The Effects of Auditory Consequences on Visuomotor Adaptation and Motor Memory

by

Gemma Malagón Meza

B.Sc. (Biomedical Engineering), Tecnológico de Monterrey, 2020

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biomedical Physiology and Kinesiology
Faculty of Science

SIMON FRASER UNIVERSITY
Fall 2023

Declaration of Committee

Name: **Gemma Malagón Meza**

Degree: **Master of Science**

Title: **The Effects of Auditory Consequences on Visuomotor Adaptation and Motor Memory**

Committee: **Chair:** **David C. Clarke**
Associate Professor, Biomedical Physiology and Kinesiology

Daniel S. Marigold
Supervisor
Professor, Biomedical Physiology and Kinesiology

Dylan F. Cooke
Committee Member
Assistant Professor, Biomedical Physiology and Kinesiology

Randy McIntosh
Committee Member
Professor, Biomedical Physiology and Kinesiology

Charles Krieger
Examiner
Professor, Biomedical Physiology and Kinesiology

Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

b. advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University

or has conducted the research

c. as a co-investigator, collaborator, or research assistant in a research project approved in advance.

A copy of the approval letter has been filed with the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, British Columbia, Canada

Update Spring 2016

Abstract

Humans have a remarkable ability to learn a wide range of motor behaviours and adapt them to different conditions. Motor learning involves rectifying movement errors and retaining corrected actions for future execution. Recent research indicates that experiencing balance-threatening physical consequences when making a movement error during adaptation can enhance motor memory. This is perhaps not surprising, as learning to avoid injury is critical for our survival and well-being. However, it remains unclear whether other forms of consequences can impact motor learning. The goal of this thesis is to determine if a non-physical consequence, a loud acoustic stimulus (LAS), can also improve motor learning, potentially through increased emotional arousal. Twenty-four participants adapted to a novel visuomotor mapping induced by prism lenses while performing a precision walking task that required them to walk and step to the center of a target projected on the ground. We randomly divided participants into two groups: an auditory consequence group and a control group. In the auditory consequence group (n = 12), participants received a LAS of 85 dB if they missed the target. Participants in the control group (n = 12) faced no consequences for a stepping error. Generalization was assessed through an interlimb transfer test (i.e., stepping to target with non-adapted foot) and obstacle-avoidance task (i.e., stepping laterally over an obstacle), both performed without prisms. The results demonstrated that the auditory consequence group exhibited greater generalization during the interlimb test, although this effect was less prominent in the obstacle-avoidance task. To evaluate consolidation, an opposite direction visuomotor mapping was introduced after initial adaptation in the first testing session and then performance with the initial mapping was re-tested one week later. Both groups showed reduced foot-placement errors during the second testing session, indicating successful consolidation. However, no significant differences were found between the groups. Overall, this thesis provides initial evidence that auditory consequences may enhance the generalization process but does little for consolidation. However, our findings suggest a connection between increased emotional arousal and improved generalization and savings. This implies that there may be potential in designing motor learning environments that enhance engagement and emotional arousal, which could be a valuable avenue for exploration, particularly in rehabilitation settings.

Keywords: sensorimotor adaptation; consolidation; emotional arousal; generalization

Dedication

To my amazing parents, who always said I could do anything I set my mind to – even if they were secretly thinking "good luck with that".

Gracias mamá y papá, por ser mis guías, mi apoyo incondicional y mi razón de ser.
A pesar de la distancia, su presencia es constante en mi vida.

Acknowledgements

I would like to express my deepest gratitude to everyone who has played a part in the completion of this master's thesis. This journey has been both challenging and rewarding, and I am truly grateful for the support and encouragement I have received along the way.

First and foremost, I would like to extend my heartfelt thanks to my supervisor, Dr. Dan Marigold. Your guidance, expertise, and dedication have been invaluable throughout this process. Your mentorship has not only shaped the content of this thesis but has also been instrumental in my personal and academic growth.

I am also grateful to the members of my thesis committee, Dr. Randy McIntosh and Dr. Dylan Cooke, for their insightful feedback and constructive criticism. Their expertise has not only enhanced the academic rigor of this work but has also broadened my perspective and deepened my understanding of the subject matter.

Special thanks go to my family and friends for their unwavering support and understanding during this demanding period away from home. Your encouragement, patience, and belief in my abilities have been a source of strength, and I am truly fortunate to have you in my life.

I am indebted to my fellow graduate friends and colleagues, who shared their knowledge and provided a collaborative and inspiring discussions. A special thank you to my BPK 801 friends Steph, Tiff and Rebekah who offered both moral support and much-needed breaks from the demands of research, thank you for being there to keep me sane and grounded. I extend the appreciation to my lab mates, Amin, Vini, and Cady, for their camaraderie, shared dedication and their constant encouragement that kept me going.

Lastly, I express my gratitude to all those who may not be mentioned explicitly but have played a role in shaping my academic and personal journey. Your contributions, whether big or small, have not gone unnoticed.

This thesis would not have been possible without the collective support of these amazing individuals and institution. Thank you all for being a part of this significant milestone in my academic journey.

Table of Contents

List of Figures

List of Acronyms

LAS	Loud Auditory Sound
SAM	Self Assessment Manikin
VR	Virtual Reality

Chapter 1.

1.1. Introduction

Learning which of our actions help to avoid injury is critical for our survival and well-being. Indeed, people can learn from the consequences of their actions. Can we exploit this idea to improve motor learning? A recent study demonstrated greater motor memory when experiencing a balance-threatening physical consequence following a movement error (Bakkum & Marigold, 2022). These authors suggested that the effect of the balance-threatening physical consequence may relate to the surprising nature of it, the balance challenge itself, the threat of a potential loss of balance, and/or heightened emotional arousal due to the surprise and/or threat. The overall goal of my thesis is to determine if a non-physical consequence, a loud acoustic stimulus, can also improve motor learning, potentially through increased emotional arousal. This knowledge may facilitate the develoment of more effective strategies to enhance motor learning in various settings.

The rest of **Chapter 1** discusses the concepts of sensorimotor adaptation, generalization, and consolidation. It also describes the impact of different error consequences on motor learning. Subsequently, it delves into the role of emotional arousal on memory. The chapter culminates with a summary of key points and a list of research aims, thus laying the groundwork for the subsequent chapter. **Chapter 2** describes the experiment to address my research aims. In **Chapter 3,** I discuss the study's limitations, broader implications of the findings, and potential future directions for the research.

1.2. Aspects of sensorimotor adaptation

Sensorimotor adaptation involves learning a new relationship between a sensory input and motor output (Bastian, 2008). It enables us to adjust and recalibrate our movements based on feedback from the environment, optimizing our motor behaviours for specific tasks and contexts. This learning concept extends to everyday scenarios. For instance, when you injure your ankle, your sensorimotor system adjusts how you move to safeguard the injured joint. It changes things like step length, movement patterns, and weight distribution to help the healing process and avoid strain. This highlights its capability to adapt to altered sensory information, promoting safer walking.

Sensorimotor adaptation involves at least two distinct components: explicit and implicit learning (Poggio & Bizzi, 2004; Kitago & Krakauer, 2013; Krakauer et al. 2019). Explicit learning in sensorimotor adaptation refers to the conscious and deliberate adjustment of motor behaviours in response to sensory feedback. (Mazzoni & Krakauer 2006; Taylor & Ivry 2011; Taylor et al. 2014). When faced with movement errors or discrepancies between expected and actual sensory outcomes, individuals strategically aim to correct their actions and reach a desired target. This form of learning involves the explicit intention to modify motor behaviours and is associated with a rapid and goal-directed adaptation process. In prism adaptation literature, this process is often referred to as strategic control (Redding et al. 2005). McDougle et al. (2017) demonstrated that the explicit component of sensorimotor learning encompasses various cognitive strategies. For example, attention can affect the speed of adaptation throughout the learning process.

In contrast to explicit learning, implicit learning in sensorimotor adaptation occurs without conscious awareness or explicit intention to modify motor behaviours. Individuals implicitly adapt their movements in response to repetitive sensory prediction errors (the error between the predicted and actual feedback) (Maeda et al. 2017a; Mazzoni & Krakauer 2006; Tseng et al. 2007). Key to this comparison is the forward internal model. It consists of two components: the forward dynamic model, which predicts the system's state changes due to actions by relying on an efference copy signal, and the forward sensory model, which predicts the sensory consequences of those state changes (Shadmehr et al. 2010; Miall & Wolpert 1996; Kandel et al. 2021). Over time, these incremental adaptations lead to gradual changes in motor actions. Specifically, the revised forward model's output can subsequently be utilized to calculate the necessary motor command for counteracting the perturbation when a task goal is specified (Izawa & Shadmehr, 2011). While implicit learning is slower and more monotonic compared to explicit learning, it can lead to more robust and enduring motor adjustments (Taylor et al. 2014). In prism adaptation literature, this process is referred to as spatial realignment (Redding et al. 2005). In my thesis work, I will use prisms to create sensory prediction errors.

Altogether, sensorimotor adaptation involves both explicit and implicit learning components. One way to assess whether a person has adapted is to determine whether they apply what they've learned in one task to other tasks. In the following section, I will discuss the transfer (or generalization) of learned motor behaviours to new situations.

1.3. Generalization

One of the hallmarks of motor learning is generalization. Generalization involves transferring a new learned behaviour to a new context (Poggio & Bizzi, 2004; Kitago & Krakauer, 2013; Krakauer et al. 2019, Torres-Oviedo et al. 2012). This process is driven by the integration of past experiences and the ability to predict and adapt to novel situations (Krakauer et al. 2000; Thoroughman & Shadmehr, 2000).

In recent years, numerous sensorimotor adaptation studies have examined the concept of generalization, primarily focusing on isolated upper limb movements. This work indicates limited generalization. For example, Thoroughman & Shadmehr (2000) and Criscimagna-Hemminger et al. (2010) reported that adaptation to forcefields during reaching did not uniformly generalize to untrained movement directions or workspace configurations. Additionally, Ghahramani et al. (1996) found evidence of limited generalization when participants experienced different visuomotor mapping perturbations. Studies using visuomotor rotations have shown similar results. For instance, Werner et al. (2015) showed that generalization was not uniform across all directions. Krakauer et al. (2000) demonstrated partial generalization across certain conditions, such as varying reaching distances (2.4 to 9.6 cm) and distinct arm trajectories. Similarly, Krakauer et al. (2006) conducted a study where participants adapted to visuomotor rotations by controlling a robotic arm. Participants showed proficient adaptation to the specific rotation they trained with; however, when confronted with a different, untrained visuomotor rotation, their ability to adapt was impaired, indicating limited generalization. Generalization can also be absent (Wang, 2008). In addition, generalization between limbs can be asymmetric (i.e., only one limb transfers to the other). Specifically, some visuomotor rotation research found that adaptation with the non-dominant arm transferred to the dominant arm, but not vice versa (Sainburg & Wang, 2002; Wang and Sainburg, 2004). In contrast, other visuomotor rotation research found that adaptation with the dominant arm transferred to non-dominant arm, but not vice versa (Balitsky & Henriques, 2010). In addition, research on prism adaptation while reaching with the dominant arm reported a lack of transfer to the non-dominant arm (Renault et al., 2020). Taken together, generalization is inconsistent in reaching studies.

There is also support for generalization following walking adaptation tasks, though also limited. Previous research during walking prism adaptation showed generalization, though incomplete, between a precision walking task and an obstacle avoidance task (Alexander et al. 2011, 2013). Adapting to prism lenses while standing or walking and balance challenged led to generalization between different standing-based reaching and walking tasks (Bakkum et al. 2020). Morton & Bastian's (2004) recent findings indicate that prism adaptation shows wide generalization from walking to reaching but not the other way around, from reaching to walking. On the other hand, Savin and Morton (2008) observed an asymmetrical pattern in the generalization of prism adapted single limb pointing movements, where arm pointing extends to the leg, but not vice versa. Taken together, it is evident in both reaching and walking studies that generalization, though present, is seldom complete. Thus, it is unclear what factors can lead to complete generalization.

Overall, generalization leverages prior experience to aid future learning, with its scope varying based on tasks and training conditions. However, it is equally important for people to retain (or consolidate) what they've learned. In the next section, I will discuss the concept of motor memory consolidation.

1.4. Consolidation

Consolidation is another hallmark of motor learning and involves transforming motor memories from a fragile to a permanent or stable state (Brashers-Krug et al. 1996). Operationally, we define consolidation as the process by which a motor memory becomes resistant to interference over time. To test for resistance to interference, a person is required to learn an opposite perturbation to the one they just learned (Krakauer et al. 2005). This opposite perturbation is the so-called interference block. Subsequently, the person is re-tested on the original perturbation. Faster rate of re-learning (i.e., savings) is evidence of motor memory consolidation.

There is evidence for and against motor memory consolidation. Some studies using reaching tasks have shown no consolidation when learning two opposing force fields one after another in close temporal proximity (i.e., A then B), (Brashers-Krug et al. 1996; Shadmehr & Brashers-Krug, 1997). However, when the fields were experienced with longer time intervals between them (e.g., ~4-6 hours), retention of A was observed. Krakauer et al. (2005) also found a lack of savings when learning opposite visuomotor rotations during reaching tasks. However, when adding washout trials in between rotation blocks, savings became evident (i.e., consolidation) and the lack of savings must have been a result of anterograde interference (Krakauer et al. 2005). Thus, these findings are evidence that new motor memories go through consolidation. In contrast, Caithness et al. (2004) argued that motor memory consolidation does not occur, as they failed to show consolidation during both reaching force field and visuomotor rotation paradigms with and without washout trials.

Interestingly, there is strong support for consolidation during walking tasks. These studies involve adapting to prism lenses while having to step onto a target or adapting to different belt speeds on a split-belt treadmill. For example, Maeda et al. (2018) and Bakkum & Marigold (2022) had participants first adapt to rightward-shifting prism lenses and then adapt to leftward-shifting lenses as the interference block of trials. They found evidence of savings when retesting adaptation to the rightward-shifting lenses one week later. This savings even remained one year later (Maeda et al. 2018). In addition, Malone et al. (2011) had participants switch between walking with treadmill belts at the same speed (tied-belts) or two different speeds (split-belts), followed by adapting to an opposite split-belt pattern. They found evidence of savings on day two that was comparable to groups that did not experience the opposite split-belt pattern. However, none of the above studies found evidence for complete consolidation.

Taken together, there is room to increase the amount of both generalization and consolidation. In the upcoming section, I will discuss how we might enhance these hallmarks of learning.

1.5. Physical consequences of movement error

There is evidence involving both animals and humans that experiencing a threatening physical consequence can impact some forms of learning and memory. Rodent studies, such as those by Stuchlík et al. (2013) and Willis et al. (2017), have demonstrated rapid learning and retention of location avoidance linked to foot shocks.

Mice navigate a rotating arena using visual cues to evade a shock zone. They quickly learn the shock zone's location and exhibit long-term memory in subsequent trials, while a control group without the shock experienced a slower learning curve. This implies that the fear of a painful physical consequence can significantly impact their learning process. Similarly, human studies have revealed that the anticipation of an aversive experience, such as an electrical shock, can lead to better declarative memory (Murty et al. 2012; Starita et al. 2019; Dunsmoor et al. 2015).

Movement errors experienced in everyday life can lead to injury. Thus, it seems reasonable to expect that physical consequences related to movement error may affect motor learning. Recent work by Bakkum & Marigold (2022) tested this idea. Participants adapted to a new visuomotor mapping created by prism lenses during a precision walking task. One group experienced an unexpected slip perturbation when making foot-placement errors, while the other group did not. The researchers tested generalization during an interlimb transfer test and an obstacle avoidance task immediately after, and they tested consolidation of the mapping one week later. The consequence group generalized better and showed greater consolidation compared to the control group. Bakkum & Marigold (2022) suggested that the balance-threatening physical consequence (slip perturbation) may have induced surprise and/or heightened perceived threat, subsequently increasing emotional arousal. This arousal could have strengthened synaptic connections in pertinent sensorimotor areas involved in learning the new visuomotor mapping. Additionally, the physical consequence may have increased the error signal, or drawn greater attention to it. However, questions remain as to whether other forms of consequences can similarly influence generalization and consolidation in this paradigm and whether this is mediated by emotional arousal. My thesis will address these questions.

1.6. How different forms of error consequences affect motor learning

The literature above discusses research using a physical consequence, which may be painful or unpleasant. However, non-physical forms of consequences may also play a role. For instance, reinforcement feedback, involving reward and punishment, can influence motor learning (Abe et al. 2011; Song & Smiley-Oyen, 2017). Specifically, using a reaching-related visuomotor rotation task, numerous studies have illustrated that these reinforcers produce distinct effects on motor learning. Punishment can enhance the learning rate (adaptation), while reward increases the retention (memory) of the motor task (Galea et al. 2015; Song & Smiley-Oyen, 2017; Quattrocchi et al. 2018). In motor skill learning, reward enhances long-term memory retention, whereas punishment does not (Abe et al. (2011). Recently, Yin et al. (2023) explored the advantages of integrating both punishment and reward in a visuomotor rotation task. Their research demonstrates that pure punishment accelerates initial learning and enhances completeness during counter-rotation learning. Pure reward, however, has no significant impact on learning or memory. Combining both punishment and reward depending on performance consistently improved learning throughout the motivational phase and even transferred to learning opposite rotations. In the context of walking, Sato et al. (2022) revealed that explicit feedback influenced both step length and step time asymmetry during 'virtual' split-belt walking adaptation. Particularly noteworthy was the punishment group's enhanced step length readaptation on the following day, suggesting the potential efficacy of punishment feedback in rectifying visuomotor errors during walking.

Auditory stimuli may also influence motor learning. Indeed, providing (descriptive or prescriptive) verbal feedback can facilitate learning of new motor skills (Magill & Anderson 2016). Recently, Leow et al. (2021) tested whether loud acoustic stimulation could alter sensorimotor adaptation during a visuomotor rotation task. Loud acoustic stimuli (83 to 123 dB) are typically used to elicit a startle reflex (Carlsen et al. 2007). The startle reflex is a rapid and involuntary response to sudden, intense auditory or tactile stimuli, characterized by a quick contraction of muscles, heightened heart rate, and increased alertness (Landis & Hunt 1939; Bradley et al. 2001). This reflex serves as a natural defensive mechanism and has been extensively studied in the context of sensory processing and motor responses (Lang et al. 1990). For instance, researchers have observed the startle reflex in response to sudden auditory stimuli, such as a loud gunshot or a surprising noise burst in controlled experiments (Brown et al. 1991b; Carlsen et al. 2007; Valls-Solé et al. 1995). In the work of Leow et al. (2021), one group of participants experienced loud acoustic stimuli (short bursts at either 94 dB or 80 dB, depending on the experiment) randomly in 50% of trials upon movement completion. The group receiving the auditory stimuli showed greater improvements in initial adaptation to sensory prediction errors and enhanced retention. However, the acoustic stimuli were not specifically related to errors. In my thesis, I will determine whether a loud acoustic stimulus following movement error can enhance generalization and consolidation like a balance-challenging physical consequence.

1.7. Impact of arousal on learning and memory

Consequences of movement error, whether physical or not, may act through an increase in emotional arousal (Bakkum & Marigold 2022). This notion aligns with the emotional tagging hypothesis, which suggests that emotionally arousing events significantly lead to a reinforcement of synaptic connections in brain regions associated with learning (Richter-Levin & Akirav, 2003) and memory consolidation (Cahill & McGaugh 1995; Cahill et al. 2003; McGaugh, 2000; Cahill et al. 1996). Researchers have studied the impact of arousal on learning and memory using diverse approaches, such as exposing participants to contextual fear conditioning (LaLumiere et al. 2003), presenting emotionally-charged pictures (Anderson & Shimamura, 2005), inducing acute stress (Marloes et al. 2009; McGaugh et al. 2002; Roozendaal et al. 2006, Roozendaal & McGaugh, 2011; Abercrombie et al. 2006), including electric shock (Dunsmoor et al. 2015; Murty et al. 2012; Starita et al. 2019; Stuchlík et al. 2013; Willis et al. 2017), and the administration of stress hormones (Morris et al. 1982; Roozendaal & McGaugh, 1996; McIntyre et al. 2003, Lupien et al. 2007). How do these approaches influence learning and/or memory?

Emotional events or stimuli are often prioritized in memory. In Dunsmoor et al. (2015), human participants engaged in a Pavlovian fear conditioning task. In this protocol, participants viewed pictures from two different categories (animals and tools) without any initial associations. Later, one category was paired with wrist shocks (fear conditioning), while the other remained unshocked. Memory tests were conducted immediately after, 6 hours later, and 24 hours later. They observed that fear conditioning substantially enhanced memory and object recognition for the pictures within the category that had been paired with wrist shocks. Importantly, this enhancement in memory persisted both retroactively, affecting recall of the previously seen images, and prospectively, influencing recognition of the same images 6 and 24 hours later. In Anderson and Shimamura (2005), participants viewed various emotional film clips, including neutral, positive, negative, and arousing content. Their findings indicated that memory performance for words connected to emotionally negative clips was poorer compared to those linked to neutral, positive, and arousing clips. Thus, the type of emotional trigger can make a difference in how one remembers.

Stress impacts learning and memory. For instance, in Lupien et al. (2007), the effects of synthetic glucocorticoid administration (stress hormones) on declarative and nondeclarative memory were examined. Participants completed a memory task involving 12 words pairs, with sets created for both stressful and non-stressful conditions. After reading the word pairs aloud and undergoing cued recall, participants engaged in a distractor task to separate declarative and nondeclarative conditions. Nondeclarative memory was assessed through a word completion task, which included syllables from previously learned word pairs, syllables from a baseline list given to another group, and randomly selected syllables. The dependent measure for the declarative memory task was the number of correctly recalled words, while the nondeclarative task calculated the difference between words generated with prior exposure and those generated without prior exposure (baseline). The study showed that stress hormones impair declarative memory function while leaving nondeclarative memory unaffected. However, the intensity and duration of the stress can have different effects (Zerbes & Schwabe, 2021). More precisely, mild, and acute stress can enhance learning and cognitive performance, while excessive and chronic stress can impair learning and negatively impact memory (Tyng et al. 2017).

There are a variety of brain regions that process arousal. For instance, studies by Amaral et al. (2003) and Schupp et al. (2003) indicate that the amygdala shows an increased response to emotional stimuli, such as fearful faces and emotional verbs (both positive and negative). The enhanced memory capacity for emotional events is attributed to the amygdala's influence on the encoding and storage of memories dependent on the hippocampus (Phelps, 2004; McGaugh et al. 1996, 2004). These regions are known for their involvement in declarative memory in humans and spatial memory in animals (Clewett et al. 2018; Tully et al. 2010; Morris et al. 1982). This is believed to occur through the release of stress hormones, such as cortisol, which modulate synaptic plasticity and strengthen memory traces (McIntyre et al. 2003).

Despite the numerous brain regions involved in processing arousal and evidence to suggest that arousal affects learning and declarative memory, it is unclear whether emotional arousal impacts sensorimotor adaptation (or motor memory in general).

Interestingly, Green et al. (2010) suggested that arousal levels, associated with perceived risk and task complexity, affect locomotor aftereffects following adaptation to a moving surface, indicating that perceived threat has the potential to modify generalization. I will determine whether arousal plays a role in a visuomotor adaptation paradigm in my thesis.

1.8. Thesis goals and specific aims

Everyday movement errors can lead to physical injuries. Our brain corrects actions that lead to movement errors to develop movement patterns that allow the body to move more safely. In previous work done in our lab (Bakkum & Marigold, 2022), experiencing a balance threatening consequence when making an error during the adaptation phase led to better learning. The authors thought that the balance-challenging aspect of the consequence (i.e., the slip), possibly through increased arousal, may explain their results. I will use the same paradigm but use a non-physical consequence for participants when they make an error during adaptation. The two aims of my thesis are:

Aim 1: Determine if a loud acoustic stimulus immediately following a movement error during adaptation can improve generalization and consolidation. To achieve Aim 1, we compared two groups. Participants in the control group (n=12) performed a precision walking task while adapting to 20-diopter prism lenses. They did not receive any auditory consequence, regardless of movement errors. In contrast, the auditory consequence group (n=12) performed the same task and experienced the same visuomotor perturbation but experienced an auditory stimulus in the form of a loud sound (85 dB) when they made an error.

Aim 2: Determine whether emotional arousal drives the learning effect. Emotional arousal can influence learning and memory. To determine if this mechanism relates to our sensorimotor adaptation paradigm, participants will complete questionnaires related to surprise and arousal. To explore this relationship, I will conduct a correlation analysis between measures of arousal and performance on the tasks.

Chapter 2.

2.1. Introduction

Motor learning is a complex aspect of human behaviour that occurs throughout our lifespan. One component of motor learning is sensorimotor adaptation. Sensorimotor adaptation involves the acquisition of a new relationship between sensory input and motor output (Bastian, 2008), but individuals must be able to retain that information and apply it (i.e., generalize it) to various contexts. Understanding these processes is essential for developing effective neurorehabilitation interventions.

There is evidence in both animals and humans that suggests that encountering unpleasant or potentially dangerous physical consequences can significantly impact the processes of learning and memory. In rodents, this is tested, for example, using a place avoidance task, where unpredictable foot shocks are administered in certain sectors of a room. Notably, mice efficiently acquire knowledge to evade these shock zone locations within a single 20-minute session, reflecting their proficiency in short-term memory acquisition and retention (Stuchlík et al. 2013; Willis et al. 2017). This suggests that the anticipation of painful consequences can profoundly influence their learning. Likewise, in humans, aversive stimuli in the form of electric shocks affects declarative memory. Memory for items from a shock-conditioned category was enhanced compared to memory for items not paired with the aversive stimulus (Dunsmoor et al. 2015; Murty et al. 2012; Starita et al. 2019). Items like those from the conditioned category were more likely to be identified as old compared to items like those from the non-conditioned category, and arousal levels measured via skin conductance during conditioning predicted this generalization of items (Starita et al. 2019). In prior research conducted within our lab (Bakkum & Marigold, 2022), introducing a balance-threatening consequence following movement errors during the adaptation phase led to enhanced learning outcomes. Specifically, one group encountered a hidden slippery surface located next to the target that caused an unexpected balance-threatening slip perturbation when making foot-placement errors. This group demonstrated better generalization to different walking tasks and showed faster relearning one week later. Given that movement errors in everyday life can result in injury, it is reasonable to expect that physical consequences related to movement errors may influence motor learning.

Non-physical consequences following movement errors, such as reward and punishment, can expedite or enhance the process of motor learning. Research studies using monetary reward and punishment to reinforce learning show evidence that punishing errors can accelerate motor learning (i.e., faster adaptation) whereas rewarding movement accuracy is beneficial for retaining motor memories (Abe et al. 2011; Song & Smiley-Oyen, 2017; Song et al. 2020; Galea et al. 2015; Quattrocchi et al. 2018; Yin et al. 2023). These findings extend to studies on walking tasks (Sato et al. 2022). Research also indicates that reward enhances movement execution by increasing feedback control and accuracy during reaching movements (Carroll et al. 2019; Manohar et al. 2019). Collectively, these studies support the idea that both reward and punishment can play a valuable role in facilitating different aspects of motor learning across various motor tasks and contexts. Beyond traditional reward and punishment strategies, consequences tied to auditory stimuli may be another way to influence generalization and consolidation.

Auditory information may impact motor learning. This includes verbal feedback that is provided to the learner both prior to, during, and after their attempt to execute a task (Moinuddin et al. 2021). This verbal feedback facilitates adjustments for subsequent movements and is categorized as either descriptive or prescriptive (Schmidt & Lee, 1999; Magill & Anderson 2016). Descriptive feedback aids learners in error detection, enhances their awareness of movement nuances, supports fine-tuning of motor skills, and fosters long-term skill development. On the other hand, prescriptive feedback offers guided improvement by providing specific recommendations for correcting errors and enhancing performance, which can lead to faster skill acquisition and increased learner confidence (Magill & Anderson 2016). Verbal feedback regarding ongoing task performance is commonly used by rehabilitation specialists to enhance learning (Johnson et al. 2013). In addition to verbal feedback, simple auditory stimuli may direct a learner’s attention in such a way as to improve performance. For instance, Leow et al. (2021) conducted a study to investigate the influence of loud acoustic stimulation (LAS) on sensorimotor adaptation in the context of a visuomotor rotation task. They found that random LAS were associated with improved initial adaptation to sensory prediction errors and better retention of learned motor skills, even though these stimuli were not explicitly linked to movement errors.

In the present study, we tested the hypothesis that introducing a LAS immediately after and linked to a movement error during adaptation, could enhance generalization and consolidation. To test this hypothesis, we conducted an experiment involving two groups of participants tasked with adapting to a new visuomotor mapping induced by prism lenses during a precision walking task (Bakkum et al. 2020, 2021, 2022; Maeda et al. 2017a). Both groups performed the same task, but the auditory consequence group experienced an auditory stimulus in the form of a loud sound (85 dB) upon making an error in foot placement. We assessed the effect of the auditory manipulation by examining initial adaptation, generalization to other walking tasks, and consolidation one week later. Bakkum & Marigold (2022) suggested that the balance-challenging physical consequence following a movement error may have increased participant's emotional arousal, leading to the enhancement in motor memory. This concept aligns with the emotional tagging hypothesis, which suggests that emotionally arousing events strengthen synaptic connections in brain regions linked to learning and memory consolidation (Richter-Levin & Akirav, 2003). Thus, we also investigated the role of emotional arousal in driving the learning effect in our experiment.

2.2. Methods and materials

2.2.1. Participants

Twenty-four participants (mean age ± SD: 20.6 ± 1.4 years; 9 males, 15 females) with no known musculoskeletal, neurological, or visual disease participated in this experiment. We calculated the sample size based on the Group x Session interaction results from Bakkum & Marigold (2022) using G*Power. To achieve at least 80% power, we required group sample sizes of 4 (total of 8 participants). We chose to use group sizes of 12 to be consistent with past research (e.g., Bakkum & Marigold 2022). During the experiments, 15 participants utilized corrective lenses, which included glasses or contact lenses. The study protocol received approval from the Office of Research Ethics at Simon Fraser University, and all participants provided informed written consent prior to participating.

2.2.2. Walking tasks and experimental groups

In this experiment, participants had to adapt to a novel visuomotor mapping created by prism lenses. This adaptation occurred while performing a precision walking task (Bakkum & Marigold 2022). This task required participants to step onto the centre of a target (3 x 36 cm) projected on the ground with an LCD projector (Epson PowerLight

5535U, brightness of 5500 lumens). Participants walked under reduced light conditions to reduce visual distractions and increase the visibility of the projected target. At the start of each trial, participants stood at the beginning of a 6-meter walkway and awaited a cue to initiate walking. Once cued, they completed a minimum of two steps before stepping with their right foot onto the centre of the target without stopping and completing three more steps. Participants were instructed to execute steps as accurately as possible to the medial-lateral (ML) centre of the target and to maintain a brisk and consistent pace to reduce the possibility of online corrections of foot trajectory during the step to the target. To prevent adaptation between trials, participants kept their eyes closed before receiving the go-cue to start each trial and while walking back to the starting position (under experimenter guidance). All participants wore a harness as a safety precaution. Kinematic data were collected at 100 Hz from infrared markers placed on the participant's chest and bilaterally on each midfoot using an Optotrak Certus motion capture camera (Northern Digital, Waterloo, Canada).

Participants were randomly assigned to one of two adaptation groups. The control group (n=12) performed the precision walking task while adapting to 20-diopter prism lenses. The auditory consequence group (n=12) performed the same task and experienced the same visuomotor perturbation, but with the addition of an auditory stimulus in the form of a loud sound (85 dB) whenever they made a foot-placement error during the task. For this consequence group, a 50 x 60 cm a pressure-sensitive mat was positioned adjacent to the target and hidden with a thin black fabric that covered the length of the walkway. The lateral edge of the mat was positioned 12 cm to the right of the target to prevent participants from receiving a consequence if their foot-placement error was within a normal range for what is expected late in the adaptation phase (Bakkum & Marigold 2022).

The pressure-sensitive mat was designed with capacitive sensors controlled by a microcontroller and operated using batteries. It consisted of an array of single-side 0.5 mm wide copper tape (3M) attached to one side of each of two compressible cardboard surfaces. 30 strips of 50 cm length, with widths ranging from 1 to 1.5 cm and separated by 1 cm, were placed in columns on the top cardboard surface. An equal number of strips with identical width and spacing were placed in rows on the bottom cardboard surface. As a result, the spatial resolution of the mat was approximately 1 cm. To establish electrical connections, thin conducting metallic wires were soldered directly to the copper tape of both the top surface (column connections) and the bottom surface (row connections). When external pressure (such as a step) was applied to the mat, it compressed the two pieces of cardboard, acting as a dielectric medium between the capacitor plates. This compression led to a change in capacitance by displacing the electrodes at the chosen location on the mat. A localized change in capacitance in response to applied pressure triggered an 85 dB sound via two computer audio speakers. The sound lasted between approximately 450 to 650 ms, depending on how fast the participant stepped away from the mat.

We tested both generalization and consolidation of the learned visuomotor mapping. To assess generalization, participants performed two different walking tasks on the same day: an interlimb transfer task and an obstacle avoidance task. The interlimb transfer task was the same as the main experimental task described above but involved stepping onto the target with the left foot. The obstacle avoidance task involved walking and stepping laterally over the middle of an obstacle (width = 6 cm; length = 80 cm; height = 25 cm), first with the left leg, then the right leg. To assess consolidation, participants returned one week later to repeat the precision walking task with the stepping to the target with the right foot (see the experiment protocol below).

2.2.3. Experimental protocols

In the initial testing session, participants completed 3 sets of 15 baseline trials for each of the tasks (precision walking, interlimb transfer, obstacle avoidance) using 0-diopter lenses. Participants performed the primary precision walking task baseline trials last and the other two tasks according to a counterbalanced order. The order of these other two tasks remained consistent for both the baseline and generalization trials. Counterbalancing the generalization trials reduced the potential of any order effects. Next, participants went through 60 adaptation trials while wearing 20-diopter rightward-shifting lenses (i.e., mapping A_1). Following this, participants completed 1 trial of each of the two generalization tasks while wearing the 0-diopter lenses. To reduce any diminishing effect of wearing 0-diopter lenses and to ensure retention of what they had learned, they proceeded with an additional 20 adaptation trials while wearing the 20-diopter rightward-shifting lenses. After this block of trials, they undertook 20 trials using the 0-diopter lenses (i.e., washout phase). Finally, participants underwent 60 adaptation trials while wearing 20-diopter leftward-shifting lenses (i.e., mapping B). This mapping allowed us to investigate consolidation, defined as the resistance of mapping A to retrograde interference from a competing mapping (Maeda et al. 2017). To assess consolidation approximately one week later (mean 7.25 ± 0.73 days), participants completed 15 baseline trials of the precision walking task, followed by 60 adaptation trials wearing the 20-diopter rightward-shifting lenses (mapping A).

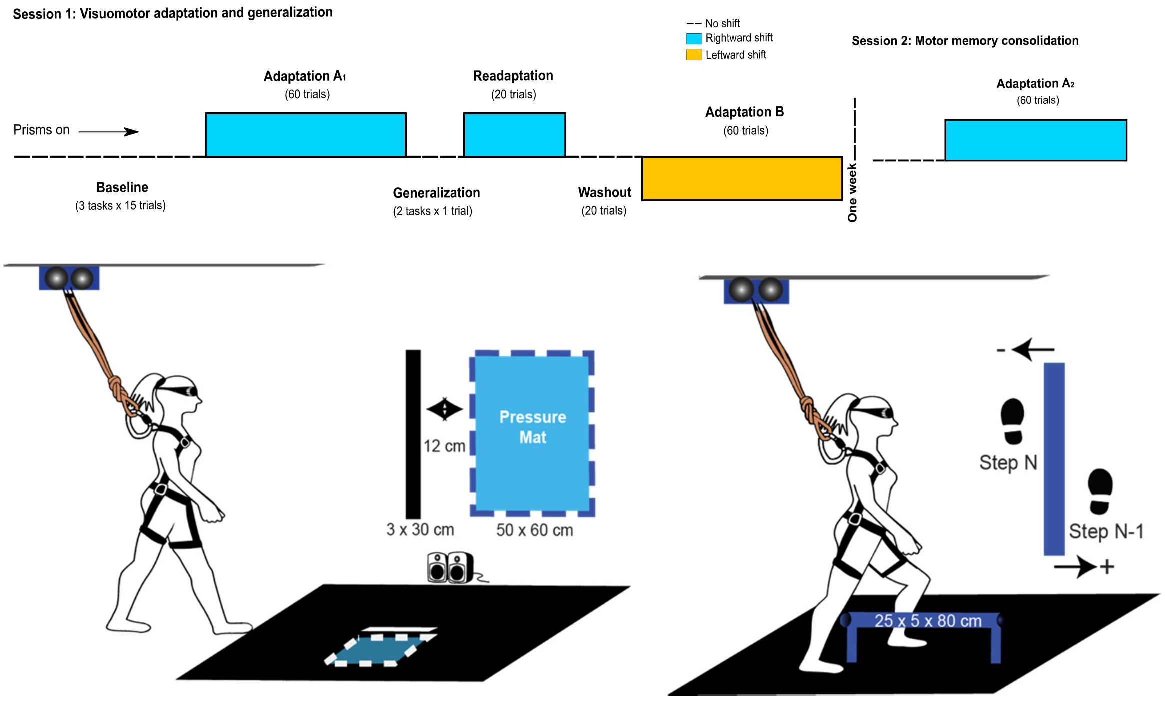

Figure 1. **Experimental task and protocol across session 1 and 2**
Top: Visual representation of the experimental protocol during both testing sessions. In the initial testing session, all participants performed baseline, adaptation, generalization, readaptation, and washout phases, then experienced an opposite visuomotor mapping to that experienced during the initial adaptation phase. Depending on the phase, participants wore either zero-diopter or 20-diopter lenses. To assess consolidation, participants repeated the baseline and adaptation phases one week later during session 2. Bottom: Illustration of the precision walking task with a pressure-sensitive mat adjacent to the stepping target. The pressure mat was concealed under black fabric and only present for the auditory consequence group. On the right side is an illustration of the obstacle avoidance task used to test generalization. Not shown is the interlimb transfer test.

To explore the relationship of emotional arousal in learning (Aim 2), we used the Self Assesment Manikin (SAM) questionnaire (Lang, 1980; Bradley & Lang, 1994) and a custom-designed single question related to surprise for all participants. The SAM questionnaire is a visual self-report tool used to evaluate and quantify emotional responses and feelings. It consists of a series of graphical figures, called "manikins," which participants use to represent their emotional states. Arousal is represented by a scale that ranges from low arousal to high arousal and participants choose a point on this scale that best represents the level of arousal they are experiencing. We administered the SAM questionnaire at the start of the experiment (immediately prior to baseline trials) and end of the adaptation phase. For the single question related to surprise, participants were verbally asked the following: "On a scale of 1 to 9, how surprised do you feel after this walking trial?" Participants were asked to provide their responses using a nine-point linear scale, where the left side indicated "Not at all surprised" and was assigned a value of 1, while the right side represented "Extremely surprised" and was designated as 9. This question was asked 16 times throughout the experiment. Specifically, it was asked once prior to the last five baseline trials, five times consecutively after the first adaptation trial, once after the initial 10 adaptation trials, and every 10 trials thereafter until the last adaptation trial (five times). Additionally it was asked once during the initial and final re-adaptation phases and once after both the initial and final washout phases. We only focus on the assessment during baseline and after the first adaptation trial to best reflect surprise and to simplify the analysis.

2.2.4. Data and statistical analysis

To analyze the kinematic data, we filtered them with a 4th-order, low-pass Butterworth filter using a cut-off frequency of 6 Hz. Foot placement during each task was determined using the vertical velocity of the mid-foot marker (Bakkum et al. 2020; O'Connor et al. 2007). The ML position of the mid-foot marker relative to the centre of the target determined the foot-placement error during the precision walking task (and interlimb transfer test). For the obstacle avoidance task, we calculated the ML distance between each foot and the obstacle for the step before (step N-1; right foot) and after crossing (step N; left foot).

To verify the groups adapted to the prisms, we compared foot-placement error during the baseline phase (mean of the last ten trials), the first adaptation trial, late adaptation (mean of the last ten trials), and the first washout trial in the first testing session using a two-way (Group x Phase) ANOVA. We did not include participant as a random effect in this model because the variance ratio was <0. In this model, we found a trial outlier (studentized residual = -4.6). Removing this data point did not influence the results and thus, we kept it in the model. To determine whether the auditory consequence improved learning, we compared groups on initial day 1 adaptation, generalization to other walking tasks, and consolidation approximately one week later. To determine differences between groups for initial adaptation, we calculated the mean foot-placement error across adaptation trials 2-8, referred to as early adaptation (Maeda et al. 2017; Bakkum et al. 2021; Bakkum & Marigold, 2022). We then performed an independent t test.

To determine if the learned visuomotor mapping generalized to the non-adapted (left) leg during the precision walking task, we compared foot-placement error during the baseline phase when using the left foot to step to the target (mean of the last ten trials) and the generalization trial using a two-way (Group x Phase) linear mixed-effects model (with the participant as a random effect). For this statistical test, we discovered a highly influential trial outlier in this model (studentized residual = -4.4), which we excluded. For the obstacle avoidance task, we compared foot-placement deviation from the obstacle during the baseline phase of this task (mean of the last ten trials) and the generalization trial for both the trailing foot (i.e., step N-1; right foot) and leading foot (i.e., step N; left foot). We used separate two-way (Group x Phase) linear mixed-effects models (with participant as a random effect). We log-transformed the step N-1 data to better conform to the assumptions of normality.

To determine if the auditory consequence improved consolidation, we quantified two measures: the first adaptation trial error and early adaptation error (i.e., mean of adaptation trials 2 – 8). The first adaptation trial error represented the initial recall of the mapping, while early adaptation error represented the rapid reduction in foot-placement error early in the adaptation phase (Bakkum & Marigold, 2022; Malone et. al 2011; Roemmich & Bastian 2015). We used separate two-way (Group x Session) linear mixed-effects models (with participant as a random effect) to determine differences in first adaptation trial error and early adaptation error between groups across sessions.

To determine if arousal influences learning, we conducted a Pearson correlation analysis. For arousal, we used the change in SAM score between the start of the experiment (immediately prior to baseline trials) and end of the adaptation phase, and the change in surprise score between baseline (prior to the last 5 baseline trials) and after the first adaptation trial. We compared these metrics to early adaptation error in session 1 (a reflection of initial adaptation), foot-placement error on the interlimb transfer test (generalization trial minus mean of last 10 baseline trials of that task), foot placement relative to the obstacle (generalization trial minus the mean of last 10 baseline trials of that task), and early adaptation error in session 2 (a reflection of savings/consolidation).

We used JMP 16 software (SAS Institute Inc., Cary, NC) with an alpha level of 0.05 for all statistical analyses. We employed Tukey's post hoc tests, where appropriate, when significant main effects or interactions were found.

2.3. Results

In this study we divided participants into two groups. Participants were adapted to a new visuomotor mapping induced by prism lenses while performing a precision walking task. One group had an additional auditory consequence when they made foot placement errors, while the other did not. We determined how the presence of auditory consequence influenced their ability to adapt to and remember the new visuomotor mapping.

2.3.1. The presence of the LAS did not change initial visuomotor adaptation

Participants in both groups successfully adapted to the novel visuomotor mapping. Initially, they showed a significant rightward foot placement deviation from the target's centre when using 20-diopter prism lenses during the walking task. Nonetheless, as they continued to adapt to the prism lenses, the end-point error gradually diminished, ultimately returning to levels close to baseline. After removing the prism lenses, participants exhibited a significant leftward deviation in foot-placement error (also-called aftereffect). These findings are visually represented in Figure 2A.

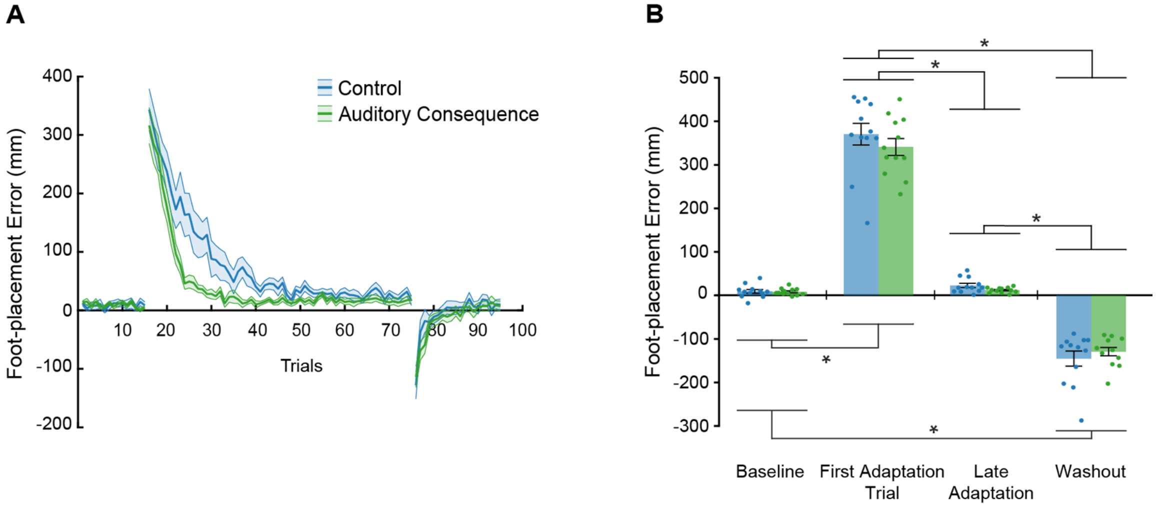

Figure 2. **Visuomotor adaptation during session 1**

A) Group mean ± SE of foot-placement errors across all trials in the baseline and adaptation phases, including the initial washout trial during the first session for both the control group (in blue) and the auditory consequence group (in green). B) Group mean ± SE of foot-placement errors for the baseline phase (averaging the last ten trials), the first adaptation trial, late adaptation (averaging the last ten trials), and the first washout trial during the first testing session for both the control group (blue) and the auditory consequence group (green). Data from each individual participant is superimposed (n =12 per group). A positive value signifies errors in the direction of the prism shift, meaning to the right of the target, while negative values indicate errors in the opposite direction of the prism shift. * Indicates values that are significantly different from each other based on post hoc tests ($p < 0.05$).

We compared foot-placement error across different phases to determine how an auditory consequence impacts visuomotor adaptation. These phases included the baseline phase (average of the last ten trials), the first adaptation trial, late adaptation (average of the last ten trials), and the initial washout trial. Our findings indicated that foot-placement errors varied significantly depending on the phase (Figure 2B; Phase main effect: $F_{3,88} = 485.5$, $p = 1.31e-54$). Post hoc tests showed that the foot-placement error was higher in the first adaptation trial than in other phases. Additionally, there was a notable difference in foot-placement error during the initial washout trial when compared to the other phases. We did not find any significant difference between the control group and the auditory consequence group throughout the different phases (non-significant Group main effect: $F_{1,88} = 0.448$, $p = 0.505$; non-significant Group x Phase interaction: $F_{3,88} = 0.995$, $p = 0.399$). To determine differences in how well groups initially adapted, we compared them using our early adaptation error measure (average of foot-placement error across trials 2 – 8). However, we did not detect significant differences (t test: $t_{22} = 1.75$, p

= 0.095). Overall, the presence of the auditory consequence did not appear to influence the ability to adapt to new visuomotor mappings. The auditory consequence did, however, significantly increase arousal. Specifically, the auditory consequence group demonstrated a greater change in SAM scores (t_{22} = 2.3, p = 0.033) and a greater change in surprise scores (t_{22} = 2.4, p = 0.026) compared to the control group.

2.3.2. The presence of the LAS associated with foot-placement errors leads to greater generalization during an interlimb transfer test but is less clear for obstacle avoidance

We examined the extent to which the acquired visuomotor mapping (mapping A) generalized to a precision walking task involving the untrained left leg (interlimb transfer test) and an obstacle avoidance task. In the interlimb transfer test (Figure 3A), our results showed that both the control and auditory consequence groups successfully extended the learned mapping to the untrained left leg, as evident by the large foot-placement errors in the direction opposite to the learned prism shift. In addition, the auditory consequence group showed greater generalization compared to the control group, as evident from difference in the generalization trial and reflected in the post hoc tests following a significant Group x Phase interaction ($F_{1,22}$ = 16.0, p = 0.0006).

In the obstacle avoidance task, we compared how far participants placed their feet from an obstacle during two phases, baseline (using the average of the last ten trials) and generalization (using a single trial). We examined both the right foot, referred to as step N-1, and the left foot, known as step N. When looking at step N-1 (right foot), a smaller distance from the obstacle signifies generalization. We observed this pattern only for the auditory consequence group (Fig. 3B), as evident from post hoc tests following a significant Group x Phase interaction ($F_{1,22}$ = 5.9, p = 0.024). However, there was no difference between auditory consequence and control groups, suggesting weak evidence of generalization for auditory consequence group. For step N (left foot), a more negative value (a greater leftward shift away from the obstacle) would suggest generalization. However, there was no evidence of generalization or differences between groups for this foot (Fig. 3B, right side; non-significant Group main effect: $F_{1,23}$ = 2.2, p = 0.149; non-significant Phase main effect: $F_{1,20}$ = 0.93, p = 0.348; non-significant Group x Phase interaction: $F_{1,20}$ = 0.63, p = 0.436). Overall, our findings suggested that exposure to an auditory consequence when making foot placement errors leads to greater generalization during an interlimb transfer test, but this is less apparent during an obstacle avoidance task.

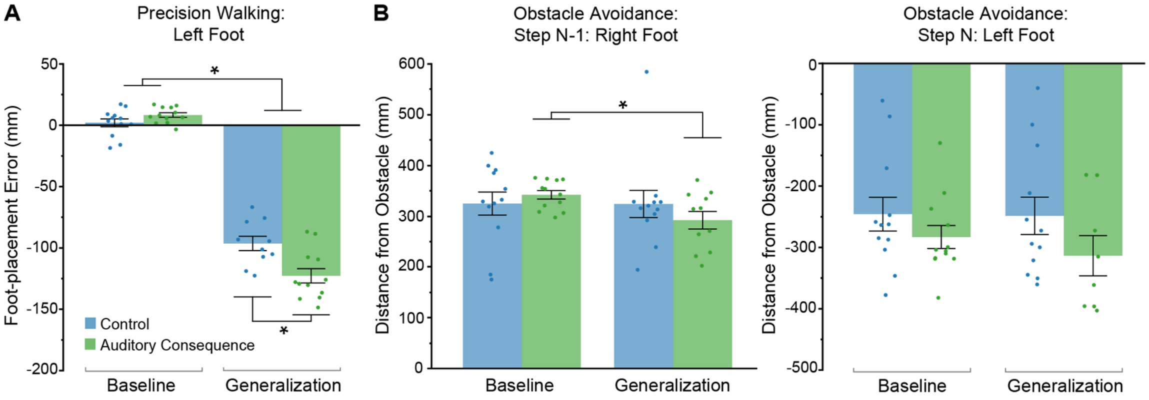

Figure 3. **Generalization during session 1**

A) Group mean ± SE of foot-placement error for both the baseline (average of the last ten trials) and the generalization phases during the precision walking task for the control (blue) and auditory consequence (green) groups. B) Group mean ± SE of foot-placement error for both the baseline phase (the average of the last ten trials) and the generalization phase during the obstacle avoidance task. These data include measurements for both the right foot (step N-1) and the left (step N) in both the control group (blue) and the auditory consequence group (green). Data from each individual participant is superimposed (n =12 per group). A smaller value signifies generalization for step N-1 (right foot), while a more negative value indicates generalization for step N (left foot). * Indicates values that are significantly different from each other based on post hoc tests ($p < 0.05$).

2.3.3. Exposure to the LAS when making foot-placement errors did not lead to enhanced consolidation across sessions

We also examined the consolidation of the novel learned mapping. To test for consolidation, after adapting to mapping A, participants adapted to an opposite prism shift (mapping B), then one week later were exposed to mapping A again. Reduced first adaptation trial error and the presence of savings (i.e., faster relearning, reflected by decreased early adaptation error) during session 2 would indicate consolidation. To determine if consolidation was present, we conducted a comparison across both testing sessions between the first adaptation trial error (which represents the initial recall of the mapping) and the early adaptation error (average of adaptation trials 2- 8). Figure 4 illustrates the results.

Both groups had reduced foot-placement error during the second testing session, as evident from the first adaptation trial error (Fig. 4C; Session main effect: $F_{1,22} = 19.5$, $p = 0.0002$) and early adaptation error (Fig. 4D; Session main effect: $F_{1,22} = 65.4$, $p = 4.94e\text{-}8$) measures. This suggests that both groups consolidated the visuomotor mapping. The auditory consequence and control groups performed differently overall, regardless of the session. Specifically, the auditory consequence group had less foot-placement error in both sessions, as reflected by a significant main effect of group for the first adaptation trial error (Fig. 4C; Group main effect: $F_{1,22} = 19.5$, $p = 0.0002$) and early adaptation error (Fig. 4D; Group main effect: $F_{1,22} = 4.9$, $p = 0.038$) measures. If the LAS had a notable impact on consolidation, we would expect a significant interaction effect. However, this was not the case for the first adaptation trial error (Fig. 4C; non-significant Group x Session interaction: F1,22 = 3.2, $p = 0.088$) or early adaptation error (Fig. 4D; non-significant Group x Session interaction: $F_{1,22} = 0.7$, $p = 0.416$) measures. In summary, our analysis reveals that there were significant differences between sessions and between groups. However, LAS did not enhance consolidation.

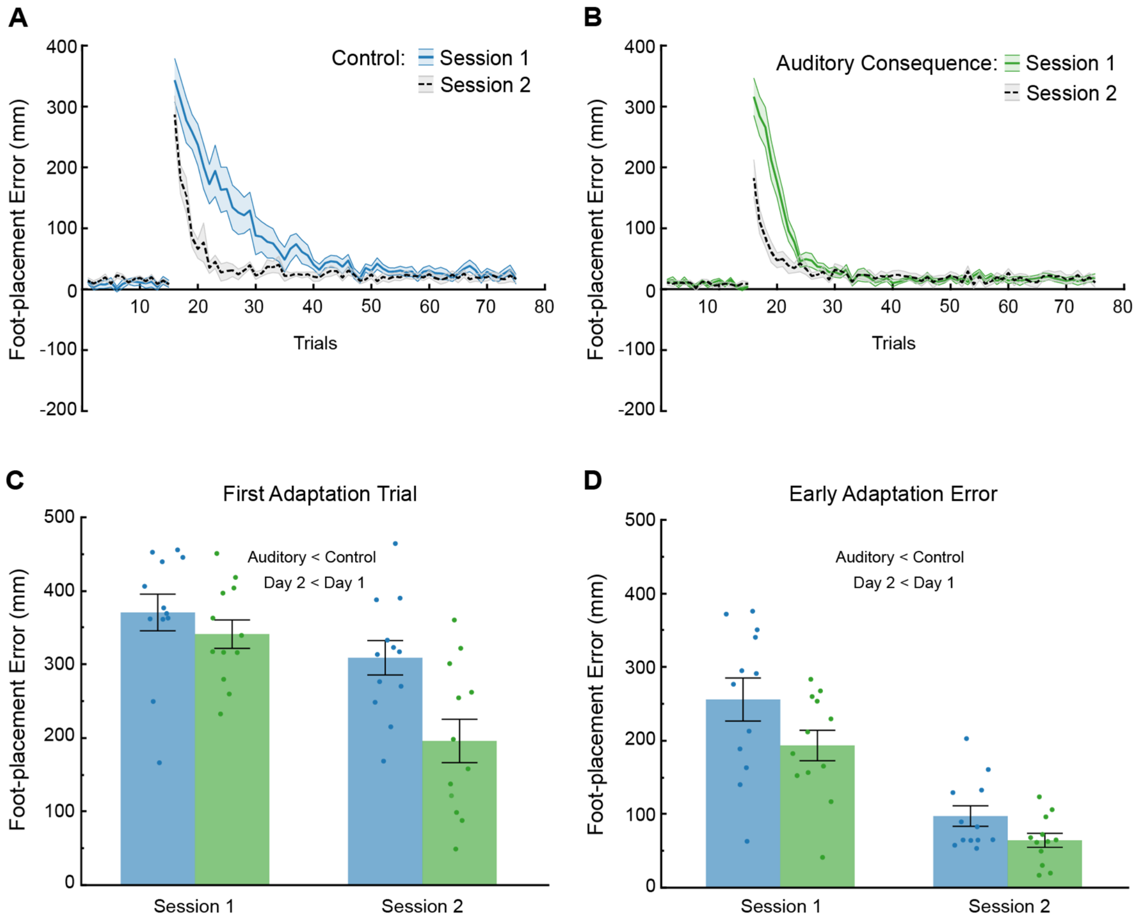

Figure 4. **Motor memory consolidation**

A) Group mean ± SE of foot-placement error across all trials in the baseline and adaptation phases for the control group (blue). The first session is represented by a solid blue line and second session is displayed with a black dotted line B) Group mean ± SE of foot-placement error across all trials in the baseline and adaptation phases for the auditory consequence group (green), including the first session represented by a solid green line and second session displayed with a black dotted line. C) Group mean ± SE of foot-placement error for the first adaptation trial across both testing sessions for the control group (blue) and the auditory consequence group (green). D) Group mean ± SE of foot-placement error for early adaptation across both testing sessions for the control group (blue) and the auditory consequence group (green). Data from each individual participant are superimposed (n =12 per group).

2.3.4. Does arousal level correlate with performance?

We peformed Pearson correlations between the change in SAM score (immediately prior to baseline trials and end of the adaptation phase) and performance measures. We also performed Pearson correlations between the change in surprise score (assessed prior to the last 5 baseline trials and after the first adaptation trial) with peformance measures. These are illustrated in Figure 5. Greater arousal correlated with reduced early adaptation error (greater savings) during session 2 ($r = -0.43$, $p = 0.037$). Greater arousal also correlated with the change in foot deviation from the obstacle for step N-1 (greater generalization) during the obstacle avoidance task ($r = -0.54$, $p = 0.008$). We found no other significant correlations with arousal or surprise ($p > 0.05$).

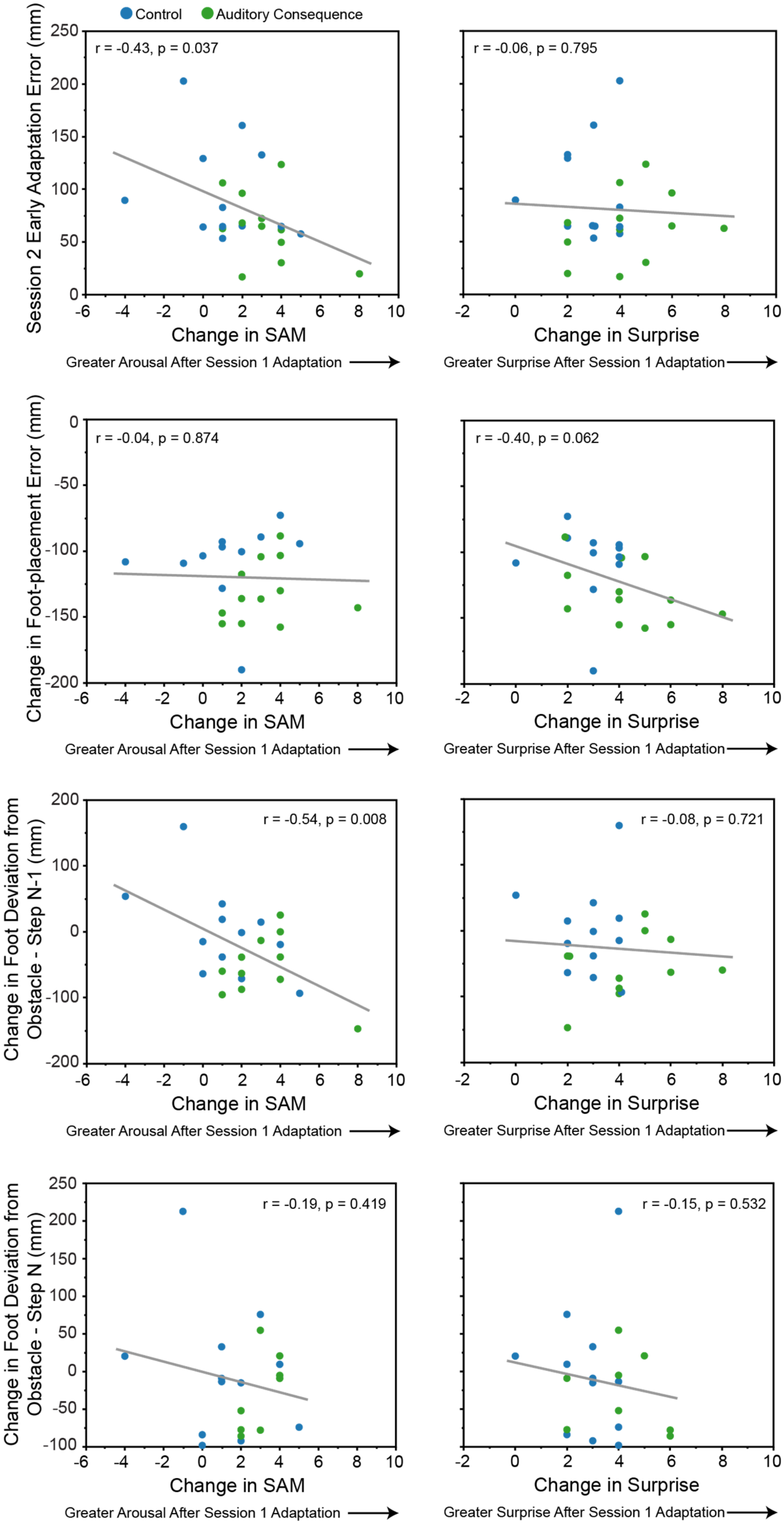
● Control ● Auditory Consequence
Session 2 Early Adaptation Error (mm)
r = -0.43, p = 0.037
r = -0.06, p = 0.795
Change in SAM
Greater Arousal After Session 1 Adaptation
Change in Surprise
Greater Surprise After Session 1 Adaptation
Change in Foot-placement Error (mm)
r = -0.04, p = 0.874
r = -0.40, p = 0.062
Change in SAM
Greater Arousal After Session 1 Adaptation
Change in Surprise
Greater Surprise After Session 1 Adaptation
Change in Foot Deviation from Obstacle - Step N-1 (mm)
r = -0.54, p = 0.008
r = -0.08, p = 0.721
Change in SAM
Greater Arousal After Session 1 Adaptation
Change in Surprise
Greater Surprise After Session 1 Adaptation
Change in Foot Deviation from Obstacle - Step N (mm)
r = -0.19, p = 0.419
r = -0.15, p = 0.532
Change in SAM
Greater Arousal After Session 1 Adaptation
Change in Surprise
Greater Surprise After Session 1 Adaptation
-6 -4 -2 0 2 4 6 8 10
-2 0 2 4 6 8 10
0 50 100 150 200 250
0 -50 -100 -150 -200
200 100 0 -100 -200
250 200 150 100 50 0 -50 -100

Figure 5. Emotional arousal correlation

Relationship between the change in SAM or change in surprise and performance. Performance measures included (from top to bottom): early adaptation error in session 2 (reflecting the amount of savings), change in foot-placement error (reflecting the amount of generalization) for the interlimb transfer test, change in foot deviation from obstacle (reflecting the amount of generalization) for step N-1 in the obstacle avoidance task, and the change in foot deviation from obstacle (reflecting the amount of generalization) for step N in the obstacle avoidance task.

2.4. Discussion

In the present study, we aimed to test the hypothesis of whether a non-physical consequence, specifically a LAS following a foot-placement error, could lead to increased generalization and consolidation, possibly due to greater emotional arousal. Both groups adapted similarly to the novel visuomotor mapping. Our findings revealed that participants who were exposed to the LAS during the adaptation phase exhibited an enhanced ability to generalize to an interlimb transfer task but not an obstacle avoidance task. Both groups showed evidence of consolidation after one week. However, we did not observe greater consolidation with the auditory consequence group compared to the control group. Taken together, the presence of the LAS only led to a limited enhancement of motor learning.

Recently, Bakkum and Marigold (2022) revealed that the introduction of a balance-threatening consequence when participants made errors during the adaptation phase resulted in improved learning. Building on the premise that incorporating a consequence can enhance motor memory consolidation and generalization, our current research adopted a similar experimental task and protocol, albeit with a notable modification. In the present study, when participants made a foot-placement error during the adaptation phase, they were exposed to a LAS consequence, in contrast to a balance-threatening consequence. We hypothesized that this auditory consequence might lead to greater generalization and consolidation. However, we did not observe strong evidence for these effects. It is possible that the contrasting effects of physical and auditory consequences on motor memory can be understood through the lens of survival and evolution. In our evolutionary history, our ancestors faced a constantly changing and often perilous environment, which required them to adapt and learn quickly. Individuals who could learn from their mistakes and adjust their behaviours had a higher likelihood of avoiding harm and securing essential resources, ultimately increasing their chances of survival and reproduction. This process of natural selection favoured those with strong learning and adaptation abilities, and these traits have been inherited by subsequent generations (Van Damme et al. 2021). Errors in maintaining balance (as in Bakkum & Marigold 2022) could lead to falls and potential injuries, making it essential to learn from these errors to prevent future mishaps. In contrast, auditory consequences may not have played as critical a role in our ancestors' survival. Alternatively, the auditory stimulus was not loud enough. Overall, it appears that not all types of consequences have the same impact on learning.

We are aware of only one other study that has explored whether auditory stimuli influence sensorimotor adaptation. While Leow et al. (2021) reported improvements in initial adaptation and retention due to auditory stimuli, our study observed enhanced generalization but no noticeable impact on consolidation. Our studies differ in key aspects. Leow et al. (2021) used LAS that were randomly introduced and were essentially uncorrelated with participants' actions and errors. These authors focused on the general impact of auditory cues on motor adaptation. In contrast, our study explored the consequences of introducing a LAS as a direct response to foot-placement errors. Furthermore, Leow et al. (2021) conducted their study using a reaching task, whereas our study focused on a walking task. The distinction between these tasks is evident in the different biomechanical constraints associated with each. However, stepping to a target and reaching to a target require similar computations to move the effector through an appropriate trajectory. Somewhat related, literature suggests that what is learned in one task can indeed be transferred to another, as emphasized by Krakauer et al. (2006) and Kitago & Krakauer (2013). This transfer of learning implies that, to some extent, the principles governing adaptation share similarities across tasks (Seidler, 2010). In line with this notion, previous research on prism adaptation led to generalization between different standing-based reaching and walking tasks (Bakkum et al. 2020). While there is evidence supporting the idea that the principles of adaptation are similar, it is worth noting that the extent of generalization may not be complete. For instance, Savin & Morton (2008) observed an asymmetrical pattern in the generalization of prism-adapted single-limb pointing movements, where the effects transferred from the arm to the leg but not the other way around. Ultimately, it is unclear what the role of task played in the differing results. Finally, Leow et al. (2021) examined retention after an overnight delay. In our study, we tested consolidation after a one week delay. Although both our groups demonstrated consolidation, if we had tested relearning of mapping A after the same interval as they did (i.e., after an overnight delay), it is possible that our auditory consequence would have led to greater consolidation. This could be because the benefit of the auditory consequence on motor memory declined with time. Regardless, both studies demonstrate some benefit of auditory stimuli on motor learning.

Punishment is known to affect motor learning, and the LAS in our study may have been perceived as a form of punishment. If the auditory consequence group perceived the LAS as a form of punishment, it may be linked to the idea that it serves as a negative consequence for errors. This, in turn, can serve as a motivator for individuals to rectify and adapt their motor behaviours. The experience of a loud, abrupt sound following an error in a motor task can elicit feelings of discomfort, surprise, or even fear, effectively acting as a deterrent that encourages participants to avoid repeating the same error in the future. This interpretation aligns with established studies on punishment and fear conditioning (Dunsmoor et al. 2015; LaLumiere et al. 2003; Skinner 1938). Our results seem to contrast with the findings of some aspects of prior research in the domain of punishment and motor learning. Several studies (Galea et al. 2015; Song & Smiley-Oyen 2017; Song et al. 2020) have explored the effects of punishment (via monetary and/or point loss) on sensorimotor adaptation and reported that it can accelerate the rate of initial adaptation. Though the auditory consequence group did show signs of error reduction in our study (Fig. 4), this reduction did not significantly differ from the control group. Similar to our results, Galea et al. (2015) found that punishment did not affect retention; though Song and Smiley-Oyen (2017) found that if punishment is reduced from 100% of trials to 50% of trials, it enhances retention.

Bakkum & Marigold (2022) proposed that increased arousal due to the error consequence, in their case a balance-challenging perturbation, might explain enhanced motor learning. They proposed that the brain assigns higher value to preserving learned visuomotor associations when they are linked to avoiding balance-threatening consequences. This aligns with the emotional tagging hypotheis (Richter-Levin & Akirav, 2003), which suggests that emotionally arousing events significantly lead to a reinforcement of synaptic connections in brain regions associated with learning. Our findings do support the idea that experiences that elicit emotional arousal can enhance specific aspects of motor memory (LeDoux, 2000; Phelps, 2004). Specifically, we observed that heightened arousal, as measured by changes in SAM scores and surprise, correlated with greater savings during session 2 and greater generalization of step N-1 during the obstacle avoidance task (Fig. 5). This idea of heightened emotional arousal enhancing specific aspects of motor memory is consistent with the broader literature on the influence of emotional arousal on memory. For example, Cahill & McGaugh (1998) have demonstrated that emotionally arousing events trigger the release of stress hormones, which strengthen memory consolidation.

Overall, our findings provide the first evidence that movement errors tied to auditory stimuli can enhance the process of generalization to some extent. However, this approach does not appear to have a lasting effect on the consolidation of motor memory. We did, however, find evidence that greater arousal relates to generalization and savings. This suggests that designing motor learning environments with elements that provoke engagement and increase emotional arousal might be an avenue to explore in rehabilitation settings.

Chapter 3.

3.1. Limitations

The present study provides valuable insights into the effects of auditory stimuli on motor memory consolidation and generalization. However, several limitations should be acknowledged. First, our use of a specific auditory stimulus in the form of a single loud sound for the duration of foot placement on the pressure mat may not fully represent the range of auditory stimuli that can influence motor learning. Variations in auditory stimuli, such as different volumes or patterns, may produce different results, indicating the potential for further research in this area. Second, the sample size for the assessment of sensorimotor learning was relatively small. However, we determined this sample size based on a combination of sample sizes used in previous research studies in our lab (Bakkum et al. 2020, 2021; Bakkum & Marigold 2022; Alexander et al. 2011; Maeda et al. 2017b) and statistical power analyses conducted using G*Power. Third, individual differences among participants may have impacted the results. Specifically, different participants may have perceived the auditory stimulus as a form of punishment (while others did not) and may have been more affected by this modality. This is partially supported by the range of SAM and surprise scores among participants within the auditory consequence group. Understanding the role of these individual differences in the context of auditory stimuli and their influence on motor learning remains a valuable area for further investigation.

It is possible that the primary measure we used to determine differences between groups in adaptation during session 1, as well as to assess consolidation, did not adequately capture performance. Specifically, our early adaptation error measure involved averaging foot-placement error across trials 2 – 8 of the adaptation phase. Past studies from our lab used this approach. This measure aims to capture the rapid reduction in error during the early stages of adaptation, providing a model-free representation of the process (Bakkum & Marigold 2022; Maeda et al. 2017b), and was first introduced by Maeda et al. (2017b). In these studies, most, if not all, foot-placement error reduction occurred within this range. These researchers also indicated that alternative trial boundaries, involving a greater number of trials in the average, produced similar qualitative results. However, examination of Figure 2 in our study suggests that error reduction continues well beyond the eighth trial for the control group and thus, performance differences between groups may not be fully represented by the average of trials 2 to 8. Therefore, a more suitable trial range for assessing adaptation and consolidation in our study might involve extending the averaging to adaptation trial 15 or 20. It is not clear at this point as to why the control group took longer to adapt than previous studies in our lab.

One final limitation of our study is the method in which we measured arousal. Instead of using a physiological measurement like galvanic skin response (GSR), we opted for a questionnaire-based approach. While physiological measurements offer the advantage of providing real-time, objective data, we encountered practical challenges when we attempted to implement GSR in our study. In our task, participant’s arms swung as they walked (as is normal). This motion artifact, in addition to sweat due to repeatedly walking in the lab, made it exceedingly difficult to extract meaningful and accurate information from the GSR signal obtained from sensors on the index and middle fingers. To address these challenges, we turned to the SAM questionnaire to measure arousal. Although it is not a physiological measure, the SAM is a well-validated and widely used tool for assessing subjective emotional experiences (Bradley & Lang, 1994; Lang, 1980; Cisnal et al. 2022; Kaufeld et al. 2022).

3.2. Implications of findings

The findings of this study, along with the comparison to the research conducted by Bakkum & Marigold (2022), offer several noteworthy implications that contribute to our understanding of motor learning and its potential applications in rehabilitation settings. The primary implication revolves around the role of consequences in the motor learning process. Both studies, though utilizing different types of consequences, auditory in our study and balance-threatening in Bakkum & Marigold's study (2022), demonstrate that consequences can significantly influence how individuals learn and adapt their motor behaviours. In our study, exposure to a LAS led to enhanced generalization but had limited effects on consolidation. This suggests that consequences, whether physical or auditory, can shape the way individuals adapt and generalize their motor behaviours. Whether it is the introduction of balance-threatening scenarios or the strategic incorporation of a LAS, the role of consequences in guiding and enhancing motor learning processes aligns with the evolutionary significance of memory systems (Meyers et al. 2020; Nairne et al. 2007).

The effective use of consequences can be a powerful tool in facilitating the transfer of motor behaviours to real-world situations. In a rehabilitation setting, therapists can effectively harness the potential of LAS. LAS can serve several functions during therapy sessions. Firstly, therapists may exploit LAS as a feedback mechanism to provide immediate and distinctive cues to patients when they successfully execute a specific motor behaviour. This approach serves as a reinforcement of correct movements, encouraging patients to replicate these movements consistently. Secondly, LAS can be seamlessly integrated into therapy sessions to establish a robust association between auditory cues and specific motor responses, building upon the concept supported by research on motor memory and auditory feedback (Roberts et al. 2018; Dewil et al. 2023). Finally, LAS can also be employed to signal errors in motor behaviours. When a patient makes a mistake or deviates from the prescribed movement pattern, therapists can trigger an auditory consequence. This approach prompts the patient to identify and correct their errors, thereby fine-tuning and improving their motor behaviours.

Another aspect to consider in the context of rehabilitation is the role of heightened emotional arousal. Our results support a role for arousal in motor learning. To optimize the learning and retention of motor behaviours, therapists can strategically employ LAS to elevate a patient's arousal during therapy sessions. Utilizing visual stimuli can also enhance emotional arousal. This might involve incorporating videos, virtual reality simulations, or dynamic visual feedback during therapy sessions. For instance, a virtual reality environment can be used to provide a visually engaging and immersive experience, where patients interact with virtual scenarios that challenge their motor behaviours. The visual appeal and novelty of such experiences can induce excitement and emotional engagement, ultimately leading to improved motor learning and retention. Another avenue to increase arousal is through the implementation of reward-based reinforcement schedules within rehabilitation sessions. This involves setting up a system where patients receive rewards or incentives for achieving specific milestones or goals. For instance, patients may earn points or tokens for completing exercises or hitting certain targets. These points can be exchanged for rewards, such as small prizes, extra break time, or even choosing the next activity. Such deliberate emotional stimulation enhances patient engagement (and motivation) and their ability to partially remember and apply learned motor behaviours.

While balance-challenging consequences enhance both generalization and consolidation of motor behaviours (Bakkum & Marigold 2022), our results suggest auditory consequences only partially enhance generalization. This suggests that physical consequences may serve as stronger modifiers in motor learning compared to non-physical ones. Therapists can, therefore, consider incorporating balance-challenging consequences, such as balance boards or virtual reality scenarios simulating real-world challenges, to further enhance motor learning outcomes while ensuring safety during rehabilitation sessions.

3.3. Future directions

This thesis has contributed valuable insights into the influence of auditory consequences on the process of motor learning, with a particular emphasis on generalization and consolidation. The results from our study have provided evidence that an auditory consequence for movement errors can indeed augment generalization to some extent. Moreover, we have established a noteworthy connection between heightened emotional arousal and improved generalization and savings. These findings not only have implications for controlled laboratory settings but also hold great promise for application in clinical rehabilitation contexts.

To explore the specific drivers of learning improvement and assess the impact of the consequence type, whether auditory or balance-threatening, on motor learning, future research can test different groups. For instance, to determine if the element of surprise explains the results of Bakkum & Marigold (2022), we could compare an unexpected slip group and an expected slip group. For the unexpected slip group, participants would experience an unexpected slippery surface as a consequence of missing the target. For the expected slip group, participants would be informed in advance about the slippery surface, thus eliminating the “surprise” component and allowing us to determine its influence in the learning process. We could also measure arousal in these groups to determine if this also influences the learning process, as proposed by Bakkum & Marigold (2022), but not directly tested. These extensions promise to enhance our comprehension of the role of balance-related consequences in the motor learning process and provide valuable insights for the design of tailored rehabilitation interventions. Moreover, we could test groups that experience different forms of auditory stimuli. This could involve variations in frequency, decibel level, and the timing of auditory stimuli. For example, one group might experience high-frequency cues for specific learned tasks, while another group encounters the same cues but at different decibel levels. Additionally, timing variations involve rapid, repeated cues for some participants and single, intermittent cues for others.

Another promising direction for future research lies in harnessing the potential benefits of virtual reality (VR) environments in the realm of motor learning and adaptation studies. The continuous advancements in VR technology provide an innovative platform for investigating the impact of different feedback mechanisms on motor learning (Sanchez-Vives & Slater, 2005). One prospective experiment could involve the creation of a VR scenario where participants engage with virtual objects or navigate through simulated environments. Within this virtual setting, feedback can be manipulated in diverse ways. For instance, instead of introducing a slippery surface, virtual obstacles or challenges could be incorporated, leading to performance errors. Alternatively, the VR environment could deliver auditory or visual cues as feedback when errors occur. VR systems can collect data on users' emotional responses through sensors like heart rate monitors or facial expression recognition. These data can be used to personalize the learning experience in real-time. For example, if a user shows signs of low engagement, the VR system can introduce interactive elements, emotionally charged encounters, or different challenges, which can induce heightened emotional arousal and in turn enhance the learning experience. By incorporating emotional arousal into VR environments for motor learning and rehabilitation, there is the possibility to create more effective and personalized training experiences.

Moreover, VR technology enables the seamless integration of rewards and penalties within a controlled and immersive context. Participants may receive virtual rewards or incur virtual losses based on their performance, serving as a form of feedback reinforcement (Galea et al. 2015). A key aspect of this integration is the ability to simulate aversive stimuli without causing any physical harm. This involves creating scenarios where individuals can encounter discomfort or negative sensations without any actual harm to their well-being. Additionally, there is the possibility to explore the potential of combining physical and auditory consequences in a motor learning context. For instance, advanced haptic feedback devices can be used to simulate physical consequences, such as collisions, falls, jolts, or other interactive scenarios. Other consequences can include vibrations or sudden visual alterations. This integration of sensory feedback can enhance motor learning experiences without exposing participants to physical risks.

Taken together, these studies will contribute to a deeper understanding of the mechanisms underlying motor learning and adaptation in various consequence scenarios. In addition, they can pave the way for introducing novel rehabilitation approaches to enhance recovery of function.

References

Abe, M., Schambra, H., Wassermann, E. M., Luckenbaugh, D., Schweighofer, N., & Cohen, L. G. (2011). Reward improves long-term retention of a motor memory through induction of offline memory gains. *Current Biology*, *21*(7), 557–562.

Abercrombie, H. C., Speck, N. S., & Monticelli, R. M. (2006). Endogenous cortisol elevations are related to memory facilitation only in individuals who are emotionally aroused. *Psychoneuroendocrinology*, *31*(2), 187–196.

Alexander, M. S., Flodin, B. W. G., & Marigold, D. S. (2013). Changes in task parameters during walking prism adaptation influence the subsequent generalization pattern. *Journal of Neurophysiology*, *109*(10), 2495–2504.

Alexander, M. S., Flodin, B. W. G., & Marigold, D. S. (2011). Prism adaptation and generalization during visually guided locomotor tasks. *Journal of Neurophysiology*, *106*(2), 860–871.

Amaral, D. G. (2003). The amygdala, social behavior, and danger detection. *Annals of the New York Academy of Sciences*, *1000*, 337–347.

Anderson, L., & Shimamura, A. P. (2005). Influences of emotion on context memory while viewing film clips. *American Journal of Psychology*, *118*(3), 323–337.

Bakkum, A., & Marigold, D. S. (2022). Learning from the Physical Consequences of Our Actions Improves Motor Memory. *ENeuro*, *9*(3).

Bakkum, A., Donelan, J. M., & Marigold, D. S. (2020). Challenging balance during sensorimotor adaptation increases generalization. *Journal of Neurophysiology*, *123*(4), 1342–1354.

Bakkum, A., Donelan, J. M., & Marigold, D. S. (2021). Savings in sensorimotor learning during balance-challenged walking but not reaching. *Journal of Neurophysiology*, *125*(6), 2384–2396.

Balitsky Thompson, A. K., & Henriques, D. Y. P. (2010). Visuomotor adaptation and intermanual transfer under different viewing conditions. *Experimental Brain Research*, *202*(3), 543–552.

Bastian, A. J. (2008). Understanding sensorimotor adaptation and learning for rehabilitation. *Current Opinion in Neurology*, *21*(6), 628–633.

Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and Motivation I: Defensive and Appetitive Reactions in Picture Processing. *Emotion*, *1*(3), 276–298.

Brashers-Krug, T., Shadmehr, R., & Bizzi, E. (1996). Consolidation in human motor memory. *Nature*, *382*(6588), 252–255.

Brown, P., Rothwell, J. C., Thompson, P. D., Britton, T. C., Day, B. L., & Marsden, C. D. (1991). New observations on the normal auditory startle reflex in man. *Brain: A Journal of Neurology*, *114 (Pt4)*(4), 1891–1902.

Cahill, L., & McGaugh, J. L. (1995). A novel demonstration of enhanced memory associated with emotional arousal. *Consciousness and Cognition*, *4*(4), 410–421.

Cahill, L., & McGaugh, J. L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*, *21*(7), 294–299.

Cahill, L., Gorski, L., & Le, K. (2003). Enhanced human memory consolidation with post-learning stress: interaction with the degree of arousal at encoding. *Learning & Memory (Cold Spring Harbor, N.Y.)*, *10*(4), 270–274.

Cahill, L., Haier, R. J., Fallon, J., Alkire, M. T., Tang, C., Keator, D., Wu, J., & McGaugh, J. L. (1996). Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(15), 8016–8021.

Caithness, G., Osu, R., Bays, P., Chase, H., Klassen, J., Kawato, M., Wolpert, D. M., & Flanagan, J. R. (2004). Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. *Journal of Neuroscience*, *24*(40), 8662–8671.

Carlsen, A. N., Dakin, C. J., Chua, R., & Franks, I. M. (2007). Startle produces early response latencies that are distinct from stimulus intensity effects. *Experimental Brain Research*, *176*(2), 199–205.

Carroll, T. J., McNamee, D., Ingram, J. N., & Wolpert, D. M. (2019). Rapid Visuomotor Responses Reflect Value-Based Decisions. *Journal of Neuroscience*, *39*(20), 3906–3920.

Clewett, D. V., Huang, R., Velasco, R., Lee, T. H., & Mather, M. (2018). Locus coeruleus activity strengthens prioritized memories under arousal. *Journal of Neuroscience*, *38*(6), 1558–1574.

Criscimagna-Hemminger, S. E., Bastian, A. J., & Shadmehr, R. (2010). Size of error affects cerebellar contributions to motor learning. *Journal of Neurophysiology*, *103*(4), 2275–2284.

Dewil, S., Kuptchik, S., Liu, M., Sanford, S., Bradbury, T., Davis, E., Clemente, A., & Nataraj, R. (2023). The cognitive basis for virtual reality rehabilitation of upper-extremity motor function after neurotraumas. *Journal on Multimodal User Interfaces 2023 17:3*, *17*(3), 105–120.

Dunsmoor, J. E., Murty, V. P., Davachi, L., & Phelps, E. A. (2015). Emotional learning selectively and retroactively strengthens memories for related events. *Nature*, *520*(7547), 345–348.

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160.

Galea, J. M., Mallia, E., Rothwell, J., & Diedrichsen, J. (2015). The dissociable effects of punishment and reward on motor learning. *Nature Neuroscience*, *18*(4), 597–602.

Ghahramani, Z., Wolpert, D. M., & Jordan, M. I. (1996). Generalization to local remappings of the visuomotor coordinate transformation. *Journal of Neuroscience*, *16*(21), 7085–7096.

Green, D. A., Bunday, K. L., Bowen, J., Carter, T., & Bronstein, A. M. (2010). What does autonomic arousal tell us about locomotor learning? *Neuroscience*, *170*(1), 42–53.

Henckens, M. J. A. G., Hermans, E. J., Pu, Z., Joëls, M., & Fernández, G. (2009). Stressed Memories: How Acute Stress Affects Memory Formation in Humans. *Journal of Neuroscience*, *29*(32), 10111–10119.

Izawa, J., & Shadmehr, R. (2011). Learning from Sensory and Reward Prediction Errors during Motor Adaptation. *PLoS Comput Biol*, *7*(3), 1002012.

Johnson, L., Burridge, J., Ewings, S., Westcott, E., Gayton, M., & Demain, S. (2023). Principles into Practice: An Observational Study of Physiotherapists use of Motor Learning Principles in Stroke Rehabilitation. *Physiotherapy*, *118*, 20–30.

Kandel, E. R, Koester J. D, Mack S. H., & Siegelbaum S. A. Principles of Neural Science. In *Principles of Neural Science, 6e*. New York, NY: McGraw Hill, 2021.

Kitago, T., & Krakauer, J. W. (2013). Motor learning principles for neurorehabilitation. *Handbook of Clinical Neurology*, *110*, 93–103.

Krakauer, J. W. (2006). Motor learning: Its relevance to stroke recovery and neurorehabilitation. *Current Opinion in Neurology*, *19*(1), 84–90.

Krakauer, J. W., Ghez, C., & Ghilardi, M. F. (2005). Adaptation to visuomotor transformations: Consolidation, interference, and forgetting. *Journal of Neuroscience*, *25*(2), 473–478.

Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L., & Haith, A. M. (2019). Motor learning. *Comprehensive Physiology*, *9*(2), 613–663.

Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience*, *20*(23), 8916–8924.

LaLumiere, R. T., Buen, T. V., & McGaugh, J. L. (2003). Post-training intra-basolateral amygdala infusions of norepinephrine enhance consolidation of memory for contextual fear conditioning. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *23*(17), 6754–6758.

Landis, C., & Hunt, W. A. (1939). The startle pattern. New York Farrar. Scientific Research Publishing.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1990). Emotion, Attention, and the Startle Reflex. *Psychological Review*, *97*(3), 377–395.

LeDoux, J. E. (2003). Emotion Circuits in the Brain. *Annurev Neuro.23.1.155*, *23*, 155–184.

Leow, L. A., Tresilian, J. R., Uchida, A., Koester, D., Spingler, T., Riek, S., & Marinovic, W. (2021). Acoustic stimulation increases implicit adaptation in sensorimotor adaptation. *European Journal of Neuroscience*, *54*(3), 5047–5062.

Lupien, S. J., Maheu, F., Tu, M., Fiocco, A., & Schramek, T. E. (2007). The effects of stress and stress hormones on human cognition: Implications for the field of brain and cognition. *Brain and Cognition*, *65*(3), 209–237.

Maeda, R. S., McGee, S. E., & Marigold, D. S. (2017). Consolidation of visuomotor adaptation memory with consistent and noisy environments. *Journal of Neurophysiology*, *117*(1), 316–326.

Maeda, R. S., McGee, S. E., & Marigold, D. S. (2018). Long-term retention and reconsolidation of a visuomotor memory. *Neurobiology of Learning and Memory*, *155*, 313–321.

Maeda, R. S., O'Connor, S. M., Donelan, J. M., & Marigold, D. S. (2017). Foot placement relies on state estimation during visually guided walking. *Journal of Neurophysiology*, *117*(2), 480–491.

Magill, R. A., & Anderson, D. (2016). *Motor learning and control : concepts and applications*. 544.

Maier, M., Ballester, B. R., & Verschure, P. F. M. J. (2019). Principles of Neurorehabilitation After Stroke Based on Motor Learning and Brain Plasticity Mechanisms. *Frontiers in Systems Neuroscience*, *13*, 463323.

Malone, L. A., Vasudevan, E. V. L., & Bastian, A. J. (2011). Motor adaptation training for faster relearning. *Journal of Neuroscience*, *31*(42), 15136–15143.

Manohar, S. G., Muhammed, K., Fallon, S. J., & Husain, M. (2019). Motivation dynamically increases noise resistance by internal feedback during movement. *Neuropsychologia*, *123*, 19–29.

Mazzoni, P., & Krakauer, J. W. (2006). An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *Journal of Neuroscience*, *26*(14), 3642–3645.

McDougle, S. D., Bond, K. M., & Taylor, J. A. (2017). Implications of plan-based generalization in sensorimotor adaptation. *Journal of Neurophysiology*, *118*(1), 383–393.

McGaugh, J. L. (2000). Memory: a century of consolidation. *Science (New York, N.Y.)*, *287*(5451), 248–251.

McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience*, *27*, 1–28.

Mcgaugh, J. L., Cahill, L., & Roozendaal, B. (1996). Involvement of the amygdala in memory storage: Interaction with other brain systems. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(24), 13508–13514.

McGaugh, J. L., McIntyre, C. K., & Power, A. E. (2002). Amygdala modulation of memory consolidation: Interaction with other brain systems. *Neurobiology of Learning and Memory*, *78*(3), 539–552.

McIntyre, C. K., Power, A. E., Roozendaal, B., & McGaugh, J. L. (2003). Role of the Basolateral Amygdala in Memory Consolidation. *Annals of the New York Academy of Sciences*, *985*(1), 273–293.

Meyers, Z. R., McCurdy, M. P., Leach, R. C., Thomas, A. K., & Leshikar, E. D. (2020). Effects of Survival Processing on Item and Context Memory: Enhanced Memory for Survival-Relevant Details. *Frontiers in Psychology*, *11*, 546229.

Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control. *Neural Networks*, *9*(8), 1265–1279.

Moinuddin, A., Goel, A., Sethi, Y., Moinuddin, A., Goel, A., & Sethi, Y. (2021). The Role of Augmented Feedback on Motor Learning: A Systematic Review. *Cureus*, *13*(11).

Morris, R. G. M., Garrud, P., Rawlins, J. N. P., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature 1982 297:5868*, *297*(5868), 681–683.

Morton, S. M., & Bastian, A. J. (2004). Prism adaptation during walking generalizes to reaching and requires the cerebellum. *Journal of Neurophysiology*, *92*(4), 2497–2509.

Murty, V. P., LaBar, K. S., & Alison Adcock, R. (2012). Threat of punishment motivates memory encoding via amygdala, not midbrain, interactions with the medial temporal lobe. *Journal of Neuroscience*, *32*(26), 8969–8976.

Nairne, J. S., Thompson, S. R., & Pandeirada, J. N. S. (2007). Adaptive memory: Survival processing enhances retention. *Journal of Experimental Psychology: Learning Memory and Cognition*, *33*(2), 263–273.

O'Connor, C. M., Thorpe, S. K., O'Malley, M. J., & Vaughan, C. L. (2007). Automatic detection of gait events using kinematic data. *Gait and Posture*, *25*(3), 469–474.

Phelps, E. A. (2004). Human emotion and memory: interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology*, *14*(2), 198–202.

Poggio, T., & Bizzi, E. (2004). Generalization in vision and motor control. *Nature*, *431*(7010), 768–774.

Quattrocchi, G., Monaco, J., Ho, A., Irmen, F., Strube, W., Ruge, D., Bestmann, S., & Galea, J. M. (2018). Pharmacological dopamine manipulation does not alter reward-based improvements in memory retention during a visuomotor adaptation task. *ENeuro*, *5*(3).

Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: a tutorial in theory and method. *Neuroscience & Biobehavioral Reviews*, *29*(3), 431–444.

Renault, A. G., Lefumat, H., Miall, R. C., Bringoux, L., Bourdin, C., Vercher, J. L., & Sarlegna, F. R. (2020). Individual movement features during prism adaptation correlate with after-effects and interlimb transfer. *Psychological Research*, *84*(4), 866–880.

Richter-Levin, G., & Akirav, I. (2003). Emotional tagging of memory formation - In the search for neural mechanisms. *Brain Research Reviews*, *43*(3), 247–256.

Roberts, B. M., Clarke, A., Addante, R. J., & Ranganath, C. (2018). Entrainment enhances theta oscillations and improves episodic memory. *Cognitive Neuroscience*, *9*(3–4), 181–193.

Roemmich, R. T., & Bastian, A. J. (2015). Two ways to save a newly learned motor pattern. *Journal of Neurophysiology*, *113*(10), 3519–3530.

Roozendaal, B., & McGaugh, J. L. (1996). Amygdaloid nuclei lesions differentially affect glucocorticoid-induced memory enhancement in an inhibitory avoidance task. *Neurobiology of Learning and Memory*, *65*(1), 1–8.

Roozendaal, B., & McGaugh, J. L. (2011). Memory Modulation. *Behavioral Neuroscience*, *125*(6), 797–824.

Roozendaal, B., Okuda, S., Van Der Zee, E. A., & McGaugh, J. L. (2006). Glucocorticoid enhancement of memory requires arousal-induced noradrenergic activation in the basolateral amygdala. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(17), 6741–6746.

Sainburg, R. L., & Wang, J. (2002). Interlimb transfer of visuomotor rotations: Independence of direction and final position information. *Experimental Brain Research*, *145*(4), 437–447.

Sanchez-Vives, M. V., & Slater, M. (2005). From presence to consciousness through virtual reality. *Nature Reviews Neuroscience 2005 6:4*, *6*(4), 332–339.

Sato, S., Cui, A., & Choi, J. T. (2022). Visuomotor errors drive step length and step time adaptation during “virtual” split-belt walking: the effects of reinforcement feedback. *Experimental Brain Research*, *240*(2), 511–523.

Savin, D. N., & Morton, S. M. (2008). Asymmetric generalization between the arm and leg following prism-induced visuomotor adaptation. *Experimental Brain Research*, *186*(1), 175–182.

Schmidt, R. A., & Lee, T. D. (1999). Motor control and learning: A behavioral emphasis, 3rd ed. In *Motor control and learning: A behavioral emphasis, 3rd ed.* Human Kinetics.

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Emotional facilitation of sensory processing in the visual cortex. *Psychological Science*, *14*(1), 7–13.

Seidler, R. D. (2010). Neural correlates of motor learning, transfer of learning, and learning to learn. *Exercise and Sport Sciences Reviews*, *38*(1), 3–9.

Shadmehr, R., & Brashers-Krug, T. (1997). Functional Stages in the Formation of Human Long-Term Motor Memory. *Journal of Neuroscience*, *17*(1), 409–419.

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual Review of Neuroscience*, *33*, 89–108.

Skinner, B. F. (1938). The Behavior of Organisms: An Experimental Analysis. - Appleton-Century; New York.

Song, Y., & Smiley-Oyen, A. L. (2017). Probability differently modulating the effects of reward and punishment on visuomotor adaptation. *Experimental Brain Research*, *235*(12), 3605–3618.

Song, Y., Lu, S., & Smiley-Oyen, A. L. (2020). Differential motor learning via reward and punishment. *Quarterly Journal of Experimental Psychology*, *73*(2), 249–259.

Starita, F., Kroes, M. C. W., Davachi, L., Phelps, E. A., & Dunsmoor, J. E. (2019). Threat learning promotes generalization of episodic memory. *Journal of Experimental Psychology: General*, *148*(8), 1426–1434.

Stuchlík, A., Petrásek, T., Prokopová, I., Holubová, K., Hatalová, H., Valeš, K., Kubík, S., Dockery, C., & Wesierska, M. (2013). Place avoidance tasks as tools in the behavioral neuroscience of learning and memory. *Physiological Research*, *62*(SUPPL 1).

Taylor, J. A., & Ivry, R. B. (2011). Flexible Cognitive Strategies during Motor Learning. *PLOS Computational Biology*, *7*(3), e1001096.

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *Journal of Neuroscience*, *34*(8), 3023–3032.

Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive combination of motor primitives. *Nature*, *407*(6805), 742–748.

Torres-Oviedo, G., & Bastian, A. J. (2012). Natural error patterns enable transfer of motor learning to novel contexts. *Journal of Neurophysiology*, *107*(1), 346–356.

Tseng, Y. W., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., & Bastian, A. J. (2007). Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *Journal of Neurophysiology*, *98*(1), 54–62.

Tully, K., & Bolshakov, V. Y. (2010). Emotional enhancement of memory: How norepinephrine enables synaptic plasticity. *Molecular Brain*, *3*(1).

Tyng, C. M., Amin, H. U., Saad, M. N. M., & Malik, A. S. (2017). The influences of emotion on learning and memory. *Frontiers in Psychology*, *8*(AUG), 235933.

Valls-Solé, J., Solé, A., Valldeoriola, F., Muñoz, E., Gonzalez, L. E., & Tolosa, E. S. (1995). Reaction time and acoustic startle in normal human subjects. *Neuroscience Letters*, *195*(2), 97–100.

Van Damme, S., De Fruyt, N., Watteyne, J., Kenis, S., Peymen, K., Schoofs, L., & Beets, I. (2021). Neuromodulatory pathways in learning and memory: Lessons from invertebrates. *Journal of Neuroendocrinology*, *33*(1), e12911.

Wang, J. (2008). A dissociation between visual and motor workspace inhibits generalization of visuomotor adaptation across the limbs. *Experimental Brain Research*, *187*(3), 483–490.

Wang, J., & Sainburg, R. L. (2004). Limitations in interlimb transfer of visuomotor rotations. *Experimental Brain Research*, *155*(1), 1–8.

Werner, S., Van Aken, B. C., Hulst, T., Frens, M. A., Van Der Geest, J. N., Strüder, H. K., & Donchin, O. (2015). Awareness of Sensorimotor Adaptation to Visual Rotations of Different Size. *PLOS ONE*, *10*(4), e0123321.

Willis, E. F., Bartlett, P. F., & Vukovic, J. (2017). Protocol for Short- and Longer-term Spatial Learning and Memory in Mice. *Frontiers in Behavioral Neuroscience*, *11*.

Yin, C., Gao, T., & Li, B. (2023). The effect of combining punishment and reward can transfer to opposite motor learning. *PLOS ONE*, *18*(4), e0282028.

Zerbes, G., & Schwabe, L. (2021). Stress-induced bias of multiple memory systems during retrieval depends on training intensity. *Psychoneuroendocrinology*, *130*.