Université de Lille - Ecole Doctorale Sciences de l'Homme et de la Société

Faculté PsySEF – Psychologie et sciences de l'Education et de la Formation

SCALab-UMR CNRS 9193

Causal attribution and selectivity of learning in saccadic adaptation

Attribution de causalité et sélectivité des apprentissages
dans l'adaptation saccadique

Thesis submitted and publicly defended by

Maxime MARTEL

For the degree of

Doctor of Psychology

Supervised by

Pr. Laurent MADELAIN

On Monday December 15th 2025

Jury members:

Pr. DORE-MAZARS Karine	Université Paris Cité	Rapporteur
Pr. MONTAGNINI Anna	Institut des Neurosciences de la Timone	Rapporteur
Pr. JOZEFOWIEZ Jérémie	Université Lille	President
Pr. MEDENDORP Pieter	Radboud University Nijmegen	Examiner
Pr. PELLON Ricardo	Universidad Nacional de Educación a Distancia	Examiner
Pr. MADELAIN Laurent	Université de Lille	Supervisor

« Vous voudriez que je fasse comme tous ceux qui n’ont rien à dire et qui le gardent pour eux ? »

– Raymond Devos, 1979

Aknowledgments

La thèse, à l’image de la démarche scientifique dans laquelle elle s’inscrit, n’est rendue possible que par la contribution de beaucoup, beaucoup de personnes. J’ai une gratitude immense pour chaque pierre que vous avez apportée à ce chemin aussi exigeant qu’épanouissant.

Ces remerciements doivent d’abord s’adresser au Professeur Laurent Madelain, qui m’a enseigné l’analyse du comportement avant de superviser ma thèse, qui a aiguisé mon esprit critique, encouragé mes prises de risques, et remis dans la bonne direction mes entreprises trop débutantes, toujours avec patience et bienveillance. Merci, Monsieur, d'avoir largement contribué à ce que cette thèse soit une expérience si riche et formatrice.

J’aimerais également remercier les membres de SCAlab, permanents et de passage, qui ont constitué un environnement de stimulation intellectuelle, d’échange et de partage d’une grande qualité. J’adresse un remerciement particulier au Pr. Yvonne Delevoye, qui a permis mon premier contact avec le monde de la recherche lors d’un stage de L3, puis qui m’a donné de précieux conseils avec le Dr. Céline Paeye lors de mon CSI de thèse. Merci au Pr. Jérémie Jozefowiez, pour les enseignements et la rigueur scientifique, conservée même sur un fond zoom de Star Wars. Merci au Pr. Anna Montagnini, pour la confiance accordée dès mon entrée en thèse et pour les échanges scientifiques de qualité. Merci à Théo Moreau et Alexis Lejeune pour une collaboration aussi passionnante qu’improbable. Un merci également à Manu et Sabine pour tout le support administratif dont j’ai largement profité pendant ces trois années.

Sincere thanks to the members of my jury for their time and dedication in evaluating my work. I am grateful for the great scientific exchange we had and the ones to come. I would also like to thank Pr. Daniel Wolpert and his team for welcoming me to their lab at the Zuckerman Institute during my PhD, and for sharing their insightful knowledge and practices.

Je remercie les partenaires de cette thèse, qui ont financé et/ou organisé les conférences et Summer School que j'ai eu la chance de joindre. Merci à SCALab, au programme ANR, aux Graduate Programmes de Lille, et à l'Académie Française, pour m'avoir permis de perfectionner ma pratique de chercheur du soleil de Floride jusqu'en Transylvanie.

Un grand merci bien sûr aux docs et post-docs de SCALab. Merci à Fanny de m'avoir accompagné en tant que représentant des docs et posts-docs. Merci à Fabri d'avoir été une super voisine. Merci à Lilas de m'avoir donné un modèle d'énergie positive par tous les temps. Merci à Constance, Marine, Clara, Léa, Marie, Mélen, Junior, Sabah, Layla, Lison, Angelica, Alice, Adrien, Louise, Nicolas, Ding, Matthieu, Clément, Paul, Robin, Melisa, Céline et tous ceux que j'oublie peut-être mais qui ont été là pour partager des petit-déjs entre docs, des gorille-cacahuètes, des soirées dans des adresses Lilloises perdues au fond de la ville et des Limoncello de survie. Vous avez donné de la couleur et de la vie à cette thèse, merci !

Un merci également à ma famille, pour qui la sélectivité des apprentissages et l'adaptation saccadique ne sont pas des préoccupations fortes mais qui a été présente et aimante pendant toute cette période. Une mention particulière à ma mère et à mon grand-père Francis, qui ont éveillé et nourri ma curiosité de petit garçon, et qui m'ont toujours encouragé à poser des questions. Un merci également à ma marraine, merci pour ton soutien inconditionnel. Merci à mon parrain pour les raclées que j'ai subies au badminton et les verres de consolation qui s'en suivaient.

Enfin, un merci particulier à mes super héros du quotidien : À mes deux super copines, Emilie et Lucie, pour tous les rires et les réunions de crises partagées. Cette thèse n'aurait pas pu se faire sans vous. À Alex, pour les week-ends option origami dans ta propriété, les divisions euclidiennes de tête et les messages vocaux de Plume qui ronronne. À Ophélie, pour m'avoir sorti du travail et rappelé que la vie c'est aussi de regarder des clowns qui font le bruit du vent. À Tim et Toto, mes deux petits frères préférés, pour avoir partagé mes hauts et mes bas. Și micului meu liliac, pentru că m-a învățat că nu trebuie să fie perfect ca să fie perfect.

Abstract of the thesis

The General Process Theory (GPT) posits that the mechanisms underlying learning are shared across species, stimuli, and contexts. However, a phenomenon referred to as selective learning challenges this generalist view. First described in 1898, selective learning occurs when, in Pavlovian or operant conditioning, learning fails to emerge despite temporal contiguity and contingency between events. An early attempt to explain this phenomenon came from the concept of belongingness, which proposed that certain associations are more easily formed when they are biologically or functionally compatible. A more recent theoretical framework, the Behavioral Systems Theory (BST), provides a richer understanding by organizing behaviors into structured systems. Yet, explaining the mechanisms and interactions of these systems remains a theoretical challenge.

We interpreted experimental results from contextual saccadic adaptation showing that the color and shape of a cue failed to induce contextual adaptation as an instance of selective learning in humans. We used a double-step paradigm to explore the underlying mechanisms of selective learning and saccadic adaptation. In a first series of studies, we replicated and extended the effect of selective learning within a contextual saccadic adaptation design. Across fourteen experiments, we observed distinct learning outcomes depending on the contextual cue provided to participants, while keeping all other parameters constant. We additionally demonstrated a clear dissociation between the perception of visual information and its integration in motor adaptation. A second study investigated higher-order conditioning to better characterize the processes involved in selective learning, and in particular, the interaction between motor and non-motor information. In a final study, we adapted a force-field learning paradigm to our saccadic framework, demonstrating that motor planning, rather than motor execution, is the critical driver of motor learning.

Together, these findings refine our understanding of the mechanisms underlying contextual saccadic adaptation. They highlight the dissociation between perceptual and motor information in both simple and higher-order conditioning. Finally, we propose a framework to map the internal organization of a motor system — structured around motor planning — that not only explains learning but also predicts its occurrence and provides a foundation for studying interactions between systems. This system provides insights about interactions between motor behaviors which should be tested in future experiments.

Keywords: Selective learning, Sensorimotor adaptation, Saccades, Contextual learning, Operant conditioning, Higher-order conditioning, Eyetracking

Table of Contents

Figures

Part I

INTRODUCTION

1. Learning Theories

1.1. A history of anomalies

1.1.1. Animal Intelligence and Belonginess

In 1898, in a paper titled “Some Experiments on Animal Intelligence” (Thorndike, 1898), Edward Thorndike describes a series of experiments he ran with cats. The method was as follows: he deprived cats of food and enclosed them in a cage (see Figure 1.A). Cats have to perform a target behavior, previously chosen by the experimenter, to exit the cage and obtain the food presented outside. Target behaviors can include turning a button, pulling a loop, or pressing down a lever. When first placed in the cage, the cat will engage in various kinds of behaviors until eventually engaging in the target behavior, resulting in the door opening. The cat will be placed in the cage again, and the next occurrence of this target behavior will open the door and give access to food again. Over the trials, all the cats consistently learned to associate the target behavior with the opening of the cage and access to the food, as evidenced by a decrease in the latency between being placed in the cage and performing the behavior (See Figure 1.B). Thorndike’s experiments illustrate instrumental conditioning, in which a stimulus (e.g., a loop) triggers a response (e.g., pulling on the loop), followed by a consequence (e.g., access to food), a relation known as the three-term contingency **(S → R → C)**. Through this process and according to Thorndike’s Law of Effect, the positive consequence of gaining access to food reinforces the stimulus-response association over trials – meaning that the presence of the stimulus will evoke the response.

In a further experiment, Thorndike selected a target behavior far from cats’ typical maneuver involved in searching for food: grooming. As in his previous studies, he starves the cats and places them in a cage, opening the door whenever the cat engages in grooming, defined as licking or scratching itself. Again, this behavior would happen accidentally at first, and the cage would open. In contrast to the previous experiments, not all of the cats learned to associate the target behavior with the opening of the cage, and the cats who learned needed a much longer period, more than double of time, with a greater variability in the latency to the target response between cats and within trials (see Figure 2 for the example of a representative cat).

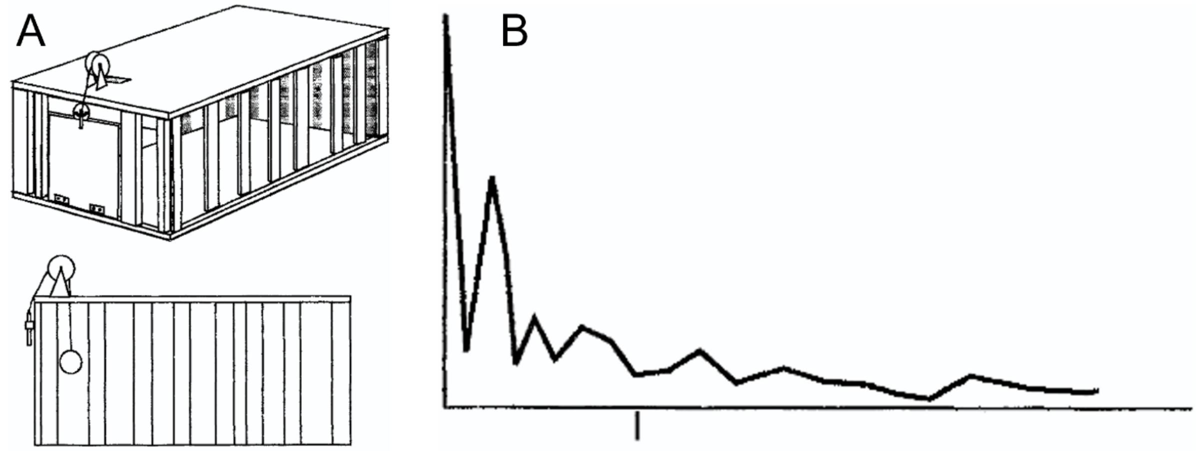

Figure 1. Pulling on the loop releases a bolt and opens the door. A. Sketch of one of Thorndike's "Puzzle Box". (From Chance,1999, Figure 1, p 434.) B. Performance of a representative cat over trials. Trials are depicted on the horizontal axis, and time to occurrence of the target behavior is depicted on the vertical axis. In this instance, escape times varied from a maximum of 160 s to a minimum of 6 s over 24 trials. The short vertical line under the horizontal axis represents a 24h interruption of training. (From Thorndike, 1898, Figure 2, p. 18.)

For Thorndike, the difference in performance between this experiment and the previous ones seems to be linked to the choice of the target behavior. The cage consistently opened whenever grooming occurred, and the three-term contingency remained intact (stimulus → response → consequence). However, grooming did not "belong" to the consequence of opening the door and accessing food, which would explain the discrepancy in the results. According to this view in terms of belongingness, some responses are naturally associated with a consequence due to the animal's evolutionary history. For example, manipulative actions such as pulling on a loop are naturally related to escaping confinement. In contrast, behaviors like grooming do not typically facilitate escape and thus are not naturally linked to the opening of the door. Despite its intuitive appeal, the concept of belongingness cannot consistently predict discrepancies across different scenarios, nor explain the mechanisms underlying the stimulus–response–consequence association when a response either does or does not 'belong' to a reinforcer. Therefore, belongingness remains primarily a post-hoc descriptive tool, lacking a theoretical basis to explain the underlying processes or to predict outcomes in novel conditioning situations.

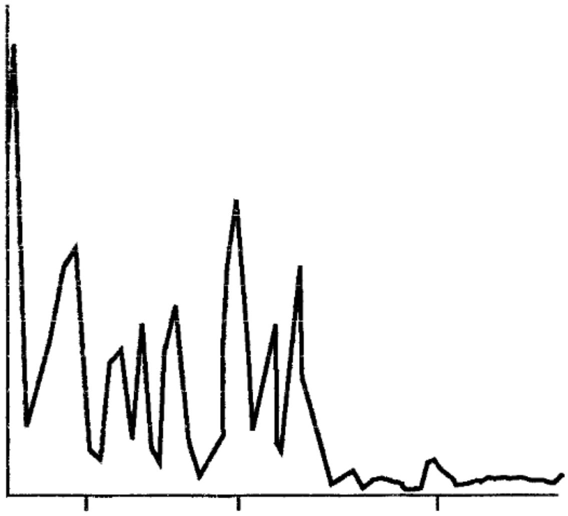

Figure 2. Performance of a representative cat over trials when grooming behavior opens the door. Convention similar to Figure 1. (From Thorndike, 1898, Figure 6, p. 22.)

1.1.2. General Process Theory

This study from Thorndike is one of the first detailed accounts of what would later be referred to as Misbehaviors, a term used for behaviors that fall outside the General Process Theory (Killeen, 2019). The General Process Theory asserts that there are universal principles governing conditioning and learning across species and situations (Domjan, 1983). While behaviorists acknowledged species-specific adaptations in sensory, motor, and motivational systems, these were assumed to affect only the expression of learning, not its underlying mechanisms (Schwartz, 1974, 1978). According to this theory, the laws of learning are independent of the specific cues, responses, and reinforcers used in experiments. Therefore, behavior analysts traditionally pursued general learning principles, with lesser interests in the differences between species or in specific cues, responses, and reinforcers. For example, one of the first principles taught in behavior analysis is the three-term contingency described earlier in this chapter: stimulus-response-consequence. According to this principle, if a response occurs in the presence of distinctive stimuli and results in the delivery of the consequence, this allows for the establishment of associations between the terms of the contingency. Note that the use of the general terms stimulus, response, and consequence is precisely meant to generalize this principle to any situation involving a similar structure. Contradictory results to the principles and laws described by behaviorists were therefore classified as Misbehavior, with the underlying idea of a probable issue in methodology rather than a questioning of the laws and theories. However, evidence from the history of behavior analysis shows that examining these phenomena more closely has refined our understanding and led to the discovery of new general principles with broad applicability. This is the case for adjunctive response, described in the 1970s as responses occurring outside any contingent reinforcement, arising instead through adventitious contiguity with a reinforcer. Adjunctive responses were initially considered anomalies or misbehaviors, lacking deeper theoretical grounding. However, their elusive nature— the difficulty of replicating them in the laboratory using pseudo-adventitious procedures (Staddon & Honig, 1977)— motivated the development of the current view in terms of response–reinforcer proximity, in a framework elaborated to account for the behavioral patterns underlying adjunctive responding (Killeen & Pellón, 2013). Thus, what were first labeled as *misbehaviors* eventually gained a theoretical foundation and expanded our understanding of learning mechanisms. Similarly, Thorndike's anomalous observation, described in the first section of this chapter, still lacks a clear understanding and has received limited interest from behaviorists, despite offering an opportunity to expand knowledge about learning processes.

1.1.3. The Bright-Noisy Water experiment

In 1966, Garcia and Koelling's bright-noisy water experiment was among the first studies to replicate a situation of the kind described by Thorndike (Garcia & Koelling, 1966). Their study is based on a classical paradigm of fear conditioning: A tone and a light are presented together upon delivery of an electric shock to a rat, leading the rat to a freezing response. In this situation, we have an unconditioned stimulus (US), the electric shock, leading to an unconditioned response (UR), freezing. The tone and light serve as a conditioned stimulus (CS) for which eliciting freezing is conditional on pairing it repeatedly with the US. Once freezing is evoked directly by the CS, we now refer to this freezing response as a conditioned response, for a conditioned stimulus evokes it. Behaviorists also use the term stimulus control, referring to the emission or suppression of a behavior contingent upon the presence or absence of a stimulus. Thus, stimuli and responses whose properties do not depend on prior conditioning are called unconditional, and stimuli and responses whose properties emerge after conditioning are called conditional. Similarly, conditioning of taste aversion is obtained by pairing a taste (the CS) to a state of illness (the US), leading to the response of avoidance of the food or liquid responsible for this illness.

In their study, Garcia and Koelling use these two kinds of conditioning together. An audiovisual stimulus (light and tone) is activated by the rat licking a drinking spout containing saccharin-flavored water. Consequently, rats were simultaneously exposed to the audiovisual stimulus and the sweetened water, two potential conditioned stimuli. One group of rats was made sick through an injection of lithium (US leading to avoidance of the source of sickness), whereas a second group received foot shock (US leading to freezing). After repeated exposure to their assigned US contingently with the two potential CS, rats were tested with each of the CS alone (see Figure 3). Surprisingly, and contrary to the prediction of equivalent conditioning for both CSs, rats exposed to foot shock showed a much stronger conditioned response to the audiovisual stimulus than to sweet water. Conversely, rats exposed to illness showed a much stronger conditioned response to sweet water than to the audiovisual stimulus.

Garcia and Koelling's experiment demonstrated a failure of association between the shock and the taste of the water, as well as between the illness and the audiovisual cue, despite the repeated pairing of these pairs. More importantly, this failure occurred with both of the CSs presented simultaneously, while the shock and audiovisual cue, as well as the taste and illness, showed the expected associations. This double dissociation between efficient and inefficient learning within a single condition was interpreted as evidence that not all responses are equally relevant for all classes of stimuli. This idea closely resembles the notion of belongingness, and the parallel with Thorndike's paradigm is instructive: in both cases, associations failed to form despite the presence of the expected contingency — whether stimulus–response–consequence in Thorndike's studies or CS–US pairing in Garcia and

Koelling's experiment. However, Garcia and Koelling's interpretation also suffers from the same theoretical fragilities, relying on post hoc description, lacking predictive power, and offering no clear account of the underlying learning mechanisms.

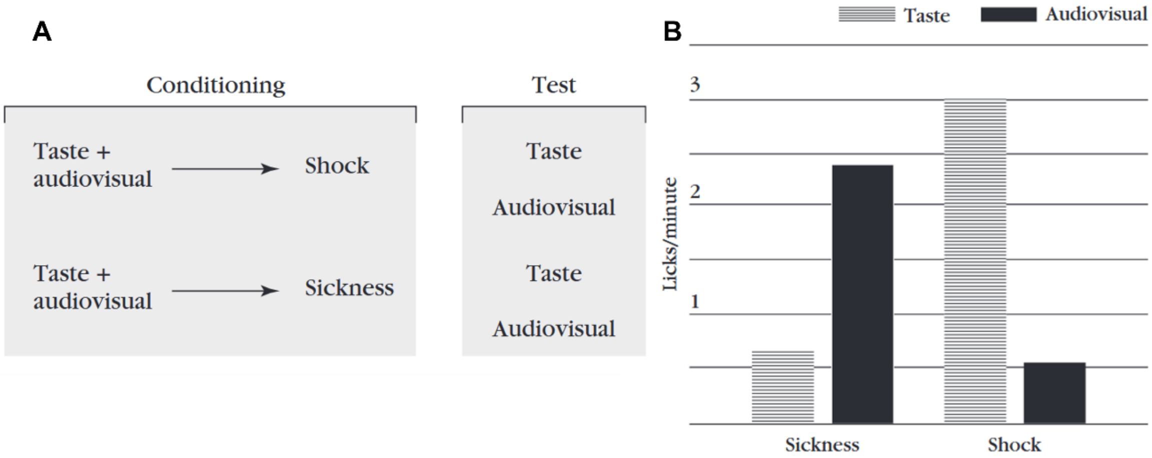

Figure 3. A. Diagram of Garcia and Koelling's experiment. A compound taste-audiovisual stimulus was first paired with either shock or sickness for separate groups of laboratory rats. The subjects were then tested with the taste and audiovisual stimuli separately. (From Domjan, 2010, Figure 4.2, p 108.) B. Rats conditioned with sickness learned a stronger aversion to taste than to audiovisual cues. By contrast, rats conditioned with shock learned a stronger aversion to audiovisual than to taste cues. (From Domjan, 2010, Figure 4.3, p 109.).

1.1.4. A theoretical attempt: *Preparedness*

In the same period, several authors tried to develop a framework accounting for these anomalous results. We will review one of them, the notion of Preparedness suggested by Seligman in 1970 (M. Seligman, 1970; M. E. Seligman & Hager, 1972), to understand the complexity of this task. Seligman presents the preparedness of associations as an alternative to the equipotentiality premise – the accepted assumption in the analysis of behavior that specific elements of a contingency may be chosen arbitrarily and interchanged without important influence on the experimental results. They suggest that organisms come biologically equipped with (1) prepared associations, allowing faster and/or stronger learning, (2) unprepared associations, neither improving nor preventing learning from happening, and (3) contraprepared associations, making them harder or even impossible to happen. Therefore, preparedness can be seen as a continuum of learning likelihood, from very likely to very unlikely associations to be learned. This preparedness of an organism for a specific association is defined by how degraded the stimulus can be before the association takes place – degraded being defined as any manipulation impacting the contingency, such as the saliency of the stimulus presentation, the number of trials, the inter-trial interval, the presence of other stimuli, etc. According to preparedness, the electric shock-audiovisual stimulus association was initially prepared in the rats. In contrast, the electric shock-taste of the water association was contraprepared, resulting in fast association on the one hand and the absence of association on the other hand. An important difference we should acknowledge between preparedness and belonginess is the emphasis of the preparedness concept on the association rather than the whole situation, which helps locate more precisely where the experimenter's interest should lie to understand this phenomenon. Additionally, preparedness attempted to introduce a metric based on the degradation of the stimulus, providing a measuring tool to compare preparedness across different associations.

This effort to integrate those anomalous results into the general principles of learning comes with several issues, which were already addressed and detailed shortly after Seligman’s publication (Schwartz, 1974): First, preparedness as it is presented does not provide explanatory insights about the mechanisms. Learning is supposed to be fast if the association is prepared, and the degree of preparedness of the association is measured by the observed learning rate. Second, measuring preparedness through stimulus degradation assumes the existence of an underlying parameter, common to all stimuli and situations, that can be captured by this measure. However, differences in the degradation of the stimuli imply modifying the structure of the procedure or the physical aspect of the stimulus, leading to a problem of how to compare changes in the inter-trial interval, the saliency of a color, or the number of trials. Thus, degradation as a measure seems very difficult to use in practice for a comparison between settings that are very different. Lastly, preparedness remains primarily a post-hoc construct with little predictive power. Relying on the idea of belongingness may give an intuitive sense of which associations are likely to form. However, as underlined by Schwartz, preparedness offers only a limited answer to questions such as whether pairing a sexual partner with an electric shock would be prepared, unprepared, or contraprepared, and provides no estimate of the degree of stimulus degradation required for such an association to emerge.

1.2. Contemporary view

1.2.1. Behavioral System Theory

The limitations of theoretical accounts such as belongingness and preparedness highlighted the need for a new conceptual framework. A major step in this direction came from ethology, with William Timberlake's Behavioral Systems Theory (Timberlake, 1993). Initially, behavioral systems are a tool used in ethology to report the behaviors of animals in different functional situations. Beyond its experimental departure from the analysis of behavior — which focuses on the modification of behavior rather than its natural occurrence — the ethologist's view also marks a decisive philosophical rupture: it assumes that organisms begin with an existing perceptual and response structure, which guides and constrains any subsequent learning process (Kline, 1898). While this idea was slowly arising in behavior analysis, the view of an organism as a blank slate for which learning will teach everything was the most common (Skinner, 1956). This difference is well underlined by Timberlake (Timberlake & Lucas, 2019):

> "Traditional learning models appear sophisticated from the viewpoint of classical physics, but from the viewpoint of biology or chemistry they are incomplete because they fail to model organismic structures and processes related to learning." (Chapter 9, p.241).

From this heritage, the Behavioral System Theory is an attempt to close the bridge between laws of learning as defined in behavioral analysis and the use of behavior systems. In this theory, a behavior system is defined as "a complex control structure related to a particular function or need of the organism, such as feeding, reproduction, defense, or body care.". Systems are organized in four critical features: (1) the subsystems, which are the current motivational state and lead to the fulfillment of a system's goal. For example, within the feeding system in rats (see Figure 4), the predatory subsystem engages in behaviors leading to finding, chasing, and eating prey. (2) Within a subsystem, the modes are generally the following: General search, Focal search, and Consumption. Modes are states related to the sequential and temporal organization of behavior. (3) The modules can be shared between modes and refer to a smaller subgroup of probabilistic linkages between particular classes of stimulus sensitivities and components of responding. They become integrated in terms of stimulus control and action patterns of learned performance. (4) Lastly, actions are the animal's external or internal behaviors. In the example of the rat, we find “locomote” in the module “travel” during the general search for prey.

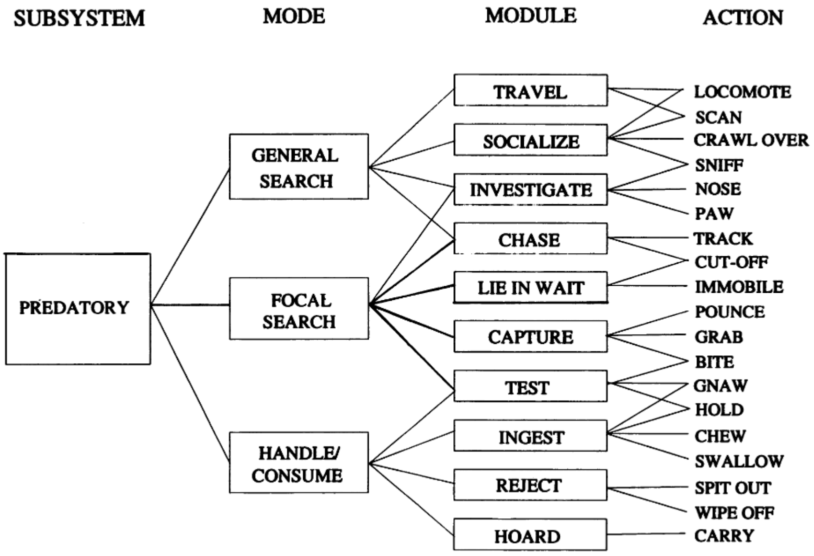

Figure 4. The structure of a behavior system includes four levels: system, subsystem, motivational mode, and perceptual-motor modules. This figure illustrates the modes and modules of the predatory subsystem in the feeding system of the rat. Response-learning effects depend upon what search modes are conditioned and the modules best supported by the stimulus environment and the search modes. (From Timberlake, 1993, P118, Figure 7).

The four different levels of the system are hierarchical, meaning that a lower level of the system would arise or disappear depending on the current state of the superior level. An initial motivational factor would induce the organism in a specific system, and from there, the next motivational states would depend on the structure of the system and on the state of the environment. The novelty of Timberlake’s approach is in its integration of Pavlovian association between all those categories. The systems described are not seen as fixed but as flexible frameworks that support and are altered by learning. From this functional perspective, learning is seen as a process that takes place within systems. A conditioning process may engage the organism in one subsystem. However, it can just as well involve a specific module or action, inducing the structural priors that such an action demands.

BST carries forward the observation that behavior is organized into subsystems, modes, and modules that prime specific actions, and that those actions, when available, reinforce those which occasioned their availability, often releasing opportunities for actions appropriate at the next module. It stresses the need to study species-specific behaviors to explain how an organism's repertoire is organized, departing from the classical view that emphasized universal laws across species. This approach enables us to transcend the circularity of Seligman's preparedness concept by introducing the notion of a system, constructed independently of and before the analysis of the organism's behavior. This also facilitates a step towards predictive power, with the idea that actions belonging to a specific subsystem should be easily associated with stimuli that engage that subsystem. For example, if the detection of a prey triggers the predatory subsystem, a grabbing or holding response should be easier to condition compared to a grooming behavior, which is not present in the predatory system. However, the predictive potential of BST also has limits, since it holds that systems are flexible and that learning can induce new behaviors within a mode. This makes it difficult to determine whether a novel response truly belongs to a mode or has been conditioned to appear there. Indeed, if a response is absent from an animal's natural behavior, is this because it cannot be integrated into the system, or simply because the ecological environment does not demand or permit its expression? One of the most common conditioning procedures in rats involves lever pressing to obtain a food pellet, yet levers and pellet dispensers are virtually absent from their natural ecological environment. This limitation is compounded by the absence of a detailed explanatory mechanism: systems are described mainly as they are observed, and the associations across their different layers remain insufficiently understood. We still lack a clear and operational account of why a given response may or may not belong to a specific system. Importantly, however, these questions stem primarily from the perspective of behavior analysis. By contrast, Behavioral Systems Theory was driven less by an effort to explain learning through behavioral systems than by the use of learning principles to analyze species-typical behaviors. The reverse perspective—using behavior to advance our understanding of learning—emerges in Domjan's work.

1.2.2. Domjan's contribution

Following the publication of Garcia and Koelling's bright–noisy water experiment, the anomalous nature of their findings prompted numerous criticisms. Many of these attempted to attribute the results to methodological flaws or external factors, thereby avoiding any challenge to the established laws of learning. However, they also had their defenders, and Domjan and colleagues in particular took care to replicate their experiment with certain modifications, addressing many of the criticisms directed at this paradigm and consistently reproducing the expected double dissociation. These replications included, for instance, the addition of a control group, the use of newborn rats, and single-trial conditioning (Domjan, 2015). These contributions established Garcia and Koelling's double dissociation as a reliable and replicable finding. Building on this foundation, Domjan and colleagues continued to investigate the phenomenon, which he refers to as biological constraints on learning, through their own studies of sexual behavior in quail.

Soon, Domjan began reinterpreting his findings and developing his theoretical reasoning within the framework of Behavioral Systems Theory, with an emphasis on the investigation of the learning processes "Our approach differs from Timberlake's in that he discussed the structure of behavior systems, not systems of learning." (Domjan & Gutiérrez, 2019). Thus, he went on to develop and analyze a behavioral system centered on his primary experimental focus: sexual behavior in quail (Figure 5). This Behavioral system will, for example, use the "copulatory imminence"**,** inspired by the "predatory imminence" continuum proposed by Fanselow (Fanselow et al., 1988) and also present in Timberlake's models. Several novel findings arise from this view, through experimental demonstration of the reinterpretation of existing studies.

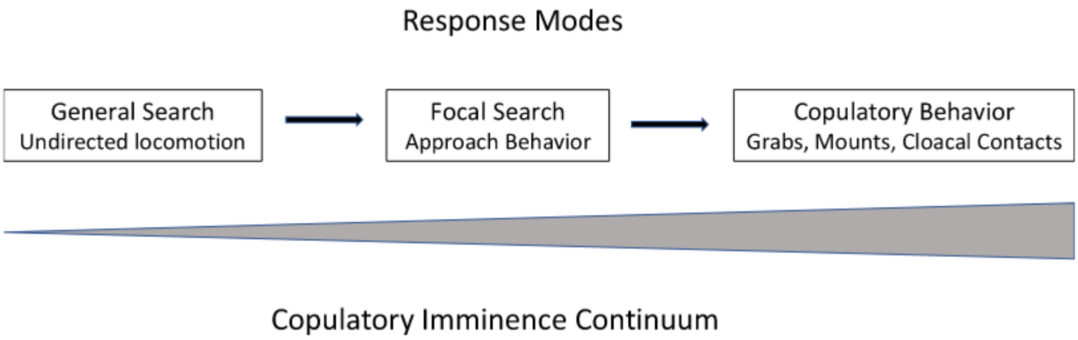

Figure 5. Response modes of the sexual behavior system organized by copulatory imminence. (Domjan 2015, Figure 1 p.185)

The first kind of contribution lies within the system, emphasizing that any element may function as a locus of conditioning. For example, he showed that the quails can be conditioned to enter the general search modes by the pairing of a distinctive context with sexual reinforcement in male quail, resulting in increased locomotor behavior in that context (Akins, 1998). Additionally, Domjan classifies the stimuli present in the environment in three major categories: (1) Spatially distributed contextual cues, defined as non-spatially localized stimuli such as overall levels of illumination, temperature, or background noises. (2) Arbitrary localized stimuli are all the stimuli that are non-specific to the species with a defined location, such as a tone or a small light. They are the ones most commonly used in classical conditioning. And (3), Species-typical localized stimuli, defined as cues being unique to a particular species, such as the physical feature of the sexual partner.

More than a classification of the stimuli, there is also a functional relevance of these categories, with different kinds of stimuli being more likely to induce a specific part of the system. For example, the presence of species-typical localized stimuli serves to identify the location of the potential sexual partner, making general search responses unnecessary, and would more likely induce a focal search or copulatory behavior. A diagram of the different stimulus categories, different response modes, and their interaction is presented in Figure 6 (Domjan & Gutiérrez, 2019). Linking this novel approach and terminology to general laws of learning, many key features of Pavlovian conditioning were demonstrated using arbitrary, localized conditioned stimuli, such as: acquisition (Domjan et al., 1986), extinction (Domjan et al., 1986; Krause et al., 2003), trace conditioning (Akins & Domjan, 1996), blocking (Köksal et al., 1994), conditioned inhibition (Crawford & Domjan, 1996), US devaluation effects (Hilliard & Domjan, 1995), second order conditioning (Crawford & Domjan, 1995), and relative waiting time effects (Burns & Domjan, 2001). Lastly, evidence demonstrates a more robust conditioning with species-typical localized stimuli, evident in their insensitivity to increases in the CS-US interval, greater resistance to extinction, and resistance to blocking (Akins & Cusato, 2015; Domjan et al., 2004).

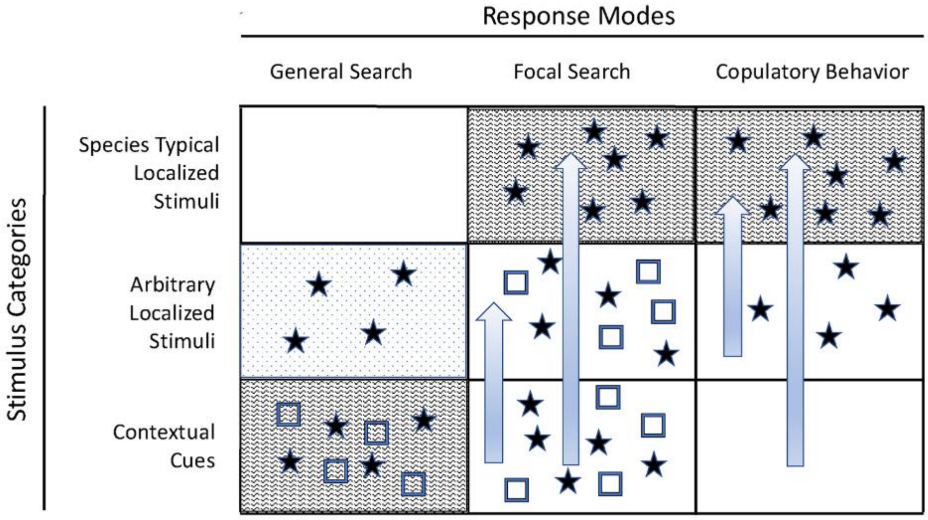

Figure 6. Modification of the sexual behavior system for males by Pavlovian conditioning. Symbols in each quadrant represent conditioning effects. Stars represent data from studies with quail. Small squares represent data from studies with rats. Arrows indicate how conditioning enables certain cues to modulate responding to other types of stimuli. The origin of each arrow represents the modulating stimulus and the tip of the arrow represents the target of the modulation. The shading of the background represents strength of control of each response component unconditionally. (Domjan, 2019, P187, Figure 4)

A second contribution to this learning-centered approach is at the whole system level. First, by suggesting a conceptual model of the evolution of the behavioral system through learning experience (Domjan & Gutiérrez, 2019). Before any learning, a pre-existing behavior system would serve as a structure for the organism when it first encounters a given situation. This situation would lead to several successes and failures of different responses, and lead to the achievement or non-achievement of the system’s main objective, e.g., the cloacal contact and fertilization of the partner in the example of the male quail's sexual behavior system. Thus, an updated behavioral subsystem would emerge from this experience, through modifications that enhance the adaptability of the system, i.e., increasing the likelihood of successfully achieving the objective in subsequent occurrences of this situation. This approach, focusing on a structured functional system rather than a specific contingency, draws a clear rupture with the traditional learning view. This allows the incorporation of the species-specific stimulus in the system, suggests boundaries to what can and cannot be learn, and proposes interactions between different systems or between features of the system.

Lastly, although grounded in quail sexual behavior, Domjan's use of a general terminology marked a departure from Timberlake's approach to the BST. By emphasizing learning principles and system functionality, his framework enables connections across species, fostering a perspective that balances the systematic generality of learning theories with the species-specific descriptions emphasized in the BST. In line with this idea, (Domjan & Hollis, 1988) suggested that variations in mating systems account for species differences in sexual learning systems, although common principles remain. Another parallel with quail findings is the induction of the general search mode by a sexually conditioned cue, evidenced by increased locomotion in rats when this cue is presented (Mendelson & Pfaus, 1989).

Linking Domjan's view to our original problem, Thorndike's experiment can be reinterpreted as follows: the cat's primary motivation was to escape the cage, engaging a system functionally directed toward exiting and obtaining the food outside. When escape attempts failed, time elapsed, and the motivational state shifted to a “self-care” system, expressed in grooming behavior. This switch, tied to a different functional objective, reduced the cat's sensitivity to external stimuli, thereby weakening any potential association between grooming and the opening of the cage. While this interpretation provides a more detailed and structured account than the initial concept of belongingness, it still falls short of providing predictive power or a clear understanding of the mechanisms differentiating efficient from inefficient associations, indicating that further theoretical development is needed.

In the present work, we adopt a behaviorist perspective, focusing on the analysis of learning processes. However, alternative approaches exist that address similar questions, such as cognitive or neurocomputational frameworks, which encounter similar issues and provide complementary insights into the mechanisms underlying selectivity

1.2.3. Outside behavior analysis

In this chapter, the discussion of learning has primarily reflected the perspective of behavior analysis. However, parallel concepts and challenges also emerge within cognitive psychology. In cognitive psychology, Thorndike’s inefficiency of learning with cats would be interpreted in terms of attention, i.e., the cat was not attentive to the opening of the door; his attention was focused on his grooming behavior. This interpretation would come from the central idea that there is a limit to the attentional resources, which constrains the information processed by the brain (Broadbent, 2013). This limit suggests that when attention is shifted toward a specific event, one becomes less aware of or blind to other events (Simons & Chabris, 1999). This perspective defines attention as a filtering agent, leading to intense debate on the location and the nature of this filter (Treisman, 1969, 2012). While this use of attention is well-established, and while neurophysiology studies have extensively corroborated the concept of filters, the question of *why* these filters arise has been less studied than *how*. In other words, attention is defined as a filter that selects information, and we then infer where attention has shifted based on the information selected. This creates a sense of circularity when attempting to explain why or when attentional shifts occur (Rosenholtz, 2024).

An alternative framework for attention has been proposed by Krauzlis et al. (Krauzlis et al., 2014) to tackle this issue. This framework places attention as an effect rather than a causal agent, with attention being a functional consequence of the neural substrates at play in the treatment of the information. A central idea is the definition of the current ‘state’ of the animal, defined through the competition of (1) the sensory data, coming from the animal's perceptual features, (2) the prior knowledge, coming from the animal's past experiences, and (3) the internal status, referring to internal stimuli (see Figure 7). States are compared to templates, each differing in the weights it assigns to the information received, and the template that best matches the current situation remains active until another one replaces it. By placing the filtering properties of attention at the neural substrate level, depending on the current state of the animal, this entails that all the perceptual information is gathered. However, only the information relevant to the current state will be processed. Because the functional need of a specific state can be specified independently of the concept of attention, this framework escapes circular reasoning.

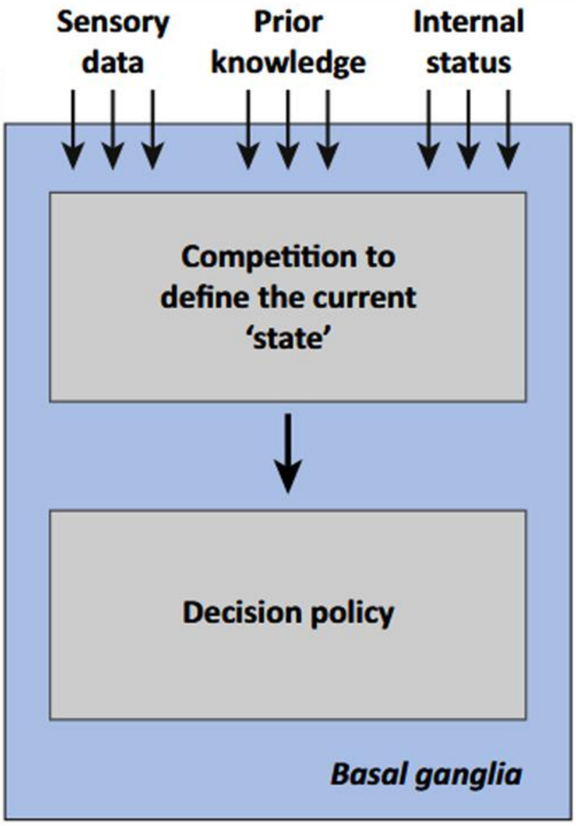

Figure 7 Attention as an effect of interpreting sensory and other data. In this framework, attention is a byproduct of circuits centered on the basal ganglia involved in value-based decision making. Here, competition does not affect how sensory inputs are represented but instead determines which estimate of the 'state' provides the best match to the current sensory data, prior knowledge, and internal status of the subject. The dominant estimate of the state then determines which decision policy is followed. (From Krauzlis 2014, Figure 1)

Critically, it is worth underlining that Krauzlis' model of attention is compatible with the BST framework we discussed in Sections 1.2.1 and 1.2.2. While the BST emphasizes the importance of sensory input, whether it belongs to the behavioral system or not, Krauzlis proposes a selection of the information to make a decision. The prior knowledge component in Krauzlis' framework can be interpreted as reflecting the organism's history of reinforcement. Lastly, the internal state may correspond to the current function being fulfilled by the organism, that is, the active response mode of the system. Beyond mere compatibility, this interpretation provides a more fine-grained view of transitions within and between systems by decomposing them into three key components.

1.2.4. Selectivity of learning

To summarize the body of work reviewed in this chapter, we observed that some experimental results conflicted with leading frameworks in learning. Despite significant theoretical and experimental progress, we remain limited in our ability to explain and predict these results. In the following of this manuscript, we will refer to this phenomenon of variable efficiency or inefficiency of the stimuli to induce learning as “Selectivity of learning”. This term of selectivity, first used by Garcia and colleagues, captures a sense of active selection of the information depending on functional requirements, which aligns with our understanding of the phenomenon. Moreover, it suggests a sense of continuity between a total absence of learning and highly efficient learning. Our theoretical starting point is the functional approach of the BST as described by Domjan. This theoretical framework raises several fundamental questions, such as the innate properties of the behavioral system: to what extent are behavioral systems innate, do they have limits to what can be introduced into a specific system, and if so, are these constraints innate as well? As it is presented, the BST suggests that the structure of a system is innate to the organism, but also that systems are flexible and can change dynamically with experience. However, none of the numerous replications of the Bright Noisy Water experiment led to an association between the electric shock and the taste of the water as efficient as the association between the shock and the audiovisual cue, suggesting a limit to the flexibility of the behavioral system.

A second fundamental question is the demonstration of the selectivity of learning in humans. To some extent, our elaborate verbal system could immunize us against this phenomenon by facilitating logical relations between events. If the selectivity of learning arises only in situations necessitating grooming to escape a cage, or when a shock is preceded by flavored water, we might figure it out through logical reasoning and learn the contingency where the cats and rats failed. Investigating further selective learning in humans and whether it is possible to find predictive features of its expression will be a central interest in this manuscript.

2. Motor Control

We interpreted experimental situations in terms of selective learning in both saccadic adaptation (eye movements) and force-field adaptation (arm movements). Since the experimental contributions presented here involve saccadic adaptation, we will focus on this paradigm and examine the properties of saccades in detail, while drawing parallels with force-field adaptation in the discussion sections.

2.1. Saccades

2.1.1. Some properties of the saccades

Saccadic adaptation is a commonly used paradigm for motor learning relying on saccades. Saccades are the most commonly produced eye movements, accounting for around 90% of all eye movements, and they enable rapid shifts in gaze direction so that the image of objects of interest falls on the fovea. Under normal conditions, humans perform two to three saccades per second, each interleaved with a fixation period during which visual information is extracted. In laboratory settings, saccades can be elicited by presenting a visual target and instructing the subject to simply ‘look’ at it. A substantial body of literature exists on the description of saccade metrics, and we will specifically focus here on: (1) The amplitude of the saccade, defined as the distance between the fixation (=starting) point and the ending point of the saccade. Saccade amplitude is usually described in degrees of visual angle (dva). (2) The latency, measured as the time between the signal for the saccade onset (usually the appearance of a visual stimulus) and the detection of this saccade onset. Under normal conditions, latencies are reported to range within 150-200ms. (3) Saccade angles, computed as the orientation of the saccade’s vector defined by the start and end points, relative to the horizontal axis. They are analyzed in a polar coordinate system, with angles ranging from 0° to 360°.

Saccades’ kinematics show regular relationships between amplitude, duration, and velocity, known as the saccadic ’main sequence’ (Bahill et al., 1975; Gibaldi & Sabatini, 2021; Straube & Buettner, 2007). The main sequence describes how saccades, within the physical and neural constraints of the oculomotor system, are executed in a way that ensures accuracy and minimizes visual disruption, thereby supporting seamless visual perception and interaction with the environment (Harris & Wolpert, 2006).

2.1.2. Saccades as an observing response

Due to their function of bringing a visual object of interest to the fovea and enabling accurate perception, saccades can be more precisely described as observing responses, a type of response first defined by Wyckoff (Wyckoff, 1952), with the modern definition of: “The observing response is a topographically different operant that functions to produce an SD or SΔ[1] depending on whether reinforcement or extinction is in effect.” (Pierce et al., 2022). This distinction is important because observing responses are reinforced by the information they provide about a stimulus, emphasizing that saccades are naturally reinforced by accurately perceiving the target of interest (Schroeder & Holland, 1968).

The definition of saccades as operant behaviors, thoroughly articulated by Madelain et al. (Madelain, Paeye, & Darcheville, 2011), was grounded in experimental evidence demonstrating the effects of reinforcement learning on various properties of saccadic movements in monkeys (Ikeda & Hikosaka, 2003; Lauwereyns et al., 2002; Takikawa et al., 2002) and in humans (e.g., Madelain et al., 2007; Madelain, Paeye, & Wallman, 2011; Montagnini & Chelazzi, 2005; Vullings & Madelain, 2018; Xu-Wilson et al., 2009). Critically, one of the arguments in favor of saccades as operant behavior lies in saccadic adaptation.

2.1.3. Saccadic adaptation

Alongside the study of saccadic characteristics, extensive attention has been devoted to the adaptability of the visual system. In this regard, saccadic adaptation was first described by McLaughlin (McLaughlin, 1967) in human participants, using the following method: the participant fixates a fixation

---

[1] SΔ. is a stimulus that indicates that reinforcement **is** not available**.**

point (A), here a red light (see Figure 8). On a signal, the participant shifted his gaze to a second light visible (B) in the periphery of his field of view. During the eye movement, the peripheral light B was turned off, and another light B’, indistinguishable from B but located 1° to its right, was turned on.

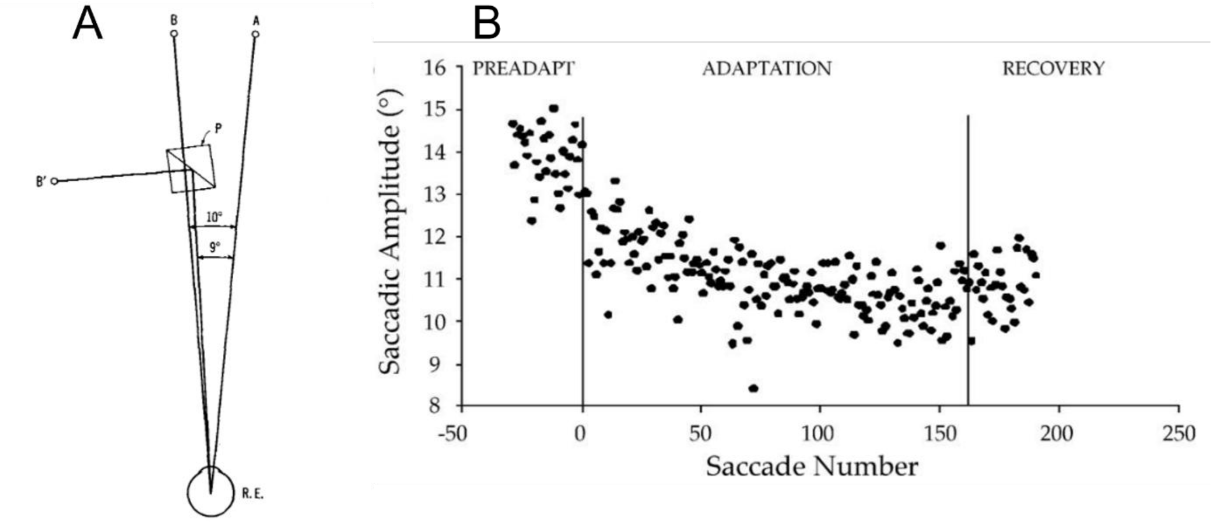

Figure 8. A. Schematic drawing of the apparatus in plan view. A, B, and B' are stimulus lights; P is a semi-reflecting prism; RE is the participant’s right eye. The participant’s task was simply to shift his gaze from A to B. During the eye movement, B was switched off and B' (indistinguishable from B) was switched on, thus inducing an overshoot with respect to B'.(From McLaughlin, 1967, Figure 1). B. Typical adaptation and recovery of saccades in a double-step paradigm. (From Hopp and Fuchs, 2004, Figure 3)

This manipulation results as a step of the light B to the location B’ during the participant’s saccade; we will refer to this step as the Intra-Saccadic-Step (ISS) for the rest of this manuscript. Initially, the saccade lands near the location of target B, and because of the intra-saccadic step, it is further away from the current location of the target, at B’. This manipulation artificially increases the retinal error—the distance between the target location and the eye position. A larger retinal error reduces the accuracy of target perception, typically triggering a second, corrective saccade toward B’. During the experiment, the participant remains unaware of the intra-saccadic step thanks to saccadic suppression: the fast nature of saccades leads to a loss of visual sensitivity that takes place around 70ms before saccade onset and lasts until saccade landing (Castet & Masson, 2000; Krock & Moore, 2014). Over the trials, the participant will experience the same ISS repeatedly, and the amplitude of the saccades will change, landing closer to the location of B’ (see Figure 8.B for a typical example). This modification is referred to as a saccadic adaptation, and is usually measured by a difference in the saccade amplitude between the beginning and the end of the experiment. In the study of motor learning, saccadic adaptation is discussed as an adjustment of the prediction, leading to Bayesian models accounting for the different features of this prediction (Shadmehr et al., 2010).

Additionally, it is important to establish the implicit nature of saccadic adaptation, confirming that we are investigating a motor learning process rather than a rule-based strategy. One evidence is the general pattern observed during this adaptation, usually a slow and progressive change of the saccade's parameters. Indeed, if participants were to use an explicit strategy, one would expect much larger and faster changes in the saccades (Schutz et al., 2014; Souto & Schütz, 2020). This slow and steady adaptation remains even when the participant is asked to saccade to half the distance between the fixation point and the target, demonstrating that even when the saccades are explicitly controlled, the adaptation remains an implicit process (Bahcall & Kowler, 2000). Moreover, Frens and Van Opstal (Frens & Van Opstal, 1995) observed that participants used to the adaptation paradigm could perceive the intra-saccadic step, whereas naive subjects could not; however, experienced and naïve participants showed similar rates of adaptation.

Along with the numerous studies on the properties of saccadic adaptation, strong evidence has been established for a directional specificity of the adaptation (Deubel, 1987; Frens & Van Opstal, 1995; Miller et al., 1981; Semmlow et al., 1989; Straube et al., 1997). This property entails a form of dependency of the saccade on the context to express adaptation, further described by Rolfs et al. (Rolfs et al., 2010). In this study, participants were trained in a saccadic adaptation paradigm that involved global, one-way, or two-way movements from the fixation point in every direction of the visual field (Figure 9). All participants were then tested in every direction, showing that adaptation proportion developed at a similar rate in all conditions, but also that adaptation was specific to the trained directions.

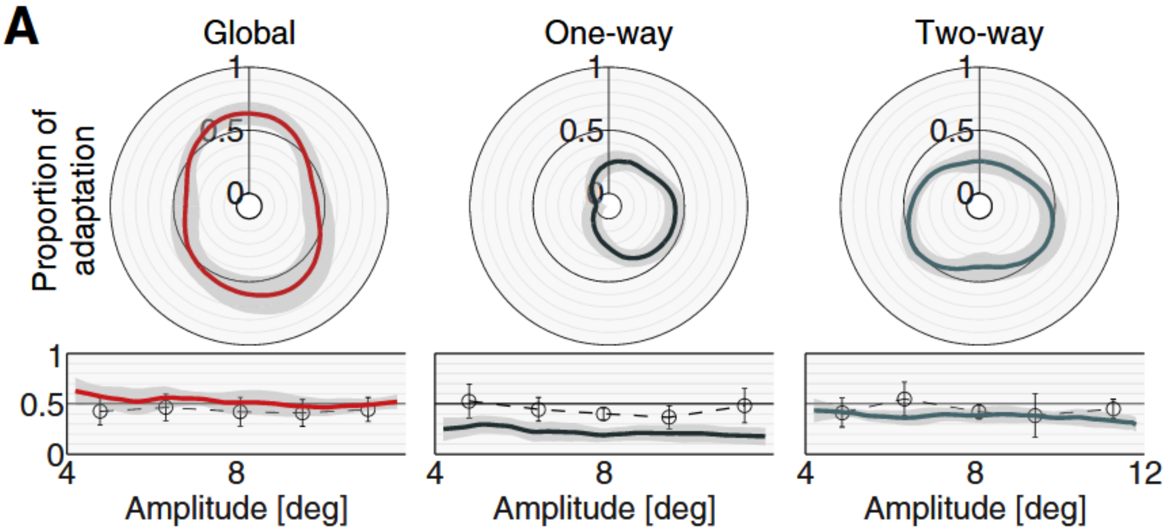

Figure 9. Spatial extent of adaptation. The proportion of adaptation after Global, One-way-, and Two-way adaptation is plotted as a function of target direction (upper panels) and amplitude (lower panels). Thick, colored lines represent the average across observers; shaded areas provide 95% confidence intervals. For comparison, dashed lines in the lower panels show the results for target directions within ±30° of the direction that was adapted in the One-way condition. Error bars are 95% confidence intervals. (From Rolfs et al., 2010, Figure 4.A).

Saccadic adaptation may be regarded as a paradigm of saccade conditioning, driven by positive reinforcement of one or more saccade parameters through the reduction of retinal error. Consequently, saccadic adaptation falls under the laws of learning and can be used as a tool for exploring learning mechanisms.

2.1.4. Contextual saccadic adaptation

Using the saccadic adaptation paradigm with different cues predicting the direction of the intra-saccadic step, contextual saccadic adaptation emerged. This novel version of the paradigm has been extensively used to investigate saccade properties, the plasticity of the saccadic circuitry, and to refine Bayesian models of saccadic adaptation (Pélisson et al., 2010). A typical situation of contextual saccadic adaptation is as follows: the participant fixates a fixation point and performs a saccade upon target displacement. The target experiences an ISS, resulting in a retinal error for the participant. The difference with the classical saccadic adaptation is that multiple, usually two, different ISS will be applied on the same saccade vector. This modification requires an adaptation of the saccades in two different directions within the same experiment. To do so, ISS directions were paired with contextual cues A and B, each associated with its specific displacement.

In Alahyane and Pelisson (Alahyane & Pelisson, 2004), the contextual cue was the location of the fixation point. The target appeared on the participant's left visual field, at one of two positions along the same vertical axis: either high or low. During baseline trials, no ISS was present after the step of the target. Baseline trials are present to measure the saccades of the participant before adaptation. In the learning trials, an ISS equal to 20% of the amplitude of the step of the target was introduced. For half of the participants, this ISS was applied backward for saccades starting from the higher fixation point and forward for saccades starting from the lower fixation point; for the other half, the directions were reversed depending on the fixation point location. This experiment demonstrated the simultaneous induction of the two opposite adaptations, with an increase in the amplitude when the fixation point was paired with the forward ISS, and a decrease in the amplitude when the fixation point was paired with the backward ISS.

Using similar designs, contextual saccadic adaptation has been demonstrated using contextual cues such as target eccentricity or depth (Chaturvedi & Van Gisbergen, 1997), horizontal or vertical orbital eye position (Alahyane & Pelisson, 2004; Shelhamer et al., 2002; Zimmermann & Lappe, 2011), head orientation (Shelhamer & Clendaniel, 2002), target motion (Azadi & Harwood, 2014), or saccade sequence (Azadi & McPeek, 2022). In each of these studies, participants experienced two different ISSs consistently paired with different contexts, resulting in two simultaneous context-specific saccadic adaptations.

As stated previously, this paradigm can be interpreted through the lens of operant conditioning: The participant is presented either with a discriminative stimulus A, the higher location, or B, the lower location, and will perform a response, the saccade, upon target appearance. The accuracy of the response will determine the outcome, the retinal error, with a greater reinforcement for a lower retinal error (for a similar argument see Madelain, Paeye, & Wallman, 2011). Over the trials, the retinal error will decrease, maximizing the reinforcement of the saccade, translated by a modification of the saccade amplitude. Because the A and the B are paired with different ISS, they require different responses, a shorter saccade or a longer saccade. These two responses are learned concurrently and expressed upon discrimination of the stimulus, e.g., the amplitude increases with the stimulus paired with the longer amplitude and decreases with the stimulus paired with the shorter amplitude.

In Bayesian models, contextual adaptation is described as a prediction process. However, due to the presence of two ISS, the prediction is now on the cue rather than being on the saccade itself. The failure of the model to predict accurately based on the saccade vector will relocate the prediction on the cue, using parallel and independent models for each cue. After every trial, the priors are updated for the current cue, leading to the simultaneous adaptation to both cues.

2.1.5. Anomalies in contextual adaptation

In another study using contextual saccadic adaptation, Deubel (Deubel, 1995) employed the color and shape of the target as contextual cues. As in previous paradigms, participants fixated the fixation point, the target underwent an initial step, and an ISS was applied at saccade onset. The target was either a green cross or a red circle, from the beginning to the end of a trial. A backward ISS was introduced in the learning trials, only for the green cross, but trials with the red circle experienced no ISS. The expected results were a decrease in the amplitude for the green cross trials and no change in the saccade amplitude for the red circle, i.e., a contextual adaptation depending on the cue. However, the results reported no contextual adaptation, with no significant difference in saccade amplitude between the green cross and the red circle trials. According to Deubel, this indicates that saccadic gain control is not specific to the visual features of the target. Those results led to replications with the color and shape of the target as a cue (Azadi & Harwood, 2014; Bahcall & Kowler, 2000; Benjamin et al., 2016), systematically aligning with Deubel's results on the inefficiency of the color and shape of the target to induce contextual learning in saccades.

In monkeys, Cecala et al. (Cecala et al., 2015), also replicated this experiment using color as a contextual cue, with a green target paired with a forward ISS and a red target paired with a backward ISS. Despite extending the experiment to 1,500 trials, the monkeys showed no significant difference in saccade amplitude as a function of cue color (Figure 10.A). In another experiment of the same study, Cecala et al. used a red colored target alone for 600 trials, showing a successful backward adaptation, followed by 600 trials of the green target alone, showing a successful forward adaptation. This additional experiment shows that cue color does not impair the monkey's ability to learn: both single adaptations are possible independently but not concurrently. In other words, when adaptation relies on a single ISS, the cue does not interfere with the process; however, the cue itself cannot support the adaptation and allow context-dependent changes.

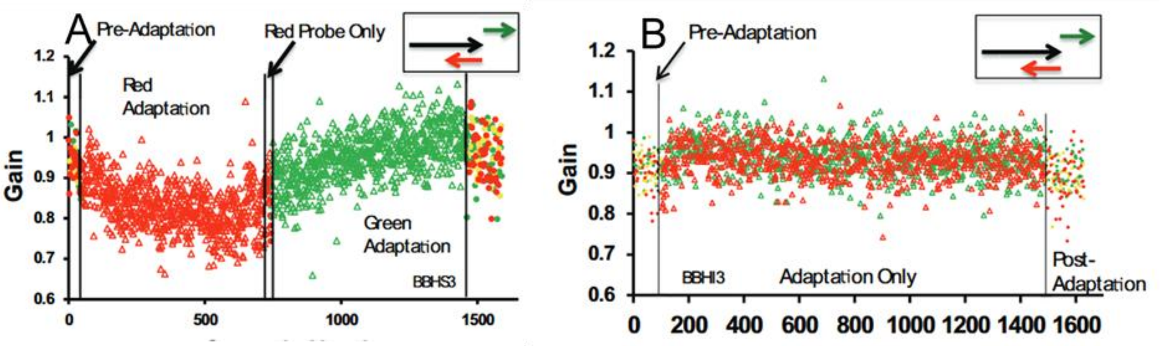

Figure 10. Color and Shape contextual cues in Rhesus Macaques. Each symbol (circle or triangle) represents data from a single trial. Circles represent probe trials; triangles represent adaptation trials; symbol colors represent the color of the targets within a given trial. Inset portrays the direction of the primary saccade (black arrow) and the direction of the intrasaccade target displacement during red (red arrow) and green (green arrow) adaptation trials. A. Adaptation using the Red cue and the Green cue in two different blocks of trials. B. Adaptation using the Red cue and the Green cue in intermixed trials.

2.1.6. Theoretical account of the anomalies

From a theoretical perspective, these results represent a persistent difficulty for research on motor learning. Bahcall and Kowler (Bahcall & Kowler, 2000), in discussing these cues, described their findings by stating that *"high-level cues are not the natural means of controlling adaptation.".* This interpretation lacks an underlying mechanism and does not offer a way to predict similar outcomes in other situations.

Azadi and al. (Azadi & Harwood, 2014) suggested a hypothesis in terms of motor state: the process of saccade adaptation is purely motor and does not have 'interest' in the perceptual properties of the target, therefore the adaptive process would have a strong prior for motor-related features, as they are relevant for the production of the saccade, but little or none for the visual features of the percept. However, this distinction between motor and visual is post-hoc since their initial expectation was that all conditions would be effective. Moreover, their discussion reveals that the problem remains unresolved: What are the underlying mechanisms that could prevent adaptation from relying on a visual cue? If adaptation can be categorized as visual or motor, what then of other potential domains—such as auditory or statistical cues?

Extending this question to research in arm movement, a very similar situation is described by Howard et al. (Howard et al., 2013). In a force field adaptation paradigm, the participant grasps the handle of a robotic manipulandum (Figure 11.A). Visual feedback of the manipulandum movements is displayed in front of the participant, and he is instructed to reach a target among 8 different locations, always starting from the same location (Figure 11.B). In every trial, a force field is applied to the handle, shifting the movement of the participant either leftward or rightward. To reach the target rapidly and accurately as instructed, the participant's arm movement has to adapt, i.e., predict the force field direction. To ensure this prediction, contextual cues are provided in each trial, a cue A paired with a leftward force field and a cue B paired with a rightward force field. In their study, they used numerous contextual cues such as the cursor color, a peripheral visual motion, or the workspace location (see Figure 12, A). Results demonstrate strong contextual adaptation for some cues, such as the workspace location, more mitigated adaptation for cues such as the peripheral visual motion, and no adaptation for cues such as the cursor color (Figure 12, B).

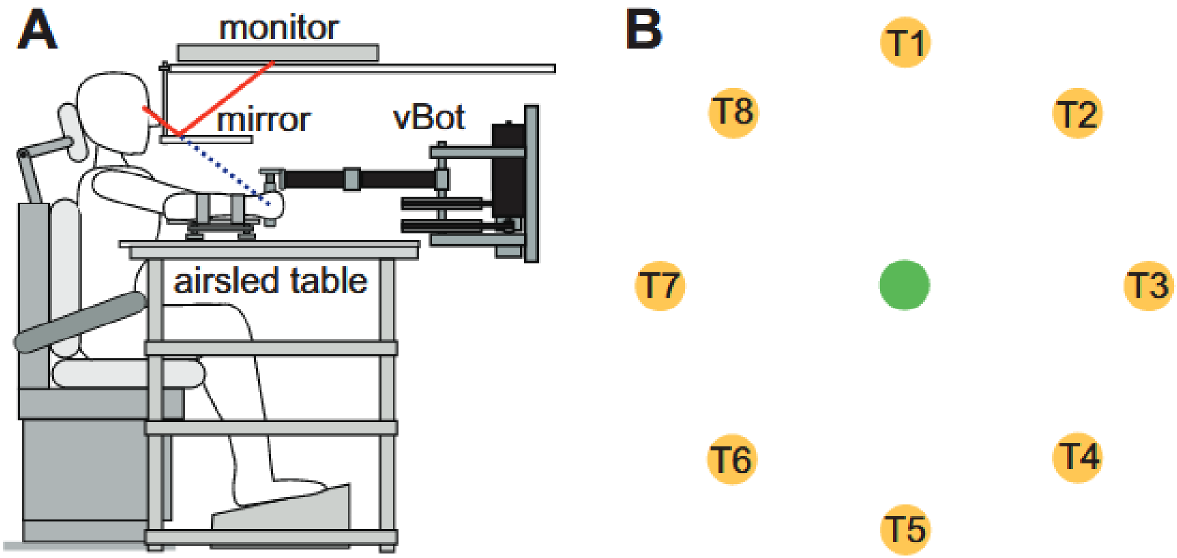

Figure 11. Experimental paradigm. A: the subject grasps the handle of the robotic manipulandum (vBOT) while seated. Visual feedback of movements is presented veridically using a horizontally mounted monitor viewed through a mirror. The subject's forearm is fixed to the handle and supported by an air sled. B: workspace layout of the experiment. There was a single starting location (green circle; note that in the experiment this was displayed as gray) and 8 targets (yellow circles: T1–T8). (From Howard et al., 2013, Figure 1).

Although slight differences across experiments limit quantitative comparisons, the authors concluded that different types of cues vary in their effectiveness at forming and recalling distinct representations in motor memory. They hypothesized that "visual movement needs to be more closely associated with the task, or even be considered part of it by the motor system, for it to have a strong contextual effect. […] the motor memories are learned as a function of the state of the limbs." (Howard et al., 2013). The analogous issue observed in force field adaptation prompted a discussion similar to that of Azadi and Harwood, offering limited insight into the underlying mechanisms and no predictive power for untested cues.

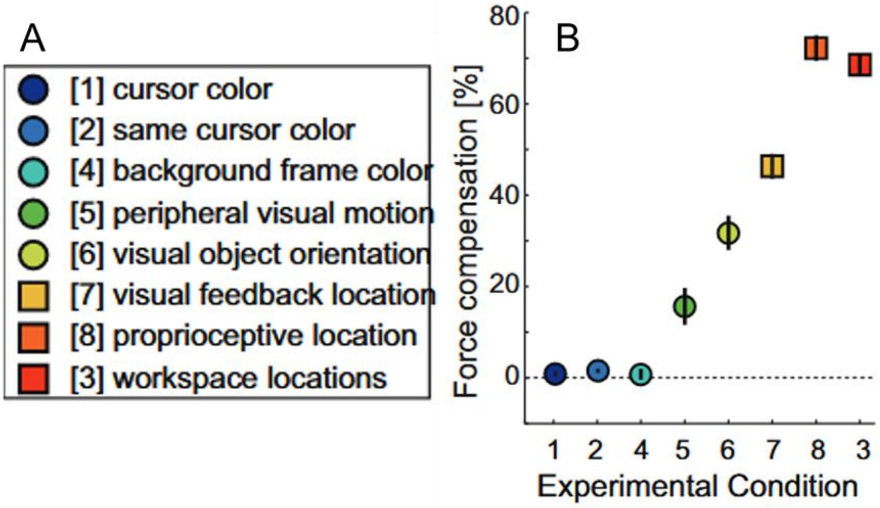

Figure 12. Contextual effects as a function of cue. B: mean force (+-SE) on clamp trials (in direction toward target T1) as a percentage of the force required for estimated complete compensation. Values for each experimental condition [on last third of trials (25 blocks) during force field exposure] are plotted sequentially along the x-axis. (adapted from Howard et al., 2013 figure 9).

3. Theoretical Rationale

3.1. Theoretical Rationale

In Chapters 1 and 2 of this Introduction, we review part of the experimental and theoretical contributions on selective learning. We presented several demonstrations of this phenomenon, as well as of the lack of a solid theoretical framework to apprehend it. We described it as a situation in which the organism is unable to associate a given stimulus with an unconditioned response in Pavlovian learning, or when the stimulus fails to elicit a response despite a perfect three-term contingency: Stimulus -> Response -> Consequence.

We then presented a case of contextual saccadic adaptation that failed to induce learning using the color and shape of a target as a cue, despite similar methods being effective with other cues. We hypothesize that these results reflect the selectivity of learning in humans. Importantly, few theoretical interpretations of these findings have been proposed, and none mention, nor contradict, the framework we are assessing.

3.2. Research Question

First, we should replicate the situation of inefficiency in learning. Our experimental settings vary from the aforementioned studies using the color and shape of the target, and establishing both effective and ineffective contextual adaptation using the same settings, besides the nature of the stimuli used, will ensure a solid basis for comparisons between the different stimuli and experimental settings.

A second major aim is to investigate a broader range of contextual cues, in order to determine which cues effectively induce learning and which fail to do so. Examining the different properties of these cues will clarify whether factors beyond the visual features of the target can control saccadic adaptation. This approach would enable a more precise quantification of learning differences across stimuli and contribute to refining and advancing the theoretical framework of selectivity.

Lastly, we aim to address selectivity of learning through two complementary approaches: an atomic approach, which examines the specificity of the saccadic system to gather detailed insights into the processes underlying discrepancies in learning efficiency; and a molecular approach, which treats eye movements as a functional system, characterizing its limitations and strengths to extend findings from saccadic adaptation to broader learning processes. Critically, we seek to propose a mechanism explaining the expression of selectivity in saccadic adaptation and motor control, along with a means to predict its occurrence.

3.3. Overview of the studies

This thesis will be centered around three main experimental studies, complemented by four additional experiments.

Section 5.1 will present the first study of this thesis, comprising 11 experiments and 106 participants. This study is a comparison of contextual cues of different natures, used in the same experimental conditions aside from this variation. Through this design, this study enabled us to confirm the effect of the selectivity of learning. We also gathered information on which cues were enabling learning and which did not, and we were able to measure differences in learning between the efficient contextual cues. Lastly, two experiments were used to demonstrate a dissociation in learning, showing that the cues inefficient for saccade adaptation were still perceived and available to the participants for other tasks.

Section 5.2 will complement this chapter with the use of additional contextual cues, serving the same comparison strategy described in the first study. Section 5.2.1 will describe an experiment using the remote distractor effect, an effect known to modify the trajectory of the saccade without modifying its starting or endpoint. Section 5.2.2 will describe two experiments manipulating temporal parameters of the saccades, namely a Gap/Overlap situation and a manipulation of the duration of the fixation period. Taken together, these experiments served to better characterize the locus of learning in saccade adaptation.

Section 6.1 will present a study aiming to use higher-order conditioning. Higher-order conditioning is introduced by using contextual features that modulate the information carried by the contextual cue. We first investigated a motor cue as the contextual feature to assess whether this higher-order design can successfully induce learning in saccadic adaptation. Then, we investigated a non-motor cue as a contextual feature to evaluate if the status of the contextual feature would bypass the selectivity of learning and help integrate the non-motor cue into the learning process.

Lastly, Chapter 7.1 will present a study replicating Sheahan et al. (Sheahan et al., 2016) paradigms on force field adaptation, investigating the key components of motor learning. This study shed new light on saccade adaptation mechanisms by demonstrating that motor planning was the key factor of motor adaptation. It allows for a more precise definition of which cues would be efficient for learning. It would be an interesting basis for an operant prediction of motor learning in general. This study replicated our previously described selective effect and provided additional data for comparison with other contextual cues we have been working with.

Summary and key points

Selectivity of learning

- Defined by the failure of an association despite the prediction of the General Process Theory.
    - In Pavlovian conditioning is the inability for a stimulus to become a conditioned stimulus; in operant conditioning it is the inefficiency for a stimulus of elicit a response.

- Had its clearest demonstration in Garcia & Koelling *Bright Noisy Water experiment*, with a double dissociation between two simultaneous conditioning.

Saccade adaptation

- Is a situation of operant conditioning in humans. This implicit learning has little sensitivity to rule-governed strategies.

- Contextual saccadic adaptation demonstrated failure of learning with the color and shape of the target as a cue. A result for which no clear theoretical account has been proposed.

Research questions

- Further demonstrate selectivity of learning in humans with our design of contextual saccadic adaptation.

- Refine the experimental and theoretical aspects of selectivity of learning through:
    - Comparison of different cues.
    - Investigating higher-order conditioning.
    - Precision of the locus of learning.

4. General method of the thesis

The experimental contributions of this thesis relied on a general method across the different experiments. The main differences between our experiments lie in the contextual cues presented, and any other difference from our usual design will be clearly stated in the experimental section of interest. Several specific methodological choices were made to best address our research questions, and these are detailed in the following section.

4.1. Contextual saccadic adaptation

We recruited participants in Lille, both through academic and non-academic channels. All participants were naïve as to the purpose of the experiments, and all had normal or corrected-to-normal vision. Participants provided consent via non-opposition, meaning they were verbally informed of all study details beforehand and explicitly told they could stop the experiment at any point. Following the standard procedures used in such protocols, no written consent has been provided to ensure the anonymity of the data. All experimental procedures received approval from the Ethical Committee in behavioral sciences of the University of Lille and conformed to the standards set by the Declaration of Helsinki. Five to ten participants were recruited for each of our 22 experiments, totaling 199 participants. All of our primary statistical analyses are made intra-participant, meaning that each participant from an experimental condition represents their own replication of this experiment. This justifies the minimal number of participants we recruited per experiment, our statistical individual lies in our amount of trials, and aligns with other authors working with a similar paradigm (Cassanello et al., 2016; Ethier et al., 2008b; Rolfs et al., 2010; Zimmermann & Lappe, 2011).

Our experimental design closely resembles the contextual saccadic adaptation designs presented in Section 2.2.1. In a typical experiment, the participant sat in a dark and quiet room facing the display monitor with his head stabilized via chin and forehead rests (60cm from the screen). Stimuli were generated and displayed on the monitor, while the right eye position was recorded by an Eyelink 1000+ Tower Mount system, sampling at 2,000 Hz.

In a session, participants started with a set of instructions and training trials designed to ensure the good functioning of the setup, and then the experimental session started. Experimental sessions were usually divided in three phases: Baseline, Learning, and Recovery trials. The baseline phase consisted of 200 trials, followed by 500 trials of learning and 150 trials of recovery. The baseline was used to assess the participants' saccades before manipulation. We designated the last two hundred trials of the learning phase as late-learning trials, based on the assumption that the learning process accumulated across trials. This final segment of the learning phase was therefore used for the main statistical comparison between contextual cues. Lastly, the recovery phase was present to ensure a smooth return to baseline as expected in motor learning, compared to a sudden and abrupt return to baseline that would have signaled a rule-governed behavior or an explicit targeting.

Within a trial, the participant fixated a fixation target and performed a saccade upon target displacement. The fixation period, as well as the amplitude of the first step, varied in each trial to avoid a prediction of the timings or localization of the next saccades. At saccade detection, the target underwent an intra-saccadic step (ISS) with an amplitude corresponding to 20% of the initial target displacement, applied in a direction orthogonal to the first-step vector. In each trial, either the contextual cue A or B was present, and A and B trials were intermixed. Every 50 trials, a short break was introduced to check whether recalibration of the EyeLink was necessary. Breaks during an adaptation session are known to facilitate the slow component of learning that is thought to consolidate learning (Shadmehr et al., 2010).

4.2. Novel features of our design

While implementing the contextual saccadic adaptation paradigm based on previous work, we introduced two main modifications to better align the design with our experimental and theoretical objectives.

First, we choose to use a 45° oblique vector for the displacement of the target, unlike the more conventional horizontal step. The fixation target was presented in the bottom left corner of the screen and stepped to the upper right corner. Therefore, the orthogonal displacement of the ISS was oblique as well, either in a North-West direction or in a South-East direction. We preferred this oblique step because of the hypometric properties of saccades, which favor gain-decreasing amplitude compared to gain-increasing amplitude (Rahmouni & Madelain, 2019). With the oblique step, we involved both the vertical and the horizontal saccade components for both the first target step and the ISS. This specificity of the design also led us to use the angle of the saccade rather than the gain as the dependent variable, with either an increase in the saccade angle when the ISS was North-West directed, or a decrease in the saccade angle when the ISS was South-East directed. For data analysis, we always normalized the value to 0° by computing the saccade angle difference to the baseline, to facilitate comparison of the results between participants and between groups.

Second, and according to Rescorla's principles of truly random procedure (Rescorla, 1967), the ISS was present in every trial, including baseline and recovery trials, as opposed to being restricted to learning trials, as is typically the case. To prevent learning in the baseline and recovery phases, we did not pair the ISS with our contextual cues; instead, each cue had a 50% chance of being followed by both ISS. This specific design allowed us to have no difference between any of the phases besides the statistical relations between the event, which may reduce the addition of motor noise in the response at the beginning of the learning phase when the ISS is usually introduced. Critically, the only difference between the learning trials versus baseline or recovery trials is the introduction of a contingency between the contextual cue and the ISS direction. Therefore, if adaptation emerges during the learning trials, it would necessarily be due to this contingency.

4.3. Statistical analysis

Before statistical analysis, a human observer validated each saccade manually. Then, we computed the angle of the first saccade in every trial. For each participant, we calculated the median baseline for each contextual cue and subtracted it from all trials sharing the same cue. This normalization of the data provided us with angles centered around 0° for all participants, facilitating comparison. It also ensured that the difference expressed in the learning trials was induced by the contingencies of the experimental design rather than from the nature of the cue we used.

For the main statistical analysis, we used a nonparametric permutation test on the difference in medians from each contextual cue in the late-learning trials (=last two hundred learning trials), with 100,000 permutations. This computation provided us with a confidence interval at 97.5% under H0, to which we compared the expressed difference in the medians of the participants, and statistical significance was reached only if the difference was in the right direction, i.e., saccades paired with the North-West ISS showed higher angles than the saccades paired with the South-East ISS.

To quantify the normalized difference between the angles of saccades performed in each context, we computed the Kolmogorov–Smirnov (KS) distance (Berger & Zhou, 2014). The two-sample Kolmogorov–Smirnov test compares the empirical distributions of two samples by measuring the maximum distance between their cumulative distribution functions, thereby assessing whether they originate from the same distribution. A distance of 1 indicates complete discrimination between the two distributions, whereas a distance of 0 reflects complete overlap, or generalization, between them. The Kolmogorov–Smirnov test directly captures the essence of discrimination learning; therefore, we used it as a descriptive tool to quantify the extent of discriminative learning across our various cues and designs, providing a more nuanced interpretation of the results than statistical significance alone.

Part II

EXPERIMENTAL CONTRIBUTION

5. Selective learning in saccadic adaptation

The article presented in Section 5.1 is published in Journal of Neurophysiology. It is presented here in its author version and the format has been adapted for the needs of the thesis. Find the published article at: doi:10.1152/jn.00148.2025

5.1. Main Study: Ineffective cues for contextual saccade adaptation

Ineffective cues for contextual saccade adaptation

Maxime Martel,[1] Laurent Madelain[1,2]

[1] UMR 9193-SCALab, CNRS, Univ. Lille, 59000 Lille, France.

[2] Institut de Neurosciences de la Timone, UMR 7289, CNRS, Aix Marseille Université, France.

Correspondence: L. Madelain (laurent.madelain@univ-lille.fr)

5.1.1. ABSTRACT

Contextual saccadic adaptation is investigated through a variant of the double-step paradigm, where two directions of intra-saccadic steps are signaled by two cues. This enables the simultaneous induction of two distinct saccadic adaptations. Surprisingly, contextual adaptation is effective only with motor-related cues, whereas visual cues such as target color and shape do not elicit significant adaptation. We tested nine different contextual cues to signal intra-saccadic steps in a contextual double-step paradigm: visual stimulus duration, lateralization of a sound, various statistical regularities across trials, symbolic cues, starting location of the target, as well as the amplitude of the first step or the target color and shape. Robust systematic contextual learning was found under the amplitude and the starting location experiments, while no learning occurred with any other cues. This lack of contextual learning further confirms that the prediction of the intra-saccadic steps depends on the nature of the context. In two additional experiments replicating those using target color and shape, as well as symbolic cues, participants were periodically prompted to explicitly report the contextual cue they had just experienced. Again, no systematic contextual adaptation was observed despite participants achieving reporting the contextual cue accurately. This dissociation between perceptual reports and motor tasks involving the same visual information aligns with previous results on the constraints for contextual learning. The saccadic system, evolutionarily specialized for spatial targeting, exhibits selective learning that prioritizes localization cues, effectively ignoring non-motor cues in its learning processes, even when such cues are explicitly perceived.

5.1.2. NEW & NOTEWORTHY

This study demonstrates that motor-related cues drive contextual saccadic adaptation, while purely perceptual cues fail to do so. We observed a dissociation between the ability to report non-motor cues and their failure to induce contextual adaptation. The results underscore the importance of spatially relevant cues for guiding contextual saccadic adaptation. These findings deepen our understanding of the selective mechanisms underlying motor learning.

Keywords: Eye movement; contextual learning; saccade adaptation; motor learning; selective learning.

5.1.3. INTRODUCTION

Saccadic eye movements play a crucial role for vision by moving the retinal image of an object of interest on the fovea (the maximally receptor-dense region of the retina), where visual acuity is highest. The saccadic motor command must be continuously adjusted to compensate for changes in the saccadic system occurring throughout the lifetime due to factors such as growth, injury, or aging, which could lead to inaccurate saccades. It is well established that the precision of saccades is maintained through saccade adaptation, a learning mechanism that rely on detecting persistent position errors to gradually adjust the saccades amplitude or angle. The mechanisms responsible for saccade adaptation and its characteristics both at the neural and behavioral levels have been subject to many experimental studies (see (Herman et al., 2013),(Hopp & Fuchs, 2004) and (Pélisson et al., 2010) for reviews) and saccadic adaptation is now regarded as a model of motor learning (Herman et al., 2013).

In the laboratory, saccadic adaptation is typically induced using a double-step paradigm in which a post-saccadic position error is created by surreptitiously shifting the visual target during the saccade (McLaughlin, 1967). Due to saccadic suppression, participants do not perceive the intra-saccadic step (ISS) as vision is impaired during the saccade. This saccadic adaptation paradigm is highly effective and after a few repetitions the initial saccade changes in amplitude or angle to partly compensate for the experimentally induced post-saccadic position error, the amount of adaptation being typically less than the amount demanded by the size of the ISS.

Importantly, contextual saccadic adaptation has been demonstrated using cues such as target eccentricity or depth (Chaturvedi & Van Gisbergen, 1997), horizontal or vertical orbital eye position (Alahyane & Pelisson, 2004) (Shelhamer et al., 2002) (Zimmermann & Lappe, 2011), head orientation (Shelhamer & Clendaniel, 2002), target motion (Azadi & Harwood, 2014), or saccade sequence (Azadi & McPeek, 2022). In these experiments participants experienced two different ISSs (for instance a forward and a backward one) which are consistently paired with different contexts (for instance saccades performed either in the upper or in the lower hemifield) resulting in two simultaneous context-specific saccadic adaptations (Pélisson et al., 2010).

Saccade adaptation is conventionally thought to rely on predictive mechanism in which the actual post-saccadic position error is compared to a predicted position error to drive changes in saccades (Herman et al., 2013; Hopp & Fuchs, 2004; Shadmehr et al., 2010). Based on this view, one might expect that any cue allowing the system to predict the characteristics of the upcoming intra-saccadic step (ISS), and thus anticipate the associated error, could support contextual adaptation. Surprisingly, although it has been repeatedly demonstrated that motor cues - i.e. cues which will actually modify the movement - such as orbital position or saccade direction might provide sufficient contexts to allow independent adaptations (Alahyane & Pelisson, 2004; Azadi & Harwood, 2014), visual cues such as target color and shape are ineffective to elicit contextual adaptation (e.g. (Azadi & Harwood, 2014)). Indeed, no changes in saccades have been reported in contextual saccadic adaptation paradigms using the target color and/or shape as a contextual cue, both in humans and monkeys ((Deubel, 1995),(Bahcall & Kowler, 2000),(Azadi & Harwood, 2014; Cecala et al., 2015)). The current study investigates the breadth of contextual cues capable of driving saccadic adaptation, extending beyond the traditional focus on visual cues. By systematically testing a diverse range of non-motor cues—including auditory, symbolic, temporal signals, and statistical regularities in trial sequences—we aim at exploring the boundaries of the saccadic system's ability to integrate contextual information into motor control. This series of experiments seek to provide insights into the specificity of contextual learning in the saccadic system, shedding light on the fundamental constraints shaping its adaptive mechanisms.

In the present study we used a contextual double step paradigm to probe the effectiveness of various contextual cues. For simplicity we will always refer to the different experimental conditions as contextual cues. Our contextual double step paradigm ensures that each experiment differs only in terms of the actual contextual cue, with all other experimental features remaining consistent across experiments. Participants experienced two possible ISSs, both orthogonal to the direction of the first target step (Fig. 13), in opposite direction, either North-West or South-East.

According to Rescorla's principles of truly random procedure (Rescorla, 1967), the ISS were present throughout every trial of an experimental session. The direction of the ISS was consistent with the cues in the learning trials, but not in the baseline and recovery trials. Crucially, the only difference between the baseline and learning phases in our design is the introduction of a contingency between the contextual cue and the ISS direction. If adaptation emerges in the learning phase, it would necessarily be due to this contingency rather than a pre-existing effect from baseline exposure. We cannot rule out the possibility that the presence of ISS during the baseline phase might introduce some interference with subsequent adaptation, a question that warrants further experimental investigation. However, if such interference occurs, it should affect all experimental conditions equally and therefore should not prevent the observation of potential differences in contextual adaptation depending on the nature of the cue.

We probed the effectiveness of nine different contextual cues. We used two motor-cues, the amplitude of the first target step and the starting location of the target. We also replicated previous experiments using a purely visual cue, the fixation target color and shape. We then used some novel contextual cues, namely, a symbolic visual cue explicitly indicating the direction of the ISS, the lateralization of an auditory stimulus, the duration of a visual event during the fixation period and three different statistical regularities across trials (i.e., different trial sequence patterns). In addition, we performed two experiments designed to assess the participants' ability to report the cue present during a trial. All contextual cues were typically ineffective in eliciting context-specific adaptation except for the first-step amplitude and the starting location experiments.

5.1.4. MATERIALS AND METHODS

Participants

A total of one hundred and twenty-two participants were recruited for this study. Sixteen were excluded for not meeting the criteria for data analysis: 13 did not reach the minimum number of correct recorded saccade criterion and 3 terminated the session early due to technical issues. The remaining one hundred and six participants (81 females and 25 males, aged 18-36 years old) participated in eleven experiments. Ten participants were included for each of the nine experiments probing the effects of the different contextual cues and eight were recruited for each of the two experiments involving a perceptual report of the contextual cue. All participants were naïve as to the purpose of the experiments and all had normal or corrected to normal vision. Participants provided consent via non-opposition, explicitly stated in the information letter provided during recruitment. All experimental procedures received approval from the Ethical Committee in behavioral sciences of the University of Lille (Agreement n° 2022-647-S111) and conformed to the standards set by the Declaration of Helsinki.

Apparatus

Participants sat in a dark and quiet room facing the display monitor (Iiyama HM204DT, 100Hz, 22 inches) with their heads stabilized via chin and forehead rests (60cm from the screen). Stimuli were generated and displayed using the Psychophysics Toolbox Extension ((Brainard, 1997),(Pelli, 1997)) for Matlab®. Recording of the right eye position was performed by an SR-Research Eyelink 1000+ Tower Mount system sampling at 2000Hz. We used the Eyelink 13-points calibration and validation routines at the beginning of the recording sessions.

General Procedure

The aim of these experiments was to compare the effect of the nature of the cues in contextual saccade adaptation. In all experiments we used a double step paradigm (Fig. 13) in which the fixation target was always in the bottom-left corner of the screen, and the first step was directed upward and to the right. The intra-saccadic step (ISS) was either upward and backward (North-West) or downward and forward (South-East) with respect to the first step. Within a session the ISS occurred in all trials.

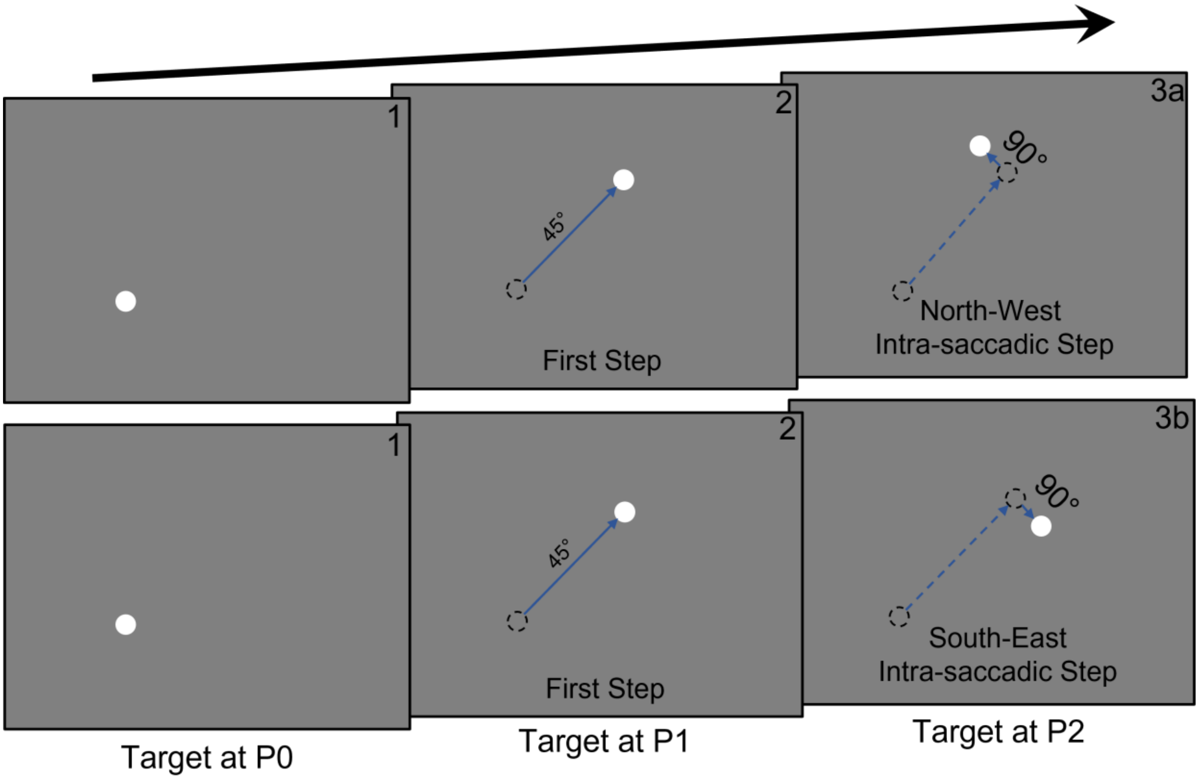

Figure 13. Schematic of a trial for all experiment. (Note: Contextual cues are not depicted in the figure). 1: The fixation point was displayed for a random period [700 ms 1,000 ms] at P0. 2: Target stepped, with a 45 angle upward and rightward and a pseudorandom amplitude [5.5 degrees of visual angle (dva); 7 dva; 8.5 dva, or 10.1 dva] at P1. 3: At saccade detection, the target stepped, during the saccade, at P2. The intrasaccadic step (ISS) amplitude was 20% of the first-step amplitude. The direction of the intrasaccadic step was either NW (3a) or SE (3b). The postsaccadic target remained visible at this position for 500 ms.

Two different cues were used in each experiment (e.g. a red triangle or a green square displayed at the beginning of each trial, during the fixation period, in the Color and Shape experiment), and were systematically paired with the ISS direction in the learning trials (e.g. the red triangle preceding a NW directed ISS and the green square a SE directed ISS). This pairing was counterbalanced across participants. Cues and ISSs were unpaired in the baseline and recovery trials (e.g. either the red square or green triangle could randomly precede each ISS directions). Therefore, in all experiments the only difference between the learning trials and the baseline and recovery trials was the systematic cue-ISS pairing. In two additional experiments we asked participants to report which cue has been present after completion of the saccade.

All trials were identical across all experiments (Fig. 13). The fixation target, a grey disk (0,4° diameter / Luminance 12,1 cd/m2) was displayed for a random duration ranging from 700 to 1000ms (drawn from a uniform distribution) against a gray background (luminance 1.7 cd/m2). During the fixation period the target was always displayed at the same location (P0, [-8,3 dva; -4.9 dva] (dva: degree of visual angle) downward and leftward with respect to the center of the screen). The target was then displaced at P1 following a 45° vector upward and rightward with four possible step amplitudes (5.5 dva; 7 dva; 8.5 dva and 10.1 dva, pseudo-randomly).

If a change in eye position was detected within an 80ms-350ms temporal window following the first step, the ISS was triggered and the target stepped at P2 during the saccade. The online saccade detection corresponded to the eye position crossing an invisible boundary 3 dva away from fixation location. The ISS direction was perpendicular (90°) to the first step of the target and its amplitude was set to 20% of the first step. Importantly, the target experienced an ISS in every trial in which a saccade was detected, including the baseline and recovery trials. Following the ISS, the target remained visible at P2 for 500ms. A unique pseudo random trial-list of ISS directions and first steps was used in all experiments such that every participant experienced the exact same series of trial characteristics. If a saccade was detected either before 80ms (anticipation) or after 350ms with respect to the first target-step onset the trial was terminated before the ISS occurred, the target was extinguished and a sound (100ms at 500 HZ) was played to signal the end of the trial.

Training

Before any experiments, participants experienced a training session. Instructions were displayed on the screen, explaining how to position themselves in the eye-tracking setup and providing a brief overview of the task. Participants were instructed to keep their eyes on the target and to shift their gaze only after the target moved. They were also informed that looking away from the target or anticipating its movement would trigger a “beep”, indicating an error. Then, following a 13-points calibration, a 50-trials training session began to familiarize the participants with the temporal sequence of a trial. These sessions were repeated until a minimum of 75% of correct saccade were recorded. During these training sessions participants experienced regular trials in which the ISS direction was randomized, with no contextual cue.

Task

Once the training criterion was reached, instructions about the task were provided again as a reminder. In the experiments involving physical stimuli (Experiments 2-7), participants were additionally informed that such stimuli would be presented (see details below). Then the experimental session started and the 13-points calibration and validation were performed again. All experimental sessions consisted in a total of 850 double step trials with 200 baseline trials, 500 learning trials and 150 recovery trials. For each experiment two possible contextual cues were used (see cue details below). Cues and ISSs were systematically present during the whole experiment but the cue-ISS pairing differed across the trial types. In the learning trials, a specific ISS direction was systematically paired with one of the cues, e.g., the ISS would always be NW for one cue and SE for the other. In the baseline and recovery trials there was no systematic cue-ISS pairing and instead, for a given cue, the target had 50% chances to have a NW-directed or a SE-directed ISS. Thus, the only difference between the learning phase and the other two phases was the systematic pairing of contextual cues with the ISS directions in the learning trials. Across the session, participants experienced short breaks every 50 trials. Rest intervals have been reported to facilitate contextual adaptation (16). Following these breaks the calibration accuracy was estimated and the experimenter conducted a 13-points calibration if necessary.

Experiments

Experiment 1: First-step amplitude (FSA) (n = 10). In this experiment the amplitude of the first target step served as a contextual cue. Contrary to all other experiments only two distinct first step amplitudes were used, either small (5.5 dva) or large (10.1 dva) ones. During the 500 learning trials, the first target step amplitude was paired with the ISS directions. For instance, the small first step was systematically paired with a NW-directed ISS while the large first step was paired with a SE-directed ISS. This pairing was counterbalanced across participants. There was no systematic pairing between the first step amplitude and the ISS direction in the baseline and recovery trials.

Experiment 2: Color and Shape. (n = 10, participants with colorblindness were not included in this experiment). For each trial, the fixation target was initially either a green square or a red triangle to serve as a contextual cue. The colored cue was displayed for 400ms at the onset of the fixation period, and was then replaced with the usual grey fixation target for the remaining fixation period. In the 500 learning trials, the color and shape contexts were each systematically paired with one direction of the ISS (counterbalanced across participants). There was no systematic pairing between the cue color and shape and the ISS direction in the baseline and recovery trials. As this experiment involved a physical contextual cue – i.e. the presentation of green square or a red triangle – participants were informed: “A colored target will be displayed at the beginning of each trial”.

Experiment 3: Color and Shape with the addition of a perceptual report. (n = 8, participants with colorblindness were not included in this experiment). This experiment was identical to experiment 2 except that prior to the beginning of the experimental session participants were verbally instructed to attend to the color and shape of the cue. In 20% of all trials the two possible cues (green square and red triangle) were displayed side by side at the center of the screen at the end of the trial. Participants were instructed to manually report which stimulus was present at the beginning of the trial using a button press on a game controller. The leftward button was always paired with the green square and the rightward button was always paired with the red triangle. A correct response was signaled by displaying “+ 10 points” in the middle of the screen. The total score was displayed every 50 trials during the breaks and again at the end of the experimental session. Participants were informed that no monetary gain was associated with the points. These perceptual reports occurred every 5 trials on average in a random fashion.

Experiment 4: Symbolic Cue (n = 10). On each trial, a grey arrow (0.5 dva length; luminance 12,1 cd/m2) pointing either toward the north west or south east direction was displayed at the fixation location (P0) to serve as a contextual cue. After 400ms following the onset of the fixation period it was then replaced with the grey fixation target for the remaining fixation period and trials resumed as previously described. In the 500 learning trials the orientation of the arrow was systematically paired with the direction of the ISS. The arrow orientation and the ISS were always consistent (i.e. the NW arrow was paired with the NW-directed ISS and the SE arrow with the SE-directed ISS). This pairing was not counterbalanced across participants. There was no systematic pairing between the arrow orientation and the ISS direction in the baseline and recovery trials. As this experiment involved a physical stimulus – i.e. the presentation of an arrow– participants were informed: “An arrow will be displayed at the beginning of each trial”.

Experiment 5: Symbolic Cue with the addition of a perceptual report (n = 8). This experiment was identical to experiment 4 except that prior to the beginning of the experimental session participants were verbally instructed to attend to the arrow direction. In 20% of all trials, the two possible arrows were displayed side by side at the end of the trial at the center of the screen. Participants were instructed to manually report which arrow was present at the beginning of the trial using a button press on a game controller. The leftward button was always paired with the North-West arrow and the rightward button was always paired with the South-East arrow. A correct response was signaled by displaying “+ 10 points” in the middle of the screen. The total score was displayed every 50 trials during the breaks and again at the end of the experimental session. Participants were informed that no monetary gain was associated with the points. These perceptual reports occurred every 5 trials on average in a random fashion.

Experiment 6: Visual Stimulus Duration. (n = 10). On each trial, a grey ring (0,8 dva diameter / Luminance 12,1 cd/m2) was displayed surrounding the fixation target for either 100ms or 400ms at the onset of the fixation period. The ring then disappeared, and the grey fixation target remained visible for the remaining of the fixation period. In the 500 learning trials each possible cue duration was systematically paired with one direction of the ISS (counterbalanced across participants). There was no systematic pairing between the ring duration and the ISS direction in the baseline and recovery trials. As this experiment involved a physical stimulus – i.e. the presentation of a ring– participants were informed: “A ring will surround the target at the beginning of each trial”.

Experiment 7: Sound Lateralization. (n = 10) During this experiment participants were instructed to wear a headset (SONY MDR-ZX110). On each trial, a sound (1000HZ) was played through the headset either in the right or in the left participant’s ear for 100ms at the onset of the fixation period. To avoid discomfort, the volume of the sound was individually adjusted prior to the beginning of the experimental session. In the 500 learning trials, each location was systematically paired with one direction of the ISS (counterbalanced across participants). There was no systematic pairing between the sound position and the ISS direction in the baseline and recovery trials. As this experiment involved a physical stimulus – i.e., the presentation of a sound– participants were informed: “A sound will be played at the beginning of each trial”.

Experiment 8: Statistical Regularity 1. (n = 10). In this experiment, no physical contextual cue was displayed, only the target (Fig. 13). During the 500 learning trials the ISS directions systematically alternated between NW and SE from one trial to the next, such that if odd trials had a NW ISS, even trials had a SE ISS (counterbalanced across participants). In the baseline and recovery trials the ISS direction was not following any specific statistical regularity.

Experiment 9: Statistical Regularity 4. (n = 10). In this experiment, no physical contextual cue was displayed, only the target (Fig. 13). In the 500 learning trials the ISS directions were alternating between NW and SE by blocks of 4 consecutive trials (the ISS direction in the first block was counterbalanced across participants). In the baseline and recovery trials the ISS direction was not following any specific statistical regularity.

Experiment 10: Statistical Regularity 10. (n = 10). In this experiment, no physical contextual cue was displayed, only the target (Fig. 13). In the 500 learning trials the ISS directions were alternating between NW and SE by blocks of 10 consecutive trials (the ISS direction in the first block was counterbalanced across participants). In the baseline and recovery trials the ISS direction was not following any specific statistical regularity.

Experiment 11: Starting Location. (n = 10). In this experiment, two different starting locations of the target served as the contextual cue: Our regular starting location (i.e. the fixation location used in all the other experiments): P0a [-8,3 dva; -4.9 dva], and a rightward-shifted location: P0b [-5 dva; -4.9 dva]). Only the horizontal position was altered, with this shift applying uniformly across all target positions, preserving the target's movement but displaced along the horizontal axis. All the other parameters have been kept unchanged except that the experiment stopped at trial 700 (no recovery trials were recorded). During the 500 learning trials, P0a was paired with one ISS direction and P0b was paired to the opposite ISS (counterbalanced across participants). There was no systematic pairing between the starting location and the ISS direction in the baseline trials.

Processing of saccades

We used the Eyelink online saccade detector to identify saccades onset and offset, using 30dva/s velocity and 8000dva/s^2 acceleration thresholds. In all trials we only considered the first recorded saccade following the first target-step. Prior to statistical analysis a human observer validated each saccade manually. Then incorrect saccades, saccades with a gain lower than 0.5 or higher than 1.5, saccades with latency shorter than 80ms or longer than 350ms and saccades that were not directed toward the target at P1 (deviating more than 45° away from the target vector angle) were excluded from further analyses. A criterion of 75% correct saccades during the baseline and learning phases (first 700 trials) was used to include participants for further statistical analysis (Min: 525, Max: 683, Average: 594).

Saccade angles were computed by drawing a line between the saccade starting point and the saccade endpoint, and measuring its angle relative to the horizontal axis. For each participant and each contextual cue, we calculated the median saccade angle during baseline trials. We then subtracted this median value from each corresponding saccade angle, ensuring that the values were distributed around 0°. In this normalized space, complete adaptation would correspond to a change of +11.3° for North-East ISS and -11.3° for South-West ISS.

Statistical Analysis

We used bootstrapping methods (resampling with replacement 100,000 times) to estimate the 97.5% confidence intervals of the medians (CIs ;(Efron, 1992)). For each participant, significant differences between the two contexts in the median saccade angle changes with respect to the baseline medians were estimated by nonparametric permutation test on the difference in medians with 100,000 permutations. Permutation-based tests were implemented using custom routines in MATLAB. This test was performed on the last 200 learning trials (late-learning trials).

To quantify the normalized amount of difference between the angle of saccades performed in each context we computed the Kolmogorov-Smirnov (KS) distance. The KS distance computes the normalized amount of overlap between the two distributions of late-learning saccade angle differences with respect to baseline for each participant. A distance of 0 implies that the two distributions perfectly overlap while a distance of one implies that there is no overlap between the two distributions.

5.1.5. RESULTS

Figures 14.A and 14.B illustrate the two patterns of results we typically observed across participants in all our experiments. The trials are sorted by the two possible contextual cues. The difference in saccade angle normalized to the baseline medians is plotted as a function of the trial number. A Lowess smoothing (with a 100-trial window) is used to illustrate the general trends across the three experimental phases for each contextual cue. Fig. 14.A plots the data for a participant from experiment FSA (participant 34). Following the baseline trials (first 200 trials) in which no significant difference was observed in saccade angle between the small and large first step amplitudes (respectively 43.47 ° for the 5.5 dva trials and 41.51 ° for the 10.1 dva trials), the difference in saccade angle changes progressively increased during the learning trials (from 201 to 700), i.e. trials in which the small first step amplitude trials had a North-West ISS and the large first step amplitude trials had a South-East ISS. The difference between the two median saccade angles in the last 200 learning trials (late-learning trials, from trial 501 to 700) was statistically significant (respectively -3.16° with respect to the baseline median in the 5.5 dva trials and 3.16° in the 10.1 dva trials, difference greater than the null hypothesis 97.5% CI). These differences then decreased during the 150 recovery trials in which the first step amplitudes and the ISS angles were uncorrelated.

To summarize these results, we plotted the two median differences observed in the late learning trials against one another (Fig. 15, pink disks) for all participants in Experiment 1. In this particular experiment, the points systematically fall below the equality line as trials with a SE ISS (negative angle) are plotted with respect to the trials with a NW ISS (positive angle). We additionally plotted the average percentage of saccadic adaptation to the ISS as a function of the trial at the group level (Fig. 14.C). The differences in saccade angle changes between the two contextual cues were systematically significant (all values greater than the null hypothesis 97.5% CIs). The group median difference in saccade angle change in the late learning trials was 6.42°, ranging from 2.71 to 14.34 across participants. The only other group showing similar pattern of results to the FSA experiment is the Starting Location experiment: eight out of the ten participants demonstrated significative contextual learning (Fig. 15, dark grey disks and Fig. S9). The group median difference in saccade angle change in the late learning trials was 2.47°, ranging from 0.18° to 4.37° across participants.

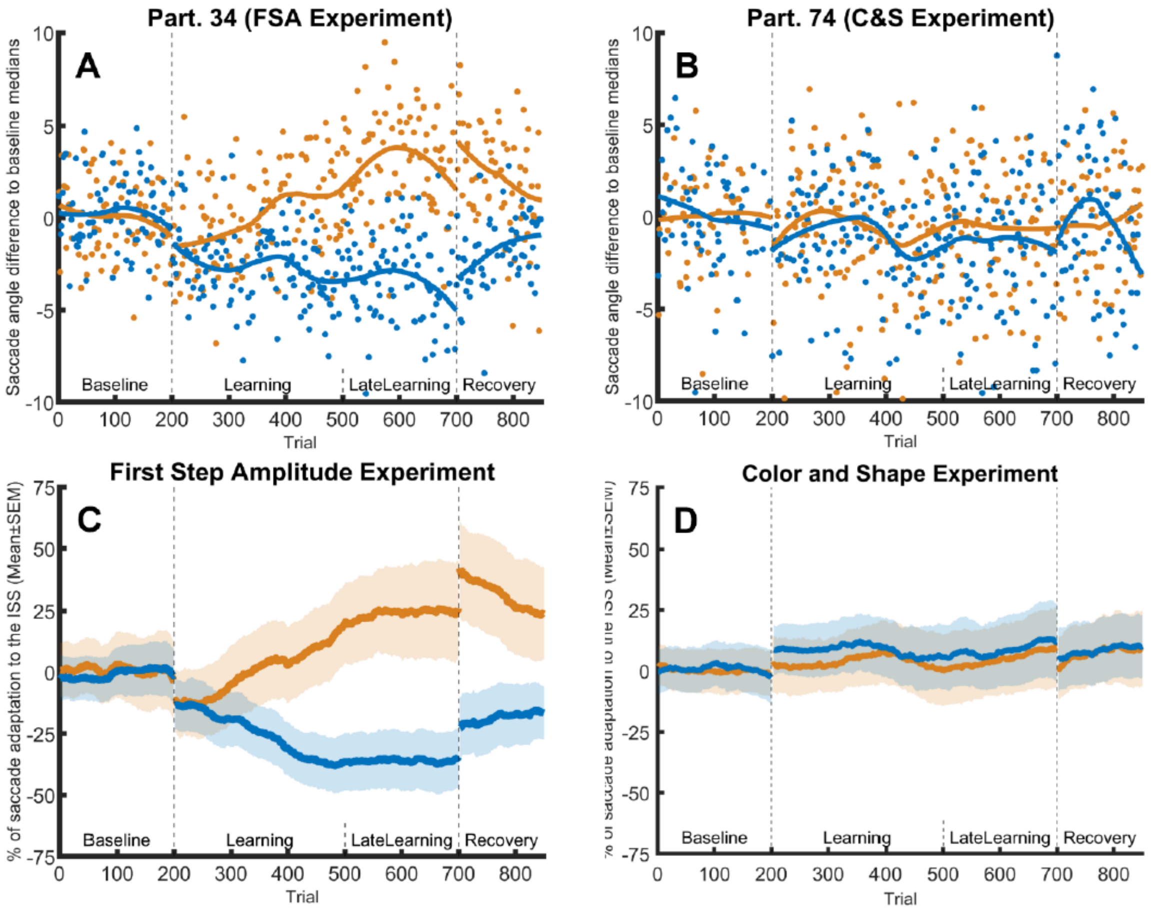

Figure 14. Effect of contextual cues on saccade adaptation in First-Step Amplitude (FSA) and Color and Shape experiments. A: representative subject (participant 34) from the First-Step Amplitude contextual cues experiment (experiment 1). Each point plots the saccade angle difference to the baseline in a trial expressed in degrees, which is the saccade angle of the trial subtracted from the median saccade angle for that context in the baseline trials. Solid lines are the Lowess smoothing of saccade angles differences to baseline with a 100-trial moving window. Orange represents the large first-step amplitude context [10.1 degrees of visual angle (dva), which was paired with the North-West intrasaccadic step (ISS) in the learning trials], blue represents the small first-step amplitude context (5.5 dva, which was paired with the South-East ISS in the learning trials). Bottom labels indicate the baseline (1200), learning (201–500), late learning (501–700), and recovery (701–850) trials. B: representative subject (participant 74) from the Color and Shape contextual cues experiment (experiment 2). Conventions are as in A. Orange represents the green square context (which was paired with the North-West ISS in the learning trials), blue represents the red triangle context (which was paired with the South-East ISS in the learning trials). C: First-Step Amplitude contextual cues experiment. Each solid line represents the moving average percentage of saccade adaptaton to the ISS. Shading represents the means ± SE. Mean and SEM are calculated independently for each of the three phase (Baseline, Learning, LateLearning, and Recovery). Bottom labels indicate the baseline (1–200), learning (201–500), late learning (501–700), and recovery (701–850) trials. A score of 0% means that participants produced saccades with no difference from the baseline, a score of 100% means that they produced a saccade with an angle change of 100% of the N-W ISS (11.3°) and a score of 100% means that they produced a saccade with an angle change of 100% of the S-E ISS (11.3°). The orange color represents the trials in which a North-West cue (i.e. the cue paired with the NW ISS during the learning trials) was presented; blue color represents the trials in which a South-East cue was presented. D: Color and Shape contextual cues experiment. All conventions are similar as for C.

The second pattern of results is well exemplified when considering the results for a participant from the Color and Shape experiment (Fig. 14.B, participant 74). Much like participant 34, there was no difference between the saccade angle changes depending on the two contextual cues (either a green square or a red triangle displayed during the initial fixation period) for the baseline trials (median saccade angle 41.27° and 41.11 °, respectively). This lack of difference persisted throughout the learning trials as well, indicating that there was no specific adaptation (difference in median angle changes 0.60, within the null hypothesis 97.5% CIs). When plotting the median change in saccade angle observed for each contextual cues in the late learning trials against one another (Fig. 14.E, blue disks and triangles) all points fall close to the equality line and no significant differences were observed for any participant in this experiment. The group median difference in saccade angle change in the late learning trials was 0.04°, ranging from -1.15 to 0.94 across participants. We additionally plotted the average percentage of saccadic adaptation to the ISS as a function of the trial for the group (Fig. 14.D). This pattern of results was replicated in Experiment 3 - Color and Shape with the addition of a perceptual report (Fig. S1). No participant showed a significant context effect (Fig. 16, yellow disks). The group median difference in saccade angle in the late learning trials was 0.13°, ranging from -3.48 to 2.40 across participants. In this experiment, participants had to report the color and shape shown during fixation after saccade completion. On average, perceptual reports were correct 87 % of the time

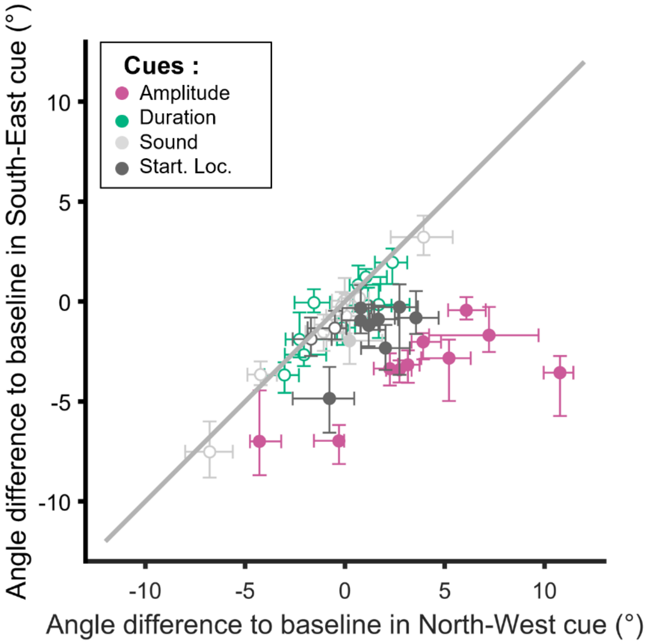

Figure 15. Median, and 95% confidence intervals (CIs), saccade angle difference to median baseline across contexts for each participant in the First-Step Amplitude (experiment 1, n=10), Visual Stimulus Duration (experiment 6, n=10), Sound Lateralization (experiment 7, n=10), and Starting Location (experiment 11, n=10) experiments. Filled symbols indicate a difference greater than the null hypothesis 97.5% CIs. The oblique gray line marks equal values.

(Min: 69%; Max: 99%), demonstrating the ability to discriminate and report the contextual cues at the end of the trial. No significant difference in saccade latencies was found between Experiment 2 (Color and Shape) and Experiment 3 (Color and Shape with Perceptual Report) (mean difference = 2.29 ms; t-test, NS).

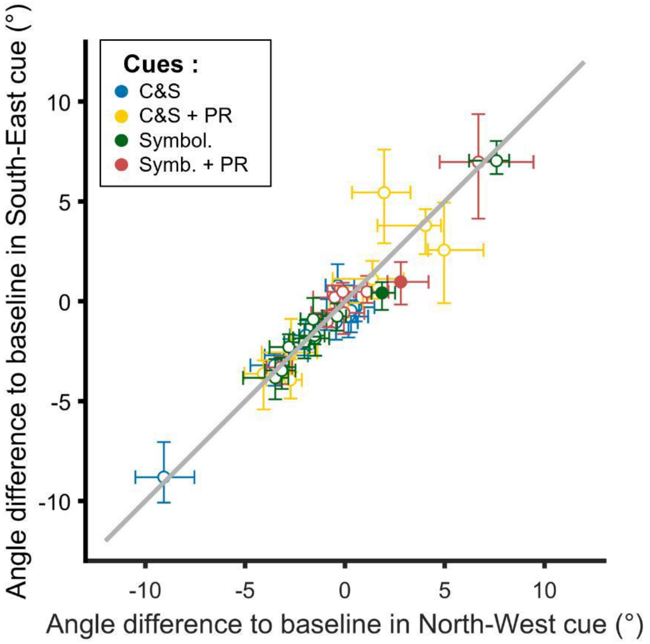

Figure 16.Conventions are the same as for Fig. 15. Here, a represented Color and Shape (experiment 2, n=10), Color and Shape with perceptual report (experiment 3, n= 8), Symbolic Cue (experiment 4, n= 10), and Symbolic Cue with perceptual report (experiment 5, n= 8) experiments.

Overall, we observed that our contextual cues did not induce specific saccade adaptation in any non-motor cue experiment, apart for some minor differences. In the Symbolic Cue experiment (Fig. 16 green disks and Fig. S3) one participant (P. 32) exhibited a significant difference in saccade angle (1.44°, greater than the null hypothesis 97.5% CIs) the group median difference in saccade angle in the late learning trials was 0.32° (Min -0.69; Max 1.44). Similar values were found in the Symbolic Cue with the addition of a perceptual report experiment with a 0.10° group median difference (ranging from Min -0.70 to Max 1.82). One participant (P. 12) exhibited a significant difference in saccade angle (1.82°, greater than the null hypothesis 97.5% CIs). On average participants perceptual report of the symbol direction were correct 91 % of the time (Min: 85% ; Max: 97%). No significant difference in saccade latencies was found between Experiment 4 (Symbolic Cue) and Experiment 5 (Symbolic Cue with Perceptual Report) (mean difference = 2.67 ms; t-test, NS). In the Visual Stimulus Duration experiment (Fig. 15, green symbols and Fig. S2) we found a 0.52°median difference (ranging from -1.49 to 1.85).

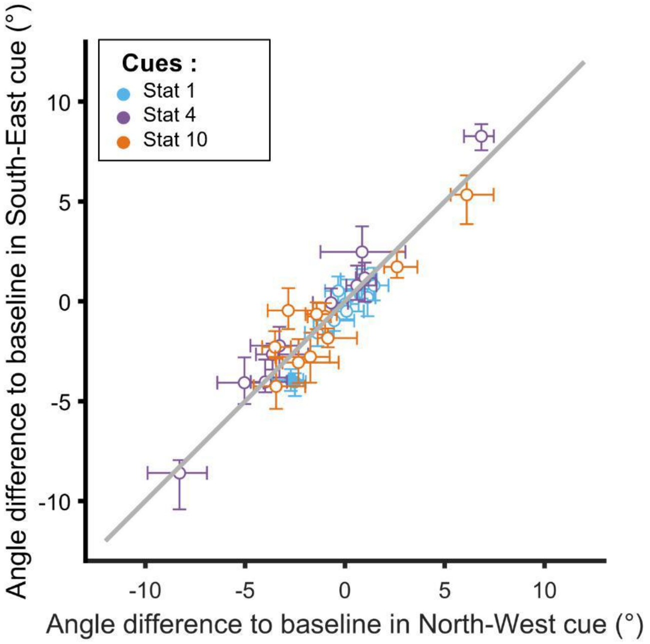

Figure 17. Conventions are the same as for Fig. 15. Here are represented Statistical Regularity 1 (n= 10), Statistical Regularity 4 (n= 10), and Statistical Regularity 10 (n= 10) experiments.

In the Sound Lateralization experiment (Fig. 15, light grey symbols and Fig. S5) the largest difference was 2.19° (greater than the null hypothesis 97.5% CIs) but all other participants did not exhibit specific adaptation with a group median difference of 0.56° (Min 0.06; Max 2.19). Manipulating the statistical regularity across trials did not induce systematic contextual effects: except for two participants in the Statistical Regularity 1 experiment (Fig. 17, light blue symbols and Fig. S6) with a difference reaching 1.22° (P. 31) and 1.53° (P. 33) (greater than the null hypothesis 97.5% CIs), all other participants did not exhibit specific adaptation with a group median difference of 0.50° (Min -0.85; Max 1.53). We found similar results in the Statistical Regularity 4 experiment (Fig. 17, purple symbols and Fig. S7) with a group median difference of 0.79° (Min -1.61; Max 0.31) and in the Statistical Regularity 10 experiment (Fig. 17, orange symbols and Fig. S8) with a group median difference of 0.75° (Min -2.38; Max 1.04). It is noteworthy that in the five participants from experiments other than the FSA experiment exhibiting a significant difference in saccade angle in the late learning trials, the observed differences were all systematically lower than the smallest difference observed in the first-step amplitude experiment (i.e. 2.71°).

Our consistent design allowed us to compare the efficacy of contextual cues across eleven experiments. We used the Kolmogorov-Smirnov distance (Berger & Zhou, 2014) to quantify the individual differences in saccade angle changes distributions for each contextual cue in the late learning trials. The greater the KS distance, the larger the difference between the two distributions. The group medians are plotted Figure 18. The median KS distance for the First-step amplitude experiment (0.73) is higher than the one for the Color and Shape experiment (0.13). For the Starting Location experiment, the median KS distance was intermediate (0.35). For all the non-motor cue experiments the median KS distances are closer to the Color and Shape results, with the largest distance observed in the Statistical Regularity 10 experiment (0.17).

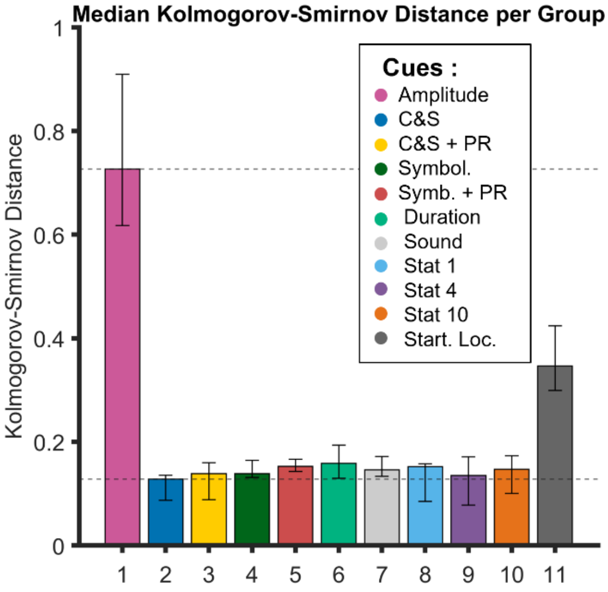

Figure 18. Median and inter-quartile range of the Kolmogorov–Smirnov distance for all experiments. The bottom dotted line marks the median KS distance for the Color and Shape experiment, the top dotted line marks the median KS distance for the First-Step Amplitude experiment.

When considering the participants who exhibited significant differences in saccade angles (filled symbols, Fig.15, Fig.16 and Fig.17) their KS distances range from 0.21 to 0.29 in experiments 2-

10 while in the FSA Experiment the smallest KS distance is 0.34 and the largest is 0.86, and in the Starting Location experiment the smallest KS distance is 0.19 and the largest is 0.48.

5.1.6. DISCUSSION

In the present study we used a conventional double-step adaptation paradigm in which a specific contextual cue was associated with each of the two intra-saccadic steps with different directions. This allowed us to quantify the contextual effects of nine different types of contexts based on their ability to elicit distinct saccadic adaptions. Learning was examined by evaluating the changes in saccade angle with respect to the baseline trials, where the intra-saccadic steps were not correlated with the contextual cues. We found large differences in the efficacy of the contexts we tested: the amplitude of the first step (Experiment 1) and the starting location (Experiment 11) elicited strong contextual saccadic adaptations (systematic for the FSA experiment and in eight out of ten participants in the Starting Location experiment) while all the other contextual cues we tested (Experiments 2-10) had little or no effect. These differences in contextual cues efficacy are well summarized when comparing the KS distances across experiments (Fig. 18): Every participant from the FSA experiment had a KS distance larger than any participants in the non-motor cue experiments, as well as six out of ten participants form the Starting Location experiment, revealing much larger contextual effects of the motor cues compared to the non-motor cues on saccade adaptation.

To our best knowledge, ours are the first results explicitly demonstrating that, in a conventional double step paradigm, pairing the first-step amplitude with the ISS direction induces strong context specific saccade adaptation. Indeed, in the learning trials, saccade angles adapted gradually to separate the saccade angles for the alternative contextual cues when the ISS was signaled by either a small (5.5 dva) or a large (10.1 dva) first target-step amplitude. This was true both at the individual level (Fig.14.A and Fig.15) and at the group level (Fig.14.C and Fig.18). It is however well established that adaptation is specific to the target vector. Adaptation fully transfers to movements with different initial eye positions but similar amplitudes and angles while the transfer decreases as the vector difference with the adapted saccade increases. Measuring adaptation fields (Frens & Van Opstal, 1995; Pélisson et al., 2010) may therefore be regarded as a quantification of contextual effects of amplitude or angle on saccade adaptation (See (Azadi & Harwood, 2014) for a similar argument). It is worth highlighting that the range of first-step amplitudes manipulated here is smaller than what is typically examined in gain field studies, and our results may therefore not be directly predictable from previous findings. Moreover, specificity of saccadic adaptation has been previously demonstrated manipulating the target distance in depth (Chaturvedi & Van Gisbergen, 1997). Overall, our results are consistent with the broader evidence that saccadic adaptation is context-dependent, with saccade direction and first-step amplitude acting as contextual cues.

It is noteworthy that a few features distinguish our experiments from previous contextual adaptation experiments. First, we chose to induce changes in saccade angle rather than saccade amplitude. In most previous saccade adaptation studies, an increase or a decrease in saccade amplitude is observed by manipulating the intra-saccadic step in the axis of the first step (on-axis paradigm) either in the backward or in the forward direction (e.g. (Noto et al., 1999; Scudder et al., 1998; Straube et al., 1997). Forward adaptation is often regarded as more difficult to achieve compared to backward adaptation as evidenced by a longer time course and a more modest amplitude change (Ethier et al., 2008a; Panouillères et al., 2009; Rahmouni & Madelain, 2019; Straube & Deubel, 1995). An adaptation-step perpendicular to the initial direction of the target (cross-axis paradigm) has also been successfully used to induce saccade adaptation (Chen-Harris et al., 2008; Deubel, 1987; Ethier et al., 2008a). Using a cross-axis paradigm in contextual saccadic adaptation should have the advantage of inducing both adaptive states with comparable efficiency. This was indeed the case in our results, and it should be noted that, although the overall contextual adaptation pattern appears similar to what has been previously reported (e.g. (Azadi & Harwood, 2014) with motion direction contexts, their figures 14.B and 15.A) we observed two simultaneous changes in saccade angle (our Fig. 14.A, Fig. 15) rather than a backward adaptation for one context associated with an absence of forward adaptation in the alternative context (their Figures 3B and 7B). Another particularity of our paradigm settings is the implementation of the ISS throughout the entire experimental sessions. Conventionally, the ISS is introduced during the learning trials. Here we rather chose to present the ISS in every trial. Critically, we manipulated its statistical relationship with the contextual cues: unpaired (50% chance for either ISS to follow each cue) in baseline and recovery trials, and paired (100% chance for a specific ISS to be preceded by a specific cue) during the learning trials. This modification allowed us to minimize the changes during a session, as nothing changes from the participant point of view except the statistical relations between the cues and ISSs.

One of the features of our results is the dramatic difference between the systematic contextual adaptation observed in the FSA and in the Starting Location experiments and the failure of all other contextual cues. Importantly, using a consistent double step paradigm across all experiments allows one to rule out a number of possible reasons for the impotence of the contextual cues used in experiments 2-10. First, all events following the fixation period were identical in every experiment, with the exception that we only used two possible first step amplitude in the FSA experiment and four in Experiments 2-11, but the range were identical in all experiments (from 5.5 deg to 10.1 deg). Moreover, the ISS directions and relative amplitudes were identical across all experiments. This was also true for the post-saccadic target duration and the other target characteristics. Second, the overall session structure and trials order were identical in Experiments 1-7 and 11. In Experiments 8-10 we manipulated the trial orders in the learning trials (from trial 201 to trial 700) to induce some specific statistical regularities (ISS directions either alternated across trials or alternated in blocks of four or ten trials).

It follows that only two candidate hypotheses might account for the differences across experiments. The first one is the specific timing of the context pairing with the ISS. In the FSA and the Starting Location experiments, the contextual cue (either small or large first target step) was present at the time of saccade but this was not the case for the other experiments. Indeed, when an actual stimulus was used for context (such as a green square versus a red triangle displayed for 400ms –

Experiments 2 and 3, an arrow pointing NW versus SE displayed for 400ms – Experiments 4 and 5, a grey ring displayed for 100ms versus 400ms – Experiment 6, or a 100ms tone delivered in the left versus right ear – Experiment 7), we presented the stimulus at the onset of the fixation period, that is 700ms to 1000ms before the target stepped, but it was absent for the remainder of the trial. One might therefore regard the lack of contextual adaptation as an effect of the absence of specific cue at the time of saccade or as resulting from the longer temporal interval between the cue offset and the ISS. However, previous studies reported failure of target color and shape as contextual cues for saccade adaptation even when the contextual cues were present throughout the trials ((Azadi & Harwood, 2014; Bahcall & Kowler, 2000; Cecala et al., 2015; Deubel, 1995). Moreover, participants correctly reported which stimulus was present at fixation at the end of the trial 89% of the time on average (Experiments 3 and 5, including a perceptual report) revealing some memory of the actual stimulus at the time of saccades and at the onset of the ISS. It is therefore unlikely that the timing of the cue presentation was solely responsible for the lack of adaption in Experiments 2-7. In the three remaining experiments, in which the order of ISS direction across trials was manipulated, there was no specific stimulus paired with each ISS direction. However, one could argue that these contextual cues were present throughout the whole learning phase as the directions of every ISS was predictable based on the trial patterns we implemented. Overall, the striking scarcity of contextual learning is therefore unlikely to be due to the temporality of events.

The second hypothesis relies on the nature of the actual contextual cues that differed across experiments. One could argue that the nature of the cues is not the critical factor here, as five participants out of the eighty-six outside the Experiment FSA and Starting Location exhibited contextual learning (one participant each from Experiments 4, 5 and 7 and two from Experiment 8). Nevertheless, the KS distances are systematically much lower compared to those observed in the FSA experiment. Additionally, our statistical hypotheses are directional, with the sign of the saccade angle differences expected to correspond to the actual directional differences in the ISS; however, when considering two-tailed differences, significant effects emerge in five other participants, one participant each from Experiments 2, 3, 6, 9, and 10, potentially reflecting idiosyncratic sensitivities to the ISSs rather than genuine contextual adaptation. Moreover, the magnitude of these observed differences is comparable with the differences observed in the five participants exhibiting some specific adaption in Experiments 2-10. In our study, when non-motor cues are manipulated, the occasional small differences observed in our results are unlikely to reflect meaningful contextual learning, as they are neither systematic nor consistent and remain quite limited. We will now discuss specifically the different types of contextual cues that we investigated and the conclusion we can draw from them.

Non-motor stimulus features are perceived but inefficient for contextual adaptation

Previous studies have investigated visual cues (target color and shape), demonstrating their inefficiency for contextual saccade adaptation (Bahcall & Kowler, 2000; Cecala et al., 2015; Deubel, 1995). We first replicated these results in the Color and Shape experiment. In a separate experiment we used symbolic cues (i.e. an oriented arrow pointing in the direction of the ISS) to probe whether an explicit information about the ISS could lead to contextual adaptation. However, the observed results show similar lack of contextual learning when using these visual cues. This raises the question: are the participant seeing the contextual cue? To address this, we replicated the two visual cue experiments with and additional perceptual report task. Every five trials on average, participants were prompted to report at the end of the trial which of the two cues (i.e. red square vs green triangle or North-West arrow vs South East arrow) was present during fixation. Their percentage of correct report in both experiments were respectively 87% on average for Experiment 3 and 91% in average for Experiment 5. Moreover, the amount of saccadic adaptation was similar compared to their single task versions. Our task was designed such that participants had to keep memory of the contextual cue throughout the trial, as the cues were presented only during the fixation period and the report occurred at the end of the trial. One could have expected that explicitly instructing participants to attend to the cue to perform the perceptual report would improve the efficiency of the contextual cues but this was not the case. This demonstrates a clear dissociation between explicit perception and motor adaptation, as participants performed two tasks involving the same cue successfully completing the perceptual task, while motor learning did not occur.

Temporal and auditory cues

To test the ability to use cues beyond purely visual features to predict the ISS direction we conducted two additional experiments manipulating either the duration of a visual stimulus during the fixation period or the lateralization of a sound. In the Visual Stimulus Duration experiment a circle surrounding the fixation point was presented for either 100 ms or 400 ms, referred to as short and long durations, respectively. The two durations were selected to ensure a marked and easily distinguishable difference. This experiment mirrored the design of the visual cue experiments, except that duration, rather than visual features, was manipulated. Because it has been established that the saccadic system can use temporal regularities in the environment to control eye movements triggering ((Hoppe & Rothkopf, 2016; Vullings & Madelain, 2018) one could expect that the stimulus durations would constitute an efficient context to predict the ISS direction. However, none of the participants in this experiment showed contextual saccade adaptation. In addition to being directed toward a visual cue, saccades can also be directed toward a localized sound. Indeed, one of the sensory maps in the superior colliculus responds to sound localization, mirroring the motor map controlling saccade endpoints (King, 2004) and auditory saccades have been shown to be accurate ((Frens & Van Opstal, 1995; Yao & Peck, 1997; Zambarbieri, 2002). We therefore designed the Sound Lateralization experiment, using rightward or leftward sounds as contextual cues. With our stimulus configuration, the auditory stimulus did not provide spatially relevant information for guiding saccades and the sound lateralization should therefore be regarded as a non-motor stimulus feature. Only one participant showed limited contextual learning, demonstrating that sound lateralization is also inefficient for contextual learning. For both stimulus features, the absence of spatially relevant information for saccades likely limited their role in predicting ISS directions and maintaining two distinct adaptive states.

Statistical regularities within trial sequences as contexts

We conducted three distinct experiments to determine whether the statistical regularity of intra-saccadic steps could facilitate contextual learning. Sequences of ISS directions occurred in blocks of either 1, 4, or 10 trials. It could be hypothesized that a sequence with a regularity of 1, where ISS directions alternate trial by trial, would be the easiest for participants to learn. Alternatively, longer sequences may be necessary for the system to identify the contextual structure: detecting changes in ISS direction and transitioning between adaptive states might be easier if the ISS direction remained consistent for several trials. Under this assumption, sequences of 10 consecutive trials should have produced the most robust effect, as they represent the longest and most stable configuration. However, none of the tested configurations succeeded in demonstrating contextual learning.

It remains unknown whether the lack of motor learning is specific to the trial sequence or whether saccades were also unaffected by the immediately preceding ISS. To address this, we performed supplementary analyses on the Statistical Regularity 10 experiment to investigate the possibility of a local learning effect (see supplementary material). We calculated the difference between the first five and last five trials within each 10-trial block and compared the median differences between late-learning trials and baseline trials. This analysis revealed a difference in the expected angle direction for all participants, with statistical significance observed in 3 out of 10 participants (Mann-Whitney, $p < 0.05$) indicating an accumulation of adaptation within the 10-trial blocks. These findings make the lack of contextual learning even more striking. Adaptation appears to rely exclusively on local error signals, with no influence from the contextual cue—i.e., the current trial sequence. Interestingly, this suggests that participants engaged with the appropriate behavior multiple times, switching effectively between sequences. However, despite the perfect correlation between the sequence and the ISS direction on the one hand and the emergence of the appropriate behavior within the trial blocks on the other hand, participants failed to exhibit any evidence of contextual learning.

The absence of learning in our Statistical Regularity experiments is striking, especially given that statistical learning has been demonstrated in various paradigms. These studies show that sequences of events, even far more complex than ours, can be successfully learned. For example, Nissen and Bullemer (Nissen & Bullemer, 1987) demonstrated clear sensitivity to statistical regularities across trials, as evidenced by shorter manual reaction times. However, researchers (Oostwoud Wijdenes et al., 2016) found that double-step sequences failed to elicit implicit motor learning in a pointing task. While some participants showed evidence of sequence learning, this occurred only when they explicitly noticed the sequence. These findings suggest that contextual adaptation may require explicit awareness of the sequence. In double-step paradigms, however, participants are often unable to explicitly perceive the ISS itself, making it impossible for them to explicitly identify any ISS sequence.

Selectivity for motor-relevant cues in contextual adaptation

As we discussed, our FSA and Starting Location experiments are the only ones leading to efficient contextual learning. The most obvious difference between those experiments and our nine others is that the contextual cues induce a modification in the saccadic movement while all the other contexts we used do not. One should point out that the observed contextual adaptation is stronger in the FSA experiment compared to the Starting Location experiment, revealing that all motor cues are not equally efficient. This difference might be attributed to the discriminability of the contextual cues we chose or to a more fundamental property of the saccadic system. However, these two experiments directly affecting the saccades clearly separate from all the other ones. We should additionally highlight that, despite a clear distinction emerging between cues that support contextual adaptation and those that do not within a single session, it remains possible that some of the cues identified here as ineffective could become effective given longer exposure or alternative task structures. This would suggest that cue effectiveness lies along a continuum, a hypothesis that warrants systematic investigation.

Our findings align with established literature, demonstrating that all effective contextual cues are spatially relevant and induce modifications in saccade planning—whether by altering the starting location, the ending location, or programming a sequence of saccades (see (Pélisson et al., 2010) for a review, (Azadi & Harwood, 2014; Azadi & McPeek, 2022)). This selective adaptation, based on motor relevance, is similarly established in arm movement learning: spatially relevant visual cues effectively facilitate contextual learning in tasks involving opposing force fields (Forano et al., 2021; Howard et al., 2013; Sarwary et al., 2015). In contrast, arbitrary motion cues or color variations lacking spatial relevance to the task failed to elicit significant contextual effects. Our results, together with previous research, demonstrate that motor-relevant cues are essential for contextual adaptation in saccadic and arm movement. This support the hypothesis originally proposed by Cecala et al (Cecala et al., 2015) for color, and extend it to non-motor cues, which, by not specifying a distinct motor-plan, may fail to engage the neural systems required for forming separate adaptative states. In contrast, contextual cues that define distinct motor commands are more likely to recruit cortical motor areas that interact with cerebellar learning mechanisms, enabling multiple adaptive states to be learned.

The observed results suggest that the saccadic system prioritizes cues that are functionally aligned with its primary role—rapid and precise spatial targeting. This aligns with Forano et al. discussion on contextual learning in force field adaptation (Forano et al., 2021). Domjan (Domjan, 2008, p. 200) offers a general framework for understanding these learning constraints, proposing that a stimulus must be compatible with the response for effective learning to occur. In other words, effective cues should inherently relate to the action being learned. This idea aligns with Timberlake's Behavior Systems Theory ((Killeen, 2019; Timberlake, 1993), which posits that learning is guided and constrained by the pre-existing organization and goals of behavioral systems. From this perspective, the saccadic system, evolutionarily specialized for spatial targeting, may have limited capacity to integrate non-motor cues into its adaptive mechanisms, even when such cues are explicitly perceived and used by other system. The functional significance of ineffective contextual saccade adaptation and difference between effective contextual cues might therefore extend well beyond motor learning.

Conclusion

Our findings highlight the remarkable selectivity of the saccadic system, which prioritizes motor-related cues and excludes non-motor information. This selectivity applies specifically to motor adaptation as we observed a dissociation between perception and learning: participants could accurately perceive and report non-motor contextual cues, yet these cues failed to drive contextual saccadic adaptation. Such goal-directed learning process reflects the system's evolutionary specialization for precise spatial targeting, ensuring rapid and accurate eye movements. However, this specialization comes with constraints, such as a limited capacity to use non-motor cues and a reliance on spatially relevant contextual factors. These results emphasize the importance of considering evolutionary pressures and the functional specialization of sensorimotor systems to fully understand the mechanisms driving their adaptability, shaping their capacity to respond to environmental demands.

DATA AVAILABILITY

The data that support the findings of this study will be openly available in data.gouv.fr.

SUPPLEMENTAL MATERIAL

Supplemental Table S1 and Supplemental Figs. S1-S9 https://doi.org/10.6084/m9.figshare.28882652

GRANTS

This research was supported by Agence Nationale de Recherche Grant ANR-21-CE28-0013 (L. Madelain)

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

M.M and L.M conceived and designed research; M.M performed experiments; M.M and L.M analyzed data; M.M and L.M interpreted results of experiments; M.M prepared figures; M.M drafted manuscript; M.M and L.M edited and revised manuscript; M.M and L.M approved final version of manuscript.

5.2. Extending to non-spatial cues

The results presented in this section have been presented at poster presentations at:

Madelain, L. & Martel, M. (2025): Remote Distractor Location as a Motor-Relevant Cue for Contextual Saccadic Adaptation. ECVP 2025, Mainz, Germany

Martel, M. & Madelain, L. (2025). Exploring the Influence of Temporal Cues on Contextual Saccadic Learning. GDR Vision, Leuven, Belgium.

Cues successfully inducing contextual saccade adaptation in our study *Ineffective cues for contextual saccade adaptation* directly modified the saccade starting or ending location. In their discussion, Azadi and Harwood (Azadi & Harwood, 2014) underline the importance of ‘spatially relevant visual cues’ but it remains unclear whether it implies that only cues specifically involving the target displacement might be effective. In three additional experiments, we explored cues that induce a change in either the saccade’s kinematics or the saccade’s timing, without involving the target locations. In the three following experiments, all other experimental parameters and the general procedure, besides the contextual cues, were similar to those described in the Methods section of the article “Ineffective cues for contextual saccade adaptation”.

5.2.1. Investigating Remote Distractor

In a first experiment, we used a remote distractor design to assess its efficiency in inducing contextual learning in saccades. The remote distractor effect (Chaumillon et al., 2022; Ludwig et al., 2005; Walker et al., 1997) refers to the modification of one or several components of the saccade (e.g. amplitude, angle, latency, or curvature), induced by the presentation of an irrelevant distractor in the vicinity of the saccade trajectory. Since the remote distractor alters motor components of the saccade, we hypothesize that it could act as an efficient contextual cue for saccadic adaptation despite leaving untouched the actual target starting and ending point.

We probed this effect as a contextual cue by placing an irrelevant distractor, a green circle, either above (NW) or below (SE) the trajectory of the saccade between the fixation point and the target. The distractor appeared together with the first step of the target, and was located symmetrically either above or below (2.7 dva) the target vector and halfway through the step amplitude.

First, we assessed the remote distractor effect by comparing the angles of the saccades in baseline depending on the distractor location using a nonparametric permutation test on the difference in medians with 100,000 permutations. Permutation-based tests were implemented using custom routines in MATLAB. This test revealed a statistically significant difference in saccade angle between the two distractor locations for all participants (Mean: 6.69, Maximum: 16.37, Minimum: 5.60). Given that the remote distractor effect was present, we conducted a statistical analysis on the difference between contexts.

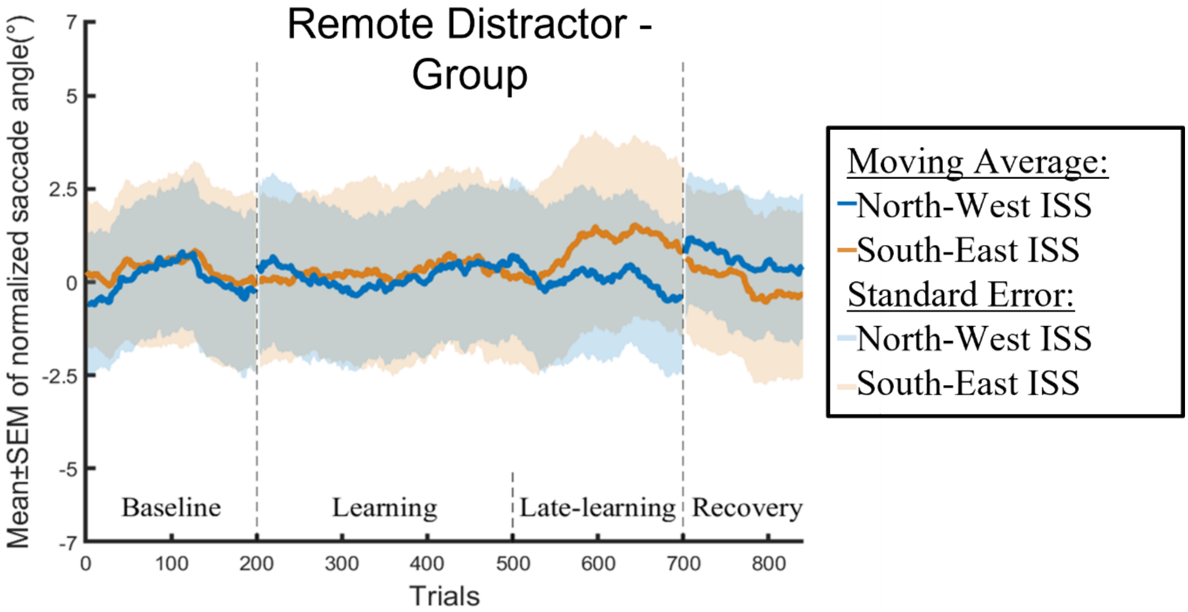

Figure 19. Remote distractor as a contextual cue. Moving average of the saccade angle difference to baseline as a function of trials for the 10 participants.

We analyzed the difference in saccade angle to estimate whether contextual saccade adaptation occurred with the same statistical procedure as in previous experiments. A nonparametric permutation test on the difference of the in late-learning trials medians normalized to the baseline with 100,000 permutations showed a consistent contextual learning in 9 out of 10 participants (Mean:3.28, Maximum: 6.68, Minimum: -1.97, See Figure 19). Additionally, we computed the Kolmogorov-Smirnov distance, showing a score similar to the Starting Location experiment with a mean of 0.30 (Maximum: 0.51, Minimum: 0.20, see Figure 22). These results will be further discussed in section 6.3.

5.2.2. Investigating Timings

Another type of non-spatial cue, which has not been investigated before, is timing. In the study "Ineffective cues for contextual saccade adaptation," we used timing through the Visual Duration experiment in which the duration of a visual object during the fixation period served as a cue. However, in this experiment, timing was only perceptual, as the duration of the cue did not affect the motor components of the saccades. To assess whether timing could be a relevant cue for contextual saccade adaptation, we ran two additional experiments manipulating the temporal properties of the saccade.

Gap and Overlap

First, we used a Gap-Overlap design (Kalesnykas & Hallett, 1987; Reuter-Lorenz et al., 1991; Saslow, 1967) as cues. In this design, the *gap* condition refers to a brief period during which no stimulus is presented on the screen following the disappearance of the fixation target. This condition is known to shorten saccade latencies. Conversely, the *overlap* condition involves a brief period of overlap between the fixation target and the saccade target, which typically results in prolonged saccade latencies (Vencato et al., 2022). Integrating gap and overlap trials into our double-step design, we extinguished the fixation point either 60ms before or after the appearance of the saccade target. Specifically, in the *overlap* condition, the fixation target remained visible when the saccade target appeared, whereas in the *gap* condition, it was extinguished prior to its onset.

Therefore, gap trials refer to trials in which the screen was left empty for 60ms after the fixation period. Participants were instructed not to move until the target appeared. On the other hand, overlap trials refer to trials during which the target is presented 60ms before the saccade-target appearance. Gap and overlap trials were each paired with an ISS direction, counterbalanced across ten participants.

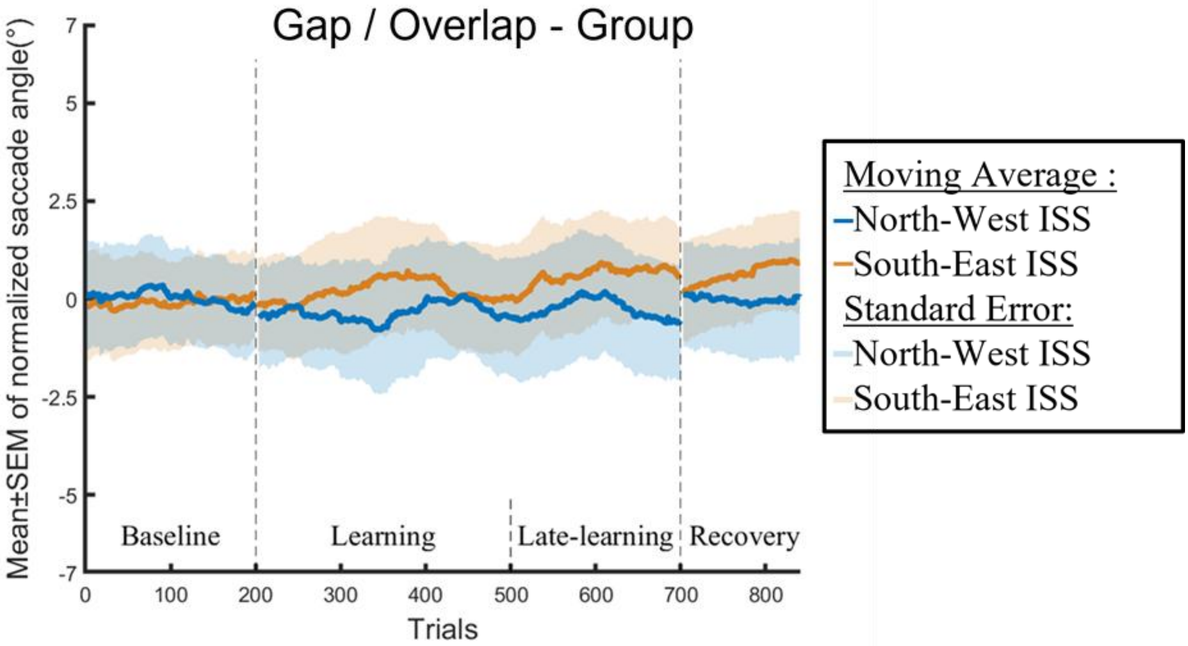

Figure 20. Gap and Overlap as contextual cues. Moving average of the saccade angle difference to baseline as a function of trials for the 10 participants.

Neither the gap nor the overlap modifies the spatial components of the target vector, and should not modify the kinematics of the saccade either. The only expected modification is on the latency, with shorter latencies in the gap trials and longer latencies in the overlap trials. This difference in the saccades' latencies modifies the temporality of the motor decision rather than the kinematics of the saccade, the *when* rather than the *where. However, b*ecause precise timings are essential for accurate motor movements, one might hypothesize that this difference in latencies should be a motor cue and lead to effective contextual adaptation.

We first evaluated the effect of the gap-overlap paradigms by comparing saccade latencies in gap versus overlap trials using a nonparametric permutation test. This test examined the difference in medians of latencies with 100,000 permutations, utilizing custom MATLAB routines. This test revealed a significant difference for all ten participants with a mean difference of 69.5ms (Maximum: 123.4ms, Minimum: 14.1ms) for an average saccade's latency of 142ms, confirming a strong effect of our design on latencies.

We then analyzed the difference in saccade angle to estimate whether contextual saccade adaptation occurred with the same statistical procedure as in previous experiments. Results showed a significant difference between the contexts for four out of ten participants (Mean: 1.88, Maximum: 4.70, Minimum: 0.19, See Figure 20). For the Kolmogorov-Smirnov distance, we observed limited and inconsistent effects across participants, with a mean of 0.25 (Maximum: 0.51, Minimum: 0.09, See Figure 22).

Fixation Time

Along with the Gap-Overlap experiment, we investigated temporal properties by manipulating the duration of the fixation preceding the saccade rather than the latency of the saccade.

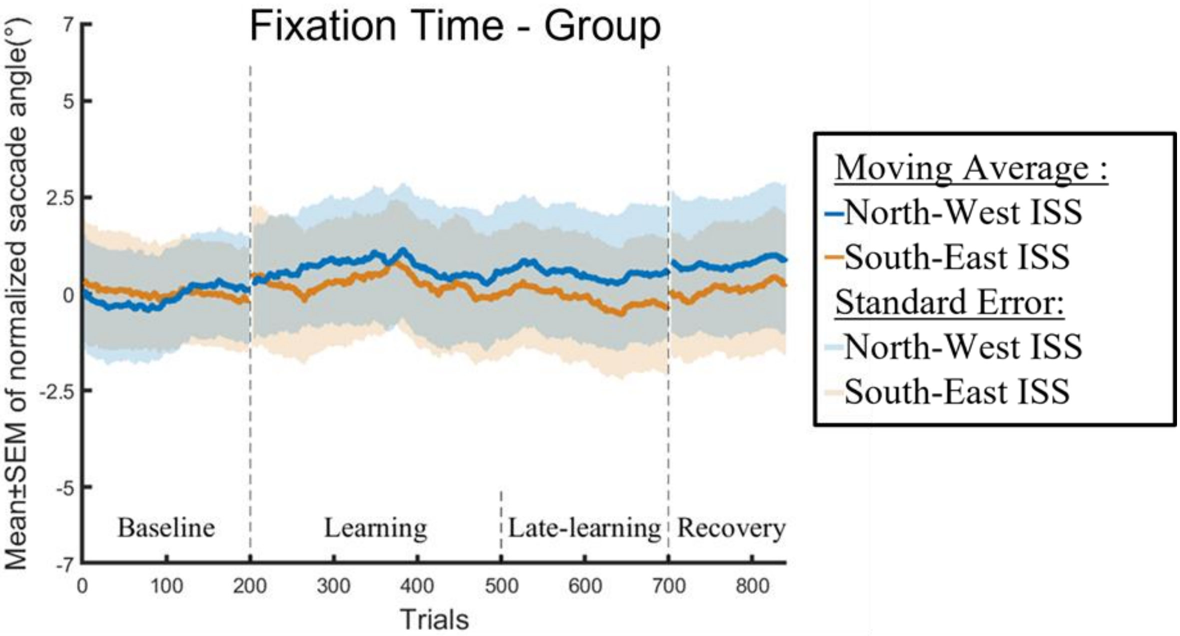

Figure 21. Fixation Time as a contextual cue. Moving average of the saccade angle difference to baseline as a functions of trials for the 10 participants.

The statistical analysis comparing the saccade angle of short-fixation trials to long-fixation trials showed a mitigated effect of contextual learning, with 3 out of 10 participants showing significant differences (Mean: 1.12, Max: 2.25, Min: 0.25, See Figure 21). For the Kolmogorov-Smirnov distance, we observed low and inconsistent scores, with a mean of 0.18 (Maximum: 0.30, Minimum: 0.07, See Figure 22).

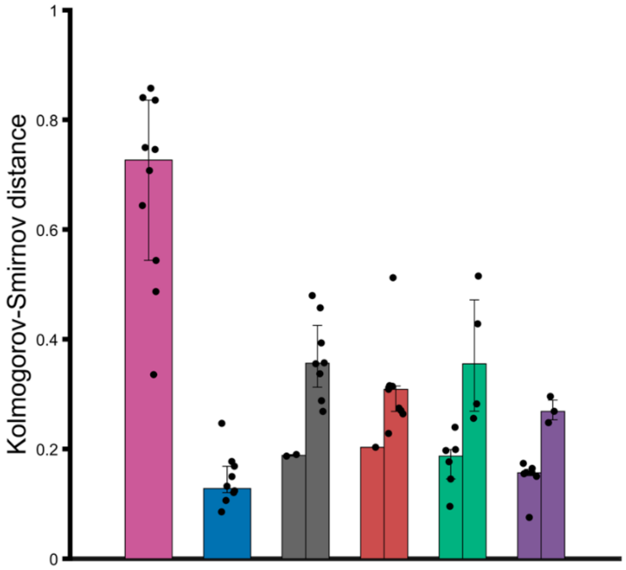

Figure 22. Median and inter-quartile range of the Kolmogorov–Smirnov distance for the experiments: First Step Amplitude (pink), Color and Shape (blue), Starting Location (grey), Remote Distractor (red), Gap/Overlap (green), and Fixation Time (purple). A split histogram always represents non-significant participants in the first bar and significant participants in the second bar. Black dots represent individual scores.

Overall, results from these three experiments extend our previous findings by showing that non-spatial cues can drive contextual saccade adaptation, provided they influence the motor properties of the saccade. Our implementation of the remote distractor effect altered the saccade trajectories without changing the target's spatial location, and proved to be an effective contextual cue for most participants. This demonstrates that modifying motor parameters is sufficient for contextual learning. In contrast, timing-related cues, such as the gap/overlap paradigms or the manipulation of the fixation duration, produced weak and inconsistent effects. Importantly, these two manipulations primarily affect the timing of saccade triggering without altering its kinematic properties. This suggests that the effectiveness of a contextual cue depends not only on its motor relevance but also on how specifically it modulates saccade execution. Overall, these experiments reveal a continuum of cue effectiveness, governed by the specific saccade parameters each cue is able to modify the motor command.

5.3. General discussion on ineffective cues

In this initial experimental contribution, we examined the effectiveness of different contextual cues in driving saccadic adaptation using a consistent double-step paradigm. The key finding is that only motor-related cues, specifically first-step amplitude and starting location, reliably produced contextual adaptation. All other cues tested—visual features (color, shape), symbolic arrows, auditory lateralization, stimulus duration, or statistical regularities across trials—were largely ineffective.

In Section 6.2, we investigated whether only spatially relevant cues could be effective for learning or if different ways to alter the motor components of the saccade could lead to similar results. First, we employed a remote distractor design, which induced modification to the saccade trajectory while maintaining the starting and ending locations of the target unchanged. As a result, nine out of ten participants showed contextual adaptation. Similarly, we investigated timing through a gap/overlap design and by manipulating the duration of the fixation time. We observed four and three significant results out of ten, respectively, indicating a weaker yet present effect of timing on contextual adaptation when relevant to the motor programming of the saccade.

Our results from this first experimental contribution demonstrate a strong selectivity towards information directly tied to motor programming. By contrast, non-motor cues, even when participants explicitly perceived and reported them correctly, fail to induce contextual adaptation. This reveals a dissociation between perception and motor learning: participants can consciously recognize cues but fail to integrate them into adaptive motor control. The results align with broader evidence from force field adaptation, where spatially relevant cues support contextual adaptation, but color or arbitrary features do not (Howard et al., 2013).

The decisive effect of the nature of the cues stands as a demonstration of selective learning in this experimental design. Indeed, in similar experimental settings, motor-relevant cues can serve as effective contexts, while non-motor cues cannot. From a behavioral framework, the same contingencies led to different outcomes depending on the specific SD we used. Additionally, we revealed a dissociation between cue perception and motor integration, underlining that non-motor cues were accurately perceived but failed to take control of the saccades' kinematics. Lastly, we demonstrated that cues modifying the motor programming of the saccades could be efficient for contextual adaptation even when spatially irrelevant, such as changes in the kinematics or in the temporality of the saccade.

6. Selectivity of learning in higher-order conditioning

Section 6.1 presents a study written in article format, currently being prepared for submission to a peer-reviewed journal.

6.1. Main study: Can contextual features induce saccade adaptation?

Can contextual features induce saccade adaptation?

Maxime Martel[1], Jérémie Jozefowiez[1], Laurent Madelain[1,2]

[1] UMR 9193-SCALab, CNRS, Univ. Lille, 59000 Lille, France.
[2] Institut de Neurosciences de la Timone, UMR 7289, CNRS, Faculté de Médecine de la Timone, Aix Marseille Université, 27 Bd Jean Moulin, Marseille 13005, France.

Correspondence: L.Madelain (Laurent.madelain@univ-lille.fr)

6.1.1. Introduction

Saccadic adaptation, typically investigated with the double-step paradigm, provides a well-established framework for studying motor learning in both humans and non-human animals. This method leverages saccades—rapid, discrete eye movements that allow animals with foveal vision to bring visual targets to the center of the retina. In a classical saccadic adaptation procedure, a fixation point appears before stepping to a new location. As the participant initiates a saccade toward this new position, the target shifts again - this second displacement is known as the intra-saccadic step (ISS). Because the eye lands at the initial location of the target, the retinal error – distance between the endpoint of the saccade and the target- is large, and a secondary, corrective saccade is typically performed. With repeated trials, the primary saccade gradually adapts, reducing the retinal error induced by the ISS, i.e., landing closer to the shifted target location (McLaughlin, 1967).

While this gradual shift of the saccade is usually referred to as saccadic adaptation, it has been thoroughly demonstrated that saccades are operant behaviors (Madelain, Paeye, & Darcheville, 2011). Reinforcement of various properties of saccadic movements is grounded in experimental evidence in monkeys (Ikeda & Hikosaka, 2003; Lauwereyns et al., 2002; Takikawa et al., 2002; Watanabe et al., 2003) and in humans (Montagnini & Chelazzi, 2005; Xu-Wilson et al., 2009). Moreover, due to their function of bringing a visual object of interest to the fovea and enabling accurate perception, saccades can be more precisely described as observing responses (Wyckoff, 1952). This distinction is important because observing responses are reinforced by the information they provide about a stimulus, emphasizing that saccades are naturally reinforced by accurately perceiving the target of interest.

As an operant behavior, saccades are subject to discriminative learning, commonly referred to as contextual saccadic adaptation in vision research, which involves the following procedure: the participant fixates on a fixation target and performs a saccade upon target displacement. The target undergoes an intra-saccadic step, resulting in a retinal error for the participant. The difference with the classical and contextual saccadic adaptation is that multiple, usually two, different ISS A and B will be applied to the same saccade vector within the same experimental session. This design provides two contextual cues (or discriminative stimuli), A and B, each signaling a specific ISS direction. Following these cues, the participant must produce two types of saccades, A and B, which reduce the retinal error to their matching ISS. Discriminative learning is considered successful when the saccades are systematically different based on the contextual cue presented, thereby reducing the retinal error. From an associationist view, the stimulus A is associated with a response A and an ISS A; and the stimulus B is related to a response B and an ISS B.

As an example, in a typical double-step experiment (Alahyane & Pelisson, 2004), the contextual cue was the starting location of the fixation point. The target appeared in the participant’s left visual field at one of two possible starting locations. In the learning trials, two different ISS, forward and backward, were introduced and paired with a specific starting location. At the end of these learning trials, this contingency successfully induced simultaneous opposite adaptations: saccade amplitude increased when the starting location was paired with a forward ISS, and decreased when the starting location was paired with a backward ISS.

However, in another double-step design, Deubel (Deubel, 1995) employed the color and shape of the target as contextual cues. Similarly, a backward ISS was paired with a green cross, while an absence of ISS was paired with a red circle. The expected results were a decrease in the saccades’ amplitude for the green cross trials and no change in the saccade amplitude for the red circle trials, i.e., a contextual adaptation depending on the cue. However, the results reported no contextual adaptation, with no significant difference in saccade amplitude between the green cross and the red circle trials. According to Deubel, this indicates that control of saccadic adaptation is not specific to the visual features of the target. Those results led to replications with the color and shape of the target as a cue in humans (Azadi & Harwood, 2014; Bahcall & Kowler, 2000; Benjamin et al., 2016), and in monkeys (Cecala et al., 2015), systematically aligning with Deubel’s results on the inefficiency of the color and shape of the target to induce contextual learning in saccades.

More recently, Martel & Madelain (Martel & Madelain, 2025) investigated further this inefficiency of learning with specific stimuli. In addition to the color & shape of the target, they also investigated eight additional types of cues. Despite the three-term contingency being identical in all settings, the different nature of the SDs led to very different learning outcomes, and efficient learning occurred only with motor-related cues – cues involving a modification of the saccade’s kinematics. The absence of learning with non-motor cues revealed the strong effect of the cue's nature on eliciting or preventing learning. From an associationist view, the stimulus A failed to associate with a response A and an ISS A; and the stimulus B failed to associate with a response B and an ISS B. This failure in the association has been interpreted in terms of selective learning, arguing that the motor system is specialized in selecting motor-related cues but ignores others.

The term *selective learning* refers to a conceptual framework based on Domjan’s application and extension of the Behavioral Systems Theory (Domjan & Gutiérrez, 2019; Timberlake, 1993). This framework carries forward the observation that behavior is organized into subsystems, modes, and modules that prime specific actions, and that those actions, when available, reinforce those that occasioned their availability. It emphasizes the functional aspect of the system, enabling associations between stimuli and responses within the same system, while being less sensitive to irrelevant stimuli. Here, saccades serve the functional purpose of directing a visual target to the fovea, and as such, they are influenced by modifications of their kinematics.

In this study, we want to investigate the specificities of this selectivity of learning in saccadic adaptation by using a paradigm of higher-order conditioning. To do so, we used an occasion-setting paradigm. In this paradigm, a first cue is presented, referred to as the contextual feature, which modulates the information carried by the second stimulus, the *discriminative stimulus (SD),* thereby allowing accurate prediction of an outcome A or B (Trask & Bouton, 2014).

This method would help us answer two theoretical questions: First, whether such a higher-order conditioning can occur in saccadic adaptation. Indeed, if the motor and the non-motor information are processed differently for motor learning, we could expect that other forms of restriction could exist, leading to failure in learning with modifications to the contingency other than the nature of the cue. Second, if higher-order conditioning leads to successful learning, we could assume that more processes are at play to support this learning. Therefore, we hypothesized that using a non-motor cue as a contextual feature rather than a discriminative stimulus could bypass the selectivity of learning and help integrate a non-motor cue in contextual saccadic adaptation.

To probe this issue, we designed two experiments combining a contextual feature and a discriminative stimulus. To facilitate the association between the SD and the outcome, i.e., the ISS, we chose in both experiments the motor cue that led to the best learning performance in our previous study, the amplitude of the first step. Therefore, the only difference between our experiments lies in the cue used as a contextual feature.

In a first experiment, we used a motor cue, the starting location of the target, as a contextual feature. Therefore, the trial starts with a fixation point located either on the left side or in the middle of the monitor. Then, the ISS depends on both the starting location and the amplitude of the first step, i.e., the leftward location will predict an ISS A for the long step and an ISS B for the short step, while the central location will predict an ISS B for the long step and an ISS A for the short step.

In a second experiment, we used a non-motor cue, the color and shape of the target, as a contextual feature. Similarly to the first experiment, a green square will predict an ISS A for the short step and an ISS B for the long step, while a red triangle will predict an ISS B for the short step and an ISS A for the long step.

Our results revealed no evidence of discriminative learning in either the Starting Location or the Color and Shape experiments when conducted within a single session. However, a trend toward adaptation in the Starting Location experiment led us to replicate both experiments in a five consecutive sessions design. In these repeated replications, the Starting Location contextual feature reliably produced strong and consistent discriminative learning at the group level, whereas the Color and Shape experiment remained ineffective in inducing adaptation.

6.1.2. Method

Participant

Thirty-one participants were recruited for this study (n = 10, 10, 6, 5; 27 females, 4 males, aged 18-26 years old). All participants were naïve to the purpose of the experiments, with no prior experience with eye-movement experiments within the past 6 months, and all had normal or corrected-to-normal vision. Participants provided consent via non-opposition, explicitly informed in the information letter provided during recruitment. All experimental procedures received approval from the Ethical Committee in Behavioral Sciences of the University of Lille (Agreement No. 2022-647-S111) and conformed to the standards set by the Declaration of Helsinki.

Apparatus

Participants sat in a dark and quiet room facing the display monitor (Iiyama HM204DT, 100Hz, 22 inches) with their heads stabilized via chin and forehead rests (60cm from the screen). Stimuli were generated and displayed using the Psychophysics Toolbox Extension (Brainard, 1997; Pelli, 1997) for Matlab®. Recording of the right eye position was performed by an SR-Research Eyelink 1000+ Tower Mount system, sampling at 2000Hz. We used the Eyelink 13-point calibration and validation routines at the beginning of the recording sessions.

Training

Before any experiments, participants experienced a training session. Instructions were displayed on the screen, explaining how to position themselves in the eye-tracking setup and providing a brief overview of the task. Participants were instructed to keep their eyes on the target and to shift their gaze only after the target moved. The training trials were similar to the baseline trials from the experiments they were assigned to. Participants were informed that looking away from the target, anticipating its movement, or an absence of reaction would trigger a sound, indicating an error and the termination of the trial. Then, following a 13-point calibration, a 50-trial training session began to familiarize the participants with the temporal sequence of a trial. These sessions were repeated until a minimum of 75% of correct saccades were recorded (All participants reached the 75% criterion in one sitting). During these training sessions, participants experienced regular trials regarding the experiments they were assigned to and corresponding to baseline trials.

General procedure

The general procedure was similar for experiments 1 and 2, using a different contextual feature and similar discriminative stimuli and intra-saccadic step (ISS). Experiments 3 and 4 were respectively the replication of experiments 1 and 2, across five repeated sessions.

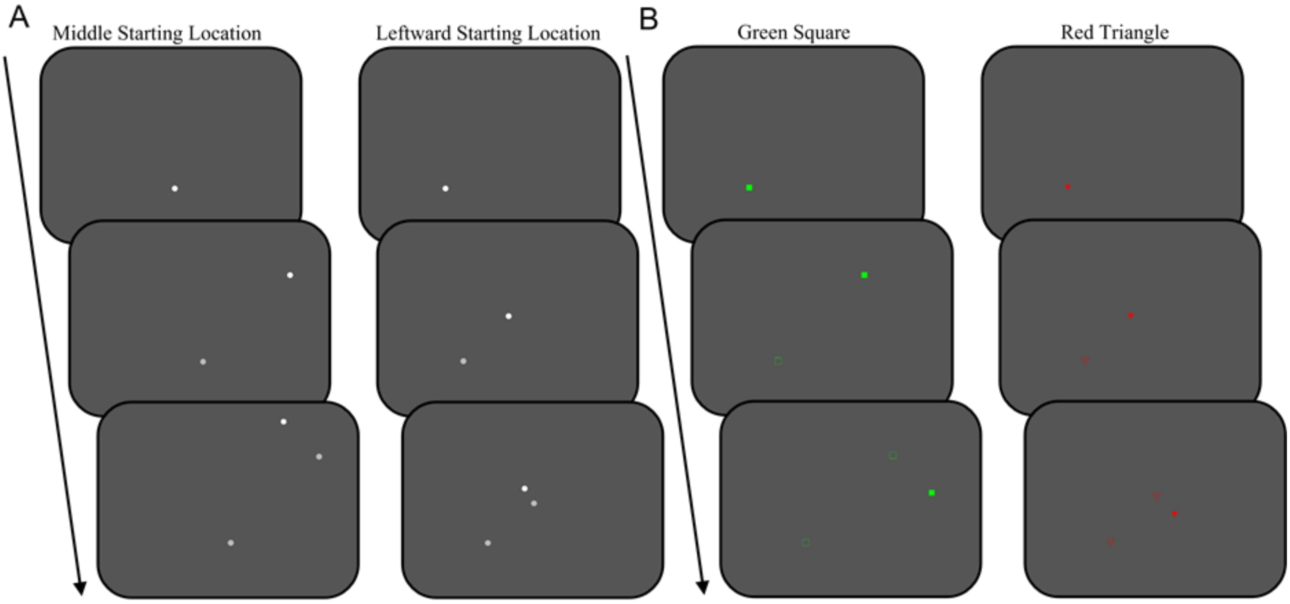

Figure 23. Panel A is a schematic of two Combination 3 and Combination 2 for the experiment Starting Location. ***1:*** *The fixation target is present for a random period [700ms 1000ms].* ***2:*** *The target steps, with a 45° angle upward and rightward.* ***3:*** *When a saccade is detected, the target steps again during the saccade. The ISS amplitude is 20% of the first step amplitude. The direction of the intra-saccadic step was either North-West or South-East, depending on the combination presented (only the North-West ISS is shown here). Panel B is a schematic of Combination 1 and Combination 4 for the experiment Color and Shape.* ***1:*** *The fixation target is present for a random period [700ms 1000ms].* ***2:*** *The target steps, with a 45° angle upward and rightward.* ***3:*** *When a saccade is detected, the target steps again during the saccade. The ISS amplitude is 20% of the first step amplitude. The direction of the intra-saccadic step was either North-West or South-East, depending on the combination presented (only the South-East ISS is shown here).*

All experiments used a double-step paradigm (Figure 23) in which the fixation target is present for a random period [700ms 1000ms], and the first step was directed upward and to the right. The ISS was either upward and backward (North-West) or downward and forward (South-East) with respect to the first step and equal to 20% of the first step amplitude. Within a session, the ISS was present in all trials. Two contextual features and two discriminative stimuli were used in each experiment. The discriminative stimuli were always the amplitude of the first step of the target, i.e., a short step [5.5 dva] or a large step [10.1 dva] (dva: degree of visual angle).

These settings led to four unique combinations in each experiment (See Figure 24). This arrangement ensures that it was impossible to rely solely on the contextual feature or on the discriminative stimuli to predict the ISS, and only the use of the combination allowed prediction of the ISS. During learning trials, each combination was 100% consistent with its paired ISS. The combination pairing was counterbalanced across participants. ISSs appeared in a random fashion during baseline trials. Therefore, in all experiments, the only difference between the learning trials and the baseline trials was the systematic pairing of a combination to an ISS.

Combination	**Features**	**Discriminative Stimulus**	**ISS**
	Experiment 1 – Starting Location		
Combination 1	Leftward Location	Large Step	North-West
Combination 2	Leftward Location	Short Step	South-East
Combination 3	Middle Location	Large Step	South-East
Combination 4	Middle Location	Short Step	North-West
	Experiment 2 – Color and Shape		
Combination 1	Green Square	Large Step	North-West
Combination 2	Green Square	Short Step	South-East
Combination 3	Red Triangle	Large Step	South-East
Combination 4	Red Triangle	Short Step	North-West

Figure 24. Four different possible combinations within an experimental session. The arrangement of the feature, the discriminative stimulus, and the ISS prevents relying on the feature or on the SD only to predict the ISS. The pairing between pairs of cues and ISS is counterbalanced across participants, such as the ISS North-West is paired with Combination 2 and 3, and the ISS South-East is paired with Combination 1 and 4 for half of the participants.

The fixation target, a grey disk 1 (0,4° diameter / Luminance 12,1 cd/m2) was displayed for a random duration ranging from 700 to 1000ms (drawn from a uniform distribution) against a gray background (luminance 3 1.7 cd/m2). Then, the target was displaced following a 45° vector upward and rightward with two possible step amplitudes (5.5 or 10.1 dva, occurring equally and in a pseudo-random order).

If a change in eye position was detected within an 80-ms to 350-ms temporal window following the first step, the ISS was triggered, and the target underwent an ISS during the saccade. The ISS was a perpendicular (90°) step regarding the first step of the target, oriented North-West or South-East, and equal to 20% of the amplitude of this first step. The online saccade detection corresponded to the eye position crossing an invisible boundary 3dva away from the fixation location. The target experienced an ISS in every trial in which a saccade was detected, including the baseline trials. Following the ISS, the target remained visible for 500ms. A unique pseudo-random trial list of the possible combinations was used in all experiments, such that every participant experienced the same series of trial characteristics. If a saccade was detected either before 80ms (anticipation) or after 350ms (absence of reaction) with respect to the onset of the trial, this trial was terminated before the ISS occurred, the target was extinguished, and a sound (100ms at 500 HZ) was played to signal the end of the trial.

Once the training criterion was reached, instructions about the task were provided again as a reminder. The experimental session started, and the 13-point calibration and validation were performed again. All experimental sessions consisted of a total of 840 double-step trials with 200 baseline trials and 640 learning trials. Across the session, participants experienced short breaks every 50 trials. Rest intervals have been reported to facilitate contextual adaptation (Ethier et al., 2008b). Following these breaks, the calibration was checked, and the experimenter conducted a 13-point calibration if necessary.

Experiment 1: Starting Location Contextual Feature

In this experiment (n=10) the contextual feature was the starting position fixation target. The fixation target was either at P0a[-12 dva; -4.9 dva], downward and leftward with respect to the center of the screen, or at P0b[-0.7 dva; -4.9 dva], downward and centered with respect to the center of the screen. The vector of the target after the first step and after the ISS was independent of the P0 location. The contextual feature was paired in combination with the SD such as: a leftward, i.e. P0a, starting location would indicate a North-West ISS for a long amplitude of the first step or a South-East ISS for a short amplitude of the first step; a centered, i.e. P0b, starting location would indicate a North-West ISS for a short amplitude of the first step or a South-East ISS for a long amplitude of the first step. This combination was 100% consistent during the learning trials, fully randomized during the baseline trials, and counterbalanced across participants.

Experiment 2: Color & Shape Contextual Feature

In this experiment (n=10), the contextual feature was the color and the shape of the fixation target. Participants with colorblindness were excluded from this experiment. The fixation target was either a green square or a red triangle. The contextual feature was paired in combination with the SD such as: a green square would indicate a North-West ISS for a long amplitude of the first step or a South-East ISS for a short amplitude of the first step – the red triangle would indicate a North-West ISS for a short amplitude of the first step or a South-East ISS for a long amplitude of the first step. This combination was 100% consistent during the learning trials, fully randomized during the baseline trials and counterbalanced across participants. All the trials started with the same P0 location for the fixation target ([-8,3 dva; -4.9 dva]; downward and leftward with respect to the center of the screen).

Experiments 3 and 4: Starting Location and Color and shape in repeated sessions

Experiment 3 and experiment 4 were identical to, respectively, experiment 1 and experiment 2 for all the parameters of the experiment. The only difference for experiments 3 and 4 was that participants performed five sessions of 840 trials across five consecutive days. The training session and the baseline trials were present only during the first day. From sessions two to five, participants started with the 13-point calibration and validation, and then would perform sessions of 840 learning trials. For experiments 3 and 4, participants received 60 euros of gratification after completion of the five sessions.

Processing of saccades

We used the Eyelink online saccade detector to identify saccade onset and offset, using 30dva/s velocity and 8000dva/s2 acceleration thresholds. In all trials, we only considered the first recorded saccade following the first step of the target. Before statistical analysis, a human observer validated each saccade manually. Incorrect saccades, saccades with a gain lower than 0.5 or higher than 1.5, saccades with latency shorter than 80ms or longer than 350ms, and saccades that were not directed toward the target at P1 (deviating more than 45° away from the target vector angle), were excluded from further analyses. A criterion of 75% correct saccades during the session was used to include participants for further statistical analysis. Saccade angles were computed by drawing a line between the saccade starting point and the saccade endpoint, and measuring its angle relative to the horizontal axis. For each participant and each contextual cue, we calculated the median saccade angle during baseline trials. We then subtracted this median value from each corresponding saccade angle, ensuring that the values were distributed around 0°. In this normalized space, complete adaptation would correspond to a change of +11.3° for North-East ISS and -11.3° for South-West ISS.

Statistical analysis

We used bootstrapping methods (resampling with replacement 100,000 times) to estimate the 97.5% confidence intervals (CIs) of the medians (Efron, 1992). For each participant, significant differences between the combinations sharing the same ISS in their median saccade angle changes with respect to the baseline medians were determined by a nonparametric permutation test on the difference in medians with 100,000 permutations. Permutation-based tests were implemented using custom routines in MATLAB. This test was performed on the last 200 learning trials (late-learning trials).

To quantify the normalized amount of difference between the angle of saccades performed in each context, we computed the Kolmogorov–Smirnov (KS) distance. The KS distance computes the normalized amount of overlap between the two distributions of late-learning saccade angle differences with respect to baseline for each participant. A distance of 0 implies that the two distributions perfectly overlap, while a distance of 1 implies that there is no overlap between the two distributions.

6.1.3. Results

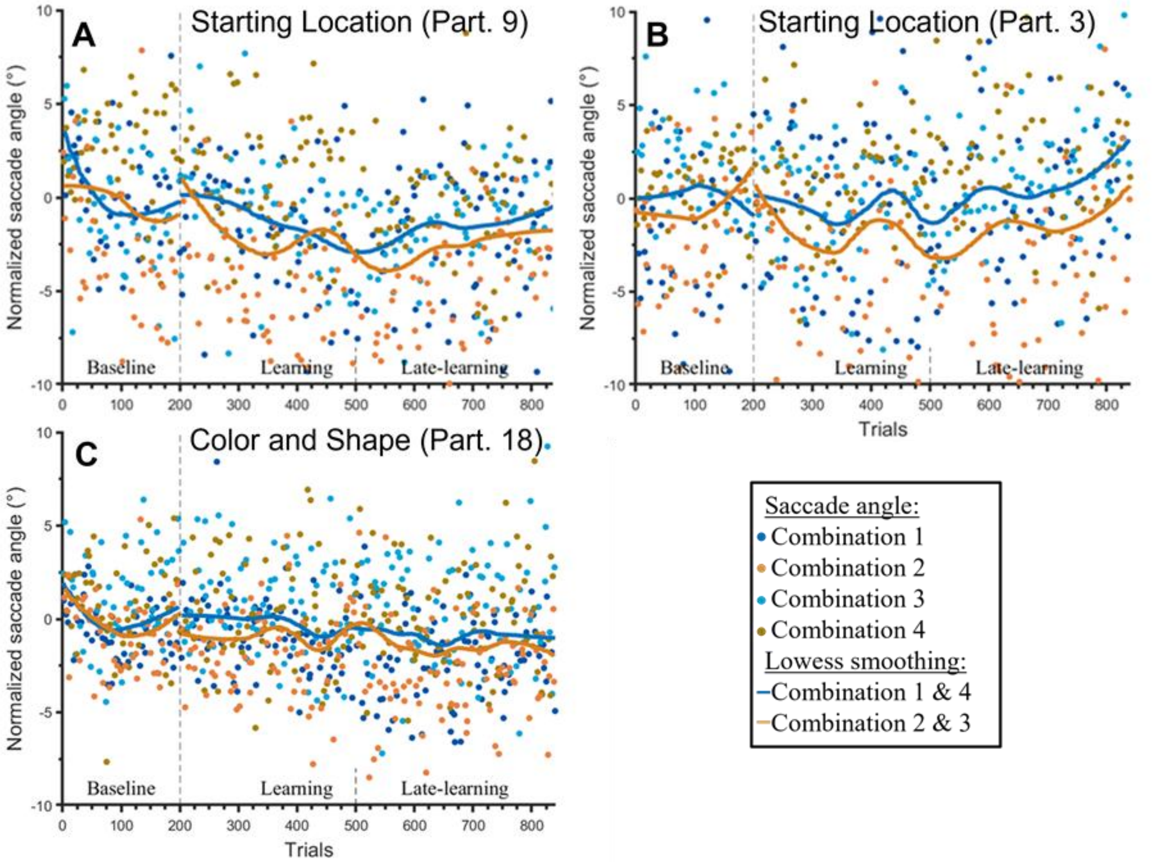

Figure 25. Typical participants from the Starting Location and the Color and Shape experiments. A: Representative non-learning participant (participant 9). Each point plots the saccade angle difference to the baseline in a trial, expressed in degrees. Solid lines are the Lowess smoothing of saccade angle differences to baseline with a 50-trial moving window. Shades of blue represent the Combination 1 and 4, sharing the North-West ISS. Shades of orange represent the combination 2 and 3, sharing the South-East ISS. Bottom labels indicate the baseline (1-200), learning (201–500) and late learning (501–840). B: Representative learning participant of the Starting location experiment (participant 3). All conventions are similar to those in A. C: Representative participant of the Color and Shape experiment (participant 18). All conventions are similar to those in A.

The difference in saccade angle normalized to the baseline medians is plotted as a function of the trial number. A Lowess smoothing (with a 100-trial window) is used to illustrate the general trends for the two pairs of combinations sharing the same ISS. Again, there was no difference between the saccade angle changes depending on the combination of the baseline trials. Saccade angles remained stable during the learning trials, indicating that there was no specific learning of the combinations (difference in median angle changes of 1.37, within the null hypothesis at 97.5% CIs). Figure 25.B, however, represents participant 3, who showed a significant difference between the pair of combination sharing the same ISS during the late-learning trials combinations (difference in median angle changes of 1.55, outside the null hypothesis at 97.5% CIs). In the Starting Location group, only two of the ten participants exhibit significant learning between the different ISS (Mean difference: 1.14, Maximum: 2.88, Minimum: -0.89). The evolution of saccade angle during the experiment at the group level for the experiment Starting Location is represented in Figure 26.A. While two participants showed significant results, the experiment showed no consistent effect at the group level. The Kolmogorov-Smirnov distance mean of the group is 0.19 (Maximum: 0.31, Minimum: 0.11).

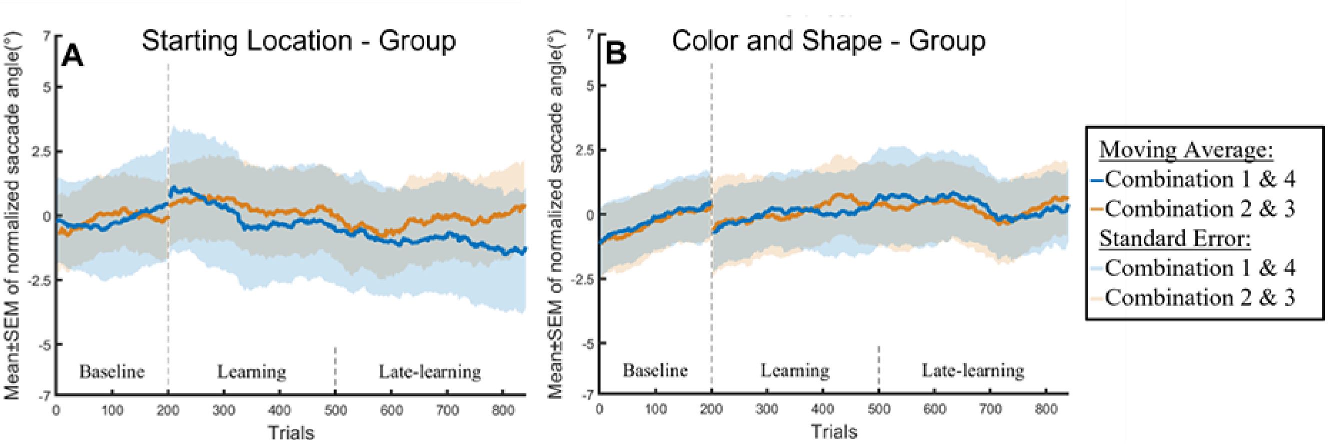

Figure 26. Moving average as a function of trials in the experiment, Starting Location, and Color and Shape. A: Starting Location experiment. Each solid line represents the moving average percentage of saccade adaptation to the ISS. Shading represents the means ± SE. Mean and SEM are calculated independently for baseline and learning trials. Bottom labels indicate the baseline (1–200), learning (201–500), and late learning trials (501–840). B: Color and Shape experiment. All conventions are similar to those in A.

There was no difference between the saccade angle changes depending on the combination of the baseline trials. Saccade angles remained stable during the learning trials, indicating that there was no specific learning of the combinations (difference in median angle changes of 0.37, within the null hypothesis at 97.5% CIs). Those results are representative of the group as none of the ten participants exhibits significant learning between the different ISS (Mean difference:0.08 Maximum: 2.66, Minimum: -2.29). The evolution of saccade angle during the experiment at the group level is for the experiment Color and Shape is represented in Figure 26.B. A Kolmogorov-Smirnov distance, used as a normalized discrimination score to compare experiments together, confirms the absence of discriminative learning with a mean group score of 0.19 (Maximum: 0.36, Minimum: 0.11), which is comparable to the starting location experiment.

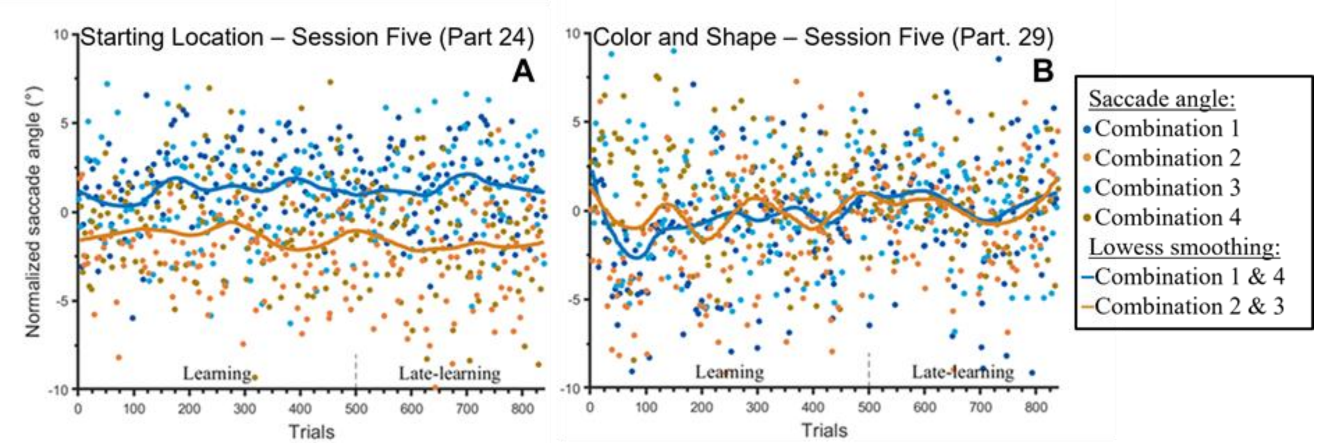

Figure 27. Typical participant for the fifth session of the Starting Location and Color and Shape experiment – repeated sessions. A: Session five of a representative participant (participant 24) of the Starting Location experiment. Each point plots the saccade angle difference to the baseline in a trial, expressed in degrees. Solid lines are the Lowess smoothing of saccade angle differences to baseline with a 50-trial moving window. Shades of blue represent the Combination 1 and 4, sharing the North-West ISS. Shades of orange represent the combination 2 and 3, sharing the South-East ISS. Bottom labels indicate the learning (1–500) and late learning (501–840). B: Session five of a representative participant (participant 29) of the Color and Shape experiment

Figure 27.A represents the typical pattern of results obtained for participant 24 after the fifth session of the Starting Location – Repeated session experiment. All conventions are similar to the initial Starting Location experiment. Because of the absence of a baseline in session five, all saccade angle is normalized on the median of the whole session to keep values around 0. Normalized saccade angles are plotted as a function of the trial number. A Lowess smoothing (with a 100-trial window) is used to illustrate the general trends across the session for each combination pair. There was a significant difference between the saccade angle depending on the combination pairs across the late-learning trials (i.e. last 340 trials) of this fifth session (difference in median angle changes of 3.03, greater than the null hypothesis at 97.5% CIs). Those results are representative of the group as five out of the six participants exhibit significant learning between the combination pairs (Mean difference: 2.60 Max: 4.73 Min: 0.50). The evolution of saccade angle during the experiment at group level for sessions one to five is represented in Figure 28.A.

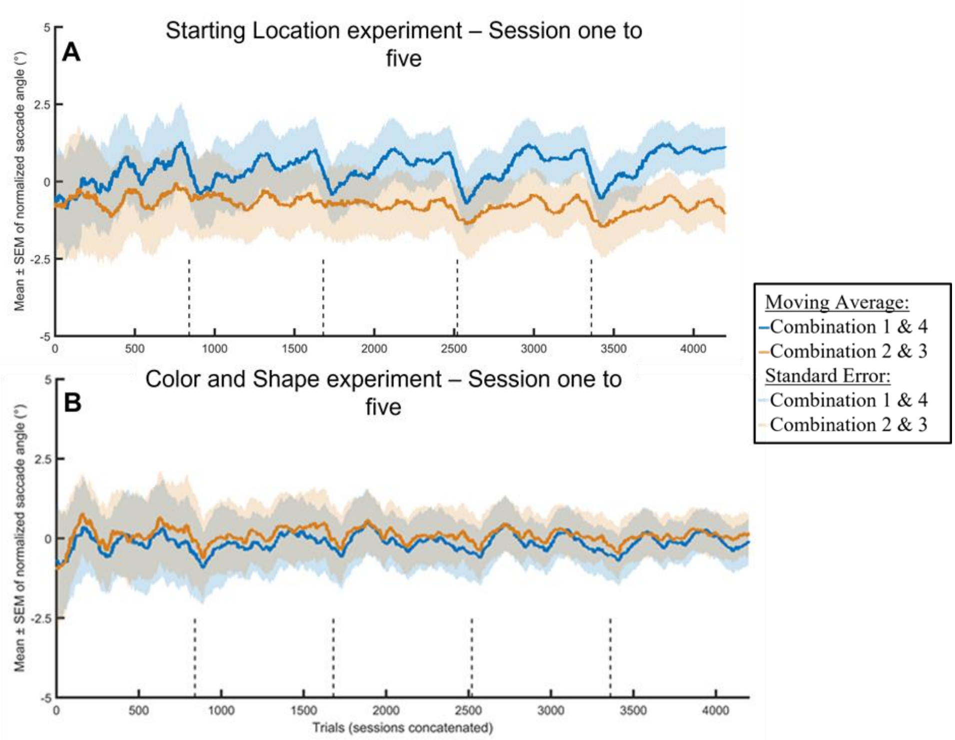

Figure 28. Moving average of the experiment Starting Location Color and Shape – repeated sessions. A: Moving average of the Starting Location experiment as a function of trials. Each solid line represents the moving average percentage of saccade adaptation to the ISS. Shading represents the means ± SE. Mean and SEM are calculated independently for baseline and learning trials. Dotted lines indicate the learning (1-500) and the late learning trials (501-840). B: Moving average of the Color and Shape experiment as a function of trials. All the conventions are similar to those in A.

This consistency of results appeared progressively trough sessions, the with respectively two out of six significative learners in session one (similar to the single session version of this experiment, mean difference: 0.95 Max:2.06 Min: -0.09), four of six significative learners for session two (Mean difference:1.77 Max:3.26 Min:0.50), five out of six significative learners for session three (Mean difference: 1.77 Max:2.42 Min:-0.62) and four out of six significative learners for session four (Mean difference: 1.69 Max: 3.11 Min: 0.19).

The temporal evolution of saccadic adaptation is well described by the Kolmogorov-Smirnov distances per participant across the session, with increasing distances at the individual level. At the group level, the KS distances were 0.20 for session one, 0.26 for session two, 0.28 for session three, 0.28 for session four, and 0.35 for session five.

Color and Shape experiment – Repeated sessions

Figure 27.B represents the typical pattern of results obtained for participant 29 during the fifth session of the Color & Shape – Repeated sessions experiment. All conventions are similarly described in the Color & Shape experiment. Because of the absence of baseline trials in session five, all saccade angles are normalized on the median of the whole session to keep values around 0. Normalized saccade angles are plotted as a function of the trial number. A Lowess smoothing (with a 100-trial window) is used to illustrate the general trends across the session for each combination pair. There was no difference between the saccade angle depending on the combination pairs across the late-learning trials (i.e., last 340 trials) of this fifth session (difference in median angle changes of 0.04, within the null hypothesis at 97.5% CIs). Those results are representative of the group, as none of the five participants exhibits significant learning between the combination pairs (Mean difference: -0.04, Maximum: 0.24, Minimum: -0.68). This absence of results was also found in each of the four previous sessions and for all participants. The evolution of saccade angle during the experiment at the group level is represented in Figure 28.B. At the group level, the Kolmogorov-Smirnov distance mean is 0.09 (Maximum: 0.11, Minimum: 0.06) and is comparable to the single-session Color and Shape experiment.

6.1.4. Discussion

We used a novel variant of the contextual double-step paradigm to investigate higher-order conditioning in contextual saccadic adaptation. In a first experiment, the starting location experiment was designed to assess the efficiency of a motor cue as a contextual feature, modulating the prediction carried by the discriminative stimulus, the amplitude of the first step. Two out of the ten participants showed significant learning after one session, and five out of the six participants showed significant learning in the repeated session. These results show that saccadic adaptation can be induced in such a higher-order design, in which the ISS prediction depends on both the SD and the contextual feature presented in the trial. Despite the need for a larger number of trials to achieve consistent learning, this demonstrates the ability of the oculomotor circuitry to integrate higher-order processes.

In a second experiment, we used a non-motor cue, the color and shape of the target, as a contextual feature. The color and shape of the target is known to lead to inefficient learning in saccadic adaptation both in human and non-animal data (Azadi & Harwood, 2014; Benjamin et al., 2016; Cecala et al., 2015; Deubel, 1995), however a previous study in our lab further confirmed that despite being inefficient for inducing saccadic adaptation, the color and the shape were accurately perceived and reported (Martel & Madelain, 2025). Here, we aimed to investigate if this non-motor cue could be used for saccadic adaptation if its role was no longer to be an SD but a contextual feature, i.e., a stimulus be present to resolve the uncertainty about the information carried by the SD. Among the ten participants, none showed discriminative learning between pairs of combinations sharing similar ISS. In the five-session replication of this experiment, none of the participants showed significant learning either. This absence of results seems to indicate that the oculomotor circuitry is unable to take the perceptual cue into account, to optimize its behavior, and reduce the retinal error. The striking difference between the color & shape and the starting location experiments further confirmed that motor cues, but not perceptual cues, can control saccadic adaptation.

The absence of learning in the Color and Shape experiment led us to consider two hypotheses to explain the efficient learning observed in the Starting Location experiment. First, the starting location feature may have acted as an occasion setter. Occasion setters are contextual features that modulate the association between a discriminative stimulus and its outcome. For instance, two different associations could be formed for the SD “short step amplitude,” one for each ISS, with the feature presented at the beginning—namely, the starting location—modulating which association is expressed. While our design allows for occasion setting to emerge, it would be an even more striking result if no learning occurred in the Color and Shape experiment, as that feature is not directly part of the contingency and is presented at an earlier stage of processing (Fraser & Holland, 2019). Such a finding would suggest that the occasion-setting process operates entirely within the oculomotor system. Further testing of this hypothesis would require additional control experiments assessing the specific properties acquired by occasion setters, which would help determine whether this modulation indeed occurs within oculomotor circuitry or if another mechanism is involved. The alternative hypothesis is that of compound SD. Under this account, participants may have learned each of the four combinations independently. This would imply that the starting location and the amplitude of the first step share part of the predictive value of the ISS and function as a compound SD composed of the two cues working together. This hypothesis is also consistent with the inefficiency observed in the Color and Shape experiment, as it again suggests that only features relevant to the programming of the motor command contribute to learning. However, it remains unclear why compound SDs would require such a large number of trials to achieve significant discrimination. Here as well, additional experiments could be designed to determine the processes at play.

While these two hypotheses could both account for the discrepancy in our results, our experimental design went beyond a simple discrimination task and consistently reproduced the phenomenon of selective learning. This suggests that, regardless of whether the process involves occasion setting or partial SDs, learning takes place within the motor system itself. Consequently, the different conditioning procedures can likely be replicated within this system, yet remain constrained by the requirement for motor-related cues. This represents an extension of the selectivity phenomenon, showing that it applies not only to simple associations but also to higher-order forms of learning.

Conclusion

In this work, we investigated the mechanisms underlying selectivity in saccadic motor learning through a novel variant of the double-step paradigm framed within an occasion setting design. By contrasting a perceptual and a motor cue in the same design, we replicated the strong selectivity of the oculomotor circuitry towards motor cues. Additionally, we demonstrated that the addition of a contextual feature modulating the prediction of the intra-saccadic-step slowed down but did not prevent saccadic adaptation. This aligns with the broader view of motor learning as a process shaped by the functional relevance of cues for motor programming, rather than by their perceptual salience alone. Taken together, our findings add empirical evidence for the selective nature of saccadic motor learning and underscore the need for models that account not only for learning outcomes but also for how the system selects information to optimize its behavior. Further studies delving into the locus of learning for contextual saccadic adaptation would help refine our understanding of the discrepancy in the results depending on the nature of the cues.

7. An underlying mechanism for motor adaptation: Planning

Section 7.1 presents a study written in article format, currently being prepared for submission to a peer-reviewed journal. These results have been presented through a poster presentation at:

Martel, M., Wolpert, D. & Madelain, L. (2025): Plan It To Learn It: Motor Planning Drives Contextual Adaptation in the Oculomotor System. *25th Vision Sciences Society, St. Pete Beach, Florida.*

7.1. Main study : Planning is the key to contextual saccadic adaptation

Planning is key to contextual saccade adaptation

Maxime Martel[1], Daniel M. Wolpert[2], Laurent Madelain[1,3]

[1] UMR 9193-SCALab, CNRS, Univ. Lille, 59000 Lille, France.
[2] Zuckerman Mind Brain Behavior Institute & Department of Neuroscience, Columbia University, New York, NY 100.
[3] Institut de Neurosciences de la Timone, UMR 7289, CNRS, Faculté de Médecine de la Timone, Aix Marseille Université, 27 Bd Jean Moulin, Marseille 13005, France.

Correspondence: L.Madelain (Laurent.madelain@univ-lille.fr)

Abstract

Contextual motor learning of saccades has faced an unresolved issue of inefficient learning despite seemingly ideal settings, particularly when using perceptual cues as contexts. By relating this problem to motor control theories, advances in the understanding of the motor cortex, and evidence from force field adaptation, we proposed a paradigm that enables the separation of perception, execution, and planning of motor actions. Previous studies have demonstrated that movement sharing a similar initial trajectory but diverging later exhibits different neural states, even in this initial part. When saccades are planned together in a sequence, the later saccade would therefore modify the plan of the first one. This allowed us to establish conditions in which a cue is used as a percept, or as a motor cue, within or outside a saccade sequence. Our results showed that participants would learn to adapt only when the motor cue is within the saccade sequence. This finding strengthens the empirical evidence that the motor system is specialized in discriminating different motor plans. At the same time, it is insensitive to motor executive and purely perceptual components of the cues.

Keywords: Contextual learning; Saccade adaptation; Motor memories; Planning; Execution; Perception

7.1.1. Introduction

Motor adaptation is a fundamental process that enables a sensorimotor system to gradually adjust motor commands to maintain accuracy and minimize errors, compensating for the continuous changes in motor systems. Studies on the oculomotor and arm movement systems have shown that, although their neural circuits differ, saccades share key features with arm movement for contextual adaptation (Heald et al., 2023). Insights from one effector system can therefore inform our understanding of the other.

Saccadic adaptation refers to the continuous modification of saccade movements to reduce endpoint errors and preserve spatial accuracy. Saccades are fast, ballistic eye movements that redirect the fovea, the region of highest visual acuity, toward objects of interest. In laboratory settings, saccadic adaptation is typically induced using the double step paradigm, in which the target undergoes an intra-saccadic step (ISS), i.e., a displacement during the saccade. Due to the movement's brevity, visual feedback cannot guide them in real time, and the motor command must be specified in advance. Participants usually remain unaware of this spatial perturbation (Bridgeman et al., 1975; Wexler & Collins, 2014), allowing for the probing of implicit forms of motor learning. It is well established that the post-saccadic position error induced by the ISS drives changes in the saccade metrics (for a review, see Pélisson et al., 2010). Specifically, saccadic adaptation is thought to be driven by prediction error, i.e. the discrepancy between the expected and actual post-saccadic retinal image (Bahcall & Kowler, 2000; Collins & Wallman, 2012; Wong & Shelhamer, 2011). The implicit nature of this process, coupled with participants’ unawareness of target displacement, further underscores its status as an implicit and robust learning mechanism.

Saccadic adaptation does not generalize across directions, an observation that gave rise to the concept of gain fields, whereby adaptation is confined to restricted regions of the oculomotor space rather than reflecting a global change in saccade metrics (Rolfs et al., 2010). This specificity suggests that adaptation is better understood as a learning process guided by contextual information. In this framework, contextual adaptation refers to situations in which changes in saccade endpoints depend on the behavioral context in which the movement is performed. Systematic investigations have shown that contextual saccadic adaptation can be driven by motor-related cues, such as orbital starting position (Albano, 1996; Deubel, 1995; Miller et al., 1981) or saccade direction (Chen-Harris et al., 2008; Xu-Wilson et al., 2009), which provide reliable signals for distinguishing motor states. In contrast, early work suggested that adaptation was insensitive to simple visual features such as target color and shape (Azadi & Harwood, 2014; Benjamin et al., 2016; Cecala et al., 2015; Deubel, 1995). This view has been reinforced by recent work from Martel and Madelain (Martel & Madelain, 2025), who systematically compared a broad range of potential contextual cues. Their findings reveal a striking dissociation: while motor-related cues such as starting position or the amplitude of an initial step reliably produced robust contextual adaptation, non-motor cues—including target color and shape, symbolic markers, or statistical regularities of the outcome—failed to do so, even while participants can explicitly perceive and report them. These results highlight the remarkable selectivity of the oculomotor system, which prioritizes motor-relevant cues and disregards other kinds of features to support adaptation.

Azadi and Harwood (Azadi & Harwood, 2014) suggested that the contextual signal might arise not from vision alone, but from motor plans associated with pursuit eye movements. More recently, Azadi and McPeek (Azadi & McPeek, 2022) showed that saccades executed within a sequence are highly sensitive to the properties of neighboring saccades. They demonstrated that the existence, direction, amplitude, and even ordinal position of preceding or following saccades within a sequence could all serve as contextual cues that drive adaptation. These findings support the hypothesis that sequential saccades are planned concurrently rather than independently, and that motor programs for future saccades are integrated into the motor plan together with the current one.

These observations resonate with findings in force field adaptation, where the role of planning in structuring motor memory in arm movements has been investigated. Sheahan, Franklin, and Wolpert (Sheahan et al., 2016) demonstrated that planning, rather than execution, is the decisive factor for the formation and discrimination of motor memories. In their experiments, participants learned to adapt to two opposing force fields when each field was associated with a distinct planned follow-through movement. Crucially, learning occurred even if the follow-through was not executed, but only planned. In contrast, when different follow-throughs were executed without being planned together, participants failed to learn and showed no discrimination of motor memories. These findings demonstrate that execution alone is insufficient for driving force field adaptation, and that motor planning establishes distinct neural states in the motor cortex that serve as the substrate for discrimination.

Despite the convergence between force field and saccade adaptation processes, the role of motor planning in saccadic adaptation has not yet been directly tested. While Azadi and McPeek (Azadi & McPeek, 2022) demonstrated concurrent planning within saccadic sequences, no study has explicitly dissociated the planning and execution of a subsequent saccade as potential contextual cues for the adaptation of a preceding saccade. The present study addresses this question through four experimental conditions that manipulate the relationship between planning and execution of a second saccade. Specifically, we test whether the mere planning of a second saccade, independent of its execution, can serve as a sufficient contextual signal to drive differential adaptation of a primary saccade. To this end, we first designed a Full Sequence experiment in which a saccade sequence is both planned and executed, and a Single Saccade experiment in which only the first saccade was planned and executed. These two experiments aimed to replicate Azadi and McPeek's results showing learning induced by saccade sequence, and to illustrate the failure of learning when there is no second saccade. In an Execution Only experiment, the delayed presentation of the cue for the second saccade ensured that participants executed the sequence without simultaneous planning. Lastly, in a Planning Only experiment, the saccade sequence was planned but canceled before execution of the second saccade.

By directly testing this hypothesis, the present study aims to establish whether motor planning, rather than execution, is the critical determinant of context-dependent saccadic adaptation. Such a finding would provide fundamental evidence for a unified principle of motor learning across effectors, underscoring the central role of internal motor plans and distinct preparatory neural states in shaping adaptive behavior.

7.1.2. Results

Participants fixated on a central white target and were instructed to make a saccade when it stepped, followed by a second saccade toward a green peripheral target. At the onset of the first saccade, the primary target stepped again - an intra-saccadic step (ISS) - in a North-West or South-East direction following a pseudo-random list. During learning trials, the direction of the ISS was consistently paired with the location of the secondary target, either in the top-left or in the bottom-right corner of the screen (see Figure 29).

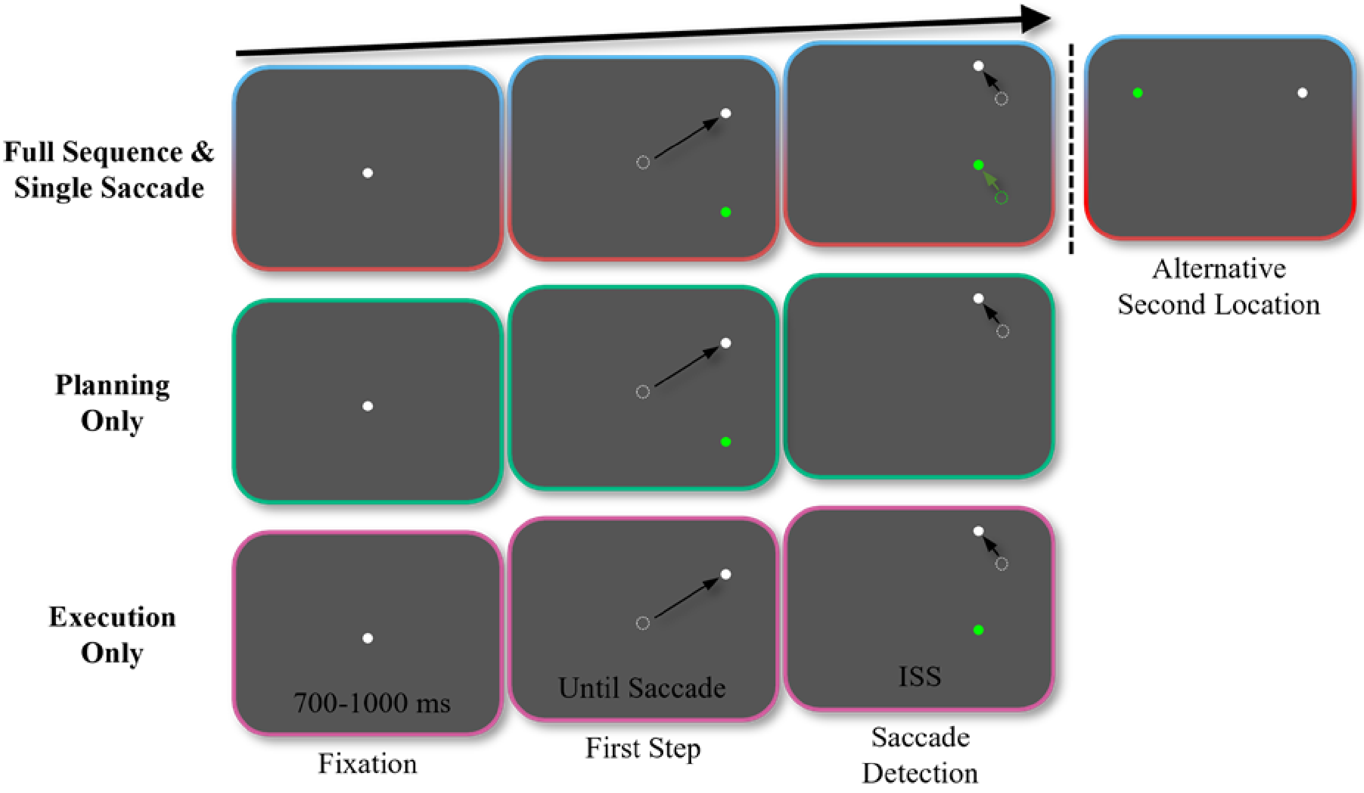

Figure 29. Schematic of a trial for all experiments. ***1:*** *The fixation point is present for a random period [700ms 1000ms] at P0.* ***2:*** *The primary target steps, with a 45° angle upward and rightward and a pseudo-random amplitude [5.5°; 7°; 8.5° or 10.1°] at P1. The secondary target appears simultaneously, except in the Execution Only experiment.* ***3:*** *When a saccade is detected, the primary target steps again during the movement, to P2. The ISS amplitude is 20% of the amplitude of the first step. The direction of the intra-saccadic step was either North-West or South-East (only the North-West ISS is shown here). In the Full Sequence and Single Saccade experiments, the secondary target moves in tandem with the primary target. In the Planning experiment, the secondary target disappears, whereas in the Execution Only experiment, it appears. In all trials, the secondary target location was either Bottom left, as represented in the main part of this schematic, or Top right, as represented in the Alternative Location panel.*

In the Full Sequence experiment, participants were instructed to always make a saccade toward the primary target, followed by a saccade toward the secondary target (see Figure 29). Figure 30.A plots the data from participant 8, illustrating the typical pattern observed in learners during the Full Sequence experiment. The trials are sorted by the two possible locations of the secondary target. For each participant, significant differences in saccade angle between the two contexts were estimated using a nonparametric permutation test on the difference in medians, with 100,000 permutations.

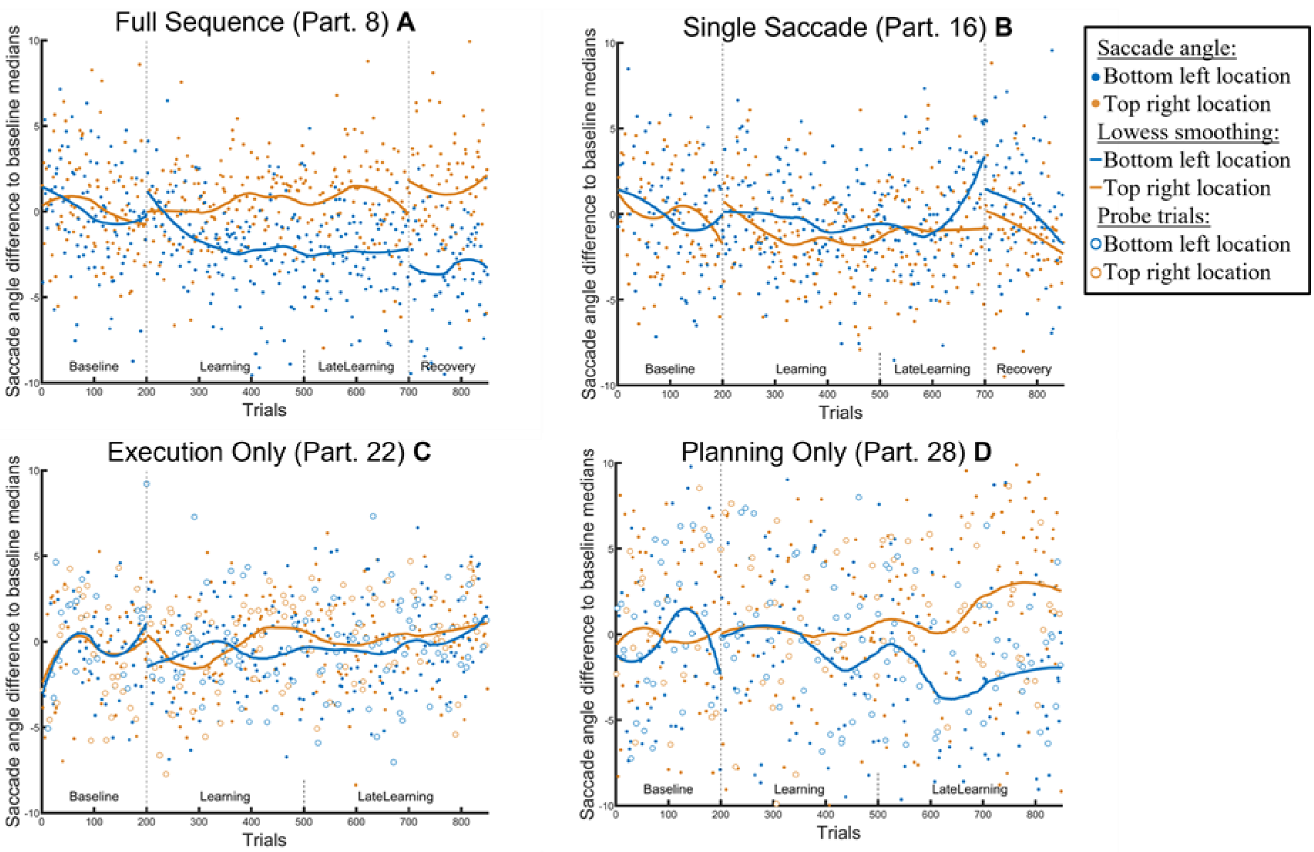

Figure 30. Individual plots of a typical participant for each experiment. ***A:*** *Participant 8 from the Full Sequence experiment. Each point plots the saccade angle difference to the baseline in a trial expressed in degrees, which is the saccade angle of the trial subtracted from the median saccade angle for that context in the baseline trials. Solid lines are the Lowess smoothing of saccade angle differences to baseline with a 100-trial moving window. Orange represents trials with the secondary target located at the top right, and blue represents trials with the secondary target located at the bottom left. For this participant, the top right location was paired with the North-West ISS, and the bottom left location was paired with the South-East ISS during learning trials. Bottom labels indicate the baseline (1-200), learning (201–500), late learning (501–700), and recovery (701–850) trials.* ***B:*** *Participant 16 from the Single Saccade experiment. All conventions are as in A.* ***C:*** *Participant 22 from the Execution Only experiment. Learning trials extend to trial 850, extending the late-learning trial window from 501 to 850. Empty discs represent the probe trials.* ***D:*** *Participant 28 from the Planning Only experiment. All conventions are as in C.*

A Lowess smoothing (with a 100-trial window) was applied to fit the general trends across the three experimental phases. After the baseline trials (first 200 trials) in which the secondary target location and the ISS were not paired, saccade angle difference increased during the learning trials (trials 201 to 700) - i.e., saccade angles increased in trials in which the secondary target was at the top right location, paired with the North-West ISS, and decreased in trials in which the secondary target was at the bottom left location, paired with the South-East ISS.

The difference between the two medians of the saccade angles in the late-learning trials (trials 501 to 700) was statistically significant for this participant (Difference of 3.52° with respect to the baseline median and greater than 1.19, the null hypothesis at 97.5% CI). At the group level, we similarly compared the medians of the two locations for the late-learning trials (trials 501-700) for each participant. Five out of the eight participants showed a significant difference in saccade angle between contexts (mean difference = 1.78, Maximum = 4.65, Minimum = -1.81), indicating that they accurately predicted and adjusted their saccades toward the primary target to minimize retinal error, depending on the secondary target location. A Kolmogorov-Smirnov analysis, which provides a measure of the distance between the two distributions of saccades, revealed a mean distance of 0.27 (Maximum = 0.54; minimum = 0.11; see Figure 31.A).

In the Single Saccade experiment, participants had the same visual display and pairing between events as described for the Full sequence experiment (Figure 29). However, they were instructed to stop after the primary target, i.e., without performing a saccade toward the secondary target. Figure 30.B plots the data from participant 16, which illustrates the typical patterns of results we observed in non-learner participants in the experiment, Single Saccade. All conventions are similar to those previously described for the Full Sequence experiment. After the baseline trials (the first 200 trials), in which the secondary target location and the ISS were not paired, the saccade angle difference remained stable during the learning trials (trials 201 to 700). The difference between the two median saccade angles in the late-learning trials (trials 501 to 700) was not statistically significant for this participant (Difference of -0.58° with respect to the baseline median and inferior to 1.21°, the null hypothesis at 97.5% CI).

At the group level, we compared medians of the two contexts for the last 200 learning trials (trials 501 to 700) for each participant. The comparison revealed no significant learning for any participant in this experiment (Mean difference = -0.08, Maximum = 1.89, Minimum = -2.51). A Kolmogorov-Smirnov analysis of the late-learning distributions revealed a mean distance of 0.19 (Maximum = 0.43, Minimum = 0.10; see Figure 31.A).

In the Execution Only experiment, the secondary target did not appear simultaneously with the primary target but together with the ISS, at saccade detection (Figure 29). This change in the order of the trial event led the participant not to perceive the secondary target before executing his first saccade; therefore, he was unable to plan the sequence of the two saccades. Participants were instructed to always perform the full saccade sequence. In this case, learning may arise from a retroactive association between the secondary target and/or the executed second saccade and the ISS. Due to this time arrangement, participants can't express contextual learning during Execution-only trials, as the context appears after the first saccade. To allow participants to express learning, one-third of the trials were probe trials. Probe trials were similar to Full Sequence trials; however, they were not consistently paired with an ISS direction to avoid learning that occurs specifically through those trials. Probe trials were present in both the baseline and learning phases. Because in one-third of the learning trials, the ISS wasn't paired with the location of the secondary target, learning trials were extended from trial 201 to trial 850, removing the recovery trials and maximizing the learning window.

Figure 30.C plots the data from participant 22, illustrating the typical patterns of results observed in non-learner participants in the experiment Execution Only. The trials are sorted by the two possible locations of the secondary target. Execution only trials are represented by colored disks, and probe trials are represented by a large colored ring. The difference in the first saccade angle normalized to the baseline medians is plotted as a function of the trial number. A Lowess smoothing (with a 100-trial window) fits the data to illustrate the general trends across the three experimental phases. After the baseline trials (first 200 trials) in which the secondary target location and the ISS were not paired, the saccade angle difference remained stable during the learning trials (trials 201 to 850). The difference between the two median saccade angles in the probe late-learning trials (from probe trials between 501 and 850) was not statistically significant for this participant (Difference of -1.44° with respect to the baseline median and inferior to 1.64°, the null hypothesis at 97.5% CI).

At the group level, we compared medians of the two contexts for the last probe learning trials (I.e., trials 501 to 850) for each participant. The comparison showed that no significant learning occurred for any of the participants in this experiment (Mean diff = 0.40, Max = 2.87, Min = -1.44). A Kolmogorov-Smirnov analysis of the late-learning distributions revealed a mean distance of 0.16 (Max=0.27; Min=0.09; see Figure 31.B).

In the Planning experiment (Figure 29), the first target and the secondary target appeared simultaneously, but the secondary target disappeared at the participant's saccade detection. Participants were instructed to stop after the first saccade if the secondary target was no longer present. The position of the secondary target dot was consistently paired with the ISS direction during learning trials. As for the Execution experiment, one-third of the trials were probe trials, ensuring that participants continued to plan the second saccade of the sequence, as well as for a fair comparison between groups. Because of the disappearance of the secondary target at saccade onset, participants weren't able to execute the second saccade of the sequence. However, learning could occur through an association of the initial motor plan and the ISS. Figure 30.D plots the data from participant 28, illustrating the typical patterns of results we observed in learner participants in the Planning experiment. All conventions are similar to those previously described for the Execution Only experiment. In contrast to the Execution experiment, saccade angles depending on the cue differ increasingly in the learning trials. The difference between the two median saccade angles in the probe late-learning trials (from probe trials 501 to 850) was statistically significant for this participant (Difference of 2.27° with respect to the baseline median and greater than 2.19°, the null hypothesis at 97.5% CI).

At the group level, we compared the medians of the two contexts for the last probe learning trials (i.e., trials 501-850) for each participant. The comparison revealed significant learning for four out of the eight participants in this experiment (Mean difference = 2.21, Maximum = 4.78, Minimum = -1.52). A Kolmogorov-Smirnov analysis of the late-learning distributions revealed a mean distance of 0.33 (Maximum = 0.64, Minimum = 0.11; see Figure 31.B).

Additionally, because participants perceived the contextual cue from the beginning of all trials, they were able to adapt their first saccade accordingly during both probe trials and planning trials. A similar bootstrap analysis to that for the Full Sequence and Single saccade experiment, comparing contexts for trials 500 to 700, reveals that six out of eight participants show a significant difference (Mean = 3.22, Maximum = 5.62, Minimum = 0.25). The Kolmogorov-Smirnov analysis of these late-learning distributions revealed a mean distance of 0.34 (Maximum = 0.55, Minimum = 0.14; see Figure 31.A).

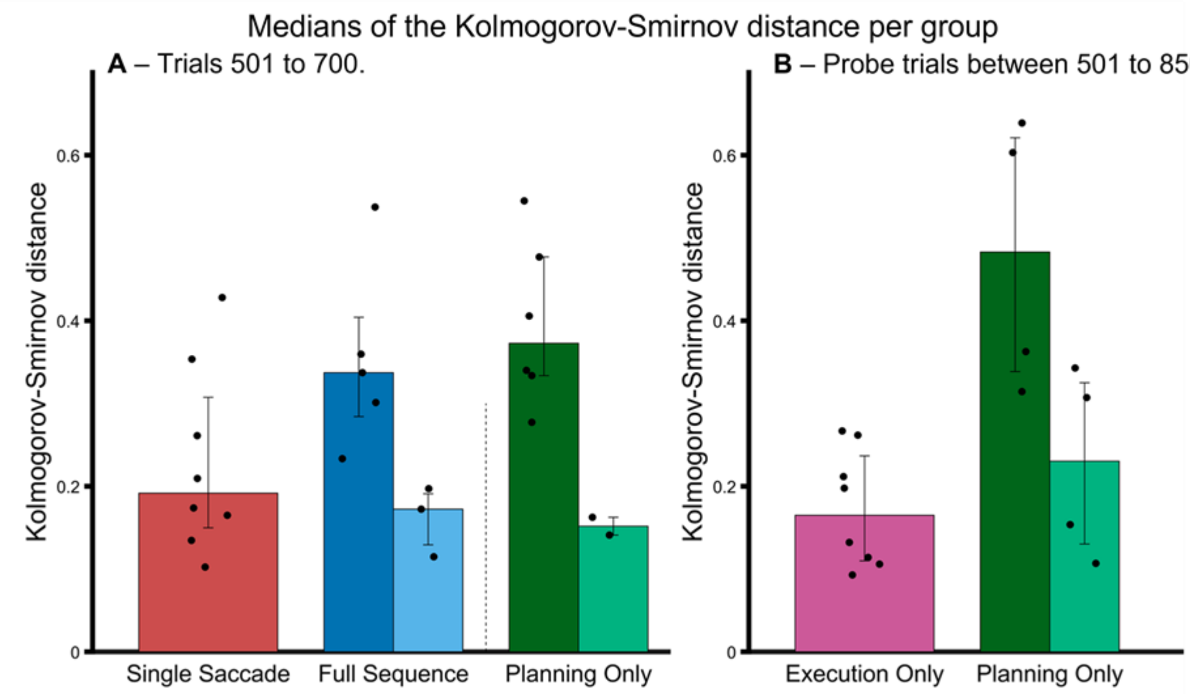

Figure 31. Median and inter-quartile range of the Kolmogorov–Smirnov distance for all experiments. Panel A is the Kolmogorov distance for trials 500 to 700 for experiments Single Saccade, Full Sequence, and Planning Only. Panel B is the Kolmogorov distance for probe trials between 500 to 850, for experiments Execution Only and Planning Only. In experiments with both learners and non-learners, the two groups are separated.

7.1.3. Discussion

In this study, we demonstrated that the planning component of the saccade is the key component for contextual learning, while neither motor execution alone nor mere perception of a peripheral target location was sufficient. We used a saccadic adaptation paradigm in which the saccade sequence served as the contextual cue, and compared learning efficiency across conditions: when the full saccade sequence was executed (*Full Saccade Sequence* experiment), when the target was present but not fixated (*Single Saccade* experiment), and when either motor execution or motor planning was isolated (*Execution Only* and *Planning Only* experiments). These findings further support the idea that saccades made within a movement sequence are planned concurrently rather than independently (Azadi & McPeek, 2022; Caspi et al., 2004), and demonstrate that the locus of learning in saccade adaptation lies primarily at the level of motor planning.

In the Full Sequence experiment - replicating Azadi & McPeek's method (Azadi & McPeek, 2022, experiment 3) with slight changes such as the diagonal step and the absence of an oriented cue to provide information about the direction - we ensured and confirmed the efficiency of saccade sequences to induce contextual learning and demonstrated that no other manipulation than the statistical contingencies of the specific sequence paired with an ISS was sufficient for this learning. We found clear evidence of contextual learning in 5 out of 8 participants, indicating a significant difference in the angles of the first saccade depending on the location of the second saccade within the sequence. This demonstrates the robustness of this contextual learning setting and further confirms the concurrent rather than independent plan of the two saccades of the sequence.

Using the same experimental settings, only with a different instruction, we asked participants to ignore the secondary target in the Single Saccade experiment. None of the eight participants showed contextual learning, replicating the absence of learning when perceptual, non-motor cues are used in contextual saccadic adaptation (Azadi & Harwood, 2014; Bahcall & Kowler, 2000; Cecala et al., 2015; Deubel, 1995; Martel & Madelain, 2025). Moreover, in a discussion about saccade sequences, Azadi & McPeek (Azadi & McPeek, 2022) emphasized the interaction between the saccades of a sequence during both planning and execution. Our results from the Full Sequence experiment are consistent with their findings, suggesting that the presence of a sequence facilitates learning, whereas its absence in the Single Saccade experiment results in no learning. This also aligns with previous work, which shows that perceptual features located away from the saccade trajectory are irrelevant to saccadic control (Walker et al., 1997). These findings raise the question of whether the critical factor is motor planning, motor execution, or their combination. Inspired by Sheahan et al. (Sheahan et al., 2016) in the context of force field adaptation, we addressed this question by designing two additional experiments to isolate the planning and execution components of the second saccade in the sequence.

The Execution-Only experiment prevented participants from planning the saccade sequence by providing the location of the secondary target after the saccade toward the primary target had begun. As a result, none of the participants showed contextual learning. This absence of learning has been measured using probe trials only, which allow participants to express their learning. These results align with previous findings on force field adaptation, suggesting that the motor execution of a movement has little effect on adapting the movement to the environment. Note that for learning to happen, the system should have associated the ISS with the upcoming second saccade, and then reuse it in the probe trials.

Lastly, the Planning Only experiment prevented participants from executing the second saccade of the sequence, while ensuring the planning of this sequence by the presence of probe trials. Looking at the probe trials only, 4 out of 8 participants showed significant contextual learning, and 6 out of 8 participants showed significant learning when performing the same analysis as for the Full Saccade Sequence and the Single Saccade experiments. Those results indicate that the execution component of the motor movement is inefficient to induce motor learning, while the planning component is efficient to do so, but additionally, the Planning Only experiments led to very similar results compared to the Full Saccade Sequence experiments, showing that removing the execution part did not affect the participant's learning process. This strongly suggests that planning is the locus of learning for discriminating between motor memories.

An important point to highlight is that our paradigm has some major differences compared to Sheahan et al (Sheahan et al., 2016), even though both were designed to probe a similar mechanism. First, in our case, the ISS is almost imperceptible to participants, and most of them report not being aware of it until the debrief at the end of the experimental session. In contrast, during force field adaptation, the presence or absence of the force field is explicitly apparent to the participant. This point may lead to some differences in the speed and strength of learning acquisition, with top-down mechanisms eventually playing a more significant role in force field adaptation. However, the implicit learning still seems to be the major factor in both paradigms, as we obtain similar results even in the Single Saccade experiment, in which the perceptual cue itself doesn't lead to contextual learning despite the participant having all the necessary information to adapt to the contexts.

A second major difference concerns timing. In force field adaptation, perception of the cue and the motor response arise from separate systems, and trial initiation is delayed by an additional 300ms after cue onset. By contrast, in saccadic adaptation, planning and execution rely on the same system, and the trial is effectively complete once the saccade is initiated toward the primary target. Reaction times are also much shorter in our paradigm (100–250ms), compared to the enforced delays in force field tasks. Moreover, Sheahan et al. imposed a strict temporal constraint—requiring movements to fall within a specific window—in order to elicit learning. No such constraint was necessary in our case, as adaptation occurred reliably without it. One plausible explanation lies in the difference between online and offline motor systems: arm movements may begin before planning is complete, thereby reducing the stability of adaptation. In contrast, saccades exhibit a tighter integration of planning and execution, which may enhance robustness.

Importantly, these methodological differences did not translate into divergent outcomes. This convergence is particularly noteworthy, as it underscores the relative independence of perceptual and motor mechanisms. Whether perception and action arise from the same or from distinct systems, and whether the delay between target onset and movement initiation is short or long, the resulting motor adaptation appears remarkably consistent.

Beyond these differences between eye and arm movements this critical function of planning for motor learning, both in saccade and force field adaptation, raises an observation on learning mechanisms. Both in force field adaptation and in saccades, contextual learning has been performed with various kinds of motor cues, allowing learning to occur. However, a closer look at participants' learning, depending on those cues, shows that their motor adaptation is not always consistent within similar experimental sessions. For instance, when comparing the Planning Only and Full Saccade Sequence experiments, we find that they produce very similar learning rates and patterns across participants, with some interindividual variability. However, comparing this with our previous study, which used comparable experimental settings (Martel & Madelain, 2025), we note that the present findings more closely resemble those of our Starting Location experiment than those of the First Step Amplitude experiment, the latter leading to much stronger and more systematic learning among participants. This phenomenon is not observed only for saccades, as 40% to 50% of force field adaptation was reported for the Planning Only and Full Follow Through experiments by Sheahan et al., which is comparable to the cues Visual Feedback Location used by Howards et al (Howard et al., 2013) in a very similar paradigm, while other cues such as proprioceptive location or workspace locations leads to up to 70% of force field adaptation for participants. These results, taken together, indicate that if a change in the motor plan is a critical component, its absence or presence is more than a binary factor in learning. One way to understand this is to consider it from a discrimination perspective: the neural state for a specific motor plan comes with a certain amount of noise, and the system must disentangle between two different memories of plans or the same plan with the addition of noise in the system. Therefore, if the planning differs significantly between two contextual cues, the discrimination might be easier and, consequently, lead to a quicker and/or stronger adaptation of the motor response. A second and complementary idea is that the motor plan is a necessary component, but not the only one, to play a role in motor learning.

Conclusion

This study demonstrated that in saccadic adaptation, the planning component of the motor response enables the learning and expression of multiple motor memories. Despite some differences in the paradigm and the system itself, we demonstrated that these results were analogous to those previously shown in force field adaptation. This extends to the visuo-motor system and, ultimately, to motor learning in general: the specific neural state of a motor plan coding for an action is the critical component for discriminating between different motor memories and learning.

7.1.4. Materials and methods

Participants

Thirty-four participants were recruited, and thirty-two met the criterion for data analysis (Two participants were under the criterion of valid saccades after pre-processing). All participants (22 females and 10 males, aged 19-31) were naïve to the purpose of the experiment, had normal or corrected-to-normal vision, and were randomly assigned to four experiments. Participants' consent was based on non-opposition, which was stipulated in the information letter sent during recruitment. All experimental procedures received approval from the Ethical Committee in Behavioral Sciences of the University of Lille (Agreement No. 2022-647-S111) and conformed to the standards set by the Declaration of Helsinki.

Apparatus

Participants sat in a dark and quiet room facing the display monitor (Iiyama HM204DT, 100Hz, 22 inches) with their heads stabilized via chin and forehead rests (60cm from the screen). Stimuli were generated and displayed using the Psychophysics Toolbox Extension (Brainard, 1997; Pelli, 1997)for Matlab®. Recording of the right eye position was performed by an SR-Research Eyelink 1000+ Tower Mount system, sampling at 2000Hz. We used the Eyelink 13-point calibration and validation routines at the beginning of the recording sessions.

Procedure

The purpose of this study was to compare the effect of planning versus execution processes in contextual saccadic adaptation across four experiments.

In Experiment 1, Full Saccade Sequence (n=8), we employed a double-step paradigm in which participants were required to perform a sequence of two saccades. The fixation point was always in the center of the screen, the primary target was always located upward and to the right of the fixation point, and the secondary target was located either downward from the primary target symmetrically to the fixation point, or leftward from the primary target symmetrically to the fixation point (see Figure 29). At saccade detection, the primary target stepped during the participant's saccade (intra-saccadic step, ISS) either upward and backward (North-West) or downward and forward (South-East). The primary and secondary targets experienced the ISS simultaneously for all trials.

For each trial, the stimulus location was identical across all experiments; only the temporality and the instructions changed. The fixation target, a grey disk (0.4° diameter; luminance 12.1 cd/m²), was displayed for a random duration ranging from 700 to 1000ms (drawn from a uniform distribution) against a grey background (luminance 1.7 cd/m²). During the fixation period, the fixation dot was always displayed at the same location (P0, centered on the screen). The primary target was then displaced following a 45° vector upward and rightward with four possible step amplitudes (4°, 4.7°, 5.4°, and 6°, pseudo-randomly). The secondary target was a green disc (0.4° diameter; Luminance 12.1 cd/m2), positioned at the same eccentricity as the primary target relative to the fixation point. Participants were instructed to saccade toward the white (primary) target first, then toward the green (secondary) target. The online saccade detection corresponded to eye position crossing an invisible boundary 3dva from the fixation location. If a change in eye position was detected within an 80-ms to 350-ms temporal window following the first step, the ISS was triggered and the target stepped at P2 during the saccade. The green cue always had the same ISS as the target. The ISS direction was perpendicular (90°) to the first step of the target, and its amplitude was set to 20% of the first step. Importantly, the primary target experienced an ISS in every trial in which a correct saccade was detected, including the baseline and recovery trials. Following the ISS, the primary target and the secondary cue remained visible for 500ms. A unique trial list of pseudo-random ISS directions and first steps was used in all experiments, such that every participant experienced the same series of trial characteristics. If a saccade was detected either before 80ms or after 350ms with respect to the first step onset, the trial was terminated before the ISS occurred, the target was extinguished, and a sound (100ms at 500 HZ) was played to signal the end of the trial.

Before any experiments, participants experienced a training session. Instructions were displayed on the screen, explaining how to position the eye recording setup and describing the task. The given instructions were identical to those for the assigned experiment. Then, following a 13-point calibration, a 50-trial training session began to familiarize the participants with the temporal sequence of a trial. Training trials were constructed in a similar way to the baseline trials of the assigned experiment. Training sessions were repeated until a minimum of 75% of correct saccades were recorded.

After training, a second 13-point calibration and validation were performed, followed by the start of the experimental session. Each session consisted of 850 double-step trials, comprising 200 baseline trials and 500 learning trials. In the Full Sequence and Single Saccade experiments, trials 700 to 850 served as recovery trials, identical to the baseline. In the Execution Only and Planning Only experiments, learning trials continued from trial 700 to 850, without a recovery phase. For each experiment, the two contextual cues were the location of the secondary target. The contextual cues and ISS were present during the whole experiment, but the cues and the ISS were paired only during the learning trials – e.g., the ISS would consistently be North-West for a secondary target at the bottom right location and the ISS would be South-East for a secondary target at the top right location (counterbalanced across participants). In the baseline and in the recovery trials, there was no systematic cue to ISS pairing, and instead, for each trial the target had 50% chances to have a North-West directed or a South-East directed ISS. There were no other differences between the baseline and the learning trials, and participants were not informed about the different types of trials they would experience, nor about the presence of an ISS. Across the experiment, participants experienced short breaks every 50 trials. Rest intervals have been reported to facilitate contextual adaptation (Ethier et al., 2008b). Following these breaks the calibration accuracy was estimated again and the experimenter would perform a new 13-point calibration if needed.

Experiments 2-4 were similar to Experiment 1, except for the following details: In Experiment 2, Single Saccade (n=8), participants were instructed to perform a saccade to the primary target and to stop there, ignoring the secondary target. The location of the secondary target served as a contextual cue. In this experiment, participants neither planned nor executed the second saccade in any trial.

In Experiment 3, Single Saccade (n = 8), participants were instructed to perform a saccade to the primary target and then to the secondary target. The location of the secondary target served as a contextual cue. Two-thirds of the trials were Execution Only trials, meaning that the secondary target appeared only at saccade detection. This made it impossible for participants to plan the saccade sequence before the onset of their saccade. The remaining one-third of the trials were probe trials. Probe trials were identical to Full Saccade Sequence trials as described above, but in those trials, the ISS was randomly paired with a secondary cue location. his random allocation of the ISS in the probe trials prevented learning from occurring in these trials, during which participants performed both the planning and execution of the saccade. Participants were instructed to always perform the two saccades. In this experiment, participants did not plan but did execute the second saccade of the sequence in 66% of the trials.

In Experiment 4, Planning Only (n = 8), participants were instructed to perform a saccade to the primary target, then to the secondary target unless it disappeared. The location of the secondary target served as a contextual cue. For two-thirds of the trials, the secondary target disappeared at saccade detection, preventing the second saccade of the sequence from being executed but allowing planning of that second saccade before the onset of the saccade sequence. The remaining one-third of the trials were probe trials. As described previously, probe trials were identical to Full Saccade Sequence trials described above, but the ISS was never consistently paired with a secondary cue location to prevent learning from happening in those trials. In this experiment, participants planned but did not execute the second saccade of the sequence in 66% of the trials.

Processing of saccades

We used the Eyelink online saccade detector to identify saccade onset and offset, using 30°/s velocity and 8000°/s^2 acceleration thresholds. In all trials, we only considered the first recorded saccade following the first target step. Before statistical analysis, a human observer manually validated each saccade. Incorrect saccades, saccades with a gain lower than 0.5 or higher than 1.5, saccades with latency shorter than 80ms or longer than 400ms, and saccades that were not directed toward the target (more than 45° away from the target vector angle) were then excluded from further analyses. A criterion of 75% correct saccades per participant was used to include the participants and perform further statistical analysis.

Saccade angles were computed by drawing a line between the saccade starting point and endpoint, and measuring its angle relative to the horizontal axis. For each participant, we calculated the median saccade angle during baseline trials for both secondary target locations. These median values were then subtracted from all corresponding saccade angles, ensuring that the resulting values were centered around 0°. In this normalized space, complete adaptation corresponds to a change of +11.3° for North-East ISS and -11.3° for South-West ISS.

Statistical Analysis

We used bootstrapping methods (resampling with replacement 100,000 times) to estimate the 97.5% confidence intervals of the medians [CIs;(Efron, 1992)]. For each participant, significant differences between the two contexts in the median angle of the first saccade were estimated using a nonparametric permutation test (100,000 permutations). Permutation-based tests were implemented using custom routines in MATLAB. For the Full Sequence and Single Saccade experiments, this test was performed on the last 200 learning trials (trials 501-700). For Execution-Only and Planning-Only experiments, the same test was used on probe trials from trial 501 to 850, comparing the angle of the first saccade.

To quantify the normalized difference between the angle of saccades performed in each context, we computed the Kolmogorov–Smirnov (KS) distance. The KS distance computes the normalized amount of overlap between the two distributions of late-learning saccade angle differences from baseline for each participant. A distance of 0 implies that the two distributions perfectly overlap, while a distance of 1 implies that there is no overlap between the two distributions (i.e., perfect discrimination between the contexts).

Part III

GENERAL DISCUSSION

8. Discussion

8.1. Experimental contribution

The experimental contribution of this thesis was driven by the objective of exploring a selectivity effect in human learning, pursued through the implementation of a motor learning paradigm based on saccadic eye movements.

8.1.1. Demonstration of the selectivity of learning

The first study presented in this thesis, in Section 6, investigated whether different types of contextual cues can drive contextual saccadic adaptation using a double-step paradigm with oblique saccades and off-axis intra-saccadic steps. Across 11 experiments, 106 participants performed saccades toward targets that underwent intra-saccadic steps (ISS) in one of two orthogonal directions (North-West or South-East). The key manipulation was the cue paired with each ISS direction during the learning trials. Tested cues included two motor-related cues (first-step amplitude and target starting location) and seven non-motor cues: target color and shape, symbolic cue, stimulus duration, lateralized sounds, and three different statistical regularities across trial sequences. In two additional experiments, participants were asked to report the cue they had just seen to ensure perception. Each experiment consisted of baseline trials (random cue–ISS pairing), learning trials (systematic pairing), and recovery trials (random cue–ISS pairing again). Eye movements were recorded with high-resolution eye tracking, and adaptation was assessed by changes in saccade angle relative to baseline.

Results demonstrated a striking dissociation between cue types. Motor cues were effective: First-step amplitude (small vs. large) produced robust and systematic context-specific adaptation across participants; Starting location also elicited contextual adaptation in most participants, though to a lesser extent compared to the first-step amplitude. On the other hand, nonmotor cues systematically failed to elicit learning: Color/shape, symbolic cues, auditory lateralization, stimulus duration, and statistical regularities did not produce reliable contextual learning. Even when participants were asked to report these nonmotor cues (>85% correct), no systematic adaptation occurred. Only the motor cues yielded significant differences in saccade angle distributions across contexts, quantified by Kolmogorov–Smirnov distances substantially larger than for nonmotor cues.

Together, findings from this study demonstrate a clear selectivity of the saccadic circuitry for motor-relevant contextual cues. In line with other research(Alahyane & Pelisson, 2004; Azadi & Harwood, 2014; Azadi & McPeek, 2022; Chaturvedi & Van Gisbergen, 1997; Shelhamer et al., 2002; Zimmermann & Lappe, 2011), contextual adaptation occurred only when cues directly modified the motor parameters of the saccade (e.g., amplitude or starting position). In contrast, purely perceptual or symbolic cues—even when explicitly processed—were ineffective. The results extend previous work showing the inefficiency of color and shape cues (Azadi & Harwood, 2014; Benjamin et al., 2016; Cecala et al., 2015; Deubel, 1995), and further establish that contextual saccadic adaptation is constrained by the motor relevance of contextual information. This dissociation suggests that only cues relevant to the function of spatial targeting are effective, consistent with the hypothesis of selectivity of learning, in which cues are efficient if they align with the system they are part of. In evolutionary terms, the system appears tuned to ignore non-motor signals for learning, reflecting its specialization for fast, precise spatial orienting.

We extended the results of this study with three additional experiments, investigating the remote distractor effect as well as two temporal manipulations. First, the remote distractor effect was particularly relevant because learning was induced by the addition of a distractor, while the information relevant to the movement—the starting and ending points—remained irrelevant for adaptation, demonstrating that the discrimination was carried by the change in the kinematics of the saccade. Moreover, since a distractor was systematically present but with a different location, this ensures that discrimination relied on the specific change brought by each of the distractor locations. Despite inducing kinematic change on saccades, the remote distractor experiment led to a reliable contextual learning, with an extent comparable to ones induced by our manipulation of the starting location when considering the Kolmogorov-Smirnov distance of the difference between contexts.

We additionally explored temporal properties of saccades through the Gap and Overlap paradigm (Kalesnykas & Hallett, 1987; Reuter-Lorenz et al., 1991; Saslow, 1967; Vencato et al., 2022) and manipulation of the fixation duration. These experiments aimed to delve deeper into the sensitivity of the system to temporal manipulation, compared to the duration of the cue present in the first study. With the duration of a cue (experiment 1), the perception of time was purely perceptual and did not affect the motor component of the saccades.

However, timing is obviously a relevant and functional factor in saccades, as it is for any motor behavior to perform accurate movement in a dynamic environment (Li et al., 2018; López-Moliner et al., 2007, 2010; Mrotek & Soechting, 2007). For example, interception of moving targets requires estimation of the speed and, therefore, a sense of timing. For this reason, we expected the manipulation of the saccade's timings to lead to a systematic differential learning effect. Surprisingly, despite a clear effect on those settings on the participants' behavior, with an effect on latencies and fixation durations, they both show limited and inconsistent control on contextual saccadic adaptation. One way to interpret these results is that the sensitivity of the system to timing is weaker compared to its sensitivity to parameters of the saccade trajectory, like its direction or its amplitude. In other words, what to do might be less important compared to when to do it. Instead of a change in the saccade program, the change in latency or in fixation duration could reflect a different 'urgency' to look, as suggested by Reddi and Carpenter (Reddi & Carpenter, 2000). Stated otherwise, our manipulation did not affect saccade planning but was limited to the timing of movement triggering, further narrowing the necessary features for efficient motor cues.

8.1.2. Higher-order conditioning

Section 7 further investigated the mechanism allowing for the induction of contextual saccadic adaptation by using contextual features. This study aimed to investigate whether higher-order conditioning (Trask & Bouton, 2014) can be induced to control contextual saccade adaptation and to explore the potential interaction between perceptual and motor information. We ran both a single-session and a repeated-sessions version of two experiments. The repeated format provided more time for learning to establish, ensuring a clearer understanding of our results and the underlying mechanisms.

In a first design, we used the starting location of the target as a contextual feature and the amplitude of the first step as a discriminative stimulus. In this setup, the contextual feature modulated the meaning of the SD, such that the same SD predicted either a North-West or a South-East ISS depending on the starting location. While the single-session experiment showed a tendency towards learning but yielded mitigated results, the repeated session confirmed that the learning mechanisms were at play, and we observed significant learning for five out of the six participants.

In a second series of experiments, we used the color and shape of the target as a contextual feature. This perceptual cue is known to be an inefficient discriminative stimulus but, as we have shown, it is explicitly available to the participant at the time of the saccade. We therefore tested whether it could contribute to the learning process when paired with a motor-related SD, namely the amplitude of the first step. Both the single and the repeated session experiments led to a systematic failure of contextual adaptation, despite perfect contingency and temporal contiguity of the elements for about 4000 trials.

We consider two hypotheses to explain the discrepancy between the two contextual features we investigated. First, the starting location may have acted as an occasion setter (Fraser & Holland, 2019), reducing uncertainty about the SD by modulating which association was selected between the North-West and the South-East ISS. Under this interpretation, the absence of learning in the color & shape experiment becomes even more striking, since this contextual feature was presented earlier in the trial, providing more time to be processed and requiring a higher-order integration with the other elements of the contingency. An argument in favor of this hypothesis is the additional time participants required to learn the contingencies. This delay may reflect the need to first establish the associations between SDs and outcomes, and then to link the occasion setter to this new association so that it can function as a modulator. A second hypothesis is that participants learned the four combinations independently, with both the starting location and the first-step amplitude acting as partial SDs associated with a given ISS. This interpretation offers a simpler explanation for the inefficiency of the color & shape experiment, consistent with the idea already proposed that non-motor cues fail because they do not directly modify the motor program. This second hypothesis raises at least two questions: how do two features with such different temporal properties as the starting location and the amplitude of the first step integrate within the same motor command to form an efficient contextual cue? Why does learning require over 2200 trials to obtain significant results? Additional experiments focusing on both simple conditioning with partial SDs and on the specific properties of occasion setters are needed to arbitrate between these hypotheses.

8.1.3. An explanatory mechanism: Planning

Lastly, we delved deeper into the specific stages of motor programming in Section 8. We adapted the method of Azadi and McPeek (Azadi & McPeek, 2022), where the direction of the second saccade served as a contextual cue for the first one. The rationale is that when planning a sequence of saccades, both movements are programmed simultaneously (Caspi et al., 2004), so the overall motor program differs even if the kinematics of the first saccade remain consistent. Azadi and McPeek demonstrated that modifying this overall sequence planning effectively drives saccadic adaptation. Adapting this method, we were able to replicate the paradigm of Sheahan and al (Sheahan et al., 2016) used in force field adaptation. The primary objective of this paradigm was to disentangle the planning and execution components of the saccade to determine which one was critical for learning or if both were necessary. This study was conducted in four experiments: the Full Sequence experiment was a control for our design, with both the planning and the execution of the second saccade being present. Participants had to perform the whole sequence of two saccades, the first saccade following a 45° step and undergoing the ISS. The second step was either leftward or downward regarding the location after the first saccade, symmetrically to the fixation point. This experiment confirmed the efficiency of the whole saccade sequence as a contextual cue, with 5 out of 8 participants showing a significant difference in the saccade angle depending on the direction of the second saccade. Then, the Single Saccade experiment was the second control of our design, with neither the planning nor the execution of the second saccade. Here, participants were instructed to stop after the first saccade and to ignore the target appearing at the secondary position. From a design perspective, participants in the Single Saccade and Full Sequence experiments were presented with identical visual stimuli; the only difference between the two conditions lay in the task instructions. This experiment confirmed the inefficiency of the sole perception of the secondary target as a contextual cue, with none of the 8 participants showing a significant difference in the saccade angles - this result also aligns with our previous experiments on the inefficiency of perceptual cues.

After a confirmation of the efficiency of learning with both planning and execution of the second saccade of the sequence, and failure of learning when they are absent, we conducted two more experiments isolating these processes. In the Execution Only experiment, we isolated the execution component by displaying the location of the secondary target at the detection of the onset of the first saccade. This way, the participant could not plan the entire sequence from the fixation point but could execute it just as well as participants in the other groups. Because the participants had access to the contextual cues after performing the saccade upon which adaptation should occur, analysis could not be conducted on those saccades and was instead conducted on probe trials. In probe trials, participants performed the entire saccade sequence, but the ISS was not consistently paired with the secondary target location, to avoid a learning effect based on those trials. Statistical analysis on the probe trials showed an absence of learning, with none of the eight participants showing significant differences between the contextual cues.

On the other hand, the Planning Only experiment isolated the planning component of the saccade by removing the secondary target at the detection of the onset of the first saccade. Participants would then plan the whole sequence before the first saccade onset, but would stop after the first saccade if the secondary target is not present anymore, preventing the execution of the saccade. To ensure the planning on both saccades, as well as fair comparison with the Execution Only group, we also introduce probe trials as described previously. Statistical analysis of the probe trials showed significant learning for four out of the eight participants. Taken together, the results of the Execution Only and the Planning Only experiments demonstrate a clear difference in the results, showing that planning of the motor command is the critical component for learning and aligning with Sheahan and al. results in force field adaptation (Sheahan et al., 2016). Moreover, the design of the Planning Only experiment gave access to the contextual information before the first saccade, allowing the adaptation based on the full sequence plan for each trial. For this reason, the statistical analysis can also be performed on the regular trials, in addition to the probe trials, which we did on trials 500 to 700 to obtain the same analysis as performed in the Full Sequence and Single Saccade experiments. This analysis revealed that six out of eight participants showed significant results, with very similar Kolmogorov-Smirnov scores compared to the Full Sequence experiments. This provides two arguments supporting the idea that planning is the critical component for contextual saccadic adaptation, serving as the locus of discriminative learning. First, learning occurred in the planning-only but not in the execution-only condition, indicating that planning is sufficient for contextual adaptation. Second, the similarity between the results of the full-sequence and planning-only experiments shows that learning was not degraded in the absence of the execution component.

8.2. Connecting the Dots: Insights Beyond Individual Studies

8.2.1. Selectivity of learning

From a behavioral analysis framework, this experimental contribution raises several challenges and provides us with new avenues to extend our understanding of the mechanisms at play.

At the molecular level, placing motor planning as the locus of learning is an uncommon proposal for learning theories. Uncommon not because an internal state might function as an SD, but because it suggests an efficiency of the learning based on the nature of the stimulus used in the contingency.

This view provides us with an operational way to predict how selectivity will be expressed in a given situation by comparing the different motor plans involved. If one had direct access to the motor plan, one could, in principle, predict whether learning will occur based on its structure. Identical motor plans would lead to no learning, highly distinct motor plans would result in rapid learning, and subtle variations between plans would produce a slower rate of learning. Indeed, if plans are the critical stimuli controlling the response, then the more motor plans are discriminable from each other, the better the learning; on the other hand, the harder they are to discriminate, the more learning is likely to fail. This interpretation resolves the anomalies observed in saccadic adaptation experiments discussed before, with the color and shape of the target being inefficient to control the saccade (Azadi & Harwood, 2014; Benjamin et al., 2016; Cecala et al., 2015; Deubel, 1995). In all those experiments, the critical component missing for an efficient adaptation is differential motor planning. Moreover, every efficient cue acted on the motor planning.

This is the case for target eccentricity or depth (Chaturvedi & Van Gisbergen, 1997), horizontal or vertical orbital eye position (Alahyane & Pelisson, 2004; Shelhamer et al., 2002; Zimmermann & Lappe, 2011), head orientation (Shelhamer & Clendaniel, 2002), target motion (Azadi & Harwood, 2014), or saccade sequence (Azadi & McPeek, 2022), which all involved a change in the starting location, the ending location, or in the planned sequence of saccades.

This interpretation can also be applied to our results. Manipulation of the amplitude of the first step or the location of a remote distractor led to modifications in the trajectory of the saccade and, therefore, different neural states resulting from the planning of those commands(Ames et al., 2014; Churchland et al., 2012; Pandarinath et al., 2015). On the contrary, the target color and shape, or the use of a symbolic cue, did not affect the actual motor plan of the target. In these situations, the system planned the same saccade and had only one state, i.e., one plan, for two different ISS, leading to a failure in learning. Lastly, the gap/overlap or the fixation effect produced the same saccades, with different timing of motor execution. We argue that sharing the same motor state with different timing in the movement triggering leads to weaker differences, arguably harder to discriminate from. This would be essentially similar to comparing how likely an organism is to discriminate between two vastly different colors, such as red and blue, versus between two close shades of orange: discrimination learning depends on the physical difference between these stimuli, facilitating specific associations to be established separately.

8.2.2. Proposition of a motor system

In Section 2.2 of the introduction, we discussed the Behavioral Systems Theory (Killeen, 2019; Timberlake, 1993; Timberlake & Lucas, 2019) and some of its limitations, particularly its limited predictive power and lack of explanatory mechanisms for system selectivity. Another aspect raised by both Timberlake (Timberlake & Lucas, 2019) and Domjan (Domjan & Gutiérrez, 2019), but with little empirical development so far, concerns the possibility for behavioral systems to be induced and to interact with one another. In this section, we will review how the experimental findings of this thesis may contribute to extending and refining this theoretical framework. We will then attempt to propose a conceptual depiction of the systems at play in saccadic adaptation. This model is not intended as a comprehensive representation of the underlying biological process, but rather as an illustrative framework to integrate and interpret the results presented in this thesis, adapting Domjan's proposition for a behavioral system of sexual behavior in quails.

First, and contrary to Domjan, who investigated a broad situation that he referred to as "sexual behaviors", our focus was instead on a specific terminal response, the saccade. Following the idea of the functionality of the behavioral system, we should depict here a *visual system. This visual system* encompasses all the processes functionally related to vision, namely eye movements and visual perception. According to Timberlake and Domjan, responses within a single behavioral system should show some degree of transversality and mutual communication. However, previous studies as well as our own findings indicate that purely visual information fails to control saccadic adaptation. The idea that motor plans, but not perceptual information, are a critical component for contextual learning in saccade movement suggests a relative independence between perceptual and motor information.

For this reason, we propose an alternative to the functional approach to determine the structure of a behavioral system, based on the underlying mechanisms. We therefore obtain a *motor system*, encompassing motor preparation, execution, and motor outcome. In this motor system, we would consequently place together motor responses, including but not limited to: saccade, smooth pursuit, or arm movements, for which motor planning may be regarded as a critical component for learning. The BST principle of interaction within a system provides a hypothesis: a sequence of movement, including arm and eye movements, planned together, should be efficient for inducing saccadic adaptation or arm adaptation.

Defining a system through its shared learning mechanism can provide both explanatory and predictive power. While Domjan's and Timberlake's models (Domjan & Gutiérrez, 2019; Timberlake & Lucas, 2019) effectively delineate what can or cannot be learned within a system, they fall short of explaining *why* such selectivity arises. Our understanding is that the functional approach they used may have integrated several different systems working together for a single goal, making it much more challenging to analyze the selective mechanisms at play with precision. By incorporating the results on selective motor learning (Howard et al., 2013; Martel & Madelain, 2025), the BST framework (Domjan & Gutiérrez, 2019; Timberlake & Lucas, 2019), and Krauzlis' approach of attentional process (Krauzlis et al., 2014), we attempted to provide an illustrative model for saccade adaptation in the motor system (Figure 32).

In the model we propose, the behavioral chain starts with the stimulus. Because we proposed that movements and perception are independent systems, we suppose a perceptual system that detects the stimulus in the periphery. Motor information about the cue will also reach the motor system, which we will describe in more detail using Krauzlis' attentional model (Krauzlis et al., 2014). This model involves three main components in decision-making: the sensory data, prior knowledge, and the internal status of the organism. First, the sensory data correspond to the stimuli from which the organism extracts information. Since our results showed that planning—but not execution—allows for discrimination, we propose that the motor plan itself constitutes the relevant sensory input for motor decisions.

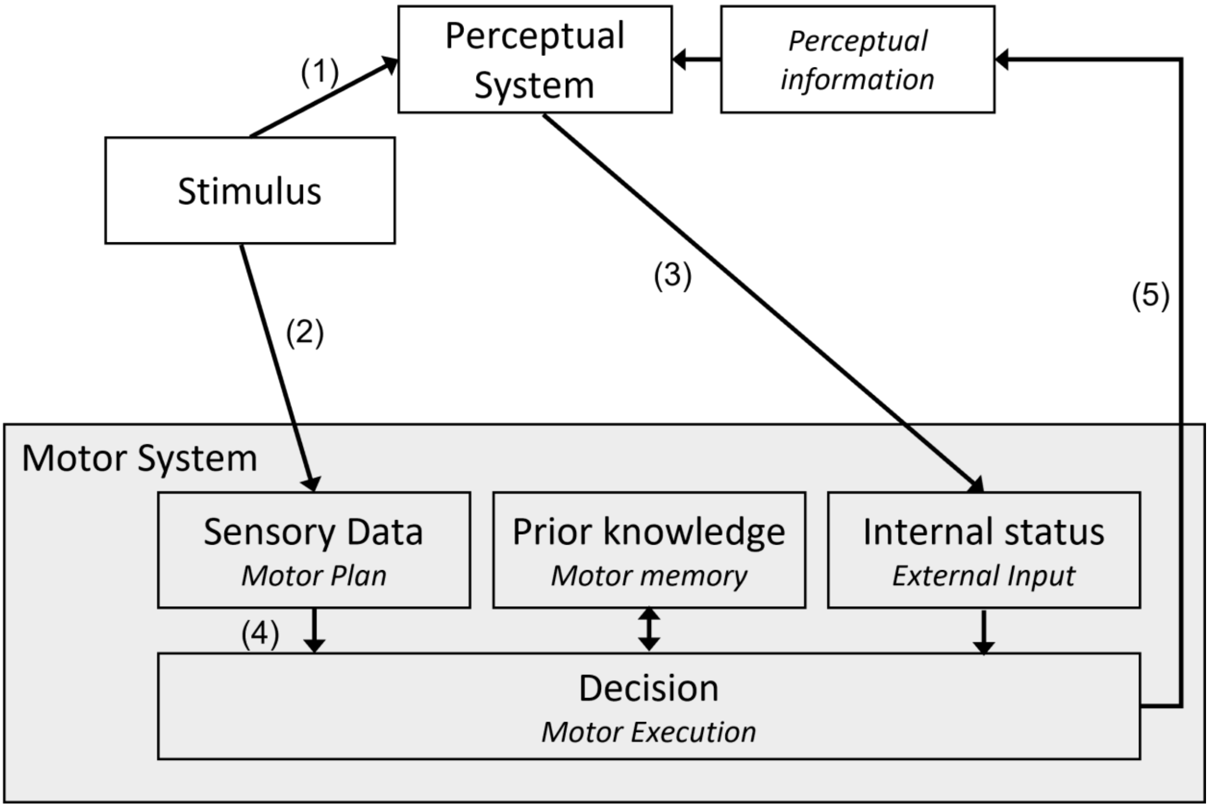

Figure 32. Illustrative example of the Motor system. (1) A stimulus of interest appears and is detected in the periphery by the perceptual system. (2) The location of the stimulus allows the motor system to build a plan to reach it. (3) The perceptual system decided to send an input to move toward the stimulus. (4) The sensory data and the internal status are present, and additionally, the motor system compares the motor plan to existing memories to adapt the kinematics. (5) After the decision and execution of the command, the motor system updates its prior knowledge depending on the motor outcome (e.g. the retinal error). The perceptual system also receives an outcome, the perception of the stimulus, and will update its own prior knowledge, increasing or decreasing the probability of sending this same motor request at the next occurrence of this stimulus.

Second, prior knowledge reflects past experiences of similar situations, namely, the motor memory. In the context of saccadic adaptation, the retinal error experienced during the previous encounter of this same motor plan is thought to serve as a feedback signal used to adjust future performance and reduce error. Finally, the internal status represents the system's current state, which may integrate influences from other behavioral systems.

Up to this point, we have repeatedly shown that perceptual cues do not directly control saccadic adaptation. However, saccades themselves clearly depend on visual perception. For instance, in the Single Saccade experiments (presented in Section 8 of this manuscript), participants refrained from looking at the secondary target, even though both targets were visible in the periphery. This demonstrates that perceptual cues determined where to go, but not how to get there: they guided target selection, but not the saccade's kinematics. We therefore suggest that the internal status component may be a top-down signal, originating from another system—likely a perceptual system—which provides task-relevant information without directly shaping motor learning.

Once these three components are allowed for the decision of motor execution, two different outcomes arise. A motor outcome, which is the prediction error of the motor system, is used to update the motor memory of the specific motor plan just performed. Then, a perceptual outcome, as the perceptual system now has access to the target's perceptual information. This outcome may increase or decrease the likelihood of the perceptual system providing an input to the motor system to reach this specific target again in the future. A similar reasoning can also account for the discrepancy in the results in force field adaptation (Howard et al., 2013).

Lastly, it is worth emphasizing that the General Process Theory (GPT) remains valid within our framework. Whenever contingency and temporal contiguity were preserved between the different motor plans and their outcomes, learning occurred successfully. The varying rates of learning observed across different contextual cues can be interpreted as differences in their motor plan—a result consistent with other discrimination tasks. Furthermore, the higher-order conditioning we implemented (presented in Section 7 of this manuscript) also conforms to the predictions of the GPT. In light of these observations, we align with Domjan's view and propose to resolve the anomaly of selective learning by reframing the GPT as: learning processes require contingency, temporal contiguity, and compatibility between the elements of the contingency and the behavioral system induced.

With these elements together, our view of behavioral systems integrates: (1) Learning theories, with the General Process Theory being reliable within a behavioral system, (2) an attentional model, describing how the organism uses information to guide responses and the possible interactions with other systems, and (3), an underlying mechanism, namely the motor plan, bearing discrimination and drawing the constraints of the system.

8.2.3. Limitations

Despite the novel perspectives brought by the behavioral system theory and the reframing we propose, some limitations still constrain its use.

First, the terminology used to describe subsystems, modes, and modules is somewhat arbitrary. While such labels help structure the model, they may also introduce ambiguity or false distinctions that arise from language. We believe that relying on the underlying mechanisms as much as possible is a way to minimize this issue.

Second, the interaction between systems remains largely misunderstood. We hypothesized that, for contextual saccade adaptation, a top-down command originates from a perceptual system, as this assumption was necessary to provide a coherent model accounting for the input driving the motor system and for their interconnectivity. However, the precise nature and relative influence of these interactions remain unknown. Moreover, additional systems may also contribute, each likely governed by its own rules of communication and integration.

Lastly, the central role of motor planning in saccade adaptation, along with its limited types of modification, makes this phenomenon particularly suitable for studying selective learning and for constructing a behavioral system. However, in his initial view, Timberlake proposed that systems were organizing the significant types of behavior of an organism, such as fleeing, fighting, or reproductive behavior. Although focusing on a more narrowly defined system provided us with valuable insights and a coherent theoretical framework, it also created a rupture with the initial BST view. In a way, Timberlake's framework was defined at a molar level—starting from large, integrated behavioral systems that probably already implied interactions among multiple systems. By contrast, our molecular perspective focused on motor behavior allowed us to identify potential underlying mechanisms and to propose a way of communication between systems. Despite these differences in scale, we believe that both approaches are complementary rather than contradictory: Timberlake's molar framework provides a broad organizational map of behavioral functions, while our molecular perspective offers a mechanistic view that can help explain how such systems emerge and interact at a finer level. Indeed, unlike saccades, other behaviors may involve multiple learning loci and more complex or meaningful interactions with different systems, and therefore benefit more from a broader approach.

8.3. Perspectives

The experimental contributions described in this manuscript and the theoretical interpretations we proposed about them raise many research questions. We already underline two studies in this manuscript: First, in Section 6.1, we discussed experiments on higher-level conditioning to help disentangle between an occasion setting or a partial SD process at play. The same reasoning on process at play within saccadic adaptation could lead us to investigate additional processes such as renewal or counter-conditioning, drawing the limit of the system and providing with a basis for fine-grain analysis of the interaction between saccades and other movements or systems.

Another kind of experiment we proposed stemmed from our illustration of a motor system integrating all the different motor behaviors. Indeed, the BST suggests that the different parts integrated into the same system should be able to interact and be relevant to each other. Accordingly, since arm and eye movement are part of the same system, a motor plan for an arm movement should also be relevant for saccade adaptation. Therefore, an experiment forcing the participant to plan a sequence of movement, including an eye movement and an arm movement, by keeping the saccade plan similar but providing two different plans for the arm movement should allow successful saccadic adaptation. Conversely, a similar arm kinematic followed by two possible saccade plans, if planned together in a motor sequence, should allow support motor adaptation.

On behavioral systems, a promising research direction following this work concerns the circumscription of a second system. For instance, defining a perceptual system could be approached by examining the effects of selectivity within a learning process based purely on perceptual information. Such a line of research would first allow for direct comparison between systems and help identify processes or rules that appear common across systems, as opposed to those that are specific to one. In a second step, it would enable a more detailed exploration of the interactions between different systems. Understanding these interactions would also constitute an essential step toward explaining more complex behaviors, as initially suggested in the BST framework—such as food seeking or mate searching.

8.4. General Conclusion

This thesis began by exposing the problem of selective learning, a phenomenon well described in research on learning, but lacking a theoretical framework. This phenomenon contradicts the General Process Theory, leading to inefficient learning in situations of perfect contiguity and contingency upon the elements. We choose the framework providing the most comprehensive account for selective learning, Domjan's view of the Behavioral System Theory, as a starting point to investigate this question. We demonstrate a situation of differential results depending on the type of cues in contextual saccadic adaptation, showing that only motor-related cues were efficient and asserting selective learning in humans. Through additional experiments, we showed that discriminative learning was not equal for all motor-related cues, and that discrepancy in the results arises between them. Then, we started to exhibit the complex interaction of systems between them, showing that higher-order conditioning could be induced by using motor-related cues but not when mixing motor and non-motor cues. Finally, we demonstrated that motor planning was the locus of learning for saccadic adaptation.

We provided a possible interpretation for the discrepancies between motor cues by illustrating the necessary and sufficient role of motor planning for learning. We suggested that the ability of the saccadic circuitry to disentangle between the different motor plans was a possible explanation for the difference in learning with motor cues. In the discussion, we aligned with Domjan's proposition of the addition of an element to the General Process Theory as a critical component of learning, namely, selective learning. Moreover, we proposed that selective learning depends on the belongingness of the elements to the same behavioral system. Stimuli within the same system are more likely to be selected for learning, whereas stimuli outside the system are more likely to be ignored.

To conclude, this work aimed not only to describe selective learning in motor adaptation but also to propose a theoretical framework capable of accounting for its mechanisms. By integrating Domjan's view of Behavioral System Theory within the molecular scope of saccadic adaptation, we sought to address the lack of an underlying mechanism proposed by the BST while promoting the theoretical benefits of this framework. This proposal opens several avenues for future research. One is to challenge the model we proposed in further experimental work on motor learning. Another is to explore how selective learning operates beyond the motor system, and whether similar principles and structures of the system can account for experimental observation. Ultimately, an important direction would be to further investigate the interaction between the systems, which could help resolve the current boundaries of the BST and facilitate its integration in General Process Theory

.

9. References

Akins, C. K. (1998). Context excitation and modulation of conditioned sexual behavior. *Animal Learning & Behavior*, *26*(4), 416–426. https://doi.org/10.3758/BF03199234

Akins, C. K., & Cusato, B. (2015). From Biological Constraints to Flexible Behavior Systems:Extending Our Knowledge of Sexual Conditioning in Japanese Quail. *International Journal of Comparative Psychology*, *28*. https://doi.org/10.46867/ijcp.2015.28.01.05

Akins, C. K., & Domjan, M. (1996). The topography of sexually conditioned behaviour: Effects of a trace interval. *The Quaterly Journal of Experimental Psychology*.

Alahyane, N., & Pelisson, D. (2004). Eye Position Specificity of Saccadic Adaptation. *Investigative Opthalmology & Visual Science*, *45*(1), 123. https://doi.org/10.1167/iovs.03-0570

Albano, J. E. (1996). Adaptive Changes in Saccade Amplitude: Oculocentric or Orbitocentric Mapping? *Vision Research*, *36*(14), 2087–2098. https://doi.org/10.1016/0042-6989(96)89627-1

Ames, K. C., Ryu, S. I., & Shenoy, K. V. (2014). Neural Dynamics of Reaching following Incorrect or Absent Motor Preparation. *Neuron*, *81*(2), 438–451. https://doi.org/10.1016/j.neuron.2013.11.003

Azadi, R., & Harwood, M. R. (2014). Visual cues that are effective for contextual saccade adaptation. *Journal of Neurophysiology*, *111*(11), 2307–2319. https://doi.org/10.1152/jn.00894.2013

Azadi, R., & McPeek, R. M. (2022). Contextual saccade adaptation induced by sequential saccades. *Journal of Neurophysiology*, *127*(3), 746–755. https://doi.org/10.1152/jn.00221.2021

Bahcall, D. O., & Kowler, E. (2000). The control of saccadic adaptation: Implications for the scanning of natural visual scenes. *Vision Research*, *40*(20), 2779–2796. https://doi.org/10.1016/S0042-6989(00)00117-6

Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence, a tool for studying human eye movements. *Mathematical Biosciences*, *24*(3–4), 191–204. https://doi.org/10.1016/0025-5564(75)90075-9

Benjamin, B., Macomb, C., Martin, A., & Cecala, A. L. (2016). *Can color act as a contextual cue in human saccadic adaptation? 87*(1).

Berger, V. W., & Zhou, Y. (2014). Kolmogorov–Smirnov Test: Overview. In N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri, & J. L. Teugels (Eds.), *Wiley StatsRef: Statistics Reference Online* (1st ed.). Wiley. https://doi.org/10.1002/9781118445112.stat06558

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, *15*(6), 719–722. https://doi.org/10.1016/0042-6989(75)90290-4

Broadbent, D. E. (2013). *Perception and communication.* (Elsevier).

Burns, M., & Domjan, M. (2001). Topography_of_spatially_directed_conditi. *Journal of the Experimental Psychology*.

Caspi, A., Beutter, B. R., & Eckstein, M. P. (2004). The time course of visual information accrual guiding eye movement decisions. *Proceedings of the National Academy of Sciences*, *101*(35), 13086–13090. https://doi.org/10.1073/pnas.0305329101

Cassanello, C. R., Ohl, S., & Rolfs, M. (2016). Saccadic adaptation to a systematically varying disturbance. *Journal of Neurophysiology*, *116*(2), 336–350. https://doi.org/10.1152/jn.00206.2016

Castet, E., & Masson, G. S. (2000). Motion perception during saccadic eye movements. *Nature Neuroscience*, *3*(2), 177–183. https://doi.org/10.1038/72124

Cecala, A. L., Smalianchuk, I., Khanna, S. B., Smith, M. A., & Gandhi, N. J. (2015). Context cue-dependent saccadic adaptation in rhesus macaques cannot be elicited using color. *Journal of Neurophysiology*, *114*(1), 570–584. https://doi.org/10.1152/jn.00666.2014

Chaturvedi, V., & Van Gisbergen, J. A. M. (1997). Specificity of saccadic adaptation in three-dimensional space. *Vision Research*, *37*(10), 1367–1382. https://doi.org/10.1016/S0042-6989(96)00266-0

Chaumillon, R., Alahyane, N., Senot, P., Lemoine-Lardennois, C., Doré-Mazars, K., Vergilino-Perez, D., & Guillaume, A. (2022). Distractor-induced saccade trajectory curvature reveals visual contralateral bias with respect to the dominant eye. *Scientific Reports*, *12*(1), 21737. https://doi.org/10.1038/s41598-022-26319-3

Chen-Harris, H., Joiner, W. M., Ethier, V., Zee, D. S., & Shadmehr, R. (2008). Adaptive control of saccades via internal feedback. *Journal of Neuroscience*, *28*(11), 2804–2813.

Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Foster, J. D., Nuyujukian, P., Ryu, S. I., & Shenoy, K. V. (2012). Neural population dynamics during reaching. *Nature*, *487*(7405), 51–56. https://doi.org/10.1038/nature11129

Collins, T., & Wallman, J. (2012). The relative importance of retinal error and prediction in saccadic adaptation. *Journal of Neurophysiology*, *107*(12), 3342–3348. https://doi.org/10.1152/jn.00746.2011

Crawford, L. L., & Domjan, M. (1995). Second-order sexual conditioning in male Japanese quail (Coturnix japonica). *Animal Learning & Behavior*, *23*(3), 327–334. https://doi.org/10.3758/BF03198929

Crawford, L. L., & Domjan, M. (1996). Conditioned inhibition of social approach in male Japanese quail using visual exposure to a female. *Behavioral Processes*.

Deubel, H. (1987). Adaptivity of gain and direction in oblique saccades. In *Eye movements from physiology to cognition* (pp. 181–190). Elsevier. https://www.sciencedirect.com/science/article/pii/B9780444701138500308

Deubel, H. (1995). Is Saccadic Adaptation Context-Specific ? In *Studies in Visual Information Processing* (Vol. 6, pp. 177–187). Elsevier. https://doi.org/10.1016/S0926-907X(05)80016-9

Domjan, M. (1983). Biological Constraints on Instrumental and Classical Conditioning: Implications for General Process Theory. In *Psychology of Learning and Motivation* (Vol. 17, pp. 215–277). Elsevier. https://doi.org/10.1016/S0079-7421(08)60100-0

Domjan, M. (2008). Adaptive Specializations and Generality of the Laws of Classical and Instrumental Conditioning. In *Learning and Memory: A Comprehensive Reference* (pp. 327–340). Elsevier. https://doi.org/10.1016/B978-012370509-9.00183-2

Domjan, M. (2015). The Garcia-Koelling Selective Association Effect: A Historical and Personal Perspective. *International Journal of Comparative Psychology*, *28*. https://doi.org/10.46867/ijcp.2015.28.01.08

Domjan, M., Cusato, B., & Krause, M. (2004). Learning with arbitrary versus ecological conditioned stimuli: Evidence from sexual conditioning. *Psychonomic Bulletin & Review*, *11*(2), 232–246. https://doi.org/10.3758/BF03196565

Domjan, M., & Gutiérrez, G. (2019). The behavior system for sexual learning. *Behavioural Processes*, *162*, 184–196. https://doi.org/10.1016/j.beproc.2019.01.013

Domjan, M., & Hollis, K. L. (1988). Reproductive behavior: A potential model for adaptive specializations in learning. *Learning and Evolution*.

Domjan, M., Lyons, R., North, C., & Bruell, J. (1986). DomjanLyonsNorthBruellJCP19861004. *Journal of Comparative Psychology*.

Efron, B. (1992). Bootstrap Methods: Another Look at the Jackknife. In S. Kotz & N. L. Johnson (Eds.), *Breakthroughs in Statistics* (pp. 569–593). Springer New York. https://doi.org/10.1007/978-1-4612-4380-9_41

Ethier, V., Zee, D. S., & Shadmehr, R. (2008a). Changes in control of saccades during gain adaptation. *Journal of Neuroscience*, *28*(51), 13929–13937.

Ethier, V., Zee, D. S., & Shadmehr, R. (2008b). Spontaneous Recovery of Motor Memory During Saccade Adaptation. *Journal of Neurophysiology*, *99*(5), 2577–2583. https://doi.org/10.1152/jn.00015.2008

Fanselow, M. S., Lester, L. S., & Helmstetter, F. J. (1988). *CHANGES IN FEEDING AND FORAGING PATTERNS AS AN ANTIPREDATOR DEFENSIVE STRATEGY: A LABORA TORY SIMULATION USING AVERSIVE STIMULATION IN A CLOSED ECONOMY*.

Forano, M., Schween, R., Taylor, J. A., Hegele, M., & Franklin, D. W. (2021). Direct and indirect cues can enable dual adaptation, but through different learning processes. *Journal of Neurophysiology*, *126*(5), 1490–1506. https://doi.org/10.1152/jn.00166.2021

Fraser, K. M., & Holland, P. C. (2019). Occasion setting. *Behavioral Neuroscience*, *133*(2), 145–175. https://doi.org/10.1037/bne0000306

Frens, M. A., & Van Opstal, A. J. (1995). A quantitative study of auditory-evoked saccadic eye movements in two dimensions. *Experimental Brain Research*, *107*(1), 103–117. https://doi.org/10.1007/BF00228022

Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science*, *4*(1), 123–124. https://doi.org/10.3758/BF03342209

Gibaldi, A., & Sabatini, S. P. (2021). The saccade main sequence revised: A fast and repeatable tool for oculomotor analysis. *Behavior Research Methods*, *53*(1), 167–187. https://doi.org/10.3758/s13428-020-01388-2

Harris, C. M., & Wolpert, D. M. (2006). The Main Sequence of Saccades Optimizes Speed-accuracy Trade-off. *Biological Cybernetics*, *95*(1), 21–29. https://doi.org/10.1007/s00422-006-0064-x

Heald, J. B., Wolpert, D. M., & Lengyel, M. (2023). The Computational and Neural Bases of Context-Dependent Learning. *Annual Review of Neuroscience*, *46*(1), 233–258. https://doi.org/10.1146/annurev-neuro-092322-100402

Herman, J. P., Blangero, A., Madelain, L., Khan, A., & Harwood, M. R. (2013). Saccade adaptation as a model of flexible and general motor learning. *Experimental Eye Research*, *114*, 6–15. https://doi.org/10.1016/j.exer.2013.04.001

Hilliard, S., & Domjan, M. (1995). Effects of sexual conditioning of devaluing the US through satiation. *The Quaterly Journal of Experimental Psychology*.

Hopp, J. J., & Fuchs, A. F. (2004). The characteristics and neuronal substrate of saccadic eye movement plasticity. *Progress in Neurobiology*, *72*(1), 27–53. https://doi.org/10.1016/j.pneurobio.2003.12.002

Hoppe, D., & Rothkopf, C. A. (2016). Learning rational temporal eye movement strategies. *Proceedings of the National Academy of Sciences*, *113*(29), 8332–8337. https://doi.org/10.1073/pnas.1601305113

Howard, I. S., Wolpert, D. M., & Franklin, D. W. (2013). The effect of contextual cues on the encoding of motor memories. *Journal of Neurophysiology*, *109*(10), 2632–2644. https://doi.org/10.1152/jn.00773.2012

Ikeda, T., & Hikosaka, O. (2003). Reward-Dependent Gain and Bias of Visual Responses in Primate Superior Colliculus. *Neuron*, *39*(4), 693–700. https://doi.org/10.1016/S0896-6273(03)00464-1

Kalesnykas, R. P., & Hallett, P. E. (1987). The differentiation of visually guided and anticipatory saccades in gap and overlap paradigms. *Experimental Brain Research*, *68*(1). https://doi.org/10.1007/BF00255238

Killeen, P. R. (2019). Timberlake's theories dissolve anomalies. *Behavioural Processes*, *166*, 103894. https://doi.org/10.1016/j.beproc.2019.103894

Killeen, P. R., & Pellón, R. (2013). Adjunctive behaviors are operants. *Learning & Behavior*, *41*(1), 1–24. https://doi.org/10.3758/s13420-012-0095-1

King, A. J. (2004). The superior colliculus. *Current Biology*, *14*(9), R335–R338.

Kline, L. W. (1898). Suggestions toward a laboratory course in comparative psychology. *American Journal of Psychology*.

Köksal, F., Domjan, M., & Weisman, G. (1994). Blocking of the sexual conditioning of differentially effective conditioned stimulus objects. *Animal Learning & Behavior*, *22*(1), 103–111. https://doi.org/10.3758/BF03199962

Krause, M. A., Cusato, B., & Domjan, M. (2003). Extinction of conditioned sexual responses in male Japanese quail (Coturnix japonica): Role of species-typical cues. *Journal of Comparative Psychology*, *117*(1), 76–86. https://doi.org/10.1037/0735-7036.117.1.76

Krauzlis, R. J., Bollimunta, A., Arcizet, F., & Wang, L. (2014). Attention as an effect not a cause. *Trends in Cognitive Sciences*, *18*(9), 457–464. https://doi.org/10.1016/j.tics.2014.05.008

Krock, R. M., & Moore, T. (2014). The Influence of Gaze Control on Visual Perception: Eye Movements and Visual Stability. *Cold Spring Harbor Symposia on Quantitative Biology*, *79*, 123–130. https://doi.org/10.1101/sqb.2014.79.024836

Lauwereyns, J., Watanabe, K., Coe, B., & Hikosaka, O. (2002). A neural correlate of response bias in monkey caudate nucleus. *Nature*, *418*(6896), 413–417. https://doi.org/10.1038/nature00892

Li, Y., Wang, Y., & Cui, H. (2018). Eye-hand coordination during flexible manual interception of an abruptly appearing, moving target. *Journal of Neurophysiology*, *119*(1), 221–234. https://doi.org/10.1152/jn.00476.2017

López-Moliner, J., Brenner, E., Louw, S., & Smeets, J. B. J. (2010). Catching a gently thrown ball. *Experimental Brain Research*, *206*(4), 409–417. https://doi.org/10.1007/s00221-010-2421-1

López-Moliner, J., Field, D. T., & Wann, J. P. (2007). Interceptive timing: Prior knowledge matters. *Journal of Vision*, *7*(13), 11. https://doi.org/10.1167/7.13.11

Ludwig, C. J. H., Gilchrist, I. D., & McSorley, E. (2005). The remote distractor effect in saccade programming: Channel interactions and lateral inhibition. *Vision Research*, *45*(9), 1177–1190. https://doi.org/10.1016/j.visres.2004.10.019

Madelain, L., Champrenaut, L., & Chauvin, A. (2007). Control of Sensorimotor Variability by Consequences. *Journal of Neurophysiology*, *98*(4), 2255–2265. https://doi.org/10.1152/jn.01286.2006

Madelain, L., Paeye, C., & Darcheville, J.-C. (2011). Operant control of human eye movements. *Behavioural Processes*, *87*(1), 142–148. https://doi.org/10.1016/j.beproc.2011.02.009

Madelain, L., Paeye, C., & Wallman, J. (2011). Modification of saccadic gain by reinforcement. *Journal of Neurophysiology*, *106*(1), 219–232. https://doi.org/10.1152/jn.01094.2009

Martel, M., & Madelain, L. (2025). Ineffective cues for contextual saccade adaptation. *Journal of Neurophysiology*. https://doi.org/10.1152/jn.00148.2025

McLaughlin, S. C. (1967). Parametric adjustment in saccadic eye movements. *Perception & Psychophysics*, *2*(8), 359–362. https://doi.org/10.3758/BF03210071

Mendelson, S. D., & Pfaus, J. G. (1989). Level searching: A new assay of sexual motivation in the male rat. *Physiology & Behavior*, *45*(2), 337–341. https://doi.org/10.1016/0031-9384(89)90136-4

Miller, J. M., Anstis, T., & Templeton, W. B. (1981). *Saccadic Plasticity: Parametric Adaptive Control by Retinal Feedback*. Journal of the Experimental Psychology.

Montagnini, A., & Chelazzi, L. (2005). The urgency to look: Prompt saccades to the benefit of perception. *Vision Research*, *45*(27), 3391–3401. https://doi.org/10.1016/j.visres.2005.07.013

Mrotek, L. A., & Soechting, J. F. (2007). Target Interception: Hand–Eye Coordination and Strategies. *The Journal of Neuroscience*, *27*(27), 7297–7309. https://doi.org/10.1523/JNEUROSCI.2046-07.2007

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology*, *19*(1), 1–32.

Noto, C. T., Watanabe, S., & Fuchs, A. F. (1999). Characteristics of Simian Adaptation Fields Produced by Behavioral Changes in Saccade Size and Direction. *Journal of Neurophysiology*, *81*(6), 2798–2813. https://doi.org/10.1152/jn.1999.81.6.2798

Oostwoud Wijdenes, L., Brenner, E., & Smeets, J. B. J. (2016). Exposing sequence learning in a double-step task. *Experimental Brain Research*, *234*(6), 1701–1712. https://doi.org/10.1007/s00221-016-4566-z

Pandarinath, C., Gilja, V., Blabe, C. H., Nuyujukian, P., Sarma, A. A., Sorice, B. L., Eskandar, E. N., Hochberg, L. R., Henderson, J. M., & Shenoy, K. V. (2015). Neural population dynamics in human motor cortex during movements in people with ALS. *eLife*, *4*, e07436. https://doi.org/10.7554/eLife.07436

Panouillères, M., Weiss, T., Urquizar, C., Salemme, R., Munoz, D. P., & Pélisson, D. (2009). Behavioral Evidence of Separate Adaptation Mechanisms Controlling Saccade Amplitude Lengthening and Shortening. *Journal of Neurophysiology*, *101*(3), 1550–1559. https://doi.org/10.1152/jn.90988.2008

Pélisson, D., Alahyane, N., Panouillères, M., & Tilikete, C. (2010). Sensorimotor adaptation of saccadic eye movements. *Neuroscience & Biobehavioral Reviews*, *34*(8), 1103–1120. https://doi.org/10.1016/j.neubiorev.2009.12.010

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Pierce, W. D., Cheney, C. D., Rasmussen, E. B., & Clay, C. J. (2022). *Behavior Analysis and Learning: A Biobehavioral Approach* (7th ed.). Routledge. https://doi.org/10.4324/9781003202622

Rahmouni, S., & Madelain, L. (2019). Inter-individual variability and consistency of saccade adaptation in oblique saccades: Amplitude increase and decrease in the horizontal or vertical saccade component. *Vision Research*, *160*, 82–98. https://doi.org/10.1016/j.visres.2019.05.001

Reddi, B. A. J., & Carpenter, R. H. S. (2000). The influence of urgency on decision time. *Nature Neuroscience*, *3*(8), 827–830. https://doi.org/10.1038/77739

Rescorla, R. A. (1967). Pavlovian conditioning and its proper control procedures. *Psychological Review*, *74*(1), 71–80. https://doi.org/10.1037/h0024109

Reuter-Lorenz, P. A., Hughes, H. C., & Fendrich, R. (1991). The reduction of saccadic latency by prior offset of the fixation point: An analysis of the gap effect. *Perception & Psychophysics*, *49*(2), 167–175. https://doi.org/10.3758/BF03205036

Rolfs, M., Knapen, T., & Cavanagh, P. (2010). Global saccadic adaptation. *Vision Research*, *50*(18), 1882–1890. https://doi.org/10.1016/j.visres.2010.06.010

Rosenholtz, R. (2024). Visual Attention in Crisis. *Behavioral and Brain Sciences*, 1–32. https://doi.org/10.1017/S0140525X24000323

Sarwary, A. M. E., Stegeman, D. F., Selen, L. P. J., & Medendorp, W. P. (2015). Generalization and transfer of contextual cues in motor learning. *Journal of Neurophysiology*, *114*(3), 1565–1576. https://doi.org/10.1152/jn.00217.2015

Saslow, M. G. (1967). Effects of Components of Displacement-Step Stimuli Upon Latency for Saccadic Eye Movement. *Journal of the Optical Society of America*, *57*(8), 1024. https://doi.org/10.1364/JOSA.57.001024

Schroeder, S. R., & Holland, J. G. (1968). OPERANT CONTROL OF EYE MOVEMENTS. *Journal of Applied Behavior Analysis*.

Schutz, A. C., Kerzel, D., & Souto, D. (2014). Saccadic adaptation induced by a perceptual task. *Journal of Vision*, *14*(5), 4–4. https://doi.org/10.1167/14.5.4

Schwartz, B. (1974). ON GOING BACK TO NATURE: A REVIEW OF SELIGMAN AND HAGER'S BIOLOGICAL BOUNDARIES OF LEARNING1. *ON GOING BACK TO NATURE: A REVIEW OF SELIGMAN AND HAGER'S BIOLOGICAL BOUNDARIES OF LEARNING1*.

Schwartz, B. (1978). *Psychology of learning and behavior.* (WW Norton&Co.). WW Norton & Co.

Scudder, C. A., Batourina, E. Y., & Tunder, G. S. (1998). Comparison of Two Methods of Producing Adaptation of Saccade Size and Implications for the Site of Plasticity. *Journal of Neurophysiology*, *79*(2), 704–715. https://doi.org/10.1152/jn.1998.79.2.704

Seligman, M. (1970). On the generality of the laws of learning. *Psychol. Rev.*

Seligman, M. E., & Hager, J. L. (1972). *Biological boundaries of learning.*

Semmlow, J. L., Gauthier, G. M., & Vercher, J.-L. (1989). Mechani~ms of Short-Term Saccadic Adaptation. *Journal of Experimental Psychology*.

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error Correction, Sensory Prediction, and Adaptation in Motor Control. *Annual Review of Neuroscience*, *33*(1), 89–108. https://doi.org/10.1146/annurev-neuro-060909-153135

Sheahan, H. R., Franklin, D. W., & Wolpert, D. M. (2016). Motor Planning, Not Execution, Separates Motor Memories. *Neuron*, *92*(4), 773–779. https://doi.org/10.1016/j.neuron.2016.10.017

Shelhamer, M., & Clendaniel, R. (2002). Sensory, motor, and combined contexts for context-specific adaptation of saccade gain in humans. *Neuroscience Letters*, *332*(3), 200–204. https://doi.org/10.1016/S0304-3940(02)00951-5

Shelhamer, M., Peng, G. C. Y., Ramat, S., & Patel, V. (2002). Context-specific adaptation of the gain of the oculomotor response to lateral translation using roll and pitch head tilts as contexts. *Experimental Brain Research*, *146*(3), 388–393. https://doi.org/10.1007/s00221-002-1235-1

Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception*.

Skinner, B. F. (1956). *A CASE HISTORY IN SCIENTIFIC METHOD*.

Souto, D., & Schütz, A. C. (2020). Task-relevance is causal in eye movement learning and adaptation. *Psychology of Learning and Motivation*, *73*, 157–193. https://doi.org/10.1016/bs.plm.2020.06.002

Staddon, J. E. R., & Honig, W. K. (1977). *Handbook of operant behavior* (Englewood Cliffs, NJ: Prentice-Hall.). Englewood Cliffs, NJ: Prentice-Hall.

Straube, A., & Buettner, U. (Eds.). (2007). *Neuro-ophthalmology: Neuronal control of eye movements*. Karger. https://doi.org/10.1159/isbn.978-3-318-01444-0

Straube, A., & Deubel, H. (1995). Rapid gain adaptation affects the dynamics of saccadic eye movements in humans. *Vision Research*, *35*(23–24), 3451–3458.

Straube, A., Fuchs, A. F., Usher, S., & Robinson, F. R. (1997). Characteristics of Saccadic Gain Adaptation in Rhesus Macaques. *Journal of Neurophysiology*, *77*(2), 874–895. https://doi.org/10.1152/jn.1997.77.2.874

Takikawa, Y., Kawagoe, R., Itoh, H., Nakahara, H., & Hikosaka, O. (2002). Modulation of saccadic eye movements by predicted reward outcome. *Experimental Brain Research*, *142*(2), 284–291. https://doi.org/10.1007/s00221-001-0928-1

Thorndike, E. (1898). Some Experiments on Animal Intelligence. *Science*, *7*(181), 818–824. https://doi.org/10.1126/science.7.181.818

Timberlake, W. (1993). BEHAVIOR SYSTEMS AND REINFORCEMENT: AN INTEGRATIVE APPROACH. *Journal of the Experimental Analysis of Behavior*, *60*(1), 105–128. https://doi.org/10.1901/jeab.1993.60-105

Timberlake, W., & Lucas, G. A. (2019). Behavior Systems and Learning: From Misbehavior to General Principles. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary Learning Theories* (1st ed., pp. 237–276). Routledge. https://doi.org/10.4324/9781315788982-12

Trask, S., & Bouton, M. E. (2014). Contextual control of operant behavior: Evidence for hierarchical associations in instrumental learning. *Learning & Behavior*, *42*(3), 281–288. https://doi.org/10.3758/s13420-014-0145-y

Treisman, A. M. (1969). Strategies and models of selective attention. *Psychological Review*.

Treisman, A. M. (2012). *Strategies and models of selective attention.*

Vencato, V., Harwood, M., & Madelain, L. (2022). Saccadic initiation biased by fixational activity. *Vision Research*, *201*, 108117. https://doi.org/10.1016/j.visres.2022.108117

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*(2), 413–421. https://doi.org/10.1152/jn.00634.2017

Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). Effect of Remote Distractors on Saccade Programming: Evidence for an Extended Fixation Zone. *Journal of Neurophysiology*, *78*(2), 1108–1119. https://doi.org/10.1152/jn.1997.78.2.1108

Watanabe, K., Lauwereyns, J., & Hikosaka, O. (2003). Neural Correlates of Rewarded and Unrewarded Eye Movements in the Primate Caudate Nucleus. *The Journal of Neuroscience*, *23*(31), 10052–10057. https://doi.org/10.1523/JNEUROSCI.23-31-10052.2003

Wexler, M., & Collins, T. (2014). Orthogonal steps relieve saccadic suppression. *Journal of Vision*, *14*(2), 13–13. https://doi.org/10.1167/14.2.13

Wong, A. L., & Shelhamer, M. (2011). Sensorimotor adaptation error signals are derived from realistic predictions of movement outcomes. *Journal of Neurophysiology*, *105*(3), 1130–1140. https://doi.org/10.1152/jn.00394.2010

Wyckoff, L. B. (1952). *The role of observing responses in discrimination learning.*

Xu-Wilson, M., Zee, D. S., & Shadmehr, R. (2009). The intrinsic value of visual information affects saccade velocities. *Experimental Brain Research*, *196*(4), 475–481. https://doi.org/10.1007/s00221-009-1879-1

Yao, L., & Peck, C. K. (1997). Saccadic eye movements to visual and auditory targets: *Experimental Brain Research*, *115*(1), 25–34. https://doi.org/10.1007/PL00005682

Zambarbieri, D. (2002). The latency of saccades toward auditory targets in humans. In J. Hyona, D. P. Munoz, W. Heide, & R. Radach (Eds.), *Progress in Brain Research* (Vol. 140, pp. 51–59). Elsevier. https://doi.org/10.1016/S0079-6123(02)40041-6

Zimmermann, E., & Lappe, M. (2011). Eye Position Effects in Oculomotor Plasticity and Visual Localization. *The Journal of Neuroscience*, *31*(20), 7341–7348. https://doi.org/10.1523/JNEUROSCI.6112-10.2011

10. Résumé en français

10.1. Introduction

10.1.1. Historique des anomalies comportementales

Intelligence animale et notion d’appartenance

En 1898, Edward Thorndike mène une série d’expériences sur l’intelligence animale, incluant des chats. Affamés, les chats sont placés dans une cage qu’ils ne peuvent ouvrir qu’en réalisant un comportement précis (tirer une corde, appuyer sur un levier, …). D’abord, les chats produisent divers comportements de manière exploratoire jusqu’à effectuer le comportement cible, ouvrant la cage et leur permettant d’accéder à de la nourriture. Au fil des essais, les chats apprennent progressivement à associer ce comportement à l’ouverture de la cage, ce qui se traduit par une diminution du temps nécessaire pour exécuter ce comportement. Ces résultats illustrent le conditionnement instrumental, avec une contingence à trois termes : stimulus → réponse → conséquence. Dans une expérience ultérieure, Thorndike choisit un comportement beaucoup moins lié à la recherche de nourriture pour le chat : le toilettage. La cage s’ouvre chaque fois que le chat se lèche ou se gratte. Contrairement aux expériences précédentes, tous les chats n’apprennent pas cette association, et ceux qui y parviennent nécessitent une plus longue période d’apprentissage, avec une forte variabilité des performances. Thorndike parle alors d’ « appartenance », et attribue cette différence au fait que le toilettage « n’appartient pas » à la conséquence contrairement à des actions manipulatoires comme tirer une corde.

Cette idée d’appartenance suggère que certaines réponses sont plus facilement associées à certaines conséquences. Toutefois, bien qu’intuitive, cette notion reste descriptive et post hoc : elle ne permet ni de prédire systématiquement les résultats dans de nouvelles situations, ni d’expliquer les mécanismes sous-jacents des associations stimulus–réponse–conséquence.

Théorie des Processus Généraux

L'étude de Thorndike est l'un des premiers exemples détaillés de ce qui sera plus tard appelé des *misbehaviors*, c'est-à-dire des comportements qui ne s'intègrent pas à la Théorie des Processus Généraux de l'apprentissage. Cette théorie postule l'existence de principes universels régissant le conditionnement et l'apprentissage, valables pour toutes les espèces et toutes les situations. Bien que les behavioristes reconnaissent l'existence d'adaptations spécifiques aux espèces, celles-ci sont considérées comme n'affectant que l'expression du comportement, et non les mécanismes fondamentaux de l'apprentissage. Dans cette perspective, les lois de l'apprentissage sont supposées indépendantes des stimuli, des réponses et des conséquences utilisés. L'analyse du comportement s'est donc longtemps concentrée sur des principes généraux, en minimisant l'importance des différences entre espèces ou entre types de comportements. Les résultats qui contredisaient ces lois étaient alors classés comme des *misbehaviors*, souvent attribués à des problèmes méthodologiques plutôt qu'à des limites théoriques. Cependant, l'histoire de l'analyse du comportement montre que l'étude approfondie de ces anomalies a permis d'affiner les théories existantes et de mettre en évidence de nouveaux principes généraux. C'est notamment le cas des « réponses adjointes », décrites dans les années 1970 comme des comportements apparaissant sans renforcement direct, mais en raison d'une proximité fortuite avec le renforçateur. Initialement considérées comme des anomalies, elles ont conduit au développement de modèles fondés sur la proximité réponse-renforçateur, enrichissant la compréhension des mécanismes d'apprentissage. À l'inverse, l'observation atypique de Thorndike sur des variabilités d'apprentissage en fonction des éléments de la contingence reste peu explorée théoriquement.

L'expérience « Bright-Noisy Water »

L'expérience de Garcia et Koelling (1966), dite de « Bright-Noisy Water », constitue l'une des premières tentatives de reproduction expérimentale de ce type d'anomalie. S'appuyant sur le conditionnement classique, elle combine conditionnement de la peur (choc électrique associé à un stimulus audiovisuel) et conditionnement de l'aversion gustative (goût associé à une maladie). Dans cette étude, des rats ont accès à un abreuvoir contenant de l'eau sucrée, ce qui déclenche simultanément un stimulus lumineux et sonore. L'un des groupes reçoit un choc électrique, l'autre une injection induisant une maladie. Les résultats montrent une dissociation claire : les rats soumis au choc développent une réponse conditionnée envers le stimulus audiovisuel, tandis que ceux rendus malades développent une aversion envers l'eau sucrée. Les associations choc–goût et maladie–stimulus audiovisuel échouent à se former malgré des appariements répétés et simultanés. Cette double dissociation suggère que tous les stimuli ne sont pas appris de façon équivalente pour toutes les réponses ou conséquences qui leur sont associées.

Ces résultats ont été interprétés comme une preuve que certaines associations sont privilégiées, une idée proche de la notion d'appartenance. Le parallèle avec Thorndike est clair : dans les deux cas, les associations attendues ne se forment pas malgré la présence des contingences nécessaires. Toutefois, comme pour Thorndike, l'interprétation de Garcia et Koelling reste principalement descriptive et post hoc, sans pouvoir prédictif ni explication mécanistique claire des processus d'apprentissage sous-jacents.

10.1.2. Une tentative théorique : La préparation

À la même période, plusieurs auteurs ont tenté de proposer un cadre théorique permettant d'expliquer ces résultats anormaux. L'un des plus influents est le concept de *préparation* (*preparedness*), proposé par Seligman en 1970. Cette notion s'oppose au principe d'équipotentialité, selon lequel les éléments d'une contingence (stimuli, réponses, conséquence) peuvent être interchangés arbitrairement sans affecter fondamentalement l'apprentissage. Selon Seligman, les organismes sont biologiquement « préparés » à former certains types d'associations. Il distingue trois catégories : les associations *préparées*, qui sont apprises rapidement et efficacement ; les associations *non préparées*, qui n'entravent ni ne facilitent l'apprentissage ; et les associations *contre-préparées*, difficiles voire impossibles à acquérir. La préparation peut ainsi être conçue comme un continuum de probabilité d'apprentissage, allant d'associations très probables à très improbables.

Le degré de préparation d'une association est défini par la capacité de l'organisme à apprendre malgré une dégradation de la contingence. Cette dégradation peut prendre diverses formes : diminution de la saillance du stimulus, modification du nombre d'essais, allongement de l'intervalle inter-essais, présence de stimuli concurrents, etc. Dans cette perspective, l'association choc électrique–stimulus audiovisuel chez le rat serait préparée, tandis que l'association choc–goût de l'eau serait contre-préparée, expliquant respectivement l'apprentissage rapide et l'absence d'apprentissage observés. Par rapport au concept d'appartenance, la préparation met davantage l'accent sur l'association elle-même plutôt que sur la situation globale. Elle introduit également l'idée d'un critère quantifiable, fondé sur la dégradation du stimulus, afin de comparer le degré de préparation entre différentes associations. Cependant, cette tentative théorique pose plusieurs problèmes majeurs. Premièrement, la préparation n'explique pas les mécanismes sous-jacents de l'apprentissage : une association est dite préparée parce qu'elle est apprise rapidement, et cette rapidité sert ensuite à mesurer la préparation, ce qui est circulaire. Deuxièmement, l'idée de mesurer la préparation par la dégradation du stimulus suppose l'existence d'un paramètre commun à toutes les situations, ce qui est difficilement défendable, car les types de dégradation sont très hétérogènes et peu comparables. Enfin, la préparation demeure essentiellement un concept descriptif et post hoc, avec un faible pouvoir prédictif. Comme le souligne Schwartz dès l'émergence de cette proposition, elle ne permet pas de répondre précisément à des questions nouvelles, par exemple déterminer si une association nouvelle serait préparée ou non, ni d'estimer les conditions nécessaires à son émergence.

10.1.3. Vues contemporaines

Théorie des systèmes comportementaux

Les limites des notions d'appartenance et de préparation ont mis en évidence la nécessité d'un nouveau cadre conceptuel pour expliquer les différences d'apprentissage liées à un changement dans la contingence à trois termes. Une avancée majeure dans cette direction provient de l'éthologie, avec la Théorie des Systèmes Comportementaux (*Behavioral Systems Theory*, BST) proposée par

Timberlake. À l'origine, les systèmes comportementaux servent à décrire les comportements animaux dans différentes situations fonctionnelles. Contrairement à l'analyse du comportement, qui s'intéresse principalement à la modification du comportement, l'éthologie adopte une position qui marque une rupture importante : elle postule que les organismes disposent dès le départ de structures perceptives et motrices préexistantes qui orientent et contraignent l'apprentissage ultérieur, s'opposant ainsi à la conception de l'organisme comme une « tabula rasa ».

La BST vise à établir un pont entre les lois générales de l'apprentissage issues de l'analyse du comportement et l'approche éthologique des systèmes comportementaux. Un système comportemental est défini comme une structure d'un ensemble de comportements liés à une fonction biologique spécifique, telle que la prédation ou la reproduction. Ces systèmes sont organisés hiérarchiquement en quatre niveaux. Les *sous-systèmes* correspondent aux états motivationnels actuels orientant l'organisme vers la satisfaction du besoin. À l'intérieur des sous-systèmes, les *modes* organisent la séquence temporelle du comportement. Les *modules* regroupent des liens probabilistes entre certains stimuli et des groupes de réponse. Finalement, les *actions* correspondent aux comportements de l'animal.

Cette organisation est hiérarchique et dynamique : l'activation d'un niveau dépend de l'état des niveaux supérieurs et de l'environnement. L'originalité de l'approche de Timberlake réside dans l'intégration des associations pavloviennes à tous les niveaux du système. Les systèmes ne sont pas considérés comme fixes, mais comme des structures flexibles façonnées par l'apprentissage. L'apprentissage y est conçu comme un processus qui se déroule à l'intérieur des systèmes comportementaux, en mobilisant et adaptant différents sous-niveaux. La BST met l'accent sur l'importance des comportements spécifiques à chaque espèce et rompt avec la recherche exclusive de lois universelles indépendantes du répertoire comportemental. Elle permet de dépasser la circularité du concept de *préparation* en postulant l'existence de systèmes définis indépendamment des comportements observés. Elle suggère que les réponses appartenant à un sous-système donné s’associent plus facilement aux stimuli qui activent ce sous-système. Par exemple, dans un contexte de prédation, des actions comme saisir ou maintenir une proie devraient être plus facilement conditionnées que le toilettage.

Toutefois, le pouvoir prédictif de la BST reste limité par la flexibilité qu’elle attribue aux systèmes : l’apprentissage peut introduire de nouveaux comportements dans un mode donné, rendant difficile la distinction entre comportements « appartenant » naturellement à un système et comportements acquis par conditionnement. Cette difficulté est illustrée par des comportements artificiels largement utilisés en laboratoire, comme l’appui sur un levier chez le rat, qui n’existent pas dans l’environnement naturel de l’espèce. De plus, la BST ne fournit pas de mécanisme explicatif précis reliant les différents niveaux des systèmes. Enfin, ces limites reflètent surtout une préoccupation issue de l’analyse du comportement. Une approche utilisant le comportement pour approfondir la compréhension des mécanismes d’apprentissage sera développée ultérieurement dans les travaux de Domjan.

Les contributions de M. Domjan

Après la publication de l’expérience Bright Noisy Water, le caractère anormal de ces résultats a suscité de nombreuses critiques. Beaucoup ont tenté d’expliquer ces effets par des défauts méthodologiques ou des facteurs externes, afin de préserver les lois classiques de l’apprentissage. Toutefois, Domjan et ses collaborateurs ont défendu ces résultats en réalisant plusieurs réplications rigoureuses, intégrant notamment des groupes contrôles, l’utilisation de rats nouveau-nés ou des conditionnements en un seul essai. Ces travaux ont confirmé de manière robuste et reproductible la double dissociation mise en évidence par Garcia et Koelling, établissant l’existence de contraintes biologiques sur l’apprentissage. À partir de ces bases, Domjan a poursuivi l’étude de ces contraintes à travers des recherches sur le comportement sexuel chez la caille. Il a progressivement reformulé ses résultats dans le cadre de la Théorie des Systèmes Comportementaux, en mettant davantage l’accent sur les processus d’apprentissage que sur la seule structure des systèmes comportementaux.

Cette approche a conduit à plusieurs contributions majeures. D'abord, elle montre que n'importe quel niveau du système peut constituer un lieu de conditionnement. Par exemple, un contexte distinctif peut conditionner l'entrée dans un mode de recherche générale, se traduisant par une augmentation de l'activité locomotrice chez la caille mâle. Domjan propose également une classification fonctionnelle des stimuli environnementaux en trois catégories : les indices contextuels diffus (comme l'éclairage ou les bruits ambiants), les stimuli localisés arbitraires (sons, lumières), et les stimuli localisés spécifiques à l'espèce (comme les caractéristiques du partenaire sexuel). Ces catégories ne sont pas seulement descriptives : elles ont une pertinence fonctionnelle, car certains types de stimuli sont plus susceptibles d'activer certaines parties du système. Les stimuli spécifiques à l'espèce, par exemple, favorisent des modes de recherche focalisée ou des comportements copulatoires plutôt qu'une recherche générale. Dans ce cadre, Domjan et ses collègues ont montré que les lois classiques du conditionnement pavlovien (acquisition, extinction, blocage, inhibition conditionnée, conditionnement de second ordre, etc.) s'appliquent aux stimuli arbitraires, tout en démontrant que les stimuli spécifiques à l'espèce produisent un conditionnement plus robuste, résistant davantage à l'extinction, au blocage et aux variations temporelles.

Une seconde contribution majeure concerne le système comportemental dans son ensemble. Domjan propose un modèle dans lequel l'apprentissage modifie progressivement la structure du système à partir d'un système préexistant. Les succès et échecs rencontrés dans une situation donnée entraînent une réorganisation fonctionnelle du système, augmentant la probabilité d'atteindre son objectif lors d'expositions futures. Cette perspective rompt avec l'approche classique centrée sur des contingences isolées, en intégrant les stimuli spécifiques à l'espèce, en posant des limites à ce qui peut être appris et en autorisant des interactions entre systèmes. Bien que fondée sur l'étude du comportement sexuel chez la caille, cette approche repose sur une terminologie générale permettant des comparaisons inter-espèces. Elle concilie ainsi la recherche de principes généraux de l'apprentissage avec la prise en compte des répertoires spécifiques aux espèces.

Appliquée au cas de Thorndike, cette perspective permet une relecture fonctionnelle : le chat serait initialement engagé dans un système orienté vers l'évasion et l'obtention de nourriture. Lorsque les tentatives d'évasion échouent et que le temps s'écoule, un changement motivationnel conduirait à l'activation d'un système lié aux soins, exprimé par le toilettage. Ce basculement réduirait la sensibilité aux stimuli externes, limitant la formation d'une association entre le toilettage et l'ouverture de la cage. Bien que cette interprétation soit plus structurée que la simple notion d'*appartenance*, elle demeure insuffisante pour prédire précisément quelles associations seront efficaces ou inefficaces, soulignant la nécessité de développements théoriques supplémentaires.

En dehors de l'analyse du comportement

Des problématiques similaires à celles que nous avons précédemment décrites apparaissent également en psychologie cognitive. Dans cette perspective, l'inefficacité de l'apprentissage observée par Thorndike chez les chats serait interprétée en termes d'attention : le chat ne prêterait pas attention à l'ouverture de la porte, son attention étant focalisée sur le toilettage. Cette interprétation repose sur l'idée centrale que les ressources attentionnelles sont limitées, ce qui contraint la quantité d'information traitée par le cerveau. Lorsque l'attention est dirigée vers un événement, d'autres événements peuvent passer inaperçus, phénomène bien documenté sous le nom de cécité attentionnelle. Dans les modèles classiques, l'attention est conçue comme un filtre qui sélectionne l'information pertinente, ce qui a donné lieu à de nombreux débats sur la localisation et la nature de ce filtre. Si cette conception est solidement étayée empiriquement, la question de l'origine de ces filtres — pourquoi et quand l'attention se déplace — a été moins étudiée. Définir l'attention comme un mécanisme de filtrage et inférer ensuite son déplacement à partir de l'information sélectionnée introduit une forme de raisonnement circulaire.

Pour répondre à cette difficulté, Krauzlis et ses collègues ont proposé un cadre alternatif dans lequel l'attention n'est plus considérée comme une cause, mais comme une conséquence fonctionnelle des mécanismes impliqués dans le traitement de l'information. Dans ce modèle, l'état attentionnel résulte de la compétition entre trois composantes : les données sensorielles issues de la perception, les connaissances préalables issues de l'expérience passée et l'état interne de l'organisme. Ces composants pondèrent différemment l'information disponible ; l'état le plus adapté à la situation reste actif jusqu'à ce qu'un autre le remplace. Dans ce cadre, toute l'information perceptive est collectée, mais seule celle qui est pertinente pour l'état actuel est effectivement traitée. Comme les besoins fonctionnels d'un état peuvent être définis indépendamment de la notion d'attention, ce modèle évite le caractère circulaire des explications traditionnelles. Enfin, ce cadre théorique est compatible avec la Théorie des Systèmes Comportementaux : les connaissances préalables peuvent être assimilées à l'histoire de renforcement de l'organisme, l'état interne à la fonction ou au mode de réponse actuellement actif, et la sélection de l'information à un mécanisme décisionnel.

Sélectivité des apprentissages

Les travaux présentés dans cette partie introductive montrent que certains résultats expérimentaux entrent en conflit avec les cadres théoriques dominants de l'apprentissage. Malgré des avancées importantes, tant sur le plan théorique qu'expérimental, notre capacité à expliquer et surtout à prédire ces résultats demeure limitée. Ce phénomène de variation de l'efficacité des stimuli à induire un apprentissage sera désigné par le terme de **sélectivité de l'apprentissage**. Introduit initialement par Garcia et collègues, ce concept renvoie à une sélection active de l'information en fonction des exigences fonctionnelles de l'organisme et implique une continuité entre l'absence totale d'apprentissage et un apprentissage très efficace.

Le point de départ théorique adopté ici est l'approche fonctionnelle de la Théorie des Systèmes Comportementaux, telle que développée par Domjan. Ce cadre soulève plusieurs questions fondamentales concernant les propriétés innées des systèmes comportementaux : dans quelle mesure ces systèmes sont-ils innés, quelles sont leurs limites d'intégration de nouveaux éléments, et ces limites sont-elles elles-mêmes innées ?

Une seconde question centrale concerne la démonstration de la sélectivité de l'apprentissage chez l'humain. Les capacités verbales et le raisonnement logique pourraient en partie masquer ou compenser ce phénomène, en permettant l'inférence explicite des contingences là où les autres espèces échouent. Si la sélectivité n'apparaît que dans des situations très spécifiques, elle pourrait être surmontée par un raisonnement explicite. L'un des objectifs majeurs de ce manuscrit est donc d'examiner l'existence de la sélectivité de l'apprentissage chez l'humain et d'identifier des caractéristiques prédictives de son expression.

10.1.4. Control Moteur

Saccades

L'adaptation saccadique est un paradigme couramment utilisé pour étudier l'apprentissage moteur impliquant les saccades. Les saccades représentent environ 90 % des mouvements des yeux et permettent de déplacer le regard afin que les objets d'intérêt soient projetés sur la fovéa. En conditions normales, l'humain effectue environ deux à trois saccades par seconde, chacun étant suivi d'une période de fixation durant laquelle l'information visuelle est extraite. En laboratoire, les saccades sont provoquées en présentant une cible visuelle et en demandant au participant de la regarder.

La littérature décrit de nombreux paramètres des saccades, dont trois sont particulièrement importants pour ce manuscrit: l'amplitude, définie comme la distance entre le point de fixation initial et le point final de la saccade, généralement exprimée en degrés d'angle visuel ; la latence, correspondant au temps écoulé entre le signal déclencheur et le début effectif de la saccade, typiquement comprise entre 150 et 200 ms ; et l'angle de la saccade, qui correspond à l'orientation du vecteur reliant les points de départ et d'arrivée, mesurée dans un système de coordonnées polaires allant de 0° à 360°. Les caractéristiques cinématiques des saccades obéissent à des relations systématiques entre amplitude, durée et vitesse, connues sous le nom de « main sequence » des saccades. Cette séquence reflète les contraintes physiques et neuronales du système oculomoteur et décrit une exécution optimisée des saccades, garantissant à la fois précision et minimisation des perturbations visuelles, afin de soutenir une perception visuelle fluide et une interaction efficace avec l'environnement.

Adaptation Saccadique

Parallèlement à l'étude des caractéristiques des saccades, de nombreux travaux se sont intéressés à la **capacité d'adaptation du système visuel**, en particulier à travers le paradigme d'**adaptation saccadique**, décrit pour la première fois par McLaughlin (1967). Dans ce paradigme, un participant fixe un point central, puis effectue une saccade vers une cible périphérique. Pendant la saccade, la cible est déplacée de manière imperceptible (saut intra-saccadique, ISS), ce qui augmente artificiellement l'erreur rétinienne, c'est-à-dire la distance entre la position de l'œil et celle de la cible après l'atterrissage de la saccade.

En raison de la **suppression saccadique**, le participant ne perçoit pas consciemment ce déplacement. Au fil des essais, cependant, la cinématique des saccades se modifie progressivement pour atterrir plus près de la position de la cible post-ISS. Cette modification graduelle correspond à l'adaptation saccadique, généralement mesurée par la différence d'amplitude des saccades entre le début et la fin de l'expérience. Dans le cadre de l'apprentissage moteur, cette adaptation est interprétée comme un ajustement des prédictions internes, souvent modélisé à l'aide d'approches bayésiennes.

Un point crucial est le **caractère implicite** de l'adaptation saccadique. Celle-ci se manifeste par des changements lents et progressifs des paramètres des saccades, incompatibles avec une stratégie explicite qui produirait des ajustements rapides et massifs. Cette adaptation persiste même lorsque les participants tentent de contrôler volontairement leurs saccades, ce qui confirme qu'il s'agit d'un processus d'apprentissage moteur automatique. De plus, bien que des participants expérimentés puissent parfois percevoir le déplacement intra-saccadique, leur taux d'adaptation reste comparable à celui de participants naïfs.

Enfin, de nombreuses études ont montré que l'adaptation saccadique est **spécifique à la direction** des mouvements entraînés. Les modifications acquises ne se généralisent pas nécessairement à des directions non entraînées, soulignant une dépendance au contexte. Ainsi, l'adaptation saccadique peut être considérée comme une forme de **conditionnement des saccades,** guidée par la réduction de l'erreur rétinienne et obéissant aux lois générales de l'apprentissage. Elle constitue donc un outil privilégié pour l'étude des mécanismes de l'apprentissage moteur.

Les saccades comme réponse d'observation

La conception des saccades comme des comportements opérants a été formalisée de manière approfondie par Madelain et collègues (2011). Elle repose sur de nombreuses preuves expérimentales montrant que les propriétés des mouvements saccadiques peuvent être modifiées par l'apprentissage par renforcement, aussi bien chez le singe que chez l'humain. Ces travaux démontrent que des variables telles que la direction, l'amplitude ou la latence des saccades sont sensibles aux contingences de renforcement. Un argument central en faveur de cette interprétation des saccades comme comportements opérants est fourni par le phénomène d'**adaptation saccadique**, qui illustre directement la capacité du système oculomoteur à modifier ses réponses en fonction des conséquences de l'action, constituant ainsi un exemple clair d'apprentissage moteur.

En raison de leur fonction consistant à amener un objet visuel d'intérêt sur la fovéa, les saccades peuvent être plus précisément décrites comme des **réponses d'observation**. Ce type de réponse,correspond à un comportement opérant dont la fonction est de produire un stimulus discriminatif signalant soit la disponibilité du renforcement, soit l'extinction. Cette distinction est essentielle, car les réponses d'observation sont renforcées par l'information qu'elles fournissent sur l'environnement. Ainsi, les saccades sont naturellement renforcées par la perception précise de la cible visuelle, ce qui souligne leur rôle fonctionnel dans l'acquisition d'information.

Adaptation contextuelle saccadique

Le paradigme d'**adaptation saccadique contextuelle** est une extension de l'adaptation saccadique classique, dans laquelle différents **indices contextuels** prédisent la direction de l'ISS. Dans ce paradigme, un participant effectue une saccade vers une cible subissant un ISS, mais contrairement à l'adaptation classique, **deux ISS différents** peuvent être appliqués sur le même vecteur de saccade, chacun associé à un contexte spécifique.

Dans l'expérience d'Alahyane et Pélisson (2004), le point de fixation servait d'indice contextuel : la cible apparaissait à une position haute ou basse. Lors des essais d'adaptation, un ISS était appliqué en avant pour le point de fixation haut et en arrière pour le point bas, entraînant simultanément **deux adaptations opposées** : augmentation de l'amplitude pour l'ISS vers l'avant et diminution pour l'ISS vers l'arrière.

D'autres études ont montré que cette adaptation contextuelle peut être induite par divers indices, comme l'excentricité ou la **profondeur de la cible**, la **position orbitale horizontale ou verticale,** l'**orientation de la tête**, le **mouvement de la cible** ou une **séquence de saccades**. Dans chaque cas, les participants apprennent deux réponses différentes simultanément, exprimées de manière spécifique au contexte. D'un point de vue du **conditionnement opérant** : l'indice contextuel (A ou B) est le stimulus discriminatif, la saccade est la réponse, et la **réduction de l'erreur rétinienne** est le renforcement. Au fil des essais, les participants ajustent leurs saccades en fonction du contexte, apprenant simultanément deux réponses différentes.

Dans les **modèles bayésiens**, l'adaptation contextuelle est vue comme un processus de **prédiction basée sur l'indice**. Chaque indice dispose de son modèle parallèle et indépendant : après chaque essai, les priors sont mis à jour pour l'indice actuel, permettant une adaptation simultanée aux deux contextes.

En résumé, l'adaptation saccadique contextuelle montre que le système oculomoteur peut apprendre **différentes réponses pour différents indices/contextes**, offrant un modèle pour étudier l'apprentissage moteur et la modélisation bayésienne des prédictions sensori-motrices.

Les anomalies dans l’adaptation saccadique

Dans une autre étude sur l’**adaptation saccadique contextuelle**, Deubel (1995) a utilisé la **couleur et la forme de la cible** comme indices contextuels. Comme dans les paradigmes précédents, les participants fixaient un point de fixation, la cible subissait un déplacement initial, et un ISS était appliqué au moment de la saccade. La cible était soit une **croix verte**, soit un **cercle rouge**. Lors des essais d’apprentissage, un ISS en arrière était appliqué uniquement pour la croix verte, tandis que le cercle rouge ne subissait aucun ISS.

On s’attendait à observer une **diminution de l’amplitude des saccades** pour la croix verte et aucun changement pour le cercle rouge, révélant ainsi une adaptation contextuelle dépendante de l’indice. Cependant, les résultats **n’ont montré aucune adaptation contextuelle** : aucune différence significative de l’amplitude des saccades entre les deux types de cibles.

Selon Deubel, cela indique que le **contrôle du gain saccadique** n’est pas spécifique aux caractéristiques visuelles de la cible. Ces résultats ont été confirmés par des réplications utilisant également la couleur et la forme comme indice, montrant systématiquement que **la couleur et la forme d’une cible sont inefficaces pour induire une adaptation contextuelle des saccades.**

Chez le singe, **Cecala et al. (2015)** ont reproduit l’expérience en utilisant la **couleur comme indice contextuel**, associant une cible verte à un ISS vers l’avant et une cible rouge à un ISS vers l’arrière. Après plus de **1 500 essais**, les singes **n’ont montré aucune différence significative** de l’amplitude des saccades en fonction de la couleur de la cible. Dans une autre expérience du même article, les auteurs ont présenté la **cible rouge seule pendant 600 essais**, entraînant une **adaptation arrière réussie**, puis la **cible verte seule pendant 600 essais,** entraînant une **adaptation avant réussie.** Ces résultats montrent que **la couleur de l’indice n’empêche pas l’apprentissage** : chaque adaptation est possible individuellement mais **pas simultanément**. Autrement dit, **lorsqu’une seule ISS est présente, l’indice ne gêne pas l’adaptation**, mais **il ne permet pas une adaptation contextuelle.**

Propositions théoriques à propos des anomalies

D’un point de vue théorique, ces résultats posent une difficulté persistante pour la recherche sur l’apprentissage moteur. Bahcall et Kowler (2000) ont suggéré que “les indices de haut niveau ne sont pas le moyen naturel de contrôler l’adaptation”, mais cette interprétation ne propose pas de mécanisme sous-jacent ni de prédiction pour d’autres situations.

Azadi et Harwood (2014) ont avancé l’hypothèse que l’adaptation des saccades est purement motrice, s’intéressant peu ou pas aux propriétés visuelles de la cible. Ainsi, le système adapterait fortement les aspects liés au mouvement, mais pas les caractéristiques visuelles. Cependant, cette distinction reste post hoc, car les auteurs s’attendaient initialement à ce que toutes les conditions soient efficaces. Le problème demeure : pourquoi certains indices visuels n’entraînent-ils pas d’adaptation ? Et qu’en est-il d’autres types d’indice, comme auditifs ou statistiques ?

Une situation similaire a été observée dans l’adaptation aux champs de force pour les mouvements de bras (Howard et al., 2013). Les participants devaient atteindre des cibles avec un bras manipulant un robot, tandis qu’un champ de force déviait le mouvement. Des indices contextuels étaient associés au champ de force (par exemple, indice A pour déviation gauche, indice B pour déviation droite). Les résultats montrent que certains indices, comme la position de départ, induisent une forte adaptation contextuelle. D’autres indices, comme un mouvement visuel périphérique, donnent une adaptation plus modérée. Enfin, certains indices, comme la couleur du curseur, n’entraînent aucune adaptation. Les auteurs concluent que l’efficacité des indices dépend de leur pertinence pour le système moteur, qui encode les mémoires motrices en fonction de l’état des membres. Comme pour les saccades, ces résultats offrent peu d’éclaircissement sur les mécanismes sous-jacents et aucun pouvoir prédictif pour des indices non testés.

10.1.5. Rationale théorique

Question de recherche

Premièrement, nous devons **répliquer la situation d’inefficacité de l’apprentissage.** Nos paramètres expérimentaux diffèrent de ceux des études précédentes utilisant la couleur et la forme de la cible. En établissant à la fois des **adaptations contextuelles efficaces et inefficaces** dans les mêmes conditions expérimentales, à l'exception de la nature des stimuli utilisés, nous disposerons d'une **base solide pour comparer les différents stimuli et paramètres expérimentaux.**

Un deuxième objectif majeur est **d'examiner un plus large éventail d'indices contextuels,** afin de déterminer **quels indices induisent effectivement l'apprentissage et quels indices échouent.** L'étude des différentes propriétés de ces indices permettra de clarifier si des facteurs **au-delà des caractéristiques visuelles de la cible** peuvent contrôler l'adaptation saccadique. Cette approche permettra de **quantifier plus précisément les différences d'apprentissage selon les stimuli** et contribuera à affiner et faire progresser le cadre théorique de la **sélectivité de l'apprentissage.**

Enfin, nous visons à **aborder la sélectivité de l'apprentissage selon deux approches complémentaires :** une **approche atomique**, qui examine la spécificité du système saccadique afin d'obtenir des **informations détaillées sur les processus sous-jacents aux différences d'efficacité de l'apprentissage.** Une **approche moléculaire**, qui considère les mouvements oculaires comme un **système fonctionnel,** permet de **caractériser ses limites et ses forces** pour étendre les résultats de l'adaptation saccadique à des processus d'apprentissage plus généraux.

De manière critique, nous cherchons à **proposer un mécanisme expliquant l'expression de la sélectivité dans l'adaptation saccadique et le contrôle moteur**, ainsi qu'un **moyen de prédire son occurrence**.

10.2. Contribution Expérimentale

10.2.1. Apprentissage sélectif dans l'adaptation saccadique

Première étude : indices inefficaces pour l'adaptation saccadique contextuelle

L'adaptation saccadique contextuelle est étudiée à travers une variante du paradigme de double saut, dans laquelle deux directions de saut intra-saccadique sont signalées par deux indices distincts. Cela permet l'induction simultanée de deux adaptations saccadiques différentes.

Dans cette étude, nous avons testé neuf indices contextuels différents pairés avec le saut intrasaccadique: durée du stimulus visuel, latéralisation d’un son, différentes régularités statistiques entre les essais, indices symboliques, position initiale de la cible, ainsi que l’amplitude du premier saut ou la couleur et la forme de la cible.

Des apprentissages contextuels robustes et systématiques ont été observés uniquement dans les expériences utilisant l’amplitude et la position de départ de la cible, tandis qu’aucun apprentissage n’a été détecté avec les autres indices. Cette absence d’adaptation contextuelle confirme que la prédiction des sauts intra-saccadiques dépend de la nature du contexte. Dans deux expériences supplémentaires, reproduisant celles utilisant la couleur et la forme de la cible, ainsi que des indices symboliques, les participants étaient périodiquement invités à rapporter explicitement l’indice contextuel qu’ils venaient de percevoir. Une fois encore, aucune adaptation contextuelle systématique n’a été observée, bien que les participants aient correctement identifié l’indice contextuel.

Cette dissociation entre le rapport perceptuel et la performance motrice, impliquant la même information visuelle, s’aligne avec les résultats précédents sur les contraintes de l’apprentissage contextuel. Le système saccadique, spécialisé dans le ciblage spatial, présente un apprentissage sélectif, privilégiant les indices de localisation et ignorant efficacement les indices non moteurs, même lorsque ceux-ci sont explicitement perçus.

Extension aux indices non-spatiaux

Les indices efficaces pour l’adaptation saccadique contextuelle sont ceux qui modifient directement la position de départ ou d’arrivée de la saccade. Azadi et Harwood (2014) soulignent l’importance des « indices visuels pertinents spatialement », mais il reste difficile de trancher si seuls les indices liés au déplacement de la cible peuvent être efficaces.

Pour répondre à cette question, nous avons mené trois expériences supplémentaires explorant des indices capables d’induire un changement soit dans la cinématique, soit dans le timing de la saccade, sans modifier les positions de la cible.

Dans une première expérience, nous avons utilisé un distracteur distant pour évaluer son efficacité comme indice contextuel. L'effet du distracteur consiste en la modification d'un ou plusieurs paramètres de la saccade induite par un distracteur présenté à proximité du trajet de la saccade. Puisque ce distracteur modifie des composantes motrices de la saccade, nous avons émis l'hypothèse qu'il pourrait constituer un indice contextuel efficace, même si les positions de départ et d'arrivée de la cible restent inchangées. Ceci a permis d'observer une adaptation saccadique robuste chez les participants, confirmant la possibilité d'induire un apprentissage contextuel sans utiliser une modification spatiale directe de la cible ou du participant.

Un autre type d'indice non spatial, les relations temporelles, restait à explorer. Pour tester si les relations temporelles pouvaient induire l'adaptation contextuelle, nous avons mené deux expériences manipulant les propriétés temporelles de la saccade.

Nous avons utilisé un design Gap-Overlap. Dans la condition Gap, le participant percevait un écran vide pendant 60 ms après la disparition du point de fixation, ce qui raccourcit la latence des saccades. Condition Overlap : le point de fixation reste visible 60 ms après l'apparition de la cible, ce qui allonge la latence. Chaque condition a été associée à une direction d'ISS, contrebalancée entre 10 participants. Cette manipulation affecte uniquement le moment du déclenchement de la saccade, pas sa cinématique et à conduit à des adaptations saccadiques. Dans une troisième étude complémentaire, nous avons manipulé la durée de fixation avant la saccade, révélant des effets d'adaptation modestes et mais présent. Ces trois expériences montrent que les indices non spatiaux peuvent induire l'adaptation contextuelle, à condition qu'ils modifient les paramètres moteurs de la saccade.

Ainsi, l'efficacité d'un indice contextuel dépend non seulement de sa pertinence motrice, mais aussi de la manière dont il modifie spécifiquement l'exécution de la saccade. Ces résultats illustrent un continuum d'efficacité des indices, gouverné par les paramètres moteurs qu'ils influencent.

10.2.2. Selectivité des apprentissages dans le conditionnement d'ordre supérieur

Seconde étude : Adaptation saccadique contextuelle et conditionnement d'ordre supérieur

Dans cette seconde étude, nous avons utilisé une variante du paradigme double-step contextuel pour étudier le conditionnement d'ordre supérieur dans l'adaptation saccadique contextuelle. Ce conditionnement d'ordre supérieur a été construit comme suit : un premier indice contextuel module l'information portée par un second indice, le stimulus discriminatif, afin de permettre la prédiction du saut intra-saccadique.

Dans une première situation expérimentale, la position de départ a été utilisée comme indice contextuel, pour moduler l'information portée par le stimulus discriminatif, l'amplitude du premier saut. Sur dix participants, deux ont montré un apprentissage significatif après une session, et cinq sur six ont montré un apprentissage significatif lors d'une réplication en 5 sessions consécutives répétée. Ces résultats indiquent que l'adaptation saccadique peut être induite dans un design d'ordre supérieur, où la prédiction de l'ISS dépend à la fois du SD et de l'indice contextuel présenté au cours de l'essai. Bien qu'un nombre plus important d'essais soit nécessaire pour obtenir un apprentissage cohérent, ces résultats démontrent la capacité du circuit oculomoteur à intégrer des processus d'ordre supérieur.

Dans une deuxième expérience, nous avons utilisé un indice non-moteur, la couleur et la forme de la cible, comme indice contextuel. La couleur et la forme de la cible sont connues pour entraîner un apprentissage inefficace dans l'adaptation saccadique, tant chez l'humain que chez l'animal. Ici, nous avons cherché à savoir si cet indice non-moteur pouvait être utilisé pour l'adaptation saccadique en tant qu'indice contextuel, c'est-à-dire comme stimulus permettant de résoudre l'incertitude sur l'information portée par le SD. Sur dix participants, aucun n'a montré d'apprentissage discriminatif. Lors d'une réplication en cinq sessions, aucun participant n'a présenté d'apprentissage significatif. Cette absence de résultats suggère que le circuit oculomoteur est incapable de prendre en compte un indice non-moteur pour optimiser son comportement et réduire l'erreur rétinienne. La différence frappante entre les expériences sur la couleur et la forme et sur la position de départ confirme que seuls les indices moteurs peuvent contrôler l'adaptation saccadique.

L'absence d'apprentissage avec la couleur et la forme a conduit à considérer deux hypothèses pour expliquer l'apprentissage efficace observé avec la position de départ.

Une interprétation en termes de modulateur contextuel : la position de départ pourrait agir comme un modulateur de l'association entre le SD et le saut intrasaccadique. Par exemple, deux associations différentes pourraient se former pour le SD « amplitude courte », une pour chaque ISS, avec la position de départ modulant quelle association est exprimée. Si cette hypothèse est correcte, le processus d'occasion setting opérerait entièrement dans le système oculomoteur. Des expériences de contrôle supplémentaires seraient nécessaires pour déterminer les propriétés spécifiques acquises par les occasion-setters et confirmer que cette modulation se produit au sein du circuit moteur.

Une seconde interprétation en termes de SD composé : les participants pourraient avoir appris chacune des quatre combinaisons indépendamment. La position de départ et l'amplitude du premier pas partageraient alors une partie de la valeur prédictive de l'ISS et fonctionneraient comme un SD composé, où les deux indices agissent conjointement. Cette hypothèse est compatible avec l'inefficacité de la couleur et de la forme, suggérant que seules les caractéristiques pertinentes pour la programmation motrice contribuent à l'apprentissage. Cependant, il reste à expliquer pourquoi un SD composé nécessiterait autant d'essais pour atteindre une discrimination significative.

Pris ensemble, nos résultats fournissent des preuves empiriques supplémentaires de la nature sélective de l'apprentissage moteur saccadique et soulignent la nécessité de modèles prenant en compte non seulement les résultats de l'apprentissage, mais aussi la manière dont le système sélectionne les informations pour optimiser son comportement.

10.2.3. Un mécanisme sous-jacent pour l'apprentissage moteur : La planification

Troisième étude : Étude du rôle de la planification motrice dans l'adaptation saccadique

La troisième contribution expérimentale de ce manuscrit s’intéresse plus précisément à la programmation des saccades. L’apprentissage moteur contextuel des saccades rencontre un problème encore non résolu d’apprentissage inefficace, même dans des conditions apparemment idéales, en particulier lorsque des indices non-moteurs sont utilisés comme contextes. En reliant ce problème aux théories du contrôle moteur, aux avancées dans la compréhension du cortex moteur et aux preuves issues de l’adaptation du bras en champ de force, nous avons proposé un paradigme permettant de séparer l’exécution et la planification des actions motrices.

Des études précédentes ont montré que des mouvements partageant une cinématique initiale similaire mais divergents dans une seconde partie du mouvement présentent des états neuronaux différents pour la planification totale du mouvement. Lorsqu’un mouvement de bras composé de deux parties (atteindre un objet, puis un second) est planifié en séquence, la seconde partie du mouvement modifie ainsi le plan total, incluant la première. De plus, cette différence de plan a été démontrée comme étant un indice nécessaire et suffisant à l’induction d’un apprentissage moteur. La conclusion tirée de ce travail est donc que la planification motrice du mouvement du bras est le composant clef de l’apprentissage.

Cette troisième étude a pour objectif d’étendre ces résultats obtenus chez le bras à la saccade, permettant ainsi une meilleure compréhension des mécanismes à l’œuvre lors d’apprentissages impliquant des mouvements de saccades, ainsi qu’une généralisation de ce principe aux apprentissages moteurs en général. Dans ce but, quatre situations expérimentales ont été comparées : Une situation de séquence complète, dans laquelle le participant devait effectuer une séquence de deux saccades et où la seconde saccade était le stimulus discriminatif. Une situation de saccade simple, où la position d’une seconde cible était le stimulus discriminatif, mais le participant ne devait pas effectuer de saccade vers celle-ci. Une situation « exécution », où l’exécution de la seconde saccade était présente, mais la planification des deux saccades en séquences était empêchée. Et enfin une situation « planification », dans laquelle le participant planifiait la séquence de saccades mais n'exécutais que la première saccade.

Nos résultats ont montré que les participants n'apprennent à adapter leurs saccades que lorsque la séquence de saccades est planifiée intégralement, indépendamment de son exécution. Cette observation renforce les preuves empiriques que le système moteur est spécialisé dans la discrimination entre différents plans moteurs, tout en étant insensible aux composantes purement perceptuelles ou à l'exécution motrice seule d'une saccade. Cette troisième contribution expérimentale souligne ainsi que la modification du plan moteur est le composant clef de l'adaptation saccadique, et probablement de l'apprentissage moteur en général.

10.3. Discussion Générale

Sélectivité des apprentissages

Dans une perspective d'analyse comportementale, les contributions expérimentales présentées ici soulèvent plusieurs défis et ouvrent de nouvelles voies pour approfondir notre compréhension des mécanismes en jeu. Au niveau moléculaire, placer la planification motrice comme le locus de l'apprentissage est une proposition peu commune dans les théories de l'apprentissage. Peu commune non pas parce qu'un état interne pourrait fonctionner comme un stimulus discriminatif (SD), mais parce qu'elle suggère que l'efficacité de l'apprentissage dépend de la nature du stimulus utilisé dans la contingence. Cette vision fournit une manière opérationnelle de prédire comment la sélectivité s'exprimera dans une situation donnée, en comparant les différents plans moteurs impliqués.

Dans cette perspective, un accès direct au plan moteur pourrait permettre de prédire si l'apprentissage se produira en fonction de sa structure : des plans moteurs identiques ne conduiraient à aucun apprentissage, des plans très distincts entraîneraient un apprentissage rapide, et des variations subtiles entre plans produiraient un apprentissage plus lent. En effet, si les plans sont les stimuli critiques contrôlant la réponse, alors plus les plans moteurs sont discriminables entre eux, meilleur est l’apprentissage ; à l’inverse, plus ils sont difficiles à discriminer, plus l’apprentissage risque d’échouer.

Cette interprétation permet de résoudre les anomalies observées dans les expériences d’adaptation saccadique précédemment discutées, où la couleur et la forme de la cible étaient inefficaces pour contrôler la saccade. Dans toutes ces expériences, le composant critique manquant pour une adaptation efficace était la différenciation de la planification motrice. De plus, chaque indice efficace agissait sur la planification motrice. C’est aussi le cas pour l’eccentricité ou la profondeur de la cible, la position orbitale horizontale ou verticale, l’orientation de la tête, le mouvement de la cible ou la séquence de saccades, qui impliquaient tous un changement de la position de départ, de la position d’arrivée ou de la séquence planifiée des saccades.

Cette interprétation peut également s’appliquer à nos résultats. La manipulation de l’amplitude du premier pas ou de la position d’un distracteur distant a conduit à des modifications de la trajectoire de la saccade et, par conséquent, à des états neuronaux différents résultant de la planification de ces commandes. En revanche, la couleur et la forme de la cible, ou l’utilisation d’un indice symbolique, n’ont pas affecté le plan moteur réel de la saccade. Dans ces situations, le système planifiait la même saccade et disposait d’un seul état, c’est-à-dire un plan, pour deux ISS différents, entraînant un échec de l’apprentissage. Enfin, les conditions gap/overlap ou la manipulation de la durée de fixation ont produit les mêmes saccades, mais avec un décalage dans le timing de l’exécution motrice. Nous soutenons que partager le même état moteur avec un timing différent lors du déclenchement du mouvement entraîne des différences plus faibles, donc plus difficiles à discriminer. Cela revient essentiellement à comparer la probabilité pour un organisme de discriminer deux couleurs très différentes, comme le rouge et le bleu, par rapport à deux nuances proches d’orange : l’apprentissage de discrimination dépend de la différence physique entre ces stimuli, facilitant l’établissement d’associations spécifiques séparément.

Proposition d’un système moteur

Dans l'introduction, nous avons discuté de la Behavioral Systems Theory (BST) et de certaines de ses limites, notamment sa capacité prédictive limitée et l'absence de mécanismes explicatifs pour la sélectivité des systèmes. Un autre aspect soulevé à la fois par Timberlake et Domjan, mais peu développé empiriquement jusqu'à présent, concerne la possibilité pour les systèmes comportementaux d'être induits et d'interagir entre eux.

Contrairement à Domjan ou Timberlake qui ont étudié des systèmes de comportements complexes, notre focus s'est porté sur une réponse terminale spécifique : la saccade. Suivant l'idée de la fonctionnalité du système comportemental, nous devrions ici représenter un système visuel. Ce système visuel englobe tous les processus fonctionnellement liés à la vision, à savoir les mouvements oculaires et la perception visuelle. Selon Timberlake et Domjan, les réponses au sein d'un même système comportemental devraient présenter un certain degré de transversalité et de communication mutuelle. Cependant, les études précédentes ainsi que nos propres résultats indiquent que l'information purement visuelle échoue à contrôler l'adaptation saccadique.

L'idée que les plans moteurs, mais pas l'information perceptuelle, constituent un élément critique pour l'apprentissage contextuel dans le mouvement saccadique suggère une relative indépendance entre perception et motricité. Pour cette raison, nous proposons une alternative à l'approche fonctionnelle pour déterminer la structure d'un système comportemental, basée sur les mécanismes sous-jacents. Nous proposons ainsi de considérer un système moteur, englobant la préparation motrice, l'exécution et le résultat moteur. Dans ce système moteur, nous placerions donc ensemble les réponses motrices, incluant, mais sans s'y limiter, : saccades, poursuites oculaires lisses ou mouvements du bras, pour lesquels la planification motrice peut être considérée comme un élément critique pour l'apprentissage.

Le principe de la BST sur l'interaction au sein d'un système fournit une hypothèse : une séquence de mouvements, incluant les mouvements oculaires et du bras, planifiée conjointement, devrait être efficace pour induire l'adaptation saccadique ou l'adaptation du bras. Définir un système par son mécanisme d'apprentissage partagé permet à la fois un pouvoir explicatif et prédictif. Tandis que les modèles de Domjan et Timberlake délimitent efficacement ce qui peut ou ne peut pas être appris au sein d'un système, ils ne permettent pas d'expliquer pourquoi cette sélectivité émerge. Notre compréhension est que l'approche fonctionnelle qu'ils ont utilisée a peut-être intégré plusieurs systèmes différents travaillant ensemble pour un seul objectif, rendant l'analyse des mécanismes sélectifs plus difficile à mener avec précision. En incorporant les résultats sur l'apprentissage moteur sélectif, le cadre BST et l'approche de Krauzlis sur le processus attentionnel, nous avons tenté de fournir un modèle illustratif de l'adaptation saccadique dans le système moteur.

Dans le modèle que nous proposons, la chaîne comportementale commence par le stimulus. Puisque nous avons proposé que mouvement et perception sont des systèmes indépendants, nous supposons un système perceptuel qui détecte le stimulus en périphérie. L'information motrice sur l'indice atteindra également le système moteur, que nous décrivons plus en détail à l'aide du modèle attentionnel de Krauzlis. Ce modèle implique trois composantes principales dans la prise de décision : les données sensorielles, les connaissances préalables et l'état interne de l'organisme. Les données sensorielles correspondent aux stimuli à partir desquels l'organisme extrait l'information. Nos résultats ont montré que la planification, mais pas l'exécution, permet la discrimination ; nous proposons donc que le plan moteur lui-même constitue l'entrée sensorielle pertinente pour les décisions motrices. Les connaissances préalables reflètent les expériences passées de situations similaires, c'est-à-dire la mémoire motrice. Dans le contexte de l'adaptation saccadique, l'erreur rétinienne rencontrée lors de l'exécution précédente de ce même plan moteur sert de signal de rétroaction pour ajuster la performance future et réduire l'erreur. Enfin, l'état interne représente l'état actuel du système, qui peut intégrer des influences d'autres systèmes comportementaux.

Nous avons montré de manière répétée que les indices perceptuels ne contrôlent pas directement l'adaptation saccadique. Cependant, les saccades dépendent clairement de la perception visuelle. Nous suggérons donc que la composante *état interne* puisse être un signal descendant, provenant d'un autre système — probablement perceptuel — fournissant des informations pertinentes pour la tâche sans façonner directement l'apprentissage moteur. Une fois ces trois composantes prises en compte pour la décision d'exécution motrice, deux issues différentes émergent : (1) Un résultat moteur, correspondant à l'erreur de prédiction du système moteur, utilisé pour mettre à jour la mémoire motrice du plan moteur spécifique exécuté. (2) Un résultat perceptuel, auquel le système perceptuel a maintenant accès aux informations perceptuelles de la cible. Ce résultat peut augmenter ou diminuer la probabilité que le système perceptuel fournisse une entrée au système moteur pour atteindre à nouveau cette cible spécifique à l'avenir.

Enfin, il convient de souligner que la General Process Theory (GPT), c'est-à-dire l'ensemble des lois connues de l'apprentissage, reste valide dans notre cadre. Chaque fois que la contingence et la contiguïté temporelle étaient préservées entre les différents plans moteurs et leurs résultats, l'apprentissage se produisait avec succès. Les différences de taux d'apprentissage observées selon les différents indices contextuels peuvent être interprétées comme des différences dans le plan moteur — un résultat cohérent avec d'autres tâches de discrimination. À la lumière de ces observations, nous nous alignons sur la vision de Domjan et proposons de résoudre l'anomalie de l'apprentissage sélectif en reformulant la GPT : les processus d'apprentissage nécessitent la contingence, la contiguïté temporelle et la compatibilité entre les éléments de la contingence et le système comportemental induit.

Conclusion générale

Cette thèse a commencé par exposer le problème de l'apprentissage sélectif, un phénomène bien décrit dans la recherche sur l'apprentissage, mais dépourvu de cadre théorique explicatif. Ce phénomène contredit la General Process Theory (GPT), entraînant un apprentissage inefficace même dans des situations où la contiguïté et la contingence entre les éléments sont parfaites. Nous avons choisi comme point de départ le cadre offrant l'explication la plus complète de l'apprentissage sélectif, à savoir la Behavioral System Theory (BST) de Domjan, pour investiguer cette question.

Nous avons démontré l'existence d'une situation de résultats différentiels selon le type d'indice dans l'adaptation saccadique contextuelle, montrant que seuls les indices liés à la motricité étaient efficaces, confirmant ainsi l'existence de l'apprentissage sélectif chez l'humain. À travers des expériences supplémentaires, nous avons montré que l'apprentissage discriminatif n'était pas équivalent pour tous les indices moteurs, et que des différences dans les résultats apparaissent entre eux. Nous avons ensuite mis en évidence la complexe interaction entre les systèmes, montrant que le conditionnement d'ordre supérieur pouvait être induit en utilisant des indices moteurs, mais pas lorsqu'on mélangeait indices moteurs et non moteurs. Enfin, nous avons démontré que la planification motrice constituait le locus de l'apprentissage pour l'adaptation saccadique.

Nous avons proposé une interprétation possible des différences observées entre indices moteurs, en illustrant le rôle nécessaire et suffisant de la planification motrice pour l'apprentissage. Nous avons suggéré que la capacité du circuit saccadique à différencier les différents plans moteurs pourrait expliquer la variation de l'apprentissage selon l'indice moteur. Dans la discussion, nous nous sommes alignés sur la proposition de Domjan d'ajouter à la GPT un élément critique de l'apprentissage, à savoir l'apprentissage sélectif. De plus, nous avons proposé que l'apprentissage sélectif dépend de l'appartenance des éléments à un même système comportemental. Les stimuli appartenant au même système sont plus susceptibles d'être sélectionnés pour l'apprentissage, tandis que ceux extérieurs au système sont plus susceptibles d'être ignorés.

En conclusion, ce travail visait non seulement à décrire l'apprentissage sélectif dans l'adaptation motrice, mais également à proposer un cadre théorique capable d'en rendre compte. En intégrant la vision de Domjan sur la BST dans le cadre moléculaire de l'adaptation saccadique, nous avons cherché à pallier le manque de mécanisme sous-jacent proposé par la BST tout en promouvant les bénéfices théoriques. Cette proposition ouvre plusieurs pistes de recherche future. L'une consiste à tester et remettre en question le modèle proposé dans des travaux expérimentaux ultérieurs sur l'apprentissage moteur. Une autre consiste à explorer comment l'apprentissage sélectif opère au-delà du système moteur, et si des principes similaires ou des structures équivalentes peuvent rendre compte des observations expérimentales. Enfin, une direction importante serait d'étudier plus avant l'interaction entre les systèmes, ce qui pourrait aider à délimiter les frontières actuelles de la BST et faciliter son intégration dans la General Process Theory.