixation durations, our study demonstrated the influence of the temporal organization of the environmental contingencies on the temporal organization of saccades. Taken together, their results and ours provide strong evidence of the possibility of finely controlling the temporal allocation of gaze by reinforcement contingencies. This is strongly compatible with observations from other preparations such as manual interception tasks, which demonstrated that prior information regarding the temporal features of the task (de la Malla, Lopez-Moliner, & Brenner, 2012; López-Moliner, Vullings, Madelain, & van Beers, 2018) affects the choice of the interceptive point favoring either spatial or temporal precisions (de la Malla & López-Moliner, 2015), or reward harvesting in complex search tasks in which humans successfully seek multiple targets under time pressure (Navalpakkam, Koch, Rangel, & Perona, 2010). Altogether these results provide strong evidence that humans may learn both the spatial and temporal regularities of the environmental contingencies to regulate their motor responses.

4.5. Costs and benefits of saccades

Most models of decision making, such as the LATER model (Carpenter & Williams, 1995; Tatler et al., 2017) or diffusion models (Ratcliff & Rouder, 1998) are based on the hypothesis of some noisy accumulation of information to decision criterion. A critical feature of these models is that a saccade is triggered as soon as enough information regarding the target location has been accumulated: SRT reveals the time needed to reach a decision. Departing from the idea of a long-lasting information accumulation, it has been proposed that saccadic decisions might be driven by the sensory information present within the first 100ms (Ludwig, 2009; Ludwig et al., 2005). Why then should SRTs be longer than 100ms? This procrastination might be a way of prioritizing actions (Harwood et al., 2008) resulting from a trade-off between the benefit of a saccade, which enhances the visual information from a newly fixated location, and associated costs such as the temporary impairment of vision and commitment cost due to the saccade refractory period (Saslow, 1967). Such a conception has also been proposed to account for switching between smooth pursuit and catch-up saccades when tracking an object (de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002; Orban De Xivry & Lefèvre, 2007), or changes in SRTs due to explicit instructions (encouraging either urgency or accuracy; Reddi & Carpenter, 2000). In our case, saccades were explicitly reinforced and did not give access to visual information, but these consequences might be regarded as functionally identical (Davison & Baum, 2006; Shahan & Cunningham, 2015). Indeed it is established that SRTs may be experimentally affected by benefit manipulation (e.g., De Vries, Azadi, & Harwood, 2016; Harwood et al., 2008; Madelain et al., 2007; Madelain, Krauzlis, & Wallman, 2005; Montagnini & Chelazzi, 2005). Our present results further confirm that observers may learn to alter their information-foraging behavior depending on the actual benefit of making a saccade.

4.6. Conclusion

About three times per second a decision is made regarding when and where to move the eyes, providing many opportunities to learn about environment regularities and the benefits of adjusting the information-foraging policy to these properties. In line with pioneer works based on the notions 1) that acquisition of information is reinforcing (Wyckoff, 1952) and 2) that saccades are controlled by reinforcement (Schroeder & Holland, 1968a, 1969), we propose that the ability to adapt the allocation of saccades in response to specific temporal organization of information further reveals the exquisite plasticity of the saccadic system and its sensitivity to the current state of the observer and the environment.

Study 2: Reinforcement reduces the size-latency phenomenon: a cost-benefit evaluation of saccade triggering

Chapter 4:

Saccadic latency depends on beneficial consequences

ABSTRACT

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 et al., 2005; Harwood et al., 2008; De Vries et al., 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. In this study, we probed 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/size ratio was equal to either 0.3 or 1.5. We used a dynamic reinforcement criterion in 2 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 phenomenon with large differences in latencies depending on the ratio in force (e.g., 152ms and 204ms, respectively for 1.5 and 0.3). After training, distributions shifted toward the shorter or longer value (e.g., 223ms and 169ms, respectively for 1.5 and 0.3). On average, latencies decreased by 31ms and increased by 75ms according to the ongoing reinforcement contingencies. These changes in saccadic latencies were not explained by changes in saccadic amplitudes. Reinforcement reduced the size-latency phenomenon, although it was not entirely suppressed.

Our results indicate that reinforcement contingencies can considerably affect saccadic latency distributions, and support the idea of a cost-benefit evaluation for saccade triggering.

VALORIZATION

This study, adapted here for the thesis, is currently in revision for the *Journal of Vision* (a link toward the corresponding manuscript has been attached in Appendix 2) and has been presented as one poster (to the international conference *Vision Sciences Society* in May 2017) and as a talk (to the national conference *Forum annuel du Groupement De Recherche Vision* in October 2017).

I. CONTEXT

If saccadic latency actually depends on a functional relationship, it should be feasible to cancel or even reverse a strong consistent phenomenon of saccadic reaction times by manipulating the beneficial consequences. We used the size-latency phenomenon (Madelain et al., 2005; Harwood et al., 2008; De Vries et al., 2016), which concentrates on the amplitude of the step in proportion to the size of the target (step/size ratio) and yields a consistent relation between the reaction time and this step/size ratio (i.e., regular latencies for a step/size ratio above 1 and longer latencies for a step/size ratio below 1). Harwood et al. (2008) proposed that this effect 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. On the one hand, the cost of a particular 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.

In this study, we aim at probing 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 the reinforcement contingencies, as it has been demonstrated that reinforcement may have a strong effect on saccade reaction times (Madelain et al., 2007; Vullings & Madelain, 2018). We reinforced on the one hand shorter latencies for the ratio with typically long ones (i.e., ratio 0.3 yielding a median latency of 229ms) and on the other hand longer latencies for the ratio with typically regular ones (i.e., ratio 1.5 yielding a median latency of 161ms).

In the event of a latency decrease in the typically delayed saccades with the small ratio, it would mean that the beneficial consequences of a saccade do consistently control

SRTs and support that saccade latency can depend on a cost-benefit relationship, compatible with our hypothesis of a functional relationship.

II. METHODS

2.1. Participants

Six adults (18–47 years old, 3 women) participated in this study. They were naïve as to the purpose of the study, except for two participants (i.e., 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. When the experimental conditions changed, the same instruction was given again. Naïve participants received 5 euros for participating, plus an additional sum depending on the points collected (one point equaled 2cts); 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 n°2017-5-S51) and conformed to the standards set by the Declaration of Helsinki. All subjects gave informed written consent.

2.2. Apparatus

Stimuli were generated using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) for Matlab® and displayed on a video monitor (Iiyama HM204DT, 100 Hz, 22”). 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 measurement errors, the subject'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.), 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 = 15.99 cd/m^2), with various diameters (ranging from 1 to 8.33deg), displayed on a dark gray background (luminance = 1.78 cd/m^2). The target randomly stepped from the screen center to the left or right with horizontal amplitudes ranging from 1.2 to 10.5 degrees. The target diameter and target step were chosen such that the step/size ratio was either 0.3 or 1.5 (see Table 1 and Figure 40).

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

Table 1: Stimulus features (diameter and amplitude in degrees) for step/size ratios 1.5 and 0.3.

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

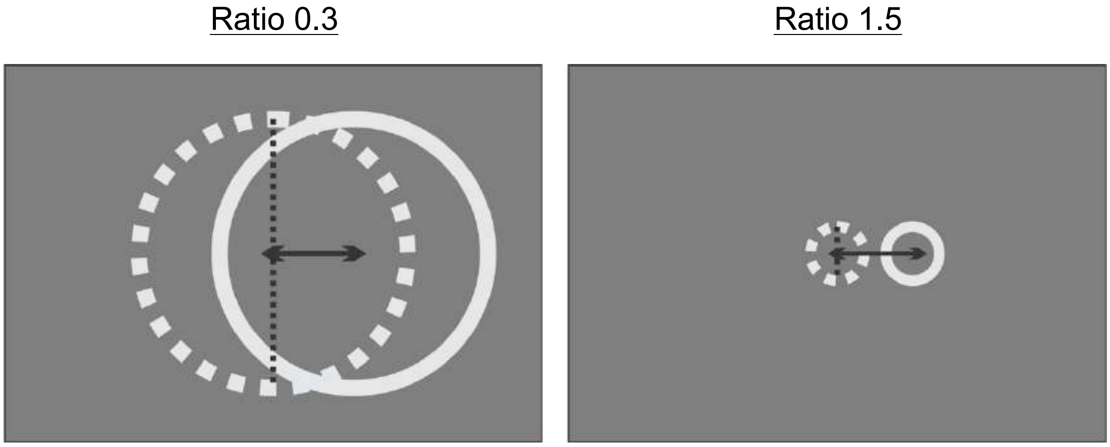

Figure 40: Illustration of the stimuli used for ratios 0.3 and 1.5 in the case of a 2.5-deg step.

2.3. Procedure

The experiment lasted thirty 320-trial sessions 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 days (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. 320-trial training sessions lasted until at least 75% of saccades were detected online (see Acquisition and data analysis). Because the probability of saccade is reduced with a 0.3 step/size ratio (Harwood et al., 2008; see Figure 10A), 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-deg step, the sizes of the outer and inner rings would be 8.33 and 1.67deg, respectively). 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 (Figure 41B). When the saccade was considered incorrect, a feedback was given consisting in a low-pitched beep (100ms, 400Hz) and a written comment (“No saccade” if the participant had blinked, anticipated or did not make a saccade, or “Wrong distance” if the participant did not correctly aim at the target center) was displayed for 500ms.

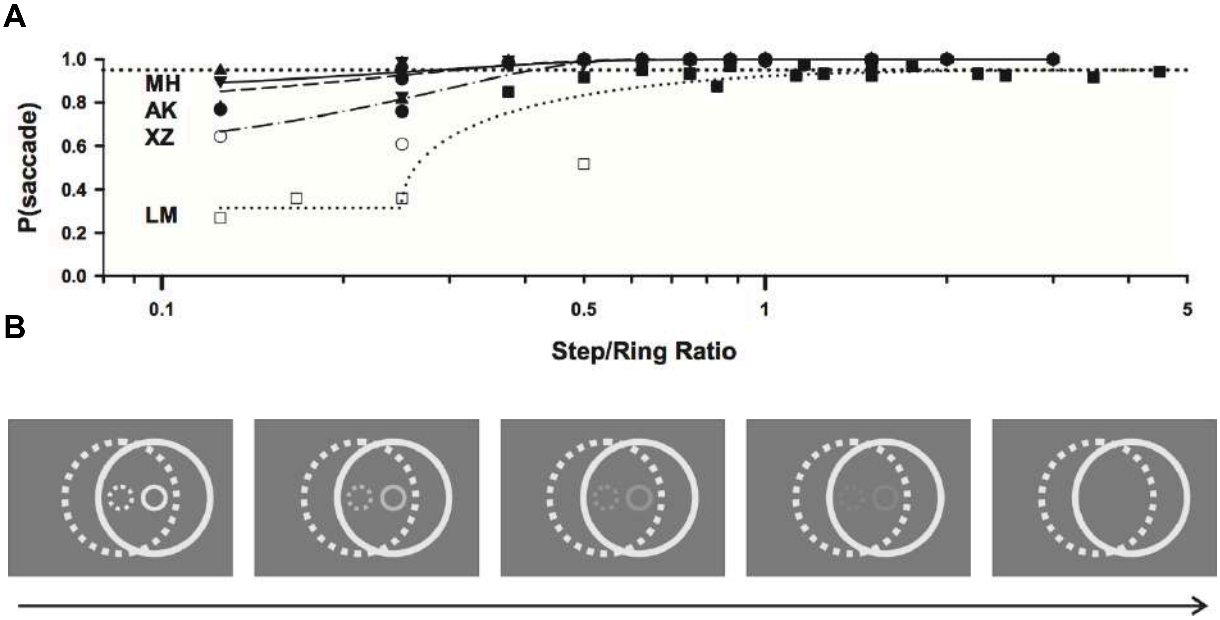

Figure 41: A) From Harwood et al. (2008). The probability of making a saccade at each step/ring ratio condition, with Weibull fits overlaid. The horizontal dotted line marks the 95% saccade probability. B) Illustration of the fading procedure used during the training phase. The inner ring corresponded to a 1.5 step/ring ratio and the outer one to a 0.3 ratio.

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 1250ms. The target then stepped randomly toward the left or right, and the participant made a saccade. If the latency was less than 80 or greater than 500ms, or if no saccade was detected, the target disappeared for the remainder of the trial (i.e. the screen remained blank) and the trial was discarded without repeat. The post-saccadic period lasted 300ms. Saccadic latency was defined as the interval of time elapsed between the target step and the saccade onset. A session was composed of 8 alternating blocks of 40 consecutive trials with either a step/size ratio of 1.5 or 0.3.

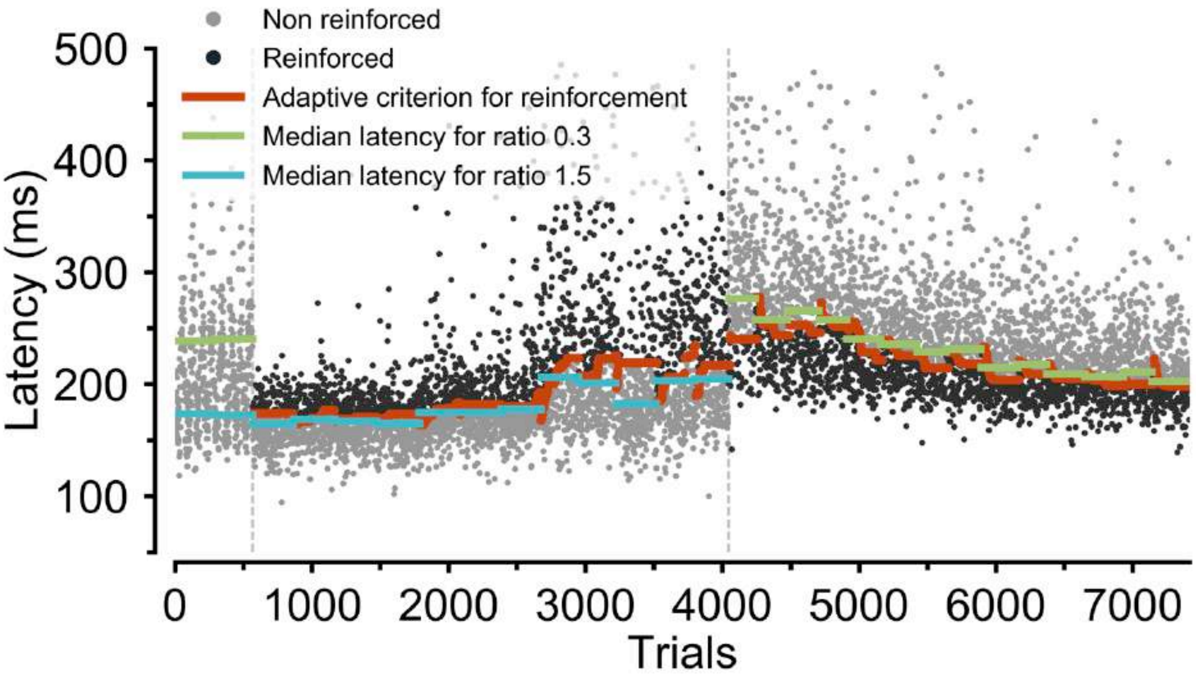

Figure 42: Time course of the experiment for the participant S4. The vertical dashed lines divide the 3 steps of the experiment: baseline, Rft 1.5, and Rft 0.3. The green and blue lines represent the median latencies for ratio 0.3 and 1.5, respectively. The red curve represents the adaptive criterion throughout the experiment. The black dots are the latencies that have been reinforced, the gray ones represent the trial on which latencies were not reinforced.

Reinforcement sessions. On average, twenty-three 320-trial reinforcement sessions were completed, separated in two counterbalanced experimental conditions: one using a step/size ratio of 1.5 and one using a step/size ratio of 0.3. During reinforcement with ratio 1.5 (Rft 1.5), the 320 trials used exclusively target sizes and steps yielding step/size ratio of 1.5 (see Table 1). We used a dynamically increasing criterion for reinforcement in order to increase saccadic latencies (see below). During the reinforcement ratio 0.3 condition (Rft 0.3), the 320 trials consisted of target sizes and steps yielding step/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 (see Figure 42 for an illustration of the adaptive criterion). The reinforcer consisted of a brief auditory feedback (100ms, 500Hz) and earning a point, which was exchanged for €0.02 collected 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, 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.

2.4. 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 $8000°/s^2$ acceleration thresholds. Saccade parameters were retrieved on average with a 12-ms delay after saccade offset. For offline analyses, a human observer first validated each saccade manually; saccades with amplitude gain (saccade amplitude/target amplitude) shorter than 0.5 or larger 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). All means and medians were compared using Fisher's exact test: the confidence intervals of the null hypothesis were computed using 100 000 permutations. Differences across latency distributions were estimated using the Kolmogorov-Smirnov distance.

III. RESULTS

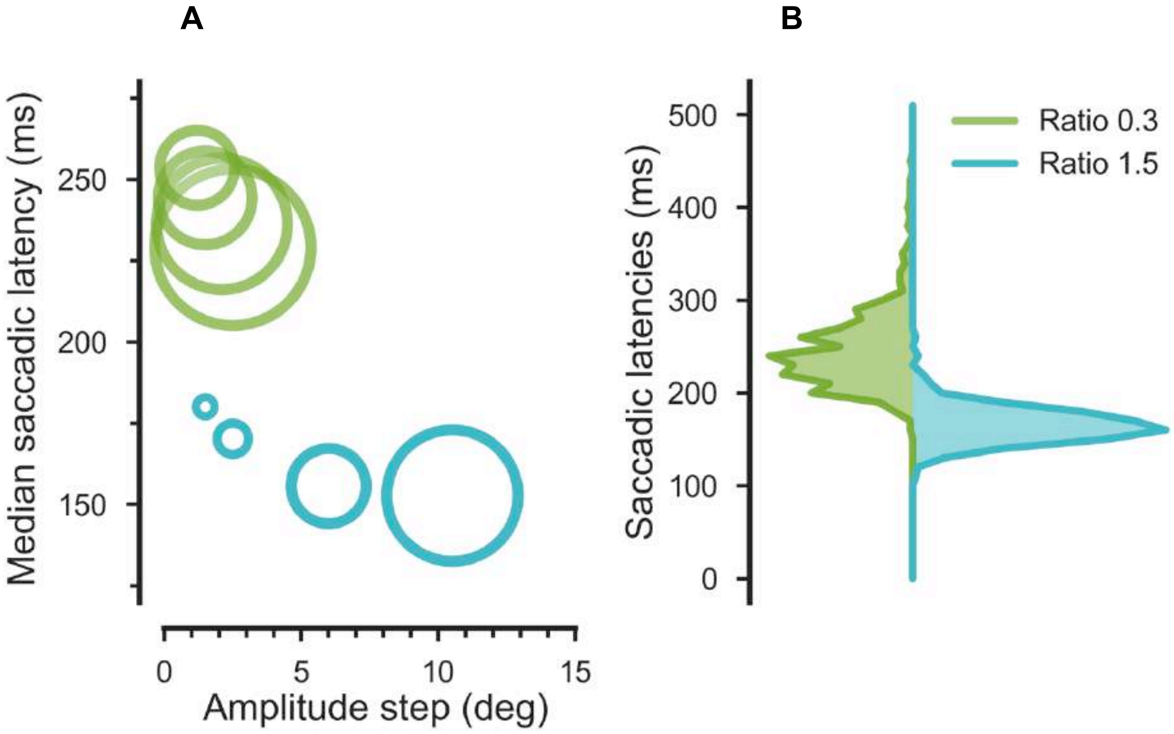

Figure 43: Illustration of the size-latency phenomenon during baseline for a representative participant. A) Median saccadic latency as a function of the amplitude step. The size of the ring represents the diameter of the stimulus (from 1 to 8.33deg). The green rings represent the stimuli used for the ratio 0.3 and the blue ones for the ratio 1.5 (actual ring color was always light gray). B) Frequency distributions of saccadic latencies for ratios 0.3 (in green) and 1.5 (in blue).

Figure 43 illustrates the baseline size-latency phenomenon for one representative participant (S6), showing that latencies were determined by the combined step/size ratio rather than by step amplitudes or target sizes alone. Large median differences between the ratios 0.3 and 1.5 (Figure 43A, green and blue, respectively, 237 and 164ms) cannot be explained by differences in either amplitude steps or target sizes: median latencies are clustered according to the step/size ratio used. Latency distributions merged across all ring sizes also show a remarkable segregation of latencies beyond the medians based on the step/size ratio (Figure 43B).

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 44, where the frequencies for the ratios 0.3 and 1.5 are represented upward and downward of 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 to S6, respectively.

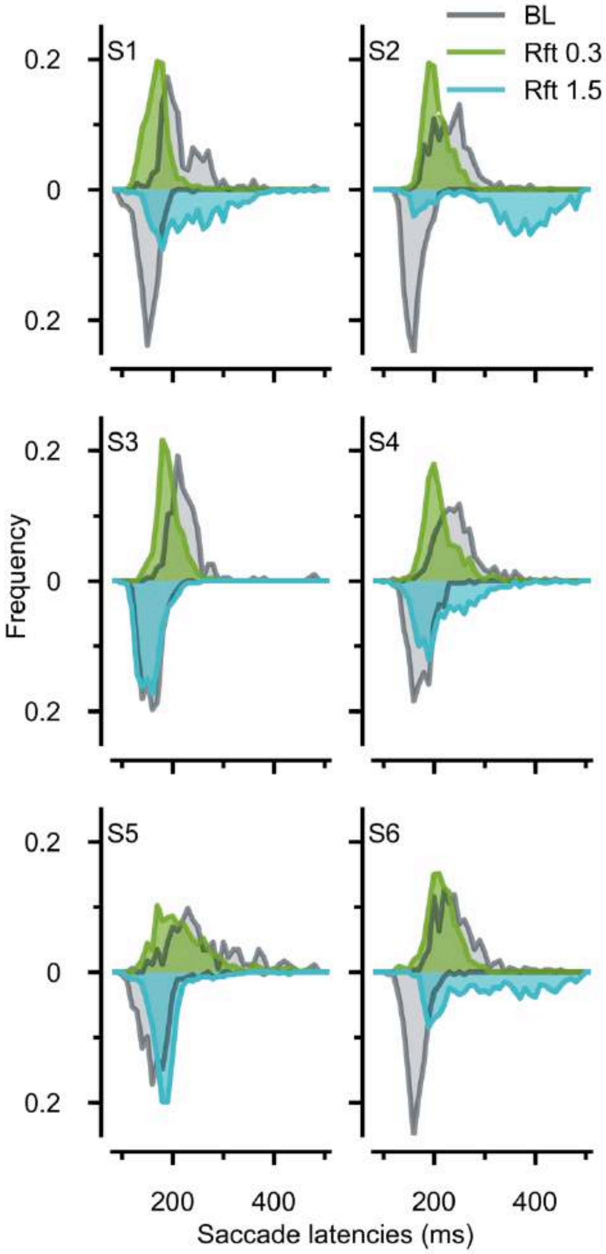

Figure 44: Frequency distributions of saccadic latencies for the baseline (light gray) and reinforcement in green and blue for ratios 0.3 and 1.5, respectively, for all participants in the last two sessions of each condition. The frequency for ratio 0.3 is represented upward of the y-axis while it is represented downward for ratio 1.5.

We used the Kolmogorov-Smirnov (KS) distance to individually assess the differences in distributions: when the KS statistic is equal to 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 were equal to 0.86, 0.82, 0.86, 0.78, and 0.87 for participants S1 to S6, respectively; all p-value < 0.0001). Our key result is how reinforcement shifts the distributions in opposite directions for each ratio (Figure 44: gray vs. green, 0.3 ratio; gray vs. blue, 1.5 ratio). Most interestingly, for the ratio 0.3, the latency distributions strongly shifted toward shorter values when shorter latencies were reinforced when compared to the baseline ones (mean latency decrease = 31ms; all values greater than the null hypothesis 98% CIs; mean KS = 0.42; all p-value < 0.0001; see Table 2). When long latencies were favored for the ratio 1.5, the distributions shifted toward longer values for all participants (mean latency increase = 90ms; all values greater than the null hypothesis 98% CIs; mean KS = 0.63; all p-value < 0.0001; see Table 2), except for S3 (latency difference = 3ms; value within the null hypothesis 98% CI; KS = 0.1; p-value = 0.0349; see Table 2). Therefore, reinforcing longer or shorter saccadic latencies strongly affected the distributions.

Table 2: Median latencies for ratios 0.3 and 1.5 in baseline and reinforcement for all participants, with the reinforcement-baseline difference in median latencies and the Kolmogorov-Smirnov distance.

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

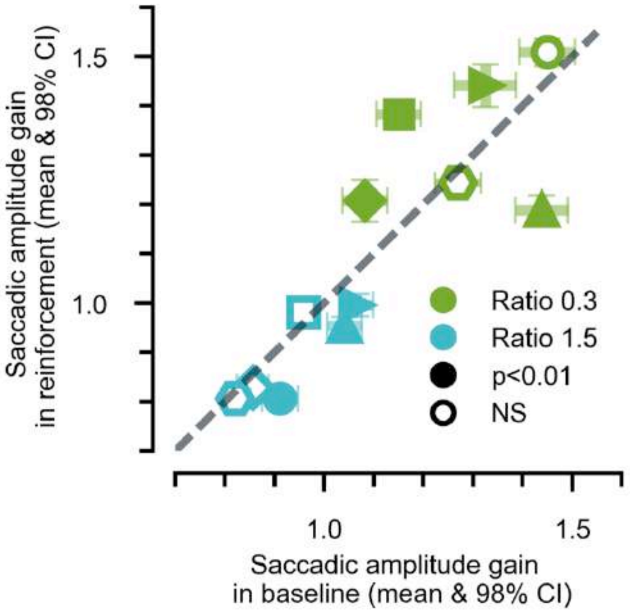

Figure 45: Mean saccadic amplitude gain in reinforcement as a function of mean saccadic amplitude gain in baseline across the last two sessions of each condition. The bootstrap 98% confidence intervals are shown for both the baseline and reinforcement means. The dashed line represents the equality line.

Furthermore, we checked whether the changes in saccadic latencies could be explained by changes in saccadic amplitudes between the baseline and reinforcement sessions. Figure 45 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. It should be noted that the overshooting in baseline and reinforcement sessions to the 0.3 ratio and undershooting to the 1.5 ratio is compatible with the range effect typically seen for smaller vs. 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 to S6, respectively (all p-value < 0.0001). There were more limited and inconsistent correlations between amplitude gain and target size: 0.27, 0.20, -0.10, 0.09, 0.09 and 0.16 for participants S1 to S6, respectively (all p-value < 0.0001). Finally, we did not observe any consistent change in peak velocities across conditions and participants.

IV. DISCUSSION

In the current paper, we aimed at experimentally probing whether the size-latency phenomenon (De Vries et al., 2016; Harwood et al., 2008; Madelain et al., 2005) 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/size ratio (averaging 68ms 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.

4.1. The size-latency phenomenon is not a function of uncertainty

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 in De Vries et al. (2016). Indeed, perhaps our observed overshooting here of the target center in the 0.3 ratio 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 in ratio 0.3. The difference in amplitude gain between the ratio 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.

4.2. A cost-benefit evaluation of saccade latencies

Our proposed explanation for the size-latency phenomenon is functional. Indeed, it has been well established that saccades are an operant behavior, i.e., a response that depends on its consequences (see Madelain et al., 2011 for a review). 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 temporary 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 of the saccadic system to prioritize fixation over movement. This explanation of saccadic latencies at a functional level 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. Interestingly, the size-latency phenomenon might also parsimoniously explain some data in past literature. For instance, Boch, Fischer, and Ramsperger (1984) investigated the effect of eccentricity, intensity and target size on express saccadic latencies with monkeys. Their Figure 5 (p227) shows what seems to be a rather complex relationship between the size, the eccentricity and the latencies: it is hard to define a clear-cut trend. They tested four different eccentricities and the last data points of the graph are really interesting: when the target size is the largest (4deg), the express saccade latencies are longer for the 1-deg step (at around 95ms), then for the 2-deg step (at around 85ms) and finally tend towards an asymptote for the 4- and 8-deg steps (around 70-65ms). One could not postulate that this effect is solely due to the target eccentricities, as shorter latencies had been found for the smallest step but with a smaller target size (e.g., around 80ms for the 1-deg step with a 1-deg target size). If we transform these data with the step/size ratio, we observe the longest latencies for the smallest ratio (95ms – ratio 0.25), then for the intermediate one (85 ms – ratio 0.5) and finally the shortest latencies for ratios above 1 (70 and 65ms for ratio 1 and 2, respectively). Therefore, the difference in latencies obtained with the 1-deg step (i.e., 95ms vs 80ms) could be explained by the step/size ratio (i.e., ratio 0.25 vs ratio 1). It is noteworthy that the size-latency phenomenon can be observed in other papers and species, but also with express saccades.

4.3. Saccade latencies and arbitrary reinforcement

Although we were able to reduce the size-latency phenomenon, it is noteworthy that we did not completely eliminate it. One explanation might be that we did manipulate the benefit associated with specific saccade latencies by giving an arbitrary reinforcer (i.e., money) while the actual benefit of having shorter or longer latencies in the size-latency phenomenon is related to the visual perception of the targeted object. In other words, our reinforcing event 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 post-saccadic ability to extract visual information as a consequence instead of a monetary reinforcer, we would have increased the changes in saccade latencies, since 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 non-visual reinforcers have been discussed before either in the context of saccade latency reinforcement (Madelain et al., 2007; Vullings & Madelain, 2018) or reinforcement-induced saccade gain change (Madelain, Paeye, & Wallman, 2011; Meermeier, Gremmler, Richert, 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.

4.4. Conclusion

We found that the size-latency phenomenon, in which saccade latencies increase when the step/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 such as the gap and overlap effects (Saslow, 1967). At the neurophysiological level this prioritization is also well explained by the recently proposed "equilibrium" hypothesis (see Krauzlis, Goffart, & Hafed, 2017 for a related discussion). 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.

Study 3: Discriminative control of saccadic reaction times using a novel latency-contingent paradigm

Chapter 5:

Stimulus control of saccadic latency

ABSTRACT

Since saccades are used to acquire information localized in our visual surroundings they are conventionally view as being solely concerned with the spatial position of objects. Yet, recent studies, including the first one in this thesis, have demonstrated that they are also influenced by the temporal regularities in dynamic environments. In this study, we asked whether discriminative control (i.e., the possibility to use external stimuli signaling the future state of the environment) of latencies in a search task can be established using reinforcement learning. Eight participants made saccades within 80-750ms toward a target displayed among distractors. For each subject we constructed two classes of latencies, “short” and “long”, using the first and last quartiles of individual baseline distributions (e.g., [80;294] and [432;750]ms respectively). We then used a latency-contingent display paradigm in which finding the target was made contingent upon specific saccadic latencies. For a first group, the target was displayed only for “short” latencies with leftward saccades, and for “long” latencies with rightward saccades. The opposite was true for a second group. When short- and long-latency saccades were reinforced (i.e., the target was displayed) depending on the saccade direction, median latencies differed by 74ms on average (all outside the 98% null hypothesis CIs). Post-training, in the absence of reinforcement, we still observed considerable differences in latency distributions, averaging 64ms for leftward versus rightward saccades. Our results demonstrate the discriminative control of saccadic latencies, further supporting the effects of

reinforcement learning for saccades. This study reveals that saccade triggering is finely controlled by learned temporal and spatial properties of the environment.

VALORIZATION

This study, adapted here for the thesis, has been submitted to the *Journal of Vision* (a link toward the corresponding manuscript has been attached in Appendix 3) and this study has been presented as two posters (to international conferences *Society for Quantitative Analysis of Behavior* in May 2017 and *European Conference on Visual Perception* in August 2017) and as a talk in a symposium (to the international conference *Association for Behavior Analysis International* in May 2018).

I. CONTEXT

Our first and second studies (chapters 3 and 4) have supported our hypothesis of a functional relationship for saccadic latencies by manipulating the effect of beneficial consequences. But it remains unclear whether these effects would hold in more complex visual contexts such as search tasks. Indeed, one has to adapt to the complexity, uncertainty and dynamic changes in natural environment, and detect the cues –also termed discriminative stimuli– signaling the actual state of the reinforcement contingencies. These discriminative stimuli represent the first term in the functional relationship between the antecedent, the behavior and the consequence. Learning the relations between these three terms of environmental contingency is crucial for an efficient information gathering. A fundamental question related to this functional relationship is whether it is possible to place saccadic latencies under discriminative control. This general ability to use the presence of cues signaling the future state of the environment, termed discriminative control, is particularly remarkable in the case of sensorimotor control as it provides a means to adapt movements to future consequences.

Most learning experiments, such as ours in the chapters 3 and 4, use extraneous consequences as reinforcers for saccades (e.g., food or liquid with non-human animals or money with humans) while the real-life benefit of saccades is associated with changes in the visual perception of the targeted object. Moreover, reduced effects have often been reported when using arbitrary reinforcement for saccade latency (Madelain et al., 2007; Vullings & Madelain, 2018; chapter 4). Because biological constraints are known to have a substantial impact on operant conditioning (e.g., Domjan & Galef, 1983), one explanation for these outcomes is that the reinforcing consequences mostly used so far might be less biologically relevant than the ones obtained in natural settings (i.e., foveating the targeted object).

In this study, we investigated whether a visual consequence –here, the ability to find a visual target– can be used to reinforce specific saccadic latencies in a visual search task and place them under discriminative control. We developed a novel latency-contingent paradigm in which finding a target among distractors depended on the latency of the current saccade. Our study is the first one to investigate the discriminative control of saccadic latencies as we aimed at training participants to have short latencies when they made saccades toward one side of the visual field and long latencies for the other side.

In the event of a differential responding in latency between the sides of the visual fields according to the reinforcement contingencies, it would mean that it is possible to place saccadic latencies under discriminative control using visual consequences as reinforcement, supporting the role of a functional relationship in the stimulus control of reaction times.

II. METHODS

2.1. Participants

Eight adults (18–26 years old, 4 women) participated in this research. They were naïve as to the purpose of the study and had normal or corrected-to-normal vision. Participants were instructed to find with one saccade a target stimulus amongst items displayed on an imaginary circle. To encourage participants to carry on the task, they were told they would earn a point every time they found the target stimulus; no further explanation was given as to how to earn points. When the experimental conditions changed, the same instruction was given again. Participants received 10 euros for participating, plus an additional sum depending on the points collected (one point equaled 2cts); they received 74 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 n°2017-2-S50) and conformed to the standards set by the Declaration of Helsinki. All participants gave informed written consent.

2.2. Apparatus

Stimuli were generated using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) for Matlab® and displayed on a video monitor (Iiyama HM204DT, 100 Hz, 22”). 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 measurement errors, the subject’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.), 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 2.2deg lines (luminance = 15.99 cd/m^2) displayed on a dark gray background (luminance = 1.78 cd/m^2). The twelve stimuli were arranged on an imaginary circle (with a radius of 9 degrees of visual angle), forming an 18deg rotated clock face, such that half of the items were on the left side of the screen and the other half on the right side (Figure 46A). Out of the twelve items, the target stimulus was a horizontal line (Figure 46B) flanked by four distractors (lines tilted by -70, -20, 20 and 70 degrees from the horizontal) and the seven other irrelevant items were vertical lines.

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

2.3. Procedure

The experiment lasted thirty 384-trial sessions divided between baseline and reinforcement sessions. Two daily sessions were typically recorded, separated by 5-min breaks during which participants were free to move. The experiment lasted 15 consecutive days (five days a week, from Monday to Friday). Regardless of the actual condition, participants were required to make a saccade toward the location at which they thought the target stimulus was. Our general goal was to create a situation in which finding the target stimulus was made contingent upon specific saccadic latencies.

Baseline. Four 384-trial baseline sessions were completed, in which participants were instructed to find the target stimulus, i.e., the horizontal line, with their first saccade. At the beginning of the trial, the participant looked at the fixation cross displayed at the center of the screen for a period varying randomly from a uniform distribution between 750 and 1250ms (Figure 46A i.). The target arrangement, consisting in the horizontal target stimulus pseudo-randomly assigned to one of the 12 possible locations (Figure 46A ii. and Figure 46D) flanked by the four distractors and seven vertical lines, was then presented for 30ms. Only five items were not vertical lines in order to cue the area where the target stimulus was displayed. Immediately after this 30ms bout, we displayed a neutral arrangement that consisted in twelve vertical lines, and the participant made a saccade (Figure 46A iii.). The saccade latency had to be comprised between 80 and 750ms (this range was defined based on latencies measured in pilot studies). Following the saccade offset, we displayed a mask consisting in 12 square noise patches at the stimulus locations during one frame (i.e., 10ms; Figure 46A iv.), then the target arrangement (i.e., the target stimulus, 4 flankers and 7 irrelevant vertical lines at the same location as it was at the beginning of the trial) for 500ms (Figure 46A v.). Finally, the neutral arrangement (i.e., the twelve vertical lines) was displayed again for 200ms (Figure 46A vi.). On cancelled trials, the target arrangement (see Figure 46A v.) was not shown and the 12-vertical lines neutral arrangement was shown for 700ms instead (see Figure 46A vi.). A trial was cancelled in four possible cases: 1) the latency was shorter than 80ms or longer than 750ms, 2) the saccade direction was such that the saccade endpoint was located between two items, 3) the participant made a saccade towards the opposite side of screen with respect to the target stimulus location, or 4) no saccade was detected. Saccadic latency was defined as the interval of time elapsed between the target onset and the saccade onset. Figure 46D plots the probability of the post-saccadic eye position to be at one of the 12-item locations as a function of the target stimulus location during baseline for the best and worst individual baseline performances. If the participants were able to systematically find the target, the diagonal would be red ($p = 1$). As it is shown, the probability of landing on target was quite low (on average $p = 0.3$) and the participants approximately aimed at either the target stimulus or its two closest flankers.

After completion of the baseline, we constructed two individual latency classes – "short" and "long" saccadic latencies– using respectively the first and last quartiles of baseline latency distributions for each participant. These individual class boundaries were fixed for the remainder of the experiment. Latencies between 80ms and the first quartile were categorized as short latencies (i.e., the shortest 25% of all baseline SRTs; e.g., 80-293ms for S1) and latencies between the last quartile and 750ms were categorized as long latencies (i.e., the longest 25% of all baseline SRTs; e.g., 430-750ms for S1). The first and last quartiles were 293 and 430ms, 236 and 321ms, 222 and 304ms, 255 and 432ms, 243 and 352ms, 241 and 287ms, 222 and 286ms, 230 and 298ms for participants S1 to S8, respectively.

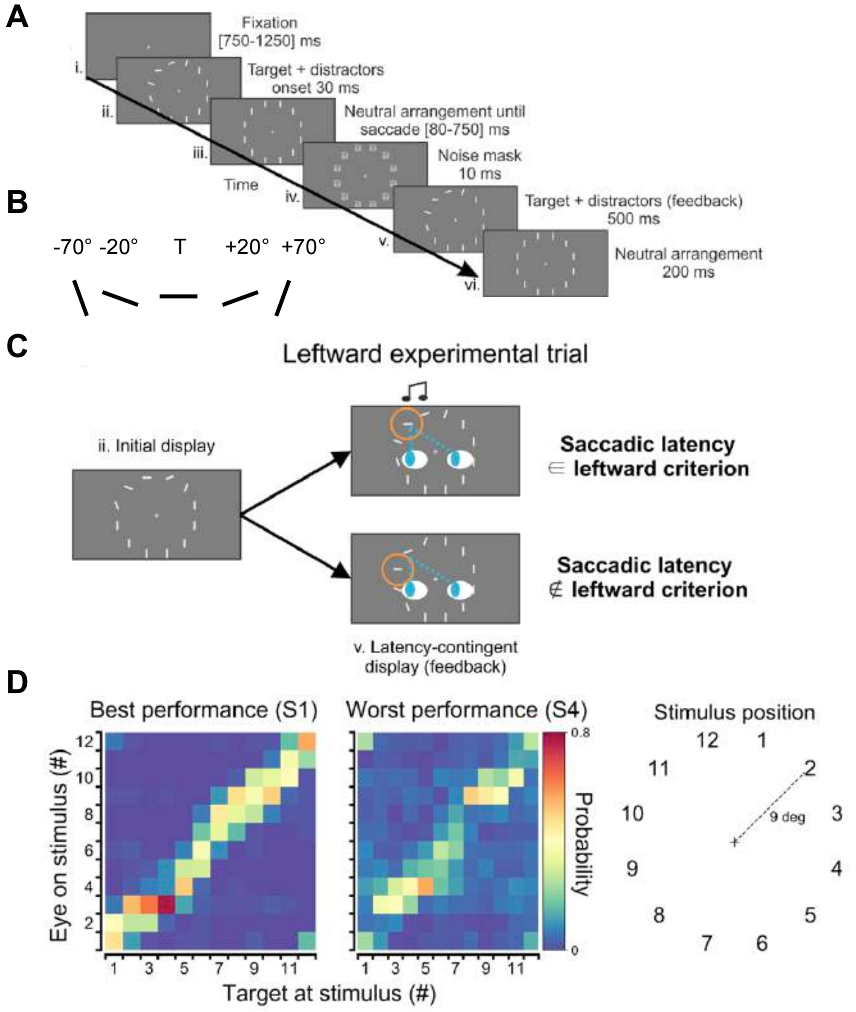

Figure 46: Illustration of the experimental design. A) Experimental design of an ongoing trial during baseline. i) The fixation cross appears at the center of the screen for a bout varying from 750 to 1250ms. ii) The target and distractors are displayed for 30ms. iii) A mask is displayed until a saccade is emitted, to which latency has to be comprised between 80 and 750ms. iv) Square patches of noise are displayed at the stimulus locations for 10ms while the eyes are moving. v) The same stimulus organization as ii) is displayed for 500ms. vi) A mask is displayed for 200ms. B) The target was always a horizontal line and the four flankers were tilted lines. C) Illustration of the latency-contingent display in a leftward experimental trial. D) Probability of the eyes to land on the target position during baseline for the best and worst performances.

Reinforcement sessions. In all reinforcement sessions, “short” and “long” latencies were independently reinforced on a multiple schedule of continuous reinforcement using a latency-contingent display, in which finding the target was made contingent upon specific latencies. In continuous schedules, reinforcement is systematically delivered contingent on a correct response –in our case, the “short” or “long” latencies. In a multiple schedule, different schedules of reinforcement are in effect during different trials signaled by particular stimuli or contexts –in our case, the target stimulus being located on either the left or right side of the screen. We aimed at training participants to have one class of latencies for the leftward target stimulus locations and the other one for the rightward target locations: for group 1, the leftward-trial criterion required short latencies and the rightward-trial criterion required long latencies; the opposite was true for group 2.

The latency-contingent display used for reinforcement consisted in displaying the target at the post-saccadic eye location upon specific latencies. Figure 46C shows an instance of the latency-contingent display for group 1, in which the target stimulus is initially located on the left, thus requiring a short latency. If the saccadic reaction time was short (as in the top right-hand corner), the 12 items were arranged such that the target was placed at the post-saccadic eye location flanked by the four distractors. If the saccadic reaction time was longer (as illustrated in the bottom right-hand panel), the 12 items were arranged such that the target was located one position away from the post-saccadic eye location, either clockwise or counter-clockwise.

Using this latency-contingent display, the participant could see the target at any of the six left item locations he would be saccading to, providing the saccade latency was short. To illustrate the procedure, we will use the case of a leftward-trial for participant S2 as an example. S2 was assigned to group 1, requiring short latencies (i.e., in his case, any latency between 80 and 236ms) for the leftward-trial criterion and long latencies (i.e., in his case, any latency between 321 and 750ms) for the rightward-trial criterion. On a given trial, the initial target arrangement was such that the target stimulus was placed at position 12. If participant S2 made a saccade to position 11, with a latency of 230ms, we would then arrange the items with the target stimulus at the post-saccadic location, in this case location 11. This would be true for any of the post-saccadic eye locations between position 7 and 12. The participant would therefore find the target stimulus for any saccade directed toward the correct side of the screen (i.e., the left side in our example) with a criterial latency. Finding the target-stimulus would then be signaled by a brief auditory feedback tone (100ms, 500Hz) and the participant would earn a point, which would be exchanged for 2cts collected at the end of the experiment. However, if the participant S2 made a saccade toward the location 11 with a latency of 237ms or longer, we would rotate the items arrangement by 30deg either clockwise or counter-clockwise with respect to position 11 such that the target stimulus would instead be randomly placed at the location 10 (as in Figure 46C, bottom right panel) or 12. In other words, the participant would not see the target stimulus at the post-saccadic eye position for saccades with non-criterial latencies. We used different types of reinforcement sessions, manipulating the initial location of the target between the left and right sides of the screen.

Massed sessions. For discrimination training, we first massed trials on one side of the screen (leftward-trial sessions followed rightward-trial sessions).

Alternating block sessions. Then, we alternated blocks of consecutive leftward/rightward trials and progressively decreased their length (24-, 12-, 6-, and 3-trial blocks). For instance, in a 12-trial block session, the participant experienced 12 leftward trials followed by 12 rightward trials and so on until 384 trials were completed.

Interleaved session. The last sessions of reinforcement consisted in pseudorandomly interleaved leftward and rightward trials.

Retention probe session. Finally, we conducted a retention probe session, in which the latency-contingent display was withdrawn. Therefore, in this session the trials were identical to the baseline ones (see Figure 46A).

The total number of 384-trial reinforcement sessions completed in each step depended on the time needed to reach stable reaction time distributions. We simultaneously used two criteria to decide when to advance the experiment from one type of reinforcement session to the next. The first learning criterion used the median, first and last quartiles of the saccadic latency distribution for the last session with the requirement that these statistics for the leftward saccades should be different (outside the 98% confidence intervals of the null hypothesis) from those of the rightward saccades. The second criterion used the same statistics for the last two sessions with the requirement that these statistics for the leftward and rightward saccades should both be different (outside the 98% confidence intervals of the null hypothesis) from those of the baseline sessions.

2.4. 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 $8000°/s^2$ acceleration thresholds. Saccade parameters were retrieved on average with a 12-ms delay after saccade offset. For offline analyses, a human observer first validated each saccade manually; we discarded the saccades with amplitude gain shorter than 0.5 or for which the distance angle between the eye and the stimulus position was greater than 10deg. On average, we kept 74% (SD = 14) 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). All means and medians were compared using Fisher's exact test: the confidence intervals of the null hypothesis were computed using 100 000 permutations.

III. RESULTS

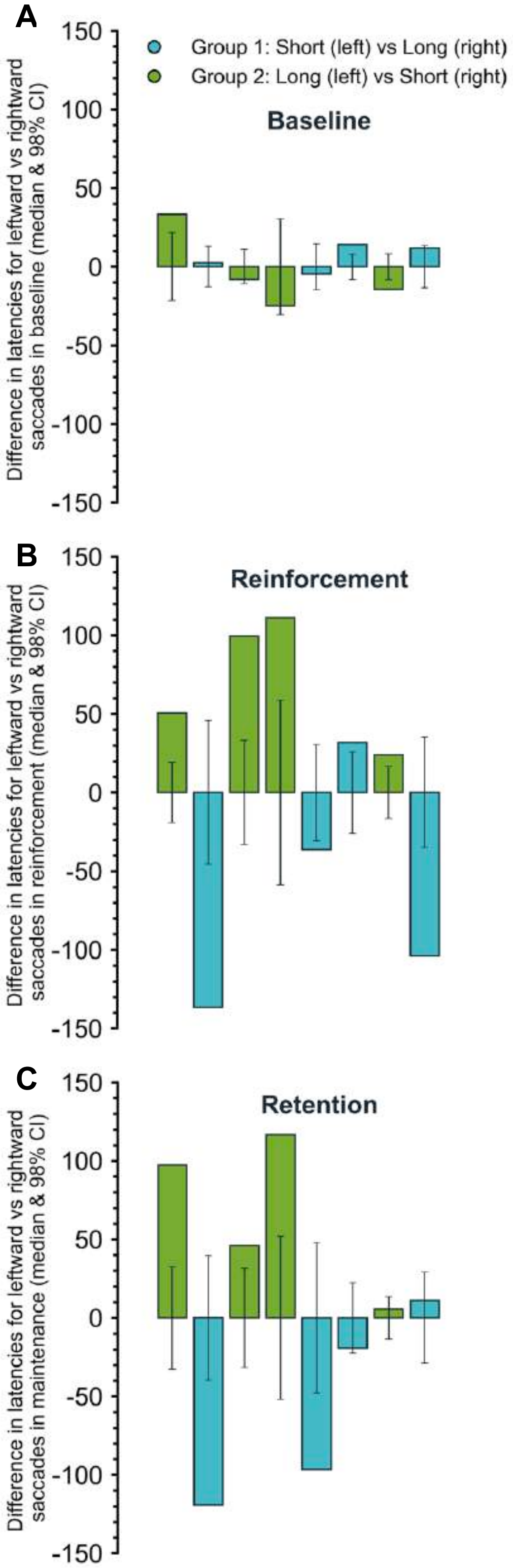

Figure 47: Differences of the medians in latencies for leftward vs. rightward saccades in baseline (A), reinforcement (B) and retention probe session (C). Groups 1 and 2 are represented in blue and green, respectively. The corresponding 98% confidence intervals of the null hypothesis (i.e., the two saccade directions have identical probability distribution) are shown.

Figure 47 represents the individual difference in latencies for leftward versus rightward saccades for the two groups of participants during the baseline session, last session of reinforcement and retention probe session. During baseline (Figure 47A), although two participants showed a latency bias, there was no significant consistent difference between the two sides across participants (absolute mean difference = 14ms). During reinforcement (Figure 47B), we were expecting a negative difference for the group 1 (as we reinforced short latencies for leftward saccades and long latencies for rightward saccades) and a positive difference for the group 2 (as we reinforced long latencies for leftward saccades and short latencies for rightward saccades). We observed a large difference in latencies between leftward and rightward saccades (absolute mean difference of 74ms; all values greater than the null hypothesis 98% CIs). This difference was systematic across participants and in the right direction for both groups, except for participant S6 for whom the difference was in the opposite direction: this participant exhibited a positive latency difference even though he was assigned to group 1, in which the leftward saccade latencies should have been shorter than the rightward ones. Finally, during retention, that is when the target location was not anymore contingent upon the latency (Figure 47C), 5 participants had significant differences that were in the right direction (S1 to S5, on average 95ms; all values greater than the null hypothesis 98% CIs). Three participants had no significant difference (S6, S7 and S8, on average 12ms; all values within the null hypothesis 98% CIs). Overall, the participants maintained a difference of 64ms in the probe retention session.

Figure 48A plots the boxplots of the saccadic latency distribution for the leftward and rightward saccades (in green and blue, respectively) during the same interleaved-location sessions for one representative participant (S3, in group 2). During baseline, there was no difference in latencies between leftward and rightward saccades (i.e., 249ms for the left and 257ms for the right; 8ms difference, within the null hypothesis 98% CI). During reinforcement, while the target location was randomized across trials, we observed a large difference in latencies between the two directions with longer latencies (median = 486ms) for leftward saccades and shorter ones (median = 386ms) for rightward saccades (100ms difference, greater than the null hypothesis 98% CI). Finally, during the retention probe session, we still observed a large latency difference between the two directions (i.e., 324ms for leftward saccades and 278ms for rightward saccades; 46ms difference, greater than the null hypothesis 98% CI). Interestingly, we observed large differences in saccadic latency distributions after learning, but also an increase of the rightward saccade latencies, which were reinforced to be shorter. Figure 48B breaks down the effect on saccadic latencies for the same participant across the phases of the experiment. We plot, on the left-hand panel, the percentage of trials in which the target was found and, on the right-hand panel, the quartiles of the respective saccadic latency distributions for the baseline, the reinforcement 24-, 12-, 6- and 3-trial alternating blocks, the reinforcement interleaved-location session and the retention probe session. First, it appears that the percentage of trials in which the target was found was always higher for the leftward saccades (on average 57.60%) than for the rightward saccades (on average 29.53%). Since the participant S3 was in group 2, this implies that long latencies were reinforced almost twice as often as short latencies. Second, we can observe that there were two kinds of effect on saccadic latency distributions throughout the time course of the experiment. On the one hand, the difference in latency was due to a shift toward shorter values for rightward saccades and a shift toward longer values for leftward saccades (as in the 24-, 12-, 6- and 3-trial alternating block sessions): the percentage of rightward trials in which the target was found was on average 37.94%. On the other hand, the difference in latency was explained by a shift toward longer values for rightward saccades and a shift toward the longest values for leftward saccades (as in the reinforcement interleaved-location session): the proportion of finding the target in rigthward trials fell to 1.34%. Interestingly, in spite of the fact that the short latencies were almost never reinforced, the difference in the saccadic latency distributions maintained. This trend was also found with the other participants, for whom long latencies were much more frequently reinforced than short latencies (see Table 3).

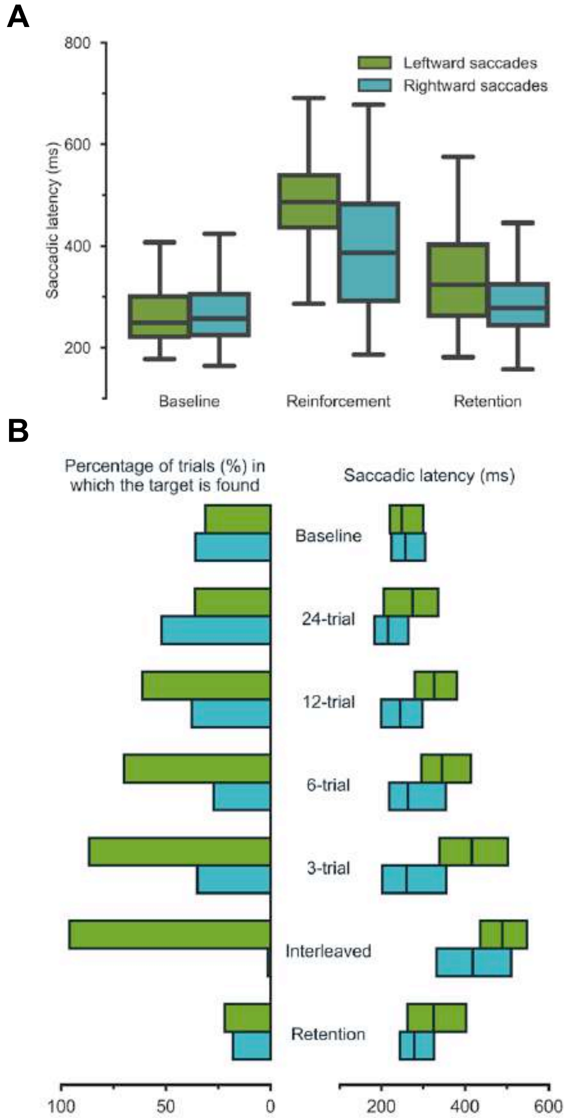

Figure 48: A) Boxplots of the saccadic latency distribution for the leftward and rightward saccades (in green and blue, respectively) during baseline, reinforcement and retention probe session for a representative participant (S3, in group 2). B) Left-hand panel: the percentage of trials in which the target was found for leftward and rightward saccades (in green an blue, respectively). Right-hand panel: the quartiles of the leftward and rightward saccadic latency distributions for the baseline, the reinforcement 24-, 12-, 6- and 3-trial alternating blocks, the reinforcement interleaved-location session and the retention probe session.

Table 3: Proportion of trials in which the target was found in leftward and rightward trials for all participants during baseline, reinforcement and retention. For the reinforcement interleaved-location session, the letter indicates whether short (S) or long (L) latencies were reinforced.

Participants	**Group**	**Baseline (%)**		**Interleaved (%)**		**Retention (%)**	
		Leftward	**Rightward**	**Leftward**	**Rightward**	**Leftward**	**Rightward**
S1	2	38.10	37.39	81.11 (L)	19.05 (S)	48.21	23.42
S2	1	23.54	29.33	17.46 (S)	91.74 (L)	18.25	29.49
S3	2	31.20	35.80	96.02 (L)	1.34 (S)	21.95	17.81
S4	2	29.18	32.02	95.77 (L)	1.79 (S)	24	29.09
S5	1	33.33	43.01	0 (S)	98.59 (L)	58.94	50.53
S6	1	21.04	22.44	0.89 (S)	82.12 (L)	34.82	20.81
S7	2	24.95	27.69	9.91 (L)	43.28 (S)	24.79	18.25
S8	1	61.18	48.44	31.12 (S)	87.50 (L)	54.81	75.30

IV. DISCUSSION

The present study introduced a novel latency-contingent paradigm to investigate discriminative control over latencies in a search task using visual reinforcement. Saccadic latency distributions were considerably affected by visual consequences and we observed significant latency differences between leftward and rightward saccades. These results provide evidence that saccadic latencies might be placed under discriminative control and further reveal the extent of reinforcement learning for saccades and sensorimotor prediction.

4.1. Inducing and maintening discriminative control of latencies

The procedure we used induced differences in latencies between leftward and rightward saccades such that saccades were on average 74ms longer for one direction than for the other. In 7 out of our 8 participants this difference was in the right direction revealing that SRTs changed according to the reinforcement contingencies. However, these differences required some training to install: participants first experienced massed training and then alternating block sessions in which they had to perform several saccades toward the same visual hemifield in a row. In these sessions, the direction of the saccade was perfectly predictable and participants learned to perform both short and long latency saccades according to the saccade direction. When leftward and rightward trials were interleaved we found that all but one (i.e., S6) participant did produce long latencies for the direction associating reinforcement with longer latencies but increased their latencies for the other direction to the point that these saccades were almost never reinforced (see Table 3 and also Figure 48 which illustrates this effect for one participant). This indicates that, although our procedure induced strong bias in latencies depending on the saccade direction, participants had a limited control over their shorter latencies in this last reinforcement session. As we have previously found, the effects of reinforcement on latencies develop over time and require quite a large number of trials to stabilize (e.g., Madelain et al., 2007, Vullings & Madelain, 2018, see their Figure 2A) and one might argue that with a longer training period participants might have increased their reinforcement rate. The necessity for a long training might be due to three possible sources of uncertainty in SRT control: the perception of the actual reinforcement contingency (Gallistel et al., 2001; Killeen & Smith, 1984), the perception of time –here the perception of one's own reaction time (Wearden, 2016), and the SRT production itself (Sumner, 2011). Although further researches are necessary to disentangle between these three sources of noise, the fact that the control of short latencies was stronger in blocked than in interleaved sessions seems to point toward a noisy discrimination of the contingencies. In the blocked sessions, participants might have taken advantage of the increased predictability due to serial dependencies across trials whereas in the interleaved session they could only rely on the appearance of the target to adjust their SRTs. In both cases, this implies discriminative control over saccade latencies but it could be that serial dependency is a more powerful contextual cue than saccade direction, particularly for short-latency saccades.

Five out of eight participants (S1-S5) exhibited a significant difference in latencies during the retention probe session while the remaining two participants who also exhibited some discriminative control in the interleaved session did not (S7 and S8, see Figure 47C). The fact that not all participants showed retention is not surprising since it is commonplace to extinguish the stimulus control when reinforcement is withdrawn (Staddon, 2016) –in our case the removal of the monetary reinforcer associated with finding the visual target. In spite of not getting any monetary reinforcer, five participants still responded differentially as a function of the saccade direction, indicating that the discriminative control was firmly established in their case. Another factor that might have contributed to washing out the discriminative control in participants S7 and S8 could be that, in the retention session, any latencies were potentially reinforced by finding the visual target. Indeed, during the retention probe session, we implemented a return-to-baseline, in which the post-saccadic target was displayed at the same location as the pre-saccadic one regardless of the saccade latency (see Figure 46A). This means that participants could find the target even if their saccadic latency was not one previously reinforced (the percentage of trials in which the target was found was 21.52 and 65.06% for participants S7 and S8, respectively). Therefore, one might argue that the absence of contingency between the latency and the ability to find the target contributed to reducing the SRT differences across leftward and rightward saccades. Finally, in some trials of the retention probe session the saccadic latencies were much longer than the median latency and may not be representative of what was happening throughout the whole session. Indeed, because we used a quite large latency range (80 to 750ms), some participants presented a progressive increase in latencies (see Figure 48B). One might wonder whether a 750ms saccade latency is still a regular reaction time (Ratcliff, 1993), whether it depends on the same underlying process as a 150ms latency or whether there was a change in the participant's strategy. Interestingly, if we only consider the trials with latencies under 500ms, the differences in latencies for these two participants become significant (all values outside the 98% null hypothesis CIs): 32.38ms (S7 in group 2) and -74.56ms (S8 in group 1). Thus, the data from these participants presented a trend in favor of stimulus control.

Previous research concluded that predicting a reward tends to reduce saccadic latencies, with mean SRT being systematically shorter in rewarded than in non-rewarded condition (e.g., Dunne et al., 2015; Glaser et al., 2016; Takikawa et al., 2002; Watanabe et al., 2003a). This was not the case in our experiment and the fact that participants collected more reinforcers for saccades requiring longer latencies indicate that reward expectancy does not necessarily imply a decrease in saccade latencies. One key specificity of our procedure is that we established a latency-contingent reinforcement program so that reward expectancy was associated with both longer and shorter SRTs depending on the saccade direction. Previous research using a latency-contingent paradigm also found that there is no systematic relation between reward expectancy and reduced latencies (Madelain et al., 2007; Vullings & Madelain, 2018). One should therefore conclude that the SRTs truly adapt to the actual contingency in force rather than being reduced by the outcome expectation.

4.2. Reinforcers

Previous studies have investigated the impact of reinforcement learning on gaze control both in experimental and natural settings (for reviews, see Glimcher, 2003; Hayhoe & Matthis, 2018; Madelain, Paeye, & Darcheville, 2011; Trommershäuser, Glimcher, & Gegenfurtner, 2009). Most learning experiments use extraneous consequences as reinforcers for saccades (e.g., food or liquid with non-human animals or money with humans) while the real-life benefit of saccades is associated with changes in the visual perception of the targeted object. It has been well documented that extraneous reinforcers such as monetary profits affect saccade target selection (e.g., Chen et al., 2013; Liston & Stone, 2008; Lou, Hsu, & Sajda, 2015; Schütz et al., 2012; Stritzke et al., 2009) and influence saccade latencies (e.g., Madelain et al., 2007; Milstein & Dorris, 2007; Rothkirch et al., 2013; Vullings & Madelain, 2018). However, limited effects have often been reported when using arbitrary reinforcement for saccade latency (Madelain et al., 2007; Vullings & Madelain, 2018) or saccade amplitude (Madelain, Paeye, & Wallman, 2011; Meermeier, Gremmler, Richert, et al., 2017). Because biological constraints are known to have a substantial impact on operant conditioning (e.g., Domjan & Galef, 1983), one explanation for these effects is that the extraneous reinforcing consequences commonly used so far might be less biologically relevant than the ones obtained in natural settings (i.e., foveating the targeted object). In line with the fact that acquisition of information is reinforcing (Wyckoff, 1952), some studies demonstrated that visual consequences could as well act as a reinforcer for saccadic amplitude (Madelain, Paeye, & Wallman, 2011; Meermeier et al., 2017; Paeye & Madelain, 2014). It has also been shown that humans exhibit shorter latencies when the target remains visible after the saccade than when it is systematically extinguished (Collins, 2012). Furthermore, Montagnini and Chelazzi (2005) elegantly demonstrated that making the visual perception of a target contingent on short latencies has a dramatic effect on saccadic latency distributions in a visual-discrimination task. Taken together these results imply that saccades are reinforced by the ability to carry on a visually guided task. That a reinforcer might be a behavior rather than an object (such as food or money) has been established before (e.g., Timberlake, 1995; Timberlake & Allison, 1974). In the case of saccades, the outcome is information: saccades enhance the perceived high spatial frequency of a visual object by placing its retinal image on the center of the retina. One could argue that whether this information is meaningful depends on the flow of activities in which the organism is engaged. In other words, changing what one sees constitutes a favorable outcome if the ongoing task benefits from this additional information. Paradigms such as ours (see also Montagnini & Chelazzi, 2005) attempt to mimic this natural state of affair by establishing relations between a specific dimension of saccadic eye movements, in our case their latency, and the ability to perform a visually guided task. That these relations come to change the saccades reveal the reinforcing effect of these outcomes.

4.3. Saccadic latencies and Discriminative control

Participants had either a positive or negative latency differences between leftward and rightward saccades depending on the reinforcement contingencies (Figure 47). Although, it has already been shown that saccade latencies could become shorter (e.g., Ikeda & Hikosaka, 2007; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Montagnini & Chelazzi, 2005; Watanabe et al., 2003) or longer (e.g., De Vries, Azadi, & Harwood, 2016; Harwood et al., 2008; Madelain et al., 2005) depending on the contingencies in force, our study is to our best knowledge the first demonstrating that one can induce a discriminative control of saccadic latencies using reinforcement. The discriminative control of behavior, demonstrated by differential responding associated with changes in stimuli or context, is a fundamental aspect of how organisms are sensitive to specific features of the environment and adjust to it (Cowie & Davison, 2016) as their survival depends on the ability to behave in a way that is appropriate to future circumstances (Domjan, 2010). Unraveling the conditions under which a behavior comes under discriminative control is critical for a better comprehension of how an organism interacts with its environment (Bouton, Todd, & León, 2014). Indeed, discriminative control of saccades results in responses that are controlled by the present state of the environment in such a way that they are adapted to the future state of the environment. Understanding how the outcome of saccades might be predicted provides critical insights about how these motor responses are attuned to environmental exigencies.

The ability to use the current state of the environment to adjust saccades according to future outcomes has been explored before. For instance, Fleuriet and Goffart (2012) proposed that saccade endpoint in the presence of a moving target might be accounted for by the spatiotemporal characteristics of the target at the time of saccade onset. As we previously discussed, saccade adaptation may be placed under discriminative control such that an amplitude increase might be associated with one context while an amplitude decrease is associated with another context (e.g., Azadi & Harwood 2016). More generally, when exploring a visual scene, eye movements are perturbed by the presence of an inconsistent object or by having objects violating the laws of physics (Võ & Henderson, 2011). In other words, eye movements are perturbed by unfamiliar context revealing that familiar context usually do control exploration saccades. Research also demonstrated that saccade may become predictive (i.e., with a 0ms latency) when a visual target steps between two locations with a fixed inter-stimulus interval (Lee et al., 2016): the context formed by the spatiotemporal regularities of the target appearance comes to control saccade triggering.

Importantly, discriminative control may also be observed in situations in which the reinforcer delivery itself forms the context. For instance, it has been shown that monkeys might learn to adequately choose between two physical targets depending on the probability of reinforcement associated with each target (Sugrue et al., 2004). When the reinforcement probabilities changed, the probability of saccading toward one or the other target changed as well such that the local relative frequency of choice matched the local relative frequency of reinforcement. This indicates that monkeys were able to discriminate among the various contingencies which in return came to control the saccades. Research also demonstrated that human observers may learn the temporal properties of a dynamical environment to allocate their gaze toward a specific region based on the associated frequency of reinforcement (Hoppe & Rothkopf, 2016). A similar result was obtained in a latency-contingent paradigm in which changes in reinforcement contingencies induced changes in saccade latency distributions (Vullings & Madelain, 2018). That organisms may adjust their behavior to reinforcement contingencies despite the absence of explicit cues in the environment has been taken as evidence that reinforcers themselves have discriminative properties as they signal a change in differential reinforcement (Cowie & Davison, 2016).

Previous research established that manipulating reinforcement contingencies induce changes in SRT distributions (e.g., Madelain et al., 2007, Vullings & Madelain, 2018) and we previously proposed that the allocation of saccade in time depends on the specific temporal organization of the environment. Indeed, one could argue that saccades are information-foraging responses that must take into account the ways information is distributed in space but also in time (see Hoppe & Rothkopf, 2016 for a similar argument): the ability to use the temporal properties of our environments to shift gaze toward potentially informative locations at the right time allows efficient exploration of the visual environment. The present results reveal that human observers were able to learn to use environmental cues to adjust their saccade latencies. Taken together, these results indicate that saccade latencies are constrained by the environmental temporal properties, allowing information-foraging to be attuned to the specific dynamics of our environment.

4.4. Saccadic latency and Associative learning

That our participants differentially responded to different stimuli opens new perspectives for research on saccadic latencies and decision-making models. Indeed, decision models such as the LATER model, or its newest version the LATEST (Tatler et al., 2017), cannot account for our current and prior results. Therefore, our findings challenge the understanding of what saccadic latencies really underpin. Because the discriminative control of saccadic latencies is possible, it means that the control of reaction times by the environment depends on associative learning as well (Staddon, 2016). Associative learning or classical conditioning has not been investigated within the scope of saccades yet. Further research should therefore be conducted on this topic since it could be an excellent means to thoroughly investigate discriminative control on saccadic latencies. Our current study used biologically relevant contexts for saccadic eye movements (i.e., the left and right visual fields) but it would be interesting to probe whether saccadic latencies can be placed under discriminative control with other kinds of stimuli. To draw a parallel with saccadic adaptation, it has been shown that contexts triggering different motor responses such as target directions or velocities can establish a stimulus control over saccade amplitude (e.g., Alahyane & Pélisson, 2004; Azadi & Harwood, 2014; Chaturvedi & Van Gisbergen, 1997; Shelhamer & Clendaniel, 2002) whereas contexts that trigger the same motor response such as target color or shape fail to do so (e.g., Azadi & Harwood, 2014; Bahcall & Kowler, 2000;

Deubel, 1995). It would be pertinent to assess whether saccadic latencies are under the same apparent restrictions.

4.5. Conclusion

Expanding prior findings showing that saccades are affected by reinforcement, we demonstrated that saccadic latencies can be placed under discriminative control by operant conditioning. Our results indicate that the outstanding plasticity of the saccadic system depends on the state of the environment at the time of the saccade. The ability to use predictive signals to adapt the temporal allocation of saccades in response to the specific organization of information sheds a new light on the mechanisms by which reinforcing events affect motor control.

Study 4 (pilot): Classical conditioning of saccadic latencies using gap and overlap paradigms

Chapter 6:

Associative learning of saccadic latency

ABSTRACT

This pilot study aimed at investigating to what extent learned environmental contingencies affect the temporal allocation of saccade and the involvement of classical conditioning in this process. It is well established that a stimulus-onset-asynchrony between the fixation-target offset and the saccade-target onset considerably affects saccade latencies. A gap (fixation-target disappearing before the saccade-target onset) triggers short latency saccades. An overlap (fixation-target disappearing after the saccade-target onset) triggers long latency saccades. In this study, we probed the possibility to control saccadic latencies using classical conditioning by systematically pairing a gap with one saccade direction and an overlap with the other. In classical conditioning (Pavlov, 1927), unconditional stimuli (US; e.g., food) –eliciting unconditional responses (UR; e.g., salivation)– are paired with initially neutral stimuli (NS; e.g., bell). After repeated pairing, the NS –then called conditional stimuli (CS)– come to elicit conditional responses (CR) comparable with the UR. We first associated a saccade direction (i.e., leftward or rightward, NS1 or NS2) with either a 100ms gap (US1) or a 150ms overlap (US2). We then introduced leftward and rightward probe-trials in which there was no SOA (CS1 and CS2; 20% of trials). Once steady state was observed, we did a return-to-baseline and then reversed the direction pairing. During baseline, we observed no difference in latencies across saccade directions. During training (6200 pairing trials on average), the gap and overlap (US) resulted in shorter and longer latencies (UR), respectively (median latencies differed by 144ms on average; all outside the 98% null hypothesis CIs). For

the probe-trials, we observed considerable differences in latency distributions (CR; i.e., on average 31ms; all outside the 98% null hypothesis CIs) consistent with direction pairing (CS). Interestingly, during the return-to-baseline sessions (200 trials), there was a slight retention of the CR for three participants out of seven. Our results demonstrate control of saccadic latencies by saccade direction using classical conditioning. This study further establishes that learned environmental contingencies affect the temporal allocation of saccades (Vullings & Madelain, 2018).

VALORIZATION

This pilot study on classical conditioning of saccadic reaction times has been presented as a poster (to the international conference *Vision Sciences Society* in May 2018) and will be further carried on in the near future.

I. CONTEXT

The previous chapters have investigated the influence of instrumental conditioning and the manipulation of antecedent stimuli and consequences on reaction times, supporting a functional interpretation of SRTs. Because we observed stimulus control in the chapter 5, it raises the issue of the effect of associative learning on saccadic latency. Indeed, discriminative control is tightly related to associative learning processes (Staddon, 2016). Recently, Jóhannesson et al. (2018) have demonstrated that training express saccades toward specific targets using a gap paradigm could transfer to the untrained eye, suggesting that classical conditioning of saccade latencies is possible.

In this study, we further investigated the stimulus control over saccadic latencies, using this time classical conditioning. We systematically paired a saccade direction (NS1) with a gap SOA (US1) and the other saccade direction (NS2) with an overlap SOA (US2), and then introduced probe trials with no SOA to assess whether control of saccade latencies by saccade direction could be observed.

In the event of a differential responding in latency between saccade direction according to the pairings (i.e., shorter latencies for CS1 and longer latencies for CS2), it would mean that it is possible to place saccadic latencies under stimulus control through classical conditioning, emphasizing the necessity to consider learning and historical effects when studying reaction time. Also, if we observe that SRT distributions in probe trials are affected simply by a consistent pairing between saccade direction and a gap or overlap, it would further challenge the current interpretation of saccadic latencies and express saccades.

II. METHODS

2.1. Participants

Seven adults (3 women and 4 men, mean age = 26.1, age range: 18-47 years) participated in this study. They were naïve as to the purpose of the study, except for two participants (i.e., the authors, S1 and S2), and had normal or corrected-to-normal vision. Participants were instructed to look at a fixation ring that could appear on the left or right side of the screen, then to make a saccade toward the target and to not anticipate. No further explanation was given. Participants could listen to music or podcasts during the experiment. Naïve participants received 50 euros for participating. All experimental procedures conformed to the standards set by the Declaration of Helsinki. All participants gave informed written consent.

2.2. Apparatus

Stimuli were generated using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997) for Matlab® and displayed on a video monitor (Iiyama HM204DT, 100 Hz, 22"). Participants were seated on an adjustable stool in a darkened quiet room, facing the center of the computer screen at a viewing distance of 60cm. To minimize 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 recorded and 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.), sampled at 2000Hz. Data were transferred, stored, and analyzed via programs written in Matlab® running on an Ubuntu Linux computer.

Stimuli were light gray disk and ring (luminance = 15.99 cd/m^2), diameter 0.5°, displayed on a dark gray background (luminance = 1.78 cd/m^2). The fixation position pseudo-randomly alternated between two fixed locations on the screen (left or right), both located at 7.9 degrees horizontally with respect to the center of the monitor.

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

2.3. Procedure

The experiment lasted on average 18 500-trial sessions divided between baseline, pairing, probe, and reversal sessions. Two daily sessions were typically recorded, separated by 5-min breaks during which participants were free to move. On average, the experiment lasted 10 consecutive days (five days a week, from Monday to Friday). We aimed at probing the possibility to control saccadic latencies using classical conditioning.

Baseline. One 500-trial baseline session was completed, in which participants fixated a left or right position and made saccades toward the target horizontally stepping to the opposite direction. At the beginning of the trial, the participant looked at the fixation ring for an unpredictable period varying between 750 and 1250ms (sampled from a uniform distribution). At the same time as the fixation offset, the target disk appeared horizontally in the opposite direction at pseudo-randomly 7, 10, 13, 16 or 19 degrees from the fixation. The participant made a saccade with a latency that had to be ranging from 60 to 1000ms. If the latency was outside this range or if no saccade was detected the target disappeared and the trial was discarded for offline analysis. The post-saccadic period lasted 400ms. Saccadic latency was defined as the interval of time elapsed between the target onset and the saccade onset.

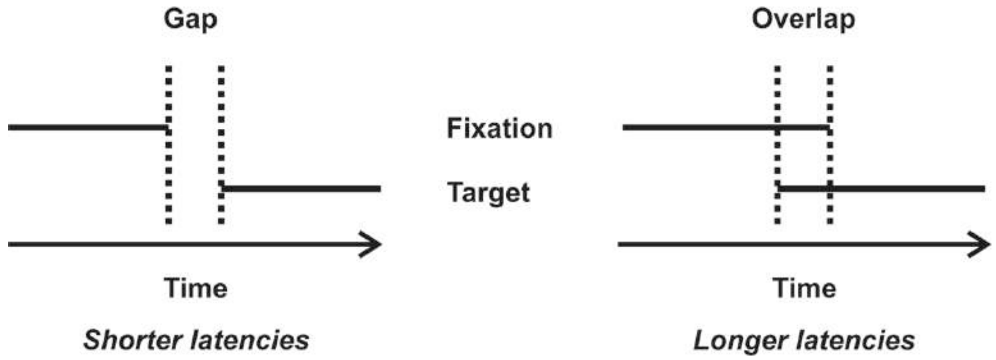

Figure 49: Illustration of the gap and overlap paradigm. A gap consists of the fixation-target disappearing before the saccade-target onset whereas an overlap consists of the fixation-target disappearing after the saccade-target onset. A gap triggers short latencies, as opposed to an overlap that triggers long latencies.

Pairing. It is well established that a stimulus-onset-asynchrony (SOA) between the fixation-target offset and the saccade-target onset considerably affects saccade latencies (Kalesnykas & Hallett, 1987). A gap (the fixation-target disappearing before the saccade-target onset) triggers short-latency saccades. An overlap (the fixation-target disappearing after the saccade-target onset) triggers long-latency saccades (Figure 49). To probe how contexts and stimuli come to trigger certain saccadic latencies, we investigated whether it is possible to establish classical conditioning over saccadic latencies. In classical conditioning (Pavlov, 1927), unconditional stimuli (US; e.g., food) –eliciting unconditional responses (UR; e.g., salivation)– are paired with initially neutral stimuli (NS; e.g., metronome). After repeated pairing, the NS –then called conditional stimuli (CS)– come to elicit conditional responses (CR) comparable with the UR (Figure 50B). To probe the possibility to establish classical conditioning over saccadic latencies, we systematically paired a saccade direction (NS) with either a gap or an overlap (US). For half of the participants, the left fixation (NS1) was associated with a -100ms SOA gap (US1) and the right fixation (NS2) with a 150ms SOA overlap (US2; see Figure 50A); the opposite was true for the other participants. The US1 triggered short latencies (UR1) for rightward saccades and the US2 triggered long latencies (UR2) for leftward saccades (Figure 50C). On average, three sessions of 500-trial pairings were completed.

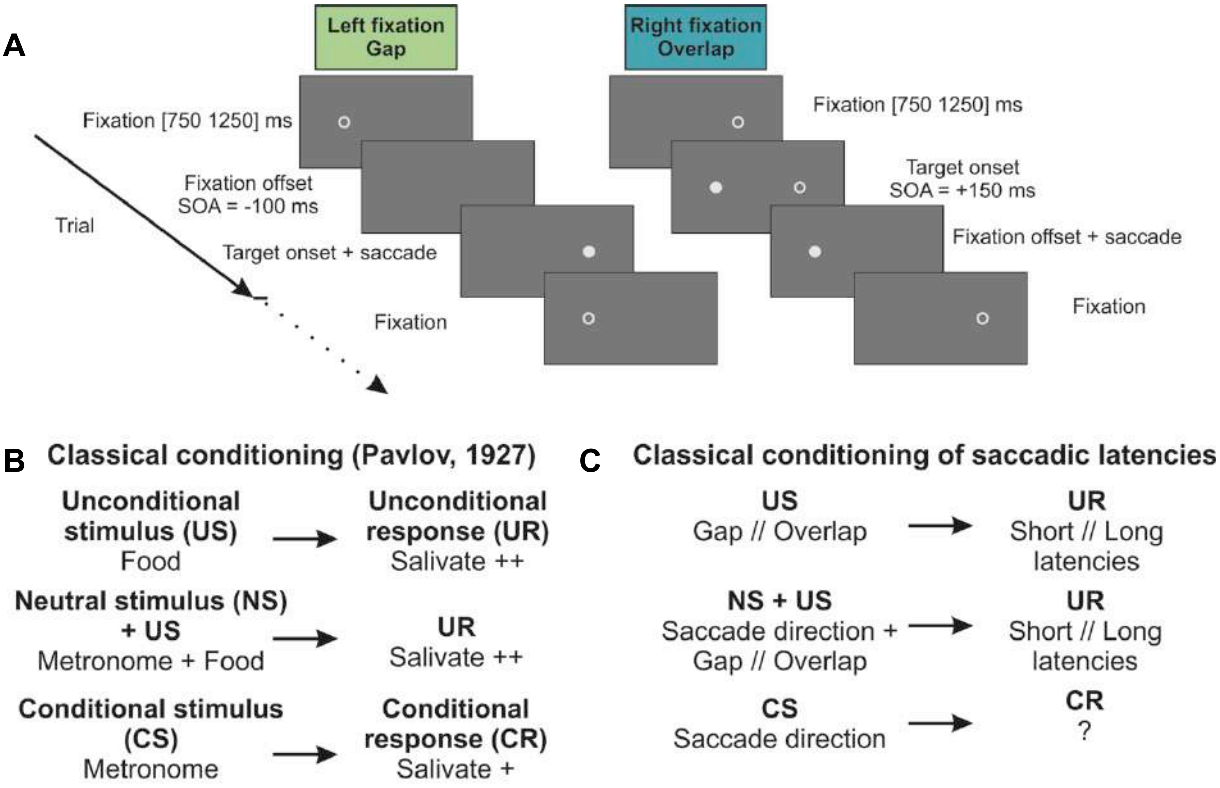

Figure 50: A) Illustration of a gap- and overlap-trial during the pairing session. B) Diagram of the common classical conditioning procedure. C) Diagram representing the classical conditioning of saccadic latencies.

Probe. We then pseudo-randomly introduced leftward and rightward probe-trials, representing 20% of trials, in which there was no SOA in order to test whether we would observe conditional responses (CR1 and CR2) depending on the saccade direction (CS1 and CS2; Figure 50C). On average, six 500-trial sessions were completed, consisting of 100 probe trials each.

Reversal. Once the results were stable, we did a return-to-baseline and then reversed the direction pairing (except for two participants, S3 and S4).

2.4. 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 saccades onset and offset, using a 30°/s velocity and $8000°/s^2$ acceleration thresholds. Saccade parameters were retrieved on average with a 12ms delay after saccade offset. For offline analyses, saccades with amplitude gain lower than 0.5 or duration longer than 100ms were automatically excluded. A human observer then validated each saccade manually. On average, we kept 82.71% (SD = 7.33) of saccades.

We used bootstrapping methods (resampling with replacement 100 000 times) to estimate all the individual statistical parameters and 98% confidence intervals (CIs; Efron, 1979). All means and medians were compared using Fisher's exact test: the confidence intervals of the null hypothesis were computed using 100 000 permutations.

III. RESULTS

Figure 51 represents the boxplots of the saccadic latency distribution for left and right fixation across experimental conditions for all participants. During baseline, we observed no consistent left-right differences across participants and only participants S5 and S7 had significant latency differences (i.e., 9ms and 10ms, respectively; both values outside the 98% CIs). Non-surprisingly, we obtained substantial and consistent differences between left-fixation saccades and right-fixation saccades when we systematically paired saccade directions with a gap or an overlap. For gap-saccades, there was strong decrease in latencies and for overlap-saccades, a critical increase, such that the average left-right difference was 144ms across participants (all values outside the 98% CIs; Table 4). During probe trials, outcomes were more diverse. Non-naïve participants (S1 and S2) had significant left-right differences (on average 75ms, all values outside the 98% CIs; see Table 4) and specifically large overlap-effect retentions (Figure 51). The same results were observed for participant S3 and S4, who had an average difference of 19ms (all values outside the 98% CIs; Table 4). However, participant S5 had no change in latencies. Participant S6 obtained a significant left-right difference in latencies, only when the overlap was associated with the left fixation and the gap with the right fixation (median latency difference outside the 98% CIs; Table 4). Finally, although participant S7 had significant –albeit small– left-right differences in latencies, it was in the right direction only when the overlap was associated with the left fixation (all values outside the 98% confidence intervals; Figure 51). Overall, the average median latency difference between leftward and rightward saccades was 31ms for probe trials. If we remove the non-naïve participants, this average difference drops at 11ms. The significant observed differences in latencies during probe trials represented on average 26% (from 11 to 50%) of the latency difference in pairing trials.

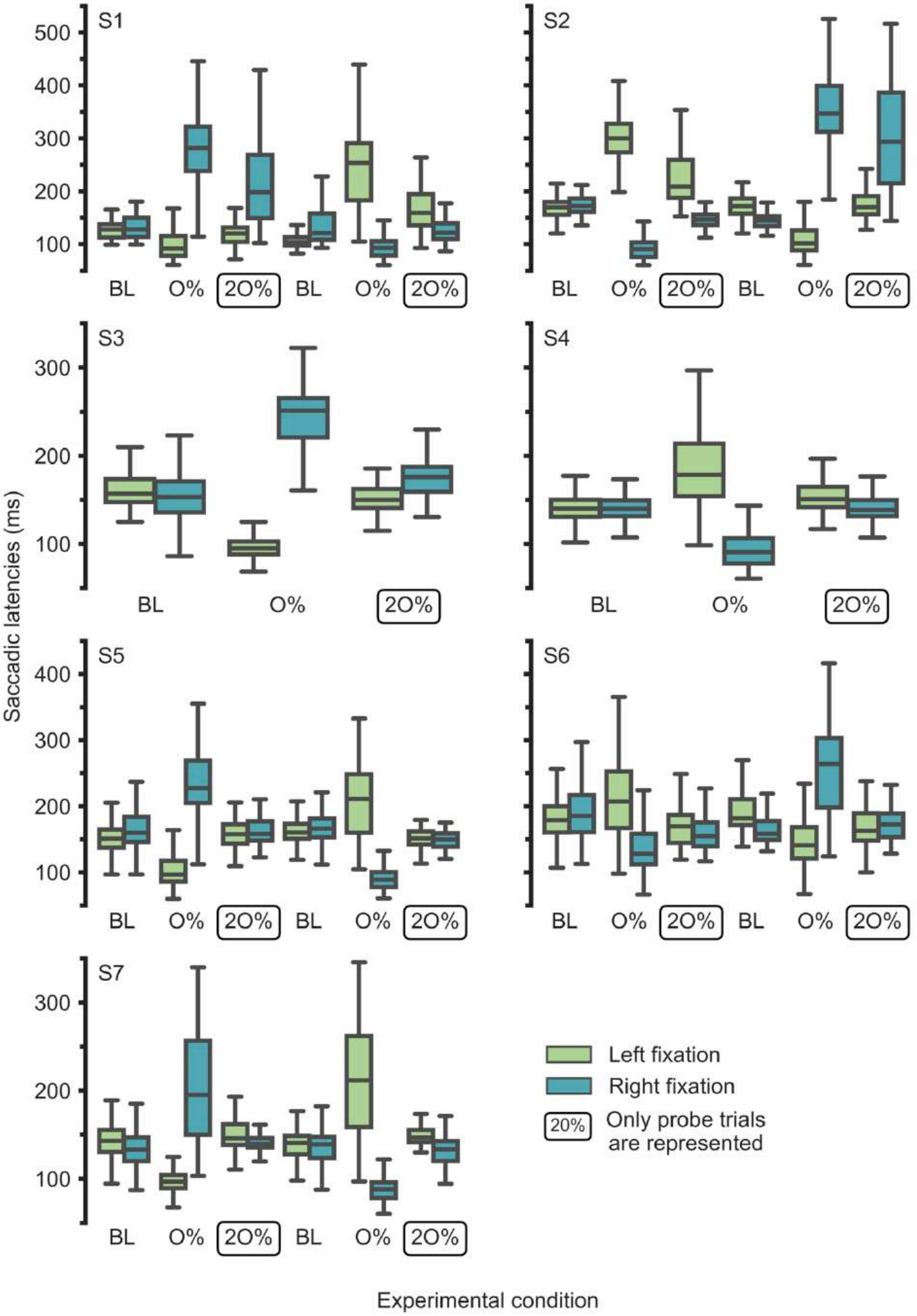

Figure 51: Boxplots of the saccadic latency distribution for left fixation (in green) and right fixation (in blue) across baseline (BL), pairing (0%) and probe sessions (20%). Note that in the probe session, only the probe trials are represented, that is 20% of the 500 trials.

Table 4: Absolute median latency difference between leftward and rightward saccades for the pairing trials and probe trials during the probe session for all participants. The 98% confidence interval of the null hypothesis is given. The significant differences in probe trials are highlighted in bold.

Latency difference (median & 98% CI)	**Pairing trials**		**Probe trials**	
S1	190ms [> 36.63]	161ms [> 57.20]	**78ms** [> 16.95]	**37ms** [> 19.38]
S2	209ms [> 20.35]	245ms [> 36.79]	**62ms** [> 21.42]	**124ms** [> 41.90]
S3	156ms [> 36.79]		**26ms** [> 9.28]	
S4	88ms [> 14.49]		**12ms** [> 7.18]	
S5	131ms [> 34.71]	122ms [> 28.39]	1ms [< 7.75]	2ms [< 6.81]
S6	79ms [> 18.13]	123ms [> 15.52]	**15ms** [> 13.68]	9ms [< 15.39]
S7	98ms [> 23.05]	124ms [> 39.14]	**6ms** [> 4.83]	**14ms** [> 6.65]

It is noteworthy that during the return-to-baseline preceding the reversal, we observed a retention of the learned difference for participant S1, S2 and S6 (i.e., 17ms, 27ms and 23ms, respectively; all values outside the 98% CIs). To check whether this significant difference in latency could explain why participant S6 did not have a larger difference in the reversal probe trials (i.e., 9 ms), we used the deltas in latencies between baseline and probe trials for both leftward and rightward saccades. With respect to the baseline latency distributions, we observed a decrease of 19ms for left fixation (previously associated with a gap) and an increase of 14ms (previously associated with an overlap) during probe trials (both values within the 98% CIs).

IV. DISCUSSION

The present pilot study investigated classical conditioning of saccadic latencies. To our best knowledge, it is the first experiment to probe associative learning with saccade latencies. Saccadic latency distributions were affected by a consistent pairing between saccade direction and a gap or overlap. These results support the fact that saccadic latencies can be controlled by classical conditioning and emphasize the necessity to consider learning and historical effects when studying reaction time.

4.1. SRTs and classical conditioning

Although the current results are not as clear-cut as the previous studies, we still observed some quite interesting outcomes. Several participants had a significant latency difference between left- and right-fixation saccades depending on the saccade direction pairing. These latency differences were always smaller than the ones observed for pairing trials (i.e., they represented at best 50% of the difference obtained with the use of the gap and overlap paradigms), however this is a well-known outcome for the conditional response to be weaker than the unconditional one. One could point out that non-naïve participants had not only the best results but also a large discrepancy with respect to the naïve participants' performances, discrediting our findings. It is true that being non-naïve might have enhanced the learning, for instance with a better attendance at the fixation-target (CS). Indeed, the conditional response observed to a CS depends on several matters, including the perceptual properties of the CS itself (Rescorla, 1988), which might have been more salient for non-naïve participants. Althought we cannot entirely discard the use of a strategy, it is noteworthy to remind that the probe trials were pseudo-randomly interleaved between pairing trials, and participants were encouraged to listen to music/podcasts so that they would not wonder about the task. Moreover, we observed a retention of the significant latency difference during the return-to-baseline for the non-naïve participants S1 and S2, and the naïve participant S6, which would have been unlikely in the case of a strategy. Therefore, despite being variable, our results are a first step in the study of associative learning with saccade latencies and the understanding of how the environment controls reaction times (Staddon, 2016). It even seems sensibly plausible to hypothesize that classical conditioning mechanism could shed a new light on why specific stimuli trigger specific latencies in a way that seems to be automatic. This pilot study provides the foundations for future research on classical conditioning with saccadic latencies.

4.2. Gap and overlap as unconditional stimuli

The main assumption of the current experiment is that the gap and overlap paradigm are unconditional stimuli that respectively trigger the unconditional responses of short and long latencies. A gap typically induces the mean latency to decrease down to 80ms (Becker, 1972; Fischer & Ramsperger, 1984; Kalesnykas & Hallett, 1987; Saslow, 1967) while the overlap leads to an increase up to 390ms (Kalesnykas & Hallett, 1987; Reulen, 1984a; Ross & Ross, 1980; Saslow, 1967). Several hypotheses has been raised to explain these phenomena, notably the fact that the foveal fixation offset disinhibits the peripheral target response in the gap condition (Reulen, 1984a, 1984b) and the necessity of cancelling fixation in the overlap condition (Hallett & Adams, 1980). The conventional explanation used to explain the fluctuations in saccadic reaction times is the sensorimotor integration in the superior colliculus (Honda, 2005; Marino et al., 2015; Reuter-Lorenz et al., 1991; Schiller et al., 1987): the disengagement of visual attention from the fixation stimulus to the target stimulus needs some time, which is added to the saccadic latency (Mayfrank, Mobashery, Kimmig, & Fischer, 1986). However, it is possible that the gap and overlap paradigms failed at being genuine unconditional stimuli, resulting in our variable performances. Indeed, some studies have found controversial results with these types of SOA: Mayfrank et al. (1986) obtained some extremely short latencies –called express saccades– in their overlap condition and Kalesnykas and Hallett (1987) observed longer latencies in the gap condition than in the overlap condition for one participant. In our current study, we observed similar outcomes for one non-included participant for whom we stopped the experiment since he had no significant difference between the gap and overlap SOAs (2ms; value within the 98% CI).

4.3. Saccades and associative learning

So far, associative learning with saccades has been explored within the framework of attentional capture (see Failing & Theeuwes, 2018 for a review). The mainstay of these experiments is to perform a visual search task that includes an irrelevant distractor associated with money either by previous pairing or by cueing the monetary benefit. Researchers use this paradigm to study the extent to which visual selection is controlled by a bottom-up process (e.g., the properties of the target) or by a top-down process (e.g., goals). Other than these experiments, only two papers have mentioned the matter of classical conditioning to explain their results on the peripheral perception of shape with or without saccadic eye movements (Paeye, Collins, Cavanagh, & Herwig, 2018) and free-operant occurrence of visual search (Daddaoua et al., 2016). Yet, classical conditioning mechanism – an hypothesis that does not invoke highly specialized internal mechanisms– appears to be essential to the understanding of how our visual surroundings come to control our saccadic eye movements.

4.4. Conclusion

The current pilot study opens up the scope of possibilities regarding the impact of learning on saccadic latencies. Our results already suggest that specific reaction times can be elicited by specific stimuli through associative learning. However, further research needs to be conducted in order to clarify why we observed such a large inter-individual variability. Especially, it would be interesting to probe whether there is a strong effect of naivety or training on the latency difference. Indeed, our three best participants (including the two authors) had been trained on previous studies on SRTs, which might explain a better plasticity of the saccadic system related to training (Bibi & Edelman, 2009) contrary to the other participants who had never been included in such a study.

DISCUSSION & PERSPECTIVES

Chapter 7:

Does saccadic latency depend on a functional relation?

1. Scope of the main experimental results

The experimental studies in this thesis have demonstrated that it is possible to control experimentally the shape of saccade latency distributions by manipulating reinforcement contingencies. Thence, saccadic reaction times appear to be an operant dimension of saccadic eye movements, which challenges the actual conception of saccade latency. The exquisite plasticity of the saccadic system has been further revealed throughout the various manipulations in this thesis.

The first study aimed at investigating the extent of control over latencies and consisted of a choice paradigm using two concurrent and independent programs of reinforcement for short and long latencies. We manipulated the relative probability of reinforcement for both latencies in three ways: 1) more reinforcers for short than for long SRTs, 2) more reinforcers for long than for short SRTs, and 3) as many reinforcers for both short and long SRTs. This study demonstrated that SRT distributions were drastically affected by reinforcement, and that choices between short and long latencies matched reinforcement contingencies. These outcomes revealed both a fine control of saccadic latencies across participants and the impacts of the temporal organization of the environment on the temporal organization of behavior.

The second study used an instance of the latency determinants reviewed in chapter 2 to illustrate our view on the functional impact of the environment on latencies. This study investigated the size-latency phenomenon (De Vries et al., 2016; Harwood et al., 2008; Madelain et al., 2005), stating that for a given amplitude step, a small object (ratio step/size > 1) triggers regular latency saccades while a large object (ratio < 1) triggers long latency saccades. To assess whether this difference in latency could be explained by an implicit cost-benefit relationship, we manipulated the benefit of making a saccade by reinforcing short latencies for a step/size ratio < 1 and long latencies for a step/size ratio > 1. The delayed saccades observed when the step/size ratio is small were reduced using an auditory reinforcement. Thus, this study showed that the size-latency phenomenon, and therefore saccadic latencies, could be evaluated by a cost-benefit relationship. This procrastination might be viewed as a way to prioritize eye movements and its manipulation highlighted the remarkable adaptability of saccadic latencies to environmental constraints in the process of movement triggering.

The third study introduced a novel latency-contingent paradigm to investigate discriminative control over latencies. Finding the target was made contingent upon specific latencies and was used as a reinforcer to train participants to produce short latency saccades toward one side of the visual field and long latency saccades toward the other one. Saccadic latency distributions were considerably affected by visual consequences proving that they can act as a reinforcer for selecting specific SRTs. Differential responding in latency was observed between leftward and rightward saccades, which provided evidence that saccadic latencies might be placed under discriminative control. This study further expanded our previous results on reinforcement learning for saccades as it demonstrated that latencies can be controlled by antecedent stimuli through operant conditioning. Therefore, the outstanding plasticity of the saccadic system also depends on the context and environmental cues.

The fourth study laid the foundations for investigating classical conditioning of saccadic latencies. We systematically paired a saccade direction with a gap SOA and the other saccade direction with an overlap SOA. Although there was a large inter-individual variability, SRT distributions in probe trials were affected by a consistent pairing between saccade direction and a gap or overlap. This pilot study is a first step towards the understanding of stimulus control over saccadic latencies and emphasized the necessity to consider learning and historical effects when studying reaction time.

Overall, this dissertation has underlined that one can control one's latencies since it is possible to choose to learn to respond within specific latency ranges (study 1) as long as the environment favors them (study 2). This work strengthens the impact of instrumental (study 3) and classical (study 4) conditioning on the temporal organizaton of saccades attuned to the temporal organization of the environment. We have shown that it is possible to allocate saccades in time as much as it is in space. Crucially, this temporal control of saccades leans on functional consequences (auditory or visual), resulting in a functional relationship between the antecedent stimuli, the saccade latency and the consequences. We conclude from these observations that saccade triggering and its temporal control depend on a general learning mechanism. Completing the previous statement that eye movements are under operant control (Madelain, Paeye, & Darcheville, 2011), it additionally appears that the mechanisms underlying classical learning do play their part both in the spatial and temporal allocation of eye movements. Accordingly, we propose that saccadic reaction times are function of environmental contingencies and cannot be limited to a measure of decision nor a byproduct of decisional processes, as it is possible to control SRTs.

2. Temporal control of saccadic latencies

2.1. Reaction times are an operant dimension of saccades

Although some research focused on the effect of reinforcement on latencies, our studies are the first to investigate choice in saccadic reaction times depending on the environmental contingencies. Throughout our various experiments, individuals have learnt to allocate their saccades in time and in space thanks to functional consequences. Importantly, considering SRTs as an operant dimension of saccades enables to reinterpret previous results and sheds a new light on the large existing literature on saccades. The malleability of the distribution of saccadic latencies echoes other preparations manipulating the temporal allocation of behaviors, such as the inter-response time (IRT). Indeed, many papers have already demonstrated that the time elapsed between behavior occurrences, i.e., the IRTs of free-operant responses, is strongly affected by reinforcement contingencies in a way similar to our findings (e.g., Blough, 1966; Platt, 1979; Reynolds & Catania, 1961; Shimp, 1969). The difference between SRTs and IRTs lie in the preceding event: a stimulus onset with the former and a behavior occurrence with the latter. We have demonstrated that the time one takes to react to an event is in fact an operant dimension of behaviors, subject to reinforcement contingencies (Skinner, 1981). More specifically, we were able to change the shape of SRT distributions with the production of specific latencies, insofar that we even obtained bimodal distributions. These outcomes contrast with the traditional conception of SRTs according to which the variability of latencies cannot be controlled (i.e., the spread will change only with the mean). There are indeed two conceptions of variability: it can be regarded as an internal noise (e.g., Faisal et al., 2008; van Beers, 2007) or as a selective functional advantage. The former considers that variability induces costs that the system must minimize (e.g., Harris & Wolpert, 2006; van Beers, 2008); whereas the latter considers the behavioral variability as an operant (e.g., Machado, 1989; Page & Neuringer, 1985), enabling organisms to produce alternative or new behaviors that might be selected by the environment, to explore new contingencies, and result in facilitating the learning of difficult target behavior (e.g., Grunow & Neuringer, 2002; Neuringer, 2009). The variability and the adaptability of the SRT distribution offer a selective and functional advantage similar to operant variability. Indeed, to react more or less rapidly to an event is functional, as it enables to favor the current action, the one about to be produced or an alternative one. In the case of saccades, it means either favoring the current fixation or one of the several potential post-saccadic locations. Contrary to the first intuition, orienting oneself as fast as possible to an event onset is not systematically beneficial for the organism.

The analysis of the saccadic system according to the general laws of learning differs from the computational view of oculomotor control and learning. Indeed, the conventional theories based upon saccadic adaptation postulate the implication of specialized mechanisms involved in comparing the predicted and actual behavior (i.e., efference copy) allowing the recalibration of the oculomotor system (e.g., Collins & Wallman, 2012; Wong & Shelhamer, 2011) and the minimization of saccade variability and movement errors (e.g., van Beers, 2008). In contrast, the control of the oculomotor system by operant learning entails the existence of behavioral selection and implies a parsimonious explanation for saccade triggering. Saccades that are followed by a beneficial consequence for the organism (i.e., the clear vision of an object in natural environment) would be repeated, unlike the ones that are not followed by this consequence (i.e., the law of effect; Thorndike, 1898). This behavioral selection, based on differential reinforcement (i.e., the reinforcement of a target behavior and the extinction of others), has been for instance evidenced in our second study. Saccadic latencies were progressively shaped to be either shorter or longer in a procedure using a dynamic criterion. The reaction times initially reinforced in the first session were not followed by reinforcement anymore during the last sessions, leading to an extinction of these reactions times and a shift in the latency distribution.

One might however question the limits of temporal saccadic control obtained with operant conditioning. Indeed, our second study –aforementioned for the use of shaping in behavioral selection– failed to completely suppress the size-latency phenomenon. That is, even though the use of auditory reinforcement reduced the occurrence of delayed saccades, the SRTs were still longer than for regular saccades. Far from being a failure, we regard this outcome as highlighting the significance of functional consequences. Indeed, our explanation for the size-latency phenomenon is based on a pre-existing functional cost-benefit relationship. The procedure we used aimed at arbitrarily manipulating the benefit of making a saccade by delivering an auditory reinforcement (associated with money). This tone did act as a reinforcer since we did observe changes in SRT occurrences depending on the reinforcement contingencies. Thus, we were able to manipulate an additional benefit to make a saccade but did not manipulate the existing relationship that did produce the phenomenon. Hence, there was a competing functional relationship that might have maintained the size-latency phenomenon. It is plausible that we would have observed a more drastic decrease in latencies if we had manipulated the visual benefit of making a saccade or added a cost to long-latency saccades. Nonetheless, this outcome questions the extent of temporal control and stresses how crucial it is to take into account the environment, reinforcement history and existing concurrent contingencies when one tries to alter a behavior.

2.2. Saccadic latencies and decision

This thesis work challenges both the conventional account of latencies and the current interpretation of the effects of the gap/overlap paradigms. Compatible with the fact that saccadic decision happens within the first 100ms of a target onset (Ludwig, 2009; Ludwig et al., 2005), we defend the idea that saccadic latencies cannot be simply reduced to a byproduct of decision processes. Instead, we support the conception of SRTs being a function of environmental contingencies. This interpretation can explain the variations in saccadic latencies without changes in saccadic amplitude (e.g., Bibi & Edelman, 2009; Madelain et al., 2007; Montagnini & Chelazzi, 2005; Vullings & Madelain, 2018), in addition to why SRTs are nearly always longer than the time needed for decision-making. It is true that this position does not however explain how is it possible to produce two distinct reaction times in a given setting, nor its neuronal reasons, which might appear puzzling. The current dissertation will not bring answers to these questions as we regard them as separate from the addressed issue. Evidently, we do not refute the fact that some neural activations might occur in these situations (e.g., see Fee, 2015 for a recent review on neural models of reinforcement learning), similar to any motor behaviors. Our argument here is that the environment shapes, selects and controls the saccadic reaction times as any other operant behaviors, because discriminative stimuli and reinforcers control them. The implication of this finding is significant as it implies that individuals have a fine temporal control of their behavior attuned to the spatial and temporal constraints of the environment. We believe that it highlights the plasticity and adaptability of the saccadic system.

This view of saccade latency also accounts for the effects obtained in a gap or an overlap paradigm. So far, the main interpretation of the short- and long-latency saccades obtained in these paradigms is that they facilitate/disrupt the sensory integration in SC receptive cells (Dorris & Munoz, 1995; Munoz & Wurtz, 1992, 1993; Reuter-Lorenz et al., 1991); yet, a growing number of studies have found that it is possible to observe short-latency saccades without a gap through training or reinforcement (e.g., Bibi & Edelman, 2009; Jóhannesson et al., 2018; Vullings & Madelain, 2018). Our explanation for the gap/overlap effects parsimoniously lies in the visual benefit of fixating the current location versus the target location. During a gap, there is no visual information at the fixation location whereas a new stimulus has appeared; the visual benefit is therefore higher to make a saccade toward the target location, leading to short-latency saccades. On the other hand, during an overlap, information at the fixation location remains while the target appears; the visual benefit of making a saccade is therefore balanced between the information at the fixation and target locations. This interpretation of the SOA effects has been supported by a recent study of Vencato et al. (2017) showing that manipulating the nature of the fixation stimulus in overlap paradigms (i.e., timing, noise, contrast or information onset) impacted the latencies of saccades. Our interpretation is close to the one based on sensory integration in that it depends on the visual information present in the environment but differs regarding the benefit of making a saccade. An interesting way to further demonstrate this viewpoint would be to study the size-latency phenomenon jointly with a gap. Indeed, if it is solely an issue of sensory integration, introducing a gap between the fixation-offset and the target-onset with a step-size ratio inferior to one should entail short latencies, instead of the long ones typically observed. On the contrary, if the effect on latency is due to a benefit manipulation, the gap should not have an impact, as the benefit of a saccade would be low with a small step-size ratio.

2.3. Temporal discrimination

“Events are perceivable but time is not.” (Gibson, 1975)

Various studies have emphasized the importance of behavior discrimination and its relationship with the associated consequences for the acquisition of a response (Grossberg & Schmajuk, 1989; Thorndike, 1898), which is also known as the credit assignment problem (i.e., behaviors and changes in the environment are connected; Staddon, 2001). In our experiments, the assessment of produced behaviors was complicated for naïve participants: they were not informed that we were working on saccadic latencies (except in our first study), that there were two types of responses or what were the requirements of the reinforcement contingencies. Because the participants in our various experiments were able to control saccadic latencies according to the reinforcement contingencies they were able to discriminate their reaction times. This temporal discrimination was quite fine since, in our first study for instance, the SRTs ranged from 80ms to 300ms and the two distinct response classes were separated by on average 38ms. Since the relative proportion of short and long latencies matched the relative rates of reinforcement, the individuals were able to learn to discriminate two very short times (in the order of hundreds of milliseconds) and to produce them as two separate responses. Moreover, because this thesis is also interested in dynamic and uncertain environments, there was no specific feedback given to the participants regarding the environmental modifications or their behavior. Only the reinforcers obtained could adopt this feedback function; and yet, the reinforcers were always identical for short and long latencies (i.e., same auditory or visual stimulus). Despite this, we systematically observed behavioral adaptation to the contingency constraints throughout our experimental manipulations. Temporal discrimination seems therefore possible for very short and close times in humans, which allows a precise temporal control.

This dissertation provides new data for the literature on temporal control in human, for which many studies deal with temporal discrimination beginning at one second (e.g., Smith, Taylor, Lidzba, & Rubia, 2003) or that directly compares two temporalities (e.g., Westheimer, 1999). Temporal discrimination has been extensively studied cognitively and behaviorally (see de Carvalho et al., 2016; Machado, Malheiro, & Erlhagen, 2009; Wearden, 2016) with paradigms requiring a passive temporal discrimination (i.e., both stimuli were presented and the choice was made retrospectively) or investigating the behavioral dynamics in interval schedules of reinforcement (e.g., distribution of behaviors when reinforcement is available on average every 30s versus 45s). For instance, Killeen and Smith (1984, experiment 2) obtained data indicating that pigeons can reliably discriminate temporal differences of 50ms, which was also found with humans (e.g., Treisman, 1963; Yunker & Herman, 1974). Our experiments are interesting for the study of temporal discrimination in that it is based here on the production of the time in question. Interestingly, parallel works in our lab have been focusing on the discrimination of saccadic reaction times and have found that humans can accurately perceive a difference of about 15% between their SRTs (Vencato & Madelain, 2017).

3. Plasticity of the saccadic system and its implication for eye movements

This thesis dissertation focuses on the operant approach of motor control. The classical computational models of motor control postulates that predictions of the physical outcome of a movement are compared with the actual sensory results of the movement in order to produce optimal responses (Wolpert & Ghahramani, 2000). These approaches focus on internal comparisons without considering the functional consequences. Studies, such as the ones by Montagnini and Chelazzi (2005), Paeye and Madelain (2014) or Rahmouni et al. (2017), have explored and nourished the literature on the functional relationships of motor behaviors. Our thesis work completes this research by focusing on the adaptation of temporal motor behaviors in various and uncertain environments and has highlighted the functional relationship of saccade latencies. It is crucial to understand how motor systems continually adjust to changes in the environment, or internal changes in the systems themselves, to analyze the maintenance of movement accuracy over the course of life. Thus, it is necessary that other studies explore the operant nature of motor control by investigating the effects of reinforcement contingencies on existing behaviors.

The plasticity of the oculomotor system extends beyond saccades and has been observed with other eye movements. For instance, Hoppe and Rothkopf (2016) designed a paradigm, quite close to the one of Schroeder and Holland (1968a), in which participants had to learn new temporal eye movement strategies. They found that observers learned to efficiently shift gaze rapidly across two locations or to maintain longer fixations depending on the durations of events occurring at each location. This study showed that environmental temporal statistics, such as event durations, might be exploited for the temporal allocation of saccades. These authors also demonstrated that, in a similar task, observers learn to blink accordingly to the environmental task demands (Hoppe, Helfmann, & Rothkopf, 2018). This means that temporal organization of the environment does influence the saccade dynamics but also the fixational eye movements. Furthermore, the gaze position after blinks is also known to be influenced by visual reinforcement. Indeed, Maus et al. (2017) observed that the post-blink eye position adapted in a few trials to a target displacement during the blink, without the observers noticing the target steps. Interestingly, when the target displacement was not consistently contingent to the blink, the effect disappeared. This plasticity and the effect of reinforcement have also been observed for smooth pursuit (e.g., Damasse, Perrinet, Madelain, & Montagnini, 2018; Damasse, Perrinet, Jozefowiez, Madelain, & Montagnini, 2016; Darcheville, Madelain, Buquet, Charlier, & Miossec, 1999; Madelain & Krauzlis, 2003b, 2003a) or with fixational eye movements (Poletti, Aytekin, & Rucci, 2015).

The plasticity of the oculomotor system is most relevant and auspicious for interventions with clinical populations. Indeed, in collaboration with Dr Preeti Verghese and Dr Chuan Hou, we have developed projects on amblyopia (i.e., vision development disorder in which an eye fails to achieve normal visual acuity, even with optical correction) and AMD (i.e., central vision loss resulting in impaired vision and erratic eye movements) that are based on the effect of reinforcement on eye movements. On the one hand, many studies have documented that the reaction time in amblyopic eyes is longer than in normal eyes (Ciuffreda, Kenyon, & Stark, 1978; McKee, Levi, Schor, & Movshon, 2016; von Noorden, 1961), which might be due to a motor component, that is fixation instability. Our project will therefore aim at training an improved fixation stability using a reinforcement procedure to eliminate the delay. On the other hand, Janssen and Verghese (2015, 2016) have demonstrated that it is possible to train efficient eye movements during visual search in individuals with AMD but failed to observe a transfer of the strategy to untrained settings. Our project will therefore focus on training individuals to identify their scotoma's location (i.e., blindspot) and to produce an efficient searching strategy in various settings to favor behavioral generalization. The fact that eye movements and their dimension are operant opens up new perspectives for both basic and clinical research.

4. Limits and research prospects

Our various paradigms provide relevant insights on the control of reaction times. However, further research should be conducted to probe whether we would find similar outcomes with manual reaction times. Indeed, Madelain et al. (2007) observed that both saccadic and manual latencies were affected by reinforcement contingencies but Harwood et al. (2008) found that the size-latency phenomenon impacted only saccadic reaction times. It is noteworthy that this outcome is not opposed to our functional interpretation of latencies, quite the reverse. Harwood et al. (2008) did not use extraneous reinforcement in their paradigm: the observers had to track the target step with their eyes and press a button as soon as they detected it. The cost-benefit relationship we use to explain the size-latency phenomenon does indeed apply solely to the saccadic eye movement and not the manual action of button pressing. Functional analyses of situations can therefore enlighten why SRTs and MRTs are sometimes affected in the same way or differentially by the environmental manipulations. Yet, further data with MRTs should be collected to strengthen and support our current interpretation to reaction times in general. It would be also interesting to evaluate the ability of behavior, once steady after learning, to withstand experimentally manipulated disturbances in order to evaluate the resistance to change, that enables a quantitative measurement of learning (Nevin, Mandell, & Atak, 1983).

The general settings in our experiments might have induced some issues, such as the weaker control of short than long reaction times, retrieved in all our experiments. In our first experiment investigating the possibility of choosing between SRTs (chapter 3), we observed 62.3% of short latencies in the 9/1 ratio condition versus 65.8% of long latencies in the 1/9 ratio condition. In our second experiment aiming at reducing the size-latency phenomenon (chapter 4), there was a mean decrease of 31ms versus a mean increase of 90ms. In our third experiment probing the discriminative control over latencies (chapter 5), observers produced on average 10.2% of short latencies for 84.5% of long latencies in the reinforcement interleaved location session. Several hypotheses could explain these outcomes. The differential effect of reinforcement on latency observed in the second experiment could be explained by biological constraints or, as discussed earlier in this dissertation, by the absence of the manipulation of the visual benefit of the saccade. Although the discriminative control experiment (chapter 5) could underline the limitations of the saccadic plasticity, the choice experiment (chapter 3) demonstrated that a fine control of SRTs is possible. On the contrary, we suppose that the experimental settings entailed these differences. First, the response range for the long SRTs was broader than for the short SRTs: a latency interval of 163ms for short

SRTs versus an interval of 411ms for long SRTs, that is 2.5 times broader and therefore easier. Second, it was the first experiment for which we used different directions (i.e., 12) while differences in latency depending on saccade directions and visual fields have been reported (Honda & Findlay, 1992). Third, there was no further instruction than to find the target; it is therefore most likely that self-instructions and rule-governed behaviors (Galizio, 1979; Vaughan, 1989) or accidentally reinforced behaviors (also termed superstitious behaviors; Skinner, 1948) controlled the performance.

The experimental environments we used can be regarded as dynamic and uncertain in that the reinforcement contingencies were changing and not signaled. Yet, natural environments are also characterized by complex stimuli, visual changes, and motions. One could therefore wonder what would happen in dynamic preparations such as interception tasks. Manual interception tasks have demonstrated that prior information regarding the temporal features of the task (de la Malla et al., 2012) affects the choice of the interceptive point favoring either spatial or temporal precision (de la Malla & López-Moliner, 2015). Recently, we have shown that these outcomes are also retrieved in saccadic interception tasks (López-Moliner et al., 2018), in which observers adjust their SRTs to intercept a moving target. This echoes the well-known saccadic plasticity of sportsmen, such as baseball player (Ceyte et al., 2017; Di Russo et al., 2003; Khanal, 2015; Land & Mcleod, 2000; Zhang & Watanabe, 2005).

5. Conclusion

About three times per second a decision is made regarding when and where to move the eyes, providing many opportunities to learn about environment regularities and the benefits of adjusting the information-foraging policy to these properties. The research presented in this thesis demonstrates that the temporal saccade triggering is dependent on the current state of the observer and the organization of the environment; in other words, the saccadic reaction time depends on a functional relationship. Indeed, saccadic latency distributions were drastically affected by reinforcement contingencies: 1) choice between short and long latencies followed relative reinforcement, 2) latencies were explained by a cost-benefit relationship, 3) latencies were placed under discriminative control and 4) specific latencies could be elicited by specific stimuli through associative learning. Overall, this dissertation has shown that one can control one's latencies through an instrumental relationship.

This work strengthens the impact of instrumental and classical conditioning on the temporal organizaton of behavior. We have shown that it is possible to choose how to allocate saccades in time, as long as this temporal control of saccades leans on functional consequences. It is essential that research on saccade triggering and decision takes into account the learning history and environmental contingencies. To conclude, this thesis work supports the notion that saccade triggering and its temporal control depends on a general learning mechanism. Accordingly, we defend that saccadic latencies are function of environmental contingencies and cannot be restricted to a byproduct of decision processes due to information accumulation.

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LIST OF PUBLICATIONS AND COMMUNICATIONS

Publications

Vullings, C., & Madelain, L. (submitted). Discriminative control of saccadic latencies. *Journal of Vision.*

Vullings, C., Harwood, M. R., & Madelain, L. (in revision). Reinforcement reduces the size-latency phenomenon: a cost-benefit evaluation of saccade triggering. *Journal of Vision.*

López-Moliner, J., Vullings, C., Madelain, L., & van Beers, R. (in review). Prediction and final temporal errors are used for trial-to-trial motor corrections. *PLOS Computational Biology.*

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.

Communications

Vullings, C., & Madelain, L. (2018, May). *One can choose one's own saccadic reaction times.* Oral communication presented at Association for Behavior Analysis International, San Diego, USA.

Vullings, C., & Madelain, L. (2018, May). *Classical conditioning of saccadic latencies using gap and overlap paradigms.* Poster presented at Vision Sciences Society, St Pete Beach, USA.

López-Moliner, J., Vullings, C., Madelain, L., & van Beers, R. J. (2018, May). *Different ways for correcting for previous temporal errors in interception tasks.* Poster presented at Vision Sciences Society, St Pete Beach, USA.

Vullings, C., & Madelain, L. (2017, November). *Control of saccadic latencies in a concurrent interval reinforcement schedule.* Oral communication presented at Association for Behavior Analysis International, Paris, France.

Vullings, C., Harwood, M., & Madelain, L. (2017, October). *Reinforcement can reduce the size-latency phenomenon.* Oral communication presented at Forum annuel du Groupement De Recherche Vision, Lille, France.

Vullings, C., & Madelain, L. (2017, August). *Contextual control of saccadic reaction times using a latency-contingent paradigm.* Poster presented at Society for European Conference on Visual Perception, Berlin, Germany.

Vullings, C., & Madelain, L. (2017, May). *Discriminative control of saccadic reaction times in a latency-contingent visual task.* Poster presented at Society for Quantitative Analysis of Behavior, Denver, USA.

Vullings, C., Harwood, M. R., & Madelain, L. (2017, May). *Effect of reinforcement on the size-latency phenomenon.* Poster presented at Vision Sciences Society, St Pete Beach, USA.

Vullings, C., & Madelain, L. (2016, November). *Reinforcement contingencies affect the allocation of saccades in time.* Oral communication presented at Forum annuel du Groupement De Recherche Vision, Toulouse, France.

Vullings, C., & Madelain, L. (2016, August). *Control of saccadic latencies in a choice paradigm.* Poster presented at European Conference on Visual Perception, Barcelona, Spain.

Vullings, C., & Madelain, L. (2016, May). *Saccadic latency and choice in a concurrent random interval reinforcement schedule.* Poster presented at Vision Sciences Society, St. Pete Beach, USA.

Vullings, C., & Madelain, L. (2015, December). *Choice and saccadic latency in a concurrent random interval reinforcement program.* Poster presented at Forum annuel du Groupement De Recherche Vision, Grenoble, France.

Published abstracts

Vullings, C., & Madelain, L. (2018). Classical conditioning of saccadic latencies using gap and overlap paradigms. *Journal of Vision, 18(10),* 1001.

López-Moliner, J., Vullings, C., Madelain, L, & van Beers, R. (2018). Different ways of correcting for previous temporal errors in interception tasks. *Journal of Vision, 18(10),* 845.

Vullings, C., Harwood, M., & Madelain, L. (2017). Effect of reinforcement on the size-latency phenomenon. *Journal of Vision, 17(10),* 908.

Vullings, C., & Madelain, L. (2016). Control of saccadic latencies in a choice paradigm. *Perception, 45,* 230.

Vullings, C., & Madelain, L. (2016). Saccadic latency and choice in a concurrent random interval reinforcement schedule. *Journal of Vision, 16(12),* 855.

APPENDIXES

Appendix 1: Article of the study 1

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. http://doi.org/10.1152/jn.00634.2017

Link: https://nextcloud.univ-lille.fr/index.php/s/MGn5JW7ZCJR7kWR

Appendix 2: Article of the study 2

Vullings, C., Harwood, M. R., & Madelain, L. (in revision). Reinforcement reduces the size-latency phenomenon: a cost-benefit evaluation of saccade triggering. *Journal of Vision.*

Link: https://nextcloud.univ-lille.fr/index.php/s/Tk85qjy4Pzn8QNH

Appendix 3: Article of the study 3

Vullings, C., & Madelain, L. (submitted). Discriminative control of saccadic latencies. *Journal of Vision.*

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Appendix 4: Article of a collaboration with Dr. López-Moliner on temporal control during a dynamic task

López-Moliner, J., Vullings, C., Madelain, L., van Beers, R. J. (in review). Prediction and final temporal errors are used for trial-to-trial motor corrections. *PLOS Computational Biology.*

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