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„From Memory Networks to Self-Regulation:
Insights into rt-fMRI Neurofeedback and Learning
Mechanisms“

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Abstract

This thesis provides a comprehensive examination of learning and memory dynamics, with a specific focus on contemporary psychological theories and their relevance to self-regulation using real-time functional magnetic resonance imaging (rt-fMRI). It delves into the multi-component model of working memory and its integration with rt-fMRI neurofeedback, highlighting the mechanisms underlying short-term and long-term memory processes. Furthermore, it explores associative learning paradigms, emphasizing the role of prediction errors and the interplay between model-free and model-based learning strategies. The thesis also investigates neurobiological underpinnings such as spike-timing-dependent plasticity and basal ganglia function in associative learning. Additionally, it examines psychological determinants including attention, motivation, and emotion, and their neural correlates in rt-fMRI neurofeedback outcomes. Finally, the thesis evaluates training protocols, discussing feedback mechanisms, reward systems, and physiological factors influencing learning success in rt-fMRI NF. Through this analysis, the thesis advances the understanding of how individuals acquire self-regulation skills in the context of rt-fMRI NF from a psychological perspective.

Abstract German

Diese Arbeit bietet eine umfassende Untersuchung der Mechanismen hinter Lern- und Gedächtnisprozessen mit besonderem Schwerpunkt auf zeitgenössischen psychologischen Theorien und deren Relevanz für die Selbstregulierung mittels funktioneller Echtzeit-Magnetresonanztomographie (eng.: real-time functional magnetic resonance imaging; rt-fMRI). Das Multikomponentenmodell des Arbeitsgedächtnisses und dessen Passung auf Lernen im Kontext von rt-fMRI-Neurofeedback wird beleuchtet, sowie die Mechanismen, die den Prozessen des Kurz- und Langzeitgedächtnisses zugrunde liegen. Außerdem werden assoziative Lernparadigmen untersucht, wobei die Rolle von Vorhersagefehlern und das Zusammenspiel zwischen modellfreien und modellbasierten Lernstrategien hervorgehoben wird. Neurobiologische Grundlagen wie die spike-timing-abhängige Plastizität und die Funktion der Basalganglien beim assoziativen Lernen werden zusätzlich diskutiert. Darüber hinaus werden psychologische Determinanten wie Aufmerksamkeit, Motivation und Emotionen sowie deren neuronale Korrelate in rt-fMRI-Neurofeedback-Ergebnissen untersucht. Schließlich werden in dieser Arbeit Trainingsprotokolle evaluiert und Feedback-Mechanismen, Belohnungssysteme

und physiologische Faktoren, die den Lernerfolg bei rt-fMRI NF beeinflussen, diskutiert. Durch diese Analyse fördert die Arbeit das Verständnis dafür, wie Individuen Selbstregulationsfähigkeiten im Kontext von rt-fMRI NF erwerben.

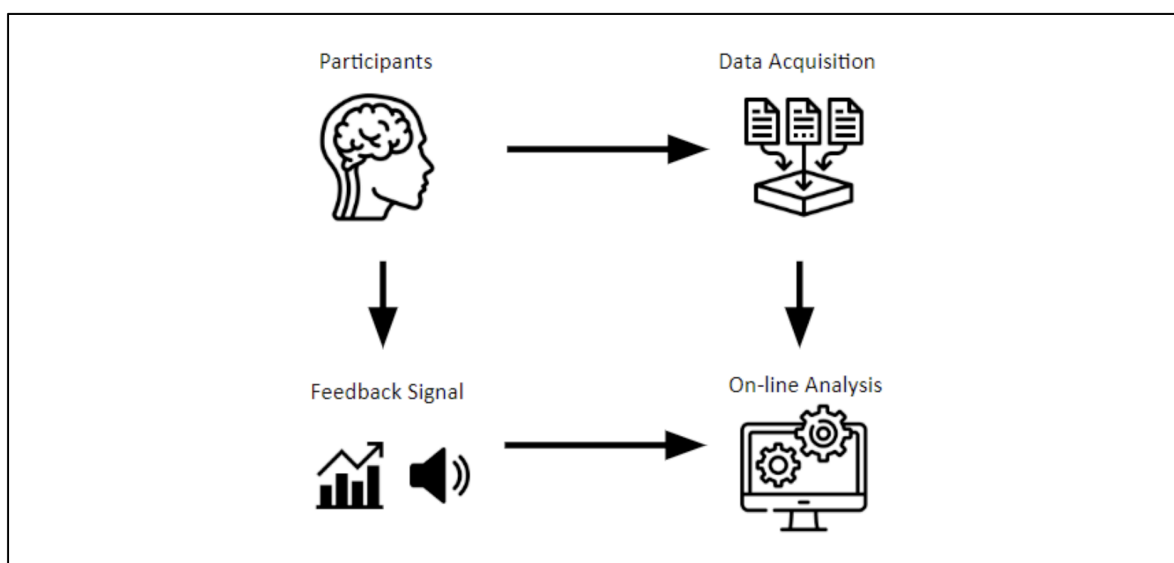
1. From Memory Networks to Self-Regulation

Learning and memory are fundamental processes that shape our understanding of the world and our ability to adapt to changing environments. Understanding the underlying mechanisms of learning and memory has been a central pursuit in neuroscience, psychology, and related fields. Brain imaging has become an indispensable method to investigate human learning and memory. Functional magnetic resonance imaging (fMRI) is an imaging technique to investigate the connectivity and organization of brain networks with high-resolution and in a non-invasive way by measuring the blood oxygen level dependent (BOLD) signal in the brain (Glover, et al. 2011). The BOLD contrast reflects physiological events in the brain by making changes in the blood oxygenation state of active brain areas visible (Logothetis et al., 2001). In most fMRI studies results become available hours or days after data acquisition, since data must be processed offline (Weiskopf et al., 2007). Real-time fMRI (rt-fMRI) is a brain imaging technique that utilizes the latest developments in data processing to make fMRI scanning results instantly available, as the analysis and display of data keep pace with data acquisition (Sulzer et al., 2013). The most prominent application of rt-fMRI in recent years has by far been rt-fMRI neurofeedback (NF). NF is a form of biofeedback, in which the subject learns to voluntarily change a neural signal or a combination of neural signals through repeated feedback on the signal in the region of interest (ROI) (Weiskopf et al., 2007). Administering NF with rt-fMRI allows the data acquisition, computation of feedback and presentation of feedback to the subject to all be processed in real-time (Birbaumer et al., 2013). Figure 1 shows the closed rt-fMRI NF loop. Participants typically receive exogenous feedback about activity in the ROI. This feedback, which informs the participant about the NF signal, can be visual, like functional maps, curves or graphical thermometers (Sulzer et al., 2013). Some studies provided auditory or, less frequently, tactile signals. A different approach is administering endogenous feedback that does not directly present the feedback signal to the participant. Instead, it alters certain experimental conditions. For instance, if a participant plays a video game where the game's content (like varying difficulty levels or bonus items) changes based on the detected neurological signal, they are receiving implicit feedback. Although they are not directly aware of their own neural signal, changes in the game's content gives them indirect access to the neural signal. Access to a neurological signal correlate can result in the lasting ability to control one's own brain activity (Caria et al., 2012). Furthermore, voluntary control of brain activity relates to behavioral changes. Successful

rt-fMRI NF thus holds much promise for understanding neural underpinnings of behavior with potential applications in various fields, including neuroscience, psychology, and in clinical settings. The possible clinical application of rt-fMRI NF has received much attention with research showing clinical improvement in populations diagnosed with medical conditions such as depression (Linden et al., 2012), ADHD (Alegria et al., 2017), posttraumatic stress disorder (Nicholson et al., 2016), and Alcohol Use Disorder (Dalkner et al., 2017), among others.

Figure 1

The Closed Neurofeedback Loop



Note. The participant's brain is scanned using fMRI, and the acquired data are processed in real time. Feedback, often in the form of visual or auditory cues, is generated based on specific brain activity patterns of interest. This feedback is then presented to the participant, who can actively modulate their brain activity in response. The updated brain activity is continuously monitored, completing the loop and allowing real-time adjustments in the feedback presentation. This closed-loop system enables individuals to learn and regulate their brain activity patterns, contributing to various applications in therapeutic interventions and cognitive enhancement. Adapted from “Improving Visual Perception through Neurofeedback”, by F. Scharnowski, et al. 2012, *Journal of Neuroscience*, 32 (49) 17830-17841; DOI: <https://doi.org/10.1523/JNEUROSCI.6334-11.2012>.

Though the general effectiveness of rt-fMRI NF has been well established, the exact mechanisms underlying learning voluntary self-control over brain activity remain unclear. A

prevalent concern within the NF literature is *NF inefficacy* (Alkoby et al., 2018). The NF inefficacy problem describes individuals unable to learn voluntary control over brain activity. Those individuals are commonly denoted as non-responders, non-performers, or non-regulators (e.g., Friedrich et al., 2014; Thibault et al., 2018; Haugg, et al. 2021). A meta-analysis has shown that between 30–50% of individuals do not achieve self-regulation in NF interventions (Alkoby et al., 2018). In studies involving rt-fMRI NF, only roughly two-thirds of participants are successful in controlling feedback through their brain signals (Friedrich et al., 2014; Haugg et al., 2020; Haugg et al., 2021). Moreover, even among those who can self-regulate, significant variability exists in how effectively they can transfer this skill outside the immediate feedback setting (Thibault et al., 2018). This inconsistency is also evident among individuals who can regulate NF, as their performance varies (Haugg et al., 2020; Stirner et al., 2022). A similar challenge is seen in Brain-Computer Interface (BCI) research, known as *BCI Illiteracy*, where 10–30% of participants do not respond to BCI interventions (Vidaurre & Blankertz, 2009). In the context of neuroprosthetics, BCIs capture brain signals and translate them into machine instructions, mirroring user intentions (Leuthardt et al., 2009). Rt-fMRI can function as a BCI, either for NF or device control (Sorger et al., 2012). Due to the notable presence of non-responders, understanding the factors leading to varied NF performance among individuals is vital. Further research into the non-responder phenomenon could improve NF efficacy (Haugg et al., 2021) which in turn could lead to more conscious use of resources in the highly time and cost demanding NF method and lessen frustrations of being unable to self-regulate in non-responders (Hasslinger et al., 2022).

Enhancing study designs, treatment efficacy, and successful transfer in the context of rt-fMRI-guided self-regulation requires a comprehensive understanding of the neuropsychological mechanisms involved in learning voluntary control of brain activity. The challenge of understanding the psychobiological process of self-regulation learning remains a pressing concern in the NF field (Emmert, Kopel, et al., 2016; Sulzer et al. 2013). Psychological learning models could play a pivotal role in offering a comprehensive understanding of the neuropsychological mechanisms underlying the acquisition of voluntary control over brain activity. These models provide a structured framework to dissect the interplay between cognitive processes, neural dynamics, and behavior during the learning process. Moreover, they shed light

on the neural substrates that underlie the acquisition, generalization, and transfer of self-regulation skills. While instrumental conditioning is widely recognized as playing a primary role in learning brain self-regulation with rt-fMRI NF (Sulzer et al., 2013; Caria et al., 2012; Sitaram et al., 2016; Fede et al., 2020), integrating principles from multiple psychological theories of learning and memory could lead to a deeper understanding of how individuals develop strategies to modulate their brain signals based on feedback. Currently, there is a lack of research providing a structured overview of contemporary insights into the psychological learning processes associated with rt-fMRI NF. Given the absence of a comprehensive theory of learning and memory, the understanding of the mechanisms involved in learned self-regulation using rt-fMRI remains incomplete.

1.1 Overview of the Thesis

Identifying an optimal strategy for enhancing brain self-regulation is crucial for advancing NF in clinical settings (Sulzer et al., 2013). This thesis explores modern learning theories and their connection to self-regulation through rt-fMRI, offering insights into the dynamics of learning and memory. It introduces the connectionist view of memory as a network of linked elements, followed by an examination of memory formation, with a focus on the multi-component model of working memory (WM) and its ties to rt-fMRI NF. The discussion extends to long-term memory (LTM) and non-declarative memory, as well as associative learning which covers both classic and instrumental conditioning, the importance of prediction errors, and the interplay between model-free and model-based learning. Additionally, the thesis details key neurobiological elements of associative learning, such as spike-timing-dependent plasticity (STDP), the basal ganglia, and dopamine. Later sections delve into psychological factors influencing rt-fMRI NF learning outcomes, including attention, motivation, and emotion, and their neural underpinnings. Lastly, the components of the training protocol, encompassing feedback, rewards, and mental strategies, along with other physiological factors, are examined. By dissecting the multifaceted aspects of learning, from foundational memory models to the nuanced physiological and psychological factors, this thesis provides valuable insights that can influence professional practices.

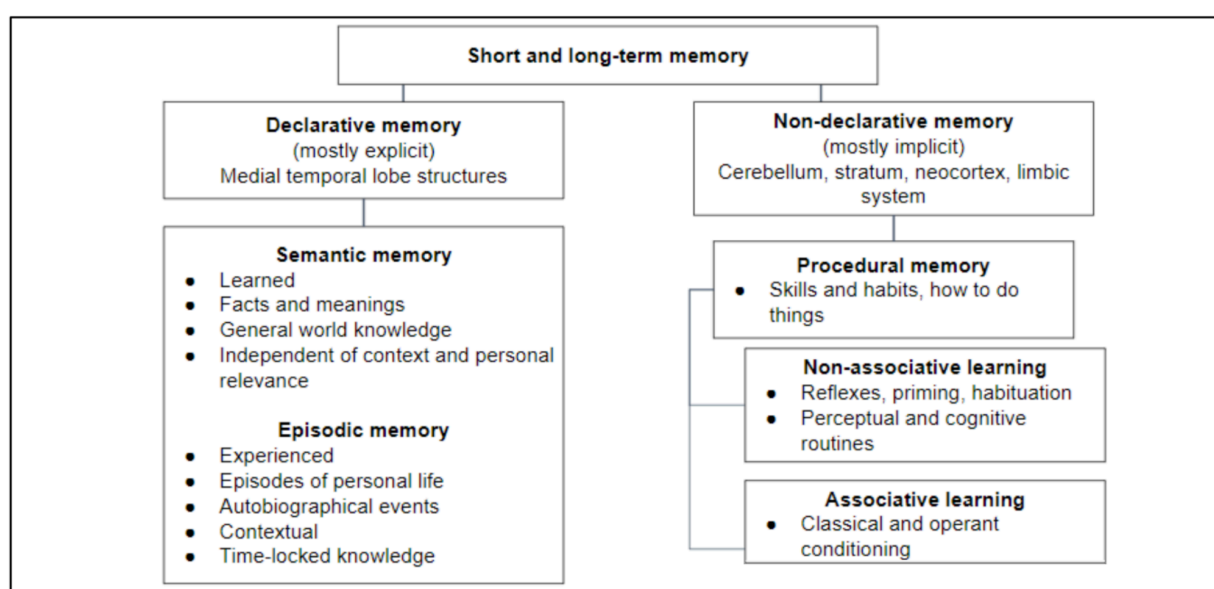
2. Foundations of Learning and Memory: Taxonomy and Frameworks.

Understanding the relationship between a system's behavior and underlying properties like *learning* and *memory* presents significant challenges in neuroscience. Despite having detailed knowledge of elements like genetics, cell types, and neural connections, there's often an incomplete understanding of how these components translate into behavior (Krakauer et al., 2017). Common ground among diverse approaches in describing the mechanisms behind learning and memory is the understanding that learning entails lasting neural changes in the brain. A contemporary approach in understanding human behavior across several scientific areas, including psychology and biology, is the information-processing perspective (Ramos, 2014). This theory suggests that the brain operates like a system processing information, producing specific neural patterns that mirror real-world events. Such neural patterns allow the interpretation and processing of observed events in a domain-specific way (Gallistel & Matzel, 2013; Ramos, 2014). Essentially, every unique observation, action, and memory corresponds to a distinct brain state, embodying the necessary information to delineate and produce these situations (Morris & Bouton, 2006). Within this framework, learning and memory are separate processes. Here, *learning* entails drawing information from experiences, while *memory* ensures this information is preserved and can be recalled for future use (Gallistel & Matzel, 2013).

Marr (1982) introduced an influential framework aimed at understanding information processing systems. The framework consists of three levels, a computational, algorithmic, and implementational level. The highest level in this framework is the computational level which focuses on the abstract problem that a cognitive system is trying to solve. This level is concerned with the overall purpose, function, and goals of the system. The algorithmic level describes what algorithm or rules the system employs, while the implementational level concerns the neural hardware or physical basis underlying the system. In recent years, neuroscientists have discussed learning and memory from this computational view proposed by Marr (Gallistel & Matzel, 2013) and even papers discussing the learning mechanisms in rt-fMRI NF cite the computational level of analysis for exploring the learning mechanisms underlying rt-fMRI NF (Sulzer et al., 2013). Investigating learning components must be complemented by understanding how the entire mechanism operates when embedded in an environment, necessitating an exploration that spans multiple levels (Krakauer et al., 2017). The study of learning and memory encompasses a wide range of levels, from the comprehensive perspective of the individual to specific anatomical

brain regions, local circuits, cells, synapses, and even down to the molecular and genetic levels. Furthermore, categorization can be based on factors like duration, content, and methods of acquisition of new information (Brem et al., 2013). The aspiration of a neurobiological theory of memory lies in its ability to seamlessly integrate insights across these varying levels (Churchland & Sejnowski, 1992). One common psychological taxonomy of learning and memory is shown in Figure 2.

Figure 2
Classification of Different Types of Memory Processes



Note. Within this conceptual framework short-term and long-term memory is categorized into two primary domains, declarative and non-declarative memory. Declarative memory can be further divided into semantic memory, encompassing concepts, ideas, and language-based information, and episodic memory, the repository for personal experiences, retaining specific events and occurrences within a temporal context. Non-declarative memory represents unconscious or automatic memory processes. It includes procedural memory, which governs motor skills and the recall of procedural knowledge required for task execution. Furthermore, procedural memory can be divided into associative memory (the formation of associations and connections between stimuli and responses) and non-associative memory (memory processes that involve changes in the response to a single stimulus, such as habituation and sensitization). Adapted from Brem, A. K., Ran, K., & Pascual-leone, A. (2013). Learning and memory. *Handbook of Clinical Neurology*, 693–737.

<https://doi.org/10.1016/b978-0-444-53497-2.00055-3>

A major intersection between experimental psychologists and neurobiologists involves the division of learning and memory into distinct temporal phases, namely encoding, storage, consolidation, and retrieval (Morris et al., 2005). During encoding, sensory input transforms into mental representations (Takeuchi et al., 2014). This information is then preserved during the storage phase, and later accessed and used during retrieval. The upcoming section offers a deeper look into the processes of memory formation, specifically the distinct phases, and key components of memory formations. Using an information-processing lens and drawing from various analytical dimensions, the section aims to explore learning and memory in the context of rt-fMRI NF.

2.1 The Connectionist Perspective

In the context of memory taxonomy, a significant classification is offered by the connectionist perspective on information processing. Connectionist models, also known as Parallel Distributed Processing models, serve as computational frameworks widely employed for simulating human perception, cognition, and behavior, including the underlying learning processes and memory functions (Cleeremans & McClelland, 2009). These models are rooted in a cognitive science perspective that seeks to align the understanding of behavior and mental states with the knowledge of neural processes. Connectionist networks utilize two main forms of representation: One form is the pattern of activation across network units, representing perceptions, processing, or memories. The other form is the values of connection weights between processing units, storing prior experiences. Connection weights represent prior experiences and are typically set through a learning process. They encode associative relationships and structured mappings between patterns, allowing for meaningful associations and mappings to be learned. Connection adjustment is used both for learning skills and for memory processes. Learning skills involves gradual adjustments to form connections that implement a skill, while memory for unique episodes requires larger connection weight changes at or around the time of the experience. Unlike traditional models in cognitive science, these models learn through repeated exposure to environmental stimuli. This perspective defines memory as comprising short-term memory (STM) and LTM (Cleeremans & McClelland, 2009). There is an ongoing debate regarding the distinction between STM and LTM (Norris, 2017; Cowan, 2019). Although past research has proposed distinct neural bases for STM and LTM,

recent arguments posit that STM and LTM are more overlapping, rather than distinct systems. Some evidence for the differentiation between STM and LTM comes from studies on STM patient populations (Norris, 2017). Patients with selective verbal STM impairments but exhibiting an intact LTM, support the idea of dissociation between these memory stores. Conversely, individuals with LTM deficits often exhibit preserved STM function, reinforcing the concept of distinct memory systems. Another finding supporting the idea of separate stores is that the LTM lacks the ability to retain spatial or temporal configurations of stimuli, necessitating a separate STM copy (Baddeley, 2003; Norris, 2017). This suggests a functional interaction between the two memory stores rather than a complete overlap. Additionally, distinctions in recall properties, such as reliance on phonological versus semantic information, further support the notion of separate memory systems (Cumming et al., 2003). Critics argue that impairments in STM tasks among LTM patients do not necessarily negate the concept of distinct memory stores, as neurologically healthy individuals also integrate STM and LTM during challenging tasks (Cowan, 2019). Task impurity may confound interpretations of deficits in STM accompanying LTM damage, advocating for a nuanced understanding of memory processes (Rhodes & Cowan, 2018).

Despite the ongoing debate, this thesis adopts the assumption of two distinct memory stores, STM and LTM, to facilitate investigation into learning models in psychology. This distinction is pragmatically beneficial as it aligns with the two primary focuses of learning models: rapid acquisition and immediate response to stimuli, as well as the encoding and retention of information for LTM storage. Moreover, in the context of rt-fMRI NF, this differentiation proves relevant as it enables the investigation of both the immediate learning and self-regulation processes, as well as the lasting transfer and retention of self-regulation abilities. By acknowledging and utilizing these distinctions, the following chapters aim to provide an overview of contemporary psychological learning models and their relevance for learning mechanisms within the context of rt-fMRI.

3. Short-Term Memory Models

This chapter explores the fundamental psychological learning models in the STM. Specifically, two prominent models are explored; the structural model and the model of WM. These models offer comprehensive frameworks for understanding the cognitive processes

involved in STM, including encoding, maintenance, and retrieval. Additionally, the neural underpinnings associated with these models are examined, shedding light on the brain regions and networks implicated in STM functioning. Furthermore, the relevance of these models in the context of rt-fMRI NF is discussed. By highlighting the theoretical foundations and neural correlates of STM, this chapter aims to provide insights into how these models can inform our understanding of cognitive processes involved in learned self-regulation.

3.1 The Structural Model

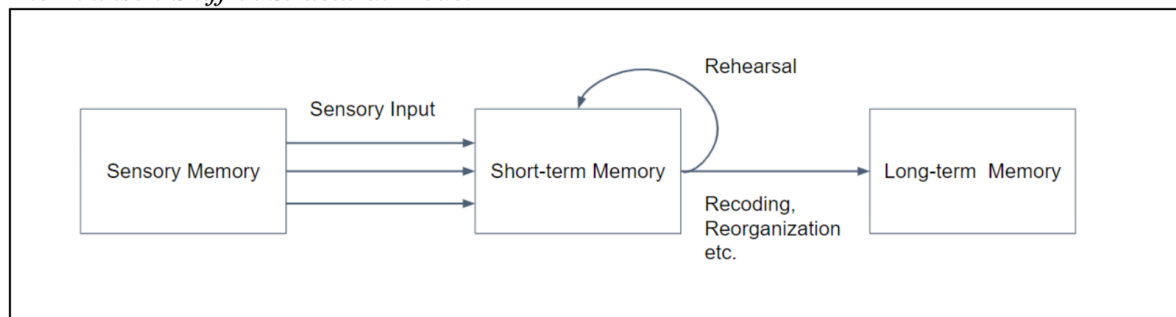
Several types of memory are distinguished, based on the idea that the memory is not a single entity, but rather consists of several entities all associated with different neural structures and processes. An early concept of memory is the structural model, which is depicted in Figure 3. The structural model proposes three different memory stores, namely a sensory memory, a STM, and a LTM store (Atkinson & Shiffrin, 1968). Although envisioning the memory system as three interconnected stores may oversimplify the complex nature of memory, it has had considerable influence on contemporary memory models. Within this framework, information initially enters the memory system through the *sensory memory*, residing there temporarily for a brief duration ranging from a few hundred milliseconds to 1-2 seconds before undergoing transfer to another memory store or fading away. STM serves as the cognitive mechanism responsible for the processing and retention of information over relatively short time intervals. Conversely, LTM enables the storage of information for extended periods, with the capacity for conscious retrieval (explicit memory) or unconscious retrieval (implicit memory). A fundamental differentiation between STM and LTM pertains to their respective durations and capacities.

Later the framework was updated to include the sensory memory's distinct stores tailored to specific types of information, such as the *iconic memory* store for visual stimuli, the *echoic memory* store for auditory stimuli, and the *haptic memory* store for tactile stimuli (Baddeley & Hitch, 1974). The structural model describes the structure and flow of information within the memory system and provides a framework for understanding how information moves from sensory input to more stable, long-term storage. However, it does not delve deeply into the active cognitive processes involved in manipulating and using information. WM, on the other hand, is a model that addresses how information is actively used by a subject. The cognitive system WM seems to play a crucial role in temporarily holding and manipulating information for various

cognitive tasks, such as problem-solving, reasoning (Cowan, 2016), and potentially self-regulation of brain activity in rt-fMRI. The following chapter delves into the WM and its role as a cornerstone of complex cognition. This chapter further unravels the neural underpinnings, theoretical models, and implications of WM for learning in rt-fMRI NF.

Figure 3

The Atkinson-Shiffrin Structural Model



Note. The Atkinson-Shiffrin structural model comprises three primary memory stores: Sensory memory (briefly holding sensory input), short-term memory (with limited capacity and short duration), and long-term memory (with vast storage and long duration). Information flows from sensory memory to short-term memory through attention and rehearsal, and then to long-term memory through encoding. Retrieval involves bringing information back from long-term memory to short-term memory. This foundational model has influenced memory research, though contemporary models incorporate more complex interactions between memory systems. Adapted from “Human Memory: A Proposed System and its Control Processes.”, by R. Atkinson & R. Shiffrin, 1968, *Psychology of Learning and Motivation*, 89–195. [https://doi.org/10.1016/s0079-7421\(08\)60422-3](https://doi.org/10.1016/s0079-7421(08)60422-3)

3.2 The Multi-Component Model of WM

The WM model is the most widely used and accepted STM model today (Oberauer et al., 2018). WM is the cognitive system that temporarily holds and manipulates information in a heightened state of availability, serving as an ensemble of components essential for ongoing information processing and mental task performance (Cowan, 2016). Baddeley and Hitch (1974) originally suggested that WM consists of five elements: the visuospatial sketchpad, the phonological loop, subsidiary slave systems, the episodic buffer, and the central executive (see Figure 4). The visuospatial sketchpad briefly holds spatial and visual information, while the phonological loop briefly stores verbal information for verbal comprehension and for acoustic

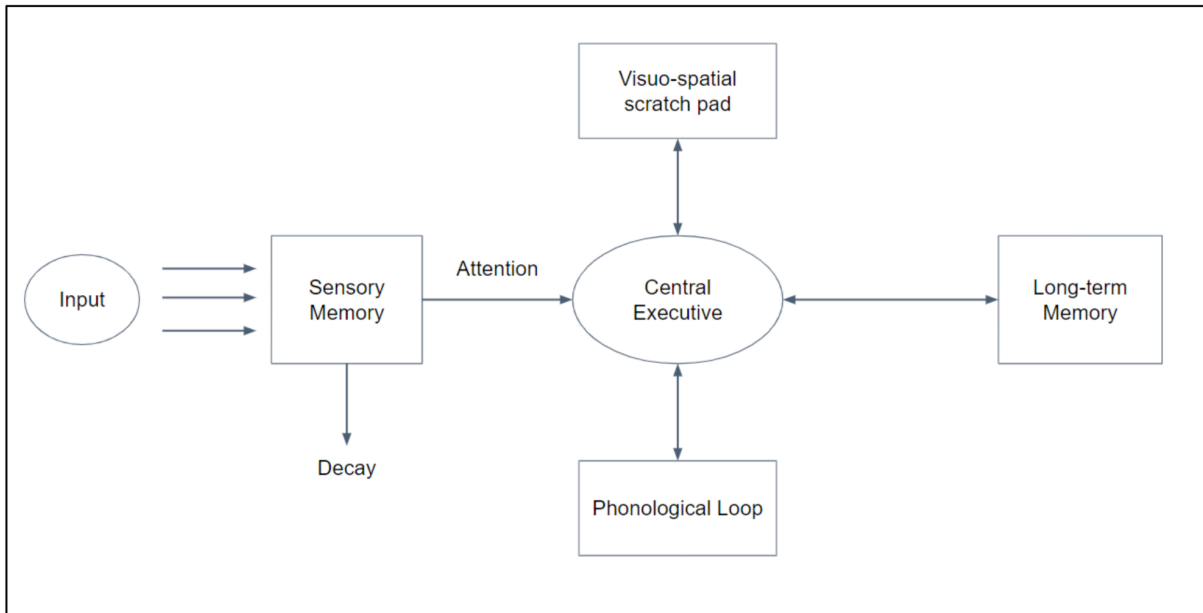
rehearsal. The subsidiary slave systems are restricted systems involved in maintaining smaller amounts of verbal or visuospatial information over short intervals. A late addition to the WM model is the episodic buffer, which allows problem solving and relating previous experiences to current information (Baddeley, 2000), but it is still a loosely defined concept with many aspects yet to be understood (Baddeley et al., 2015). The central executive oversees the workings of the WM. Given that WM has capacity limitations, the central executive determines which information is processed and the manner of its processing. Within the WM model, there are both passive and active processes. Passive processes involve storing and retrieving information, while active processes involve altering information. This combination of storing and altering information facilitates advanced cognitive functions by connecting new information to established knowledge in LTM and producing the right responses.

Historically, WM emerged as a more dynamic counterpart to STM, capturing its active and multi-faceted nature (Baddeley, 2001). While the boundaries and relationship between WM and STM have remained a topic of debate (Cowan, 2016), a prevalent view has emerged: WM is not simply a storage space, but a sophisticated cognitive system designed for both storing and manipulating information (Rose et al., 2010). This viewpoint distinguishes WM from both STM and LTM and positions it at the intersection of these memory systems. Recent research supports this stance, suggesting that WM functions at the intersection of STM and LTM, without being strictly tied to either (Aben et al., 2012; Camos & Barrouillet, 2011; Uncapher et al., 2015). Yet, the nuances of WM go beyond its relationship with STM and LTM. The capacity of WM, for instance, varies among individuals. An individual's WM capacity is typically viewed as a characteristic pertaining to how effectively they can utilize their WM system (Fukuda et al., 2015). This variance has been associated with factors like attention control ability (Fukuda & Vogel, 2009), the ability to focus on task-relevant stimuli (Fukuda & Vogel, 2011) and resistance to distractions from irrelevant stimuli (Vogel et al., 2005). Given the significance of WM in aiding the brain to retain and handle information, it is worth noting that NF training has been explored as a tool to augment WM (Jiang et al., 2022). However, the literature seems to lack investigations into how WM itself influences the learning of self-regulation through NF. The dynamics of WM, specifically its capacity and performance, may be crucial in integrating rt-fMRI signals with pre-existing knowledge in LTM and generating the appropriate neural

responses. A well-functioning WM may be a cornerstone for grasping and responding to feedback, while actively modulating one's own brain activity.

Figure 4

Working Memory Model



Note. Information first enters the sensory memory, from which it either decays or is passed to the central executive. This core mechanism then orchestrates its interactions with the visuospatial sketchpad – responsible for the temporary storage of spatial and visual details – and the phonological loop, which holds verbal data and supports acoustic rehearsal. Subsidiary slave systems play a role in maintaining select verbal or visuospatial details over short durations. Meanwhile, the episodic buffer bridges problem-solving processes by tying past experiences to current information. Adapted from “The episodic buffer: a new component of working memory?”, by A. Baddeley, 2000, *Trends in Cognitive Sciences*, 4(11), 417–423. [https://doi.org/10.1016/s1364-6613\(00\)01538-2](https://doi.org/10.1016/s1364-6613(00)01538-2)

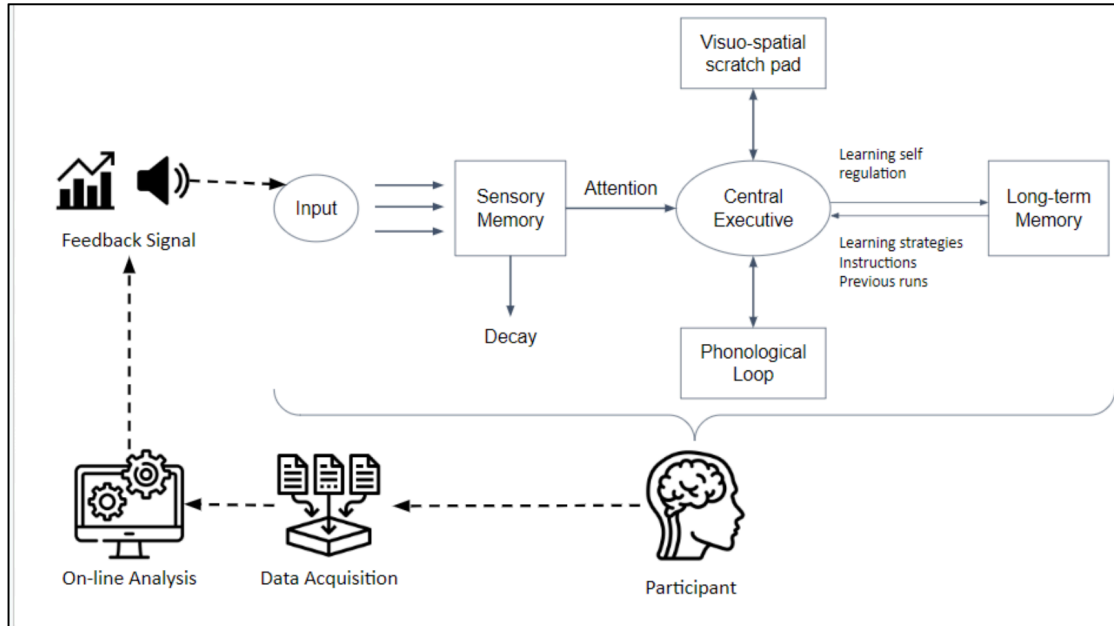
3.2.1 Neural Underpinnings

Research suggests that there are distinct components within the WM, supported by studies on patients with specific brain lesions. Patients with damage to the inferior parietal cortex, responsible for phonological processing, had difficulties in tasks associated with phonological storage and rehearsal (Baldo & Dronkers, 2006; Yue & Martin, 2022). WM ability has been shown to relate to the persistent spiking activity of neurons in the prefrontal cortex (Markowitz et al., 2015). Large-scale networks in the brain provide a framework for understanding the biological foundation of WM and its significance in rt-fMRI NF. The

central-executive network (CEN), a major system in the brain, plays a role in attention, decision-making, problem-solving, and WM (Menon, 2011). Key areas of CEN include the dorsolateral prefrontal cortex and the lateral posterior parietal cortex, with the former recognized as a central hub for WM (Markowitz et al., 2015). Although most WM studies focus on memory tasks, fMRI research shows activation in specific parts of the frontal cortex during both object and spatial WM tasks (Sala & Courtney, 2007). The CEN also plays a part in task-focused processing and practical decision-making, with reward expectation influencing goal-driven behaviors. A study revealed CEN activity during rt-fMRI NF, suggesting WM's role in this process (Emmert, Kopel, et al., 2016).

3.2.2 The WM model and NF

The WM model provides a valuable framework for understanding the processes underlying learning self-regulation in rt-fMRI NF. The basic rt-fMRI NF loop aligns well with the WM model, facilitating the integration of sensory information, attentional processes, and control mechanisms (see Figure 5). In this context, sensory information from the feedback display serves as input to the sensory memory component of the WM model. Attentional mechanisms then transfer this information to the WM, where it can be actively maintained and manipulated. This manipulation may involve encoding the feedback signal into the phonological loop or visuo-spatial memory for further processing and analysis, depending on whether the feedback signal is a visual cue or an auditory cue. The central executive component of the WM maintains attention and orchestrates cognitive control processes, allowing individuals to regulate their brain activity based on the feedback signal. Moreover, the central executive can draw upon information stored in LTM to inform and optimize self-regulation strategies. This may include knowledge of effective regulation techniques, previous experiences with NF training, or general learning strategies. Supporting the applicability of the WM model to rt-fMRI NF, research has demonstrated the effectiveness of cognitive strategies, such as attentional control and rehearsal techniques, in enhancing self-regulation performance (e.g., Emmert et al., 2016). Additionally, studies have shown that individuals can improve their NF performance over time through practice and experience, indicating a learning process guided by cognitive control mechanisms (e.g., Sulzer et al., 2013).

Figure 5*Working Memory Model Within the Closed rt-fMRI Loop*

Note. Information first enters the sensory memory, from which it either decays or is passed to the central executive. This core mechanism then orchestrates its interactions with the visuospatial sketchpad – responsible for the temporary storage of spatial and visual details – and the phonological loop, which holds verbal data and supports acoustic rehearsal. Subsidiary slave systems play a role in maintaining select verbal or visuospatial details over short durations. Meanwhile, the episodic buffer bridges problem-solving processes by tying past experiences to current information.

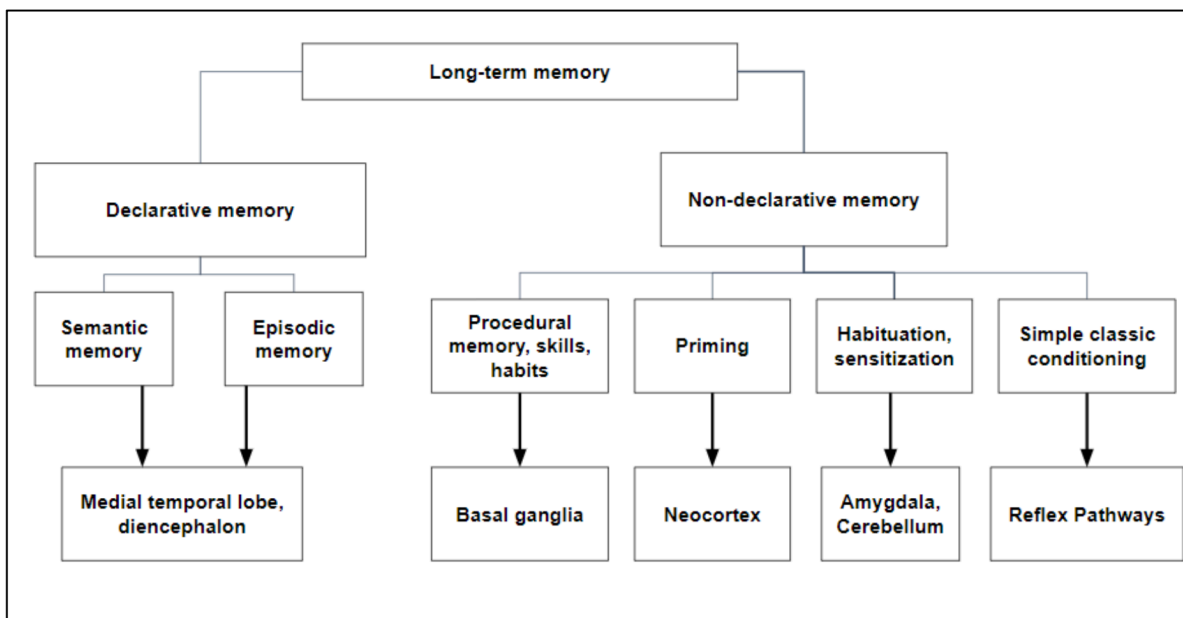
However, several limitations should be considered when applying the WM model to rt-fMRI NF. Firstly, the complexity of the NF task and the cognitive demands involved may overwhelm individuals with limited WM capacity, potentially hindering their ability to effectively regulate brain activity. Moreover, individual differences in WM capacity and cognitive control abilities may influence the efficacy of NF training, highlighting the importance of personalized approaches (see chapter 5.1). Interestingly, research has found that auditory feedback in rt-fMRI NF could potentially be more impactful than visual feedback (Harmelech et al., 2013). While WM research showed impaired performance on visual with visual interference (Park et al., 2007) and impaired performance on auditory tasks with auditory interference (Dittrich & Stahl, 2012), it can not currently explain the finding of a potentially more impactful

auditory feedback in cognitive tasks such as rt-fMRI NF. Furthermore, the WM model primarily focuses on the temporary storage and manipulation of information, rather than the mechanisms underlying long-term learning and memory consolidation. While the central executive component can incorporate information from LTM to guide self-regulation efforts, the precise interactions between WM and LTM processes during NF training are insufficiently explained by the WM model.

4. Long Term Memory Models

The WM model is a useful concept to approach learning self-guided regulation in rt-fMRI. The focus of WM however is on how information is processed in an ongoing task. In this following section, the focus is on how information from the WM is integrated into LTM. LTM plays an important role in the consolidation of the skills and strategies acquired during rt-fMRI NF. As the ultimate repository for knowledge and experiences, understanding the transition of information from WM to LTM is essential for investigating the lasting impacts and efficacy of NF interventions. Furthermore, the retrieval of these long-term stored strategies during subsequent sessions can potentially enhance self-regulation and overall learning outcomes in the rt-fMRI NF context.

A widely utilized taxonomy, established in the early stages of memory research and still prevalent today, divides the learning and memory system into declarative and nondeclarative memory, with distinct neural structures associated with each (see Figure 6; Squire & Zola, 1996; Squire, 2004; Brem et al., 2013). Declarative memory encompasses conscious recollection of facts (semantic memory) and events (episodic memory), while nondeclarative memory encompasses various learning capacities that do not require conscious effort for retrieval. Nondeclarative learning includes procedural learning, associative learning and nonassociative learning (including priming). While traditionally the concepts of explicit and implicit memory have been linked with declarative and non-declarative memory respectively, this correlation is not always accurate (Squire & Zola, 1996). Instances exist where declarative memories arise unconsciously, as is the case with memories tied to intense emotional events or those influenced subliminally (Brem et al., 2013). In contrast, some non-declarative memories stem from deliberate efforts, such as motor movements when learning to play the guitar.

Figure 6*A Long-term Memory Taxonomy*

Note. Long-term memory can be categorized it into declarative and non-declarative memory. On the declarative side, memory is further divided into semantic and episodic forms, each with its associated neural structures. In contrast, the non-declarative category encompasses procedural memory, priming, habituation, and simple classical conditioning. This classification provides a comprehensive overview of the various components and nuances of long-term memory and their respective neural underpinnings. Adapted from “Structure and function of declarative and nondeclarative memory systems.”, by L. Squire & S. Zola, 1996, *Proceedings of the National Academy of Sciences*, 93(24), 13515–13522.

4.1 Procedural Memory

Procedural memory is part of the non-declarative memory and plays a key role in encoding, storing, and retrieving skills and habits required to perform tasks (Camina & Güell, 2017). The process of acquiring information for procedural memory is skill learning. Skill learning is defined as the acquisition of a specific skill, associated with long-lasting neuronal changes of how motor activity is elicited (Cano-de-la-Cuerda et al., 2015). There are various models of skill learning (Costa et al., 2004; Floyer-Lea & Matthews, 2005), though it is mostly considered a process of three consecutive steps with gradually increasing skill-automation (Krakauer et al., 2019). During the *cognitive phase* attention is on the single components of a sequence and their combination to learn the new skill. In the *associative phase* the task becomes more automated and the attention to single components fades until the skill becomes fully

automated in various settings in the *autonomous phase* (Magill & Anderson, 2013). The involvement of attention highlights that motor learning is more than simple repetition. Numerous studies have been conducted to identify the factors influencing motor learning. Especially verbal instructions have been shown to facilitate skill acquisition (Meier et al., 2020).

4.1.1 Neural Underpinning.

Skill learning relies primarily on the primary motor cortex, the premotor area, the supplementary motor area and the parietal lobe (Magill & Anderson, 2013). Another important subcortical structure for motor learning is the basal ganglia, whose role in motor control and learning has been extensively studied in people with Parkinson's (Obeso et al., 2009) and cerebral palsy (Graham et al., 2016). Learning physical skills (Foerde & Shohamy, 2011) as well as learning to control neuroprosthetic devices (Koralek et al., 2012) has been linked to changes in the motor cortices and the striatum, which are primary input area of the basal ganglia.

4.1.2 Motor Learning and rt-fMRI.

Motor learning has been suggested to be involved in rt-fMRI NF learning (Arns et al., 2017; Yoo et al., 2008). Describing NF as a form of motor skill learning mostly stems from early biofeedback studies, where learning deliberate control of physical signals was compared to motor skill learning (Lang & Twentyman, 1976). Later, findings from studies on the control of neuroprosthetic devices and early rt-fMRI NF studies where the ROI were in areas associated with motor control also explored the similarities (deCharms et al., 2004; Yoo et al., 2008). Since the individual with a neuroprosthetic device must have continuous feedback to improve how they alter their neural signals, learning neuroprosthetic control has been compared to learning a new motor skill. Like the *phases* in motor skill learning, the user tries to identify strategies that lead to the desired change in the ROI. Additionally, there is heightened cognitive activity as feedback and strategies are processed. With repeated feedback and practice, activation in the ROI increases reflecting the acquisition of the new skill. Despite extensive scientific and clinical exploration of this theory, its application to rt-fMRI NF training has been notably absent in recent times (Sitaram et al., 2016).

4.2 Associative Learning

Associative learning stands as a foundational concept in understanding how memories are formed and connected based on experiences. In the contemporary understanding of associative learning, knowledge takes the form of representations of the relationship between events (Dickinson, 2012). Representations allow the organism to draw predictions that guide behavior. Historically, associative learning has been divided into two main paradigms: classical conditioning and instrumental conditioning. The distinctions between these two have long been a topic of debate, with researchers uncertain about whether they represent two distinct or overlapping processes (Rescorla, 1988; Cartoni et al., 2016; Ghirlanda et al., 2020). Early studies struggled with the intertwined nature of these conditioning forms, particularly given the lack of a comprehensive model system that could explain both types of conditioning at the cellular and molecular levels (Mozzachiodi et al., 2013). Both paradigms share key similarities, such as the effects of contingency (Papini & Bitterman, 1990) and associative competition (Williams, 1999; Bitterman, 2006). However, they differ in their core mechanics and influences. Classical conditioning revolves around forming associations between stimuli, leading to automatic responses, while instrumental conditioning focuses on deliberate actions influenced by intentions and goals. This dichotomy emphasizes that while classical conditioning explores associations between stimuli, instrumental conditioning describes how specific behaviors relate to outcomes and how these outcomes shape behaviors in turn.

Understanding the principles of both classical and instrumental conditioning offers valuable insights into the dynamics of learning in rt-fMRI NF. The ways in which stimuli relationships or action-outcome connections are established in these conditioning models can provide a foundational understanding of how participants might adapt and respond in NF scenarios (Caria et al., 2012). In the following, an overview of these paradigms will further clarify their relevance and applicability to rt-fMRI NF training.

4.2.1 Classic Conditioning

At its core, rt-fMRI NF training involves the association between neural activity and a feedback signal. This is analogous to the classical conditioning principle. Classical learning theory states that basic associative learning processes are essential for organisms to extract meaning from environmental relationships and thereby enabling behavioral adaptation

(Bitterman, 2006). Central to this understanding is the concept that when a neutral stimulus, referred to as the conditional stimulus (CS) is recurrently or intensively paired with another stimulus known as the unconditional stimulus (US), the mere presence of the CS can subsequently elicit the representation of the US. Modern research perspectives recognize that the US is not a monolithic entity. Instead, it comprises multiple facets, encompassing sensory, emotional, response, temporal, and hedonic dimensions (Delamater, 2012). Given this multi-dimensionality, it is inferred that the CS can form associations with various attributes of the US. This multifaceted association implies that several neural systems collaboratively engage in the process of classical conditioning (Corbit & Balleine, 2011).

A variable that is commonly observed in classic conditioning literature is that the intensity of the US determines the strength of the conditioned response, with a more intense US leading to a stronger response (e.g., Björkstrand et al., 2020; Morris & Bouton, 2006). Notably, the intensity of the CS has also been shown to be crucial for effective learning (Coulombe-Lévêque et al., 2021). Moreover, optimal conditioned learning occurs when both the CS and US are novel from the outset of the conditioning process. Exposure to the US prior to pairing with the CS impairs subsequent conditioning (Gil et al., 2014). Conversely, presenting the CS prior to pairing also negatively impacts learning, a phenomenon known as *latent inhibition* (Miller et al., 2015). Conditioned responding typically increases monotonically with the number of CS-US pairings (Gallistel & Gibbon, 2000, but see Gottlieb, 2004). The rate expectancy theory of classical conditioning postulates that when the occurrence of a US-CS pairing exceeds a certain threshold, a conditioned response emerges. Studies manipulating the temporal contiguity between CS and US onset have shown that the more closely two events occur in time, the more likely they become associated (Delamater & Holland, 2008). Gallistel et al. (2014) emphasized that experimental studies have yet to definitively determine the essential interval between the onset of the CS and US. Contrary to the idea of temporal contiguity, which might imply that simultaneous training would be the most effective for robust learning, such outcomes are infrequently seen across diverse learning paradigms. Simultaneous conditioning often leads to weaker conditioning than forward delay conditioning, where the CS is presented before the US. This reduced effectiveness of simultaneous conditioning aligns with research

suggesting that WM capacity diminishes when processing multiple stimuli at the same time (Klink et al., 2014).

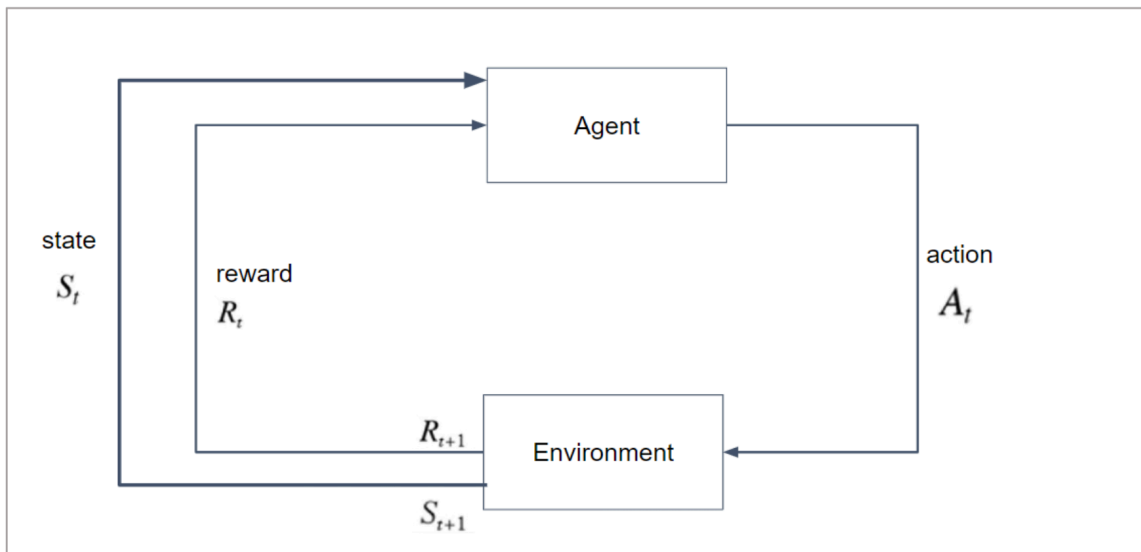
Classical conditioning lays the foundational understanding of how stimuli can evoke specific responses through association, serving as a precursor to the more complex associations in instrumental conditioning. This basic understanding of stimulus-response associations becomes central in rt-fMRI NF, where nuanced feedback is designed based on these principles to drive desired neural changes.

4.2.2 Instrumental Conditioning

Instrumental conditioning involves the facilitation of learning through predictions regarding the value of behavior, specifically in relation to the anticipated rewards it may yield (O'Doherty et al., 2017). Within this framework, the learning process is enhanced by reinforcing or punishing behaviors, ultimately resulting in modifications to the behavior itself. In the simplest form of instrumental conditioning, specific stimulus–response patterns are acquired because they lead to positive reward. Humans encode the relationship between their actions and the consequence of those actions to adapt their behavior accordingly making the action more probable or frequent (Skinner, 1965). Within the paradigm of instrumental conditioning, the consequences of behavior are characterized by four key outcomes. *Positive reinforcement* describes situations where a behavior results in the presentation of a rewarding stimulus. Conversely, *negative reinforcement* involves a behavior leading to the removal of an adverse stimulus. On the other hand, *positive punishment* is when a behavior is met with an aversive stimulus, and *negative punishment* occurs when a rewarding stimulus is taken away following a behavior. If a behavior, once reinforced, ceases to result in any of these four outcomes, it is termed as being extinguished. Several factors can influence the effectiveness of reinforcement learning. The rate of reinforcement, or how frequently a reward is given, can impact the rate of an instrumental response. Higher rates of reinforcement lead to higher rates of response. For instance, studies have shown that as the reinforcement rate increases, so does the response rate, but this relationship is not linear (Maia, 2009). Moreover, the quantity of the reinforcer plays a crucial role. Generally, larger reinforcers result in higher response rate (Trosclair-Lasserre et al., 2008). Another important factor is the quality of the reinforcer. Higher quality reinforcers, which are often preferred over lower quality ones, are typically more effective in supporting

instrumental responding (Lee et al., 2010). The response rates align with an individual's preference for a particular reinforcer, with higher response rates for more preferred items. For optimal effectiveness, reinforcement should be administered consistently and immediately following a response (DeRusso, 2010). The timing of reinforcement holds a crucial role, as an immediate consequence proves more impactful than a delayed one. While intermittent reinforcement might lead to slower learning, behaviors reinforced intermittently tend to exhibit greater resistance to extinction compared to those consistently reinforced (Nevin, 2012). Deprivation and satiation play a crucial role in determining the reinforcing value of a stimulus. Deprivation amplifies the power of both unconditioned and some conditioned reinforcers, making stimuli more effective when one has gone without them for a time (Miltenberger, 2007). Conversely, satiation diminishes a stimulus's potency as a reinforcer. Instructions and contextual rules can also modify the reinforcing value of certain stimuli, emphasizing the dynamic nature of what individuals find reinforcing under different conditions.

The computational model of reinforcement learning (RL) (Sutton & Barto, 1998) has become increasingly popular in examining instrumental learning. The fundamental principles of RL are *reward functions*, the interplay between *state* and *action*, *policy* formulation, the *significance of the value function*, and the challenges and considerations in *modeling* and *representation* (Figure 7). In RL, the reward function serves as the feedback from the environment and defines an agent's goal. It dictates what is beneficial or detrimental for the agent and cannot be changed by the agent. An action is any decision an agent makes, and a state comprises all the factors influencing that decision. The state might even include past environmental conditions. The policy function maps states to actions. This can be a stored policy or can be computed dynamically, using models of the environment to determine the most valuable action sequences. The value function maps potential states or state-action pairs to expected long-term rewards based on the current policy. It is continually updated based on the outcomes of the agent's actions. Building on this foundation of RL and its core components, the prediction error emerges as an essential factor. The next chapter will delve into the intricacies of prediction error and its role in the RL process.

Figure 7*The Reinforcement Learning Framework*

Note. In the reinforcement learning framework, an agent operates within an environment, where it observes a state S_t . Based on this state, the agent selects an action A_t . In response to this action, the environment provides the agent with a corresponding reward R_{t+1} . The objective of the agent is to choose actions that maximize its cumulative reward over a long sequence of transitions. Through this process, the agent learns the optimal strategy or policy to achieve its goal. Adapted from “Reinforcement learning and its connections with neuroscience and psychology.”, by A. Subramanian, S. Chitlangia, & V. Baths, 2022, *Neural Networks*, 145, 271–287. <https://doi.org/10.1016/j.neunet.2021.10.003>

4.2.2.1 Prediction Error. The key concept in instrumental conditioning is that learning about reward-predictive cues is regulated by the prediction error. The prediction error describes the difference between expected and actual rewards (Schultz, 2016). An individual may possess a prediction or lack a prediction regarding a behavioral outcome. An actual behavioral outcome is compared to the prediction, leading to one of three possibilities: it may be superior, equivalent, or inferior to the prediction (Ouden et al., 2012). The subsequent behavioral adjustments depend on the quantitative discrepancy experienced between the outcome and its prediction. In the presence of a prediction error, both the prediction itself and the corresponding behavior should be modified. Specifically, when the outcome surpasses the prediction (positive prediction error), the frequency of the behavior increases to attain the rewarding stimulus. Conversely, if the outcome falls short of the prediction (negative prediction error), the frequency of the behavior

decreases to avoid the aversive stimulus. In instances where the outcome aligns precisely with the prediction, the behavior remains unaltered as no prediction error arises. In RL algorithms the prediction error is modeled by optimizing the value function to minimize the reward prediction error (Subramanian et al., 2022). Thus, bidirectional prediction error serves to drive the learning process regarding cues predictive of rewards and facilitates the generation of more accurate predictions concerning future rewards. This error signal is conveyed to both the striatum and cortical areas for processing (Hare et al., 2008).

4.2.2.2 Model-Free and Model-Based Instrumental Learning. Human behavior being guided by simply seeking reward maximization and avoiding punishment in interactions with the environment does not account for its complexity. The introduction of model-free and model-based learning frameworks has allowed researchers to describe different aspects of decision-making and learning, revealing the coexistence and interplay of these two strategies in human behavior (Bouton, 2021). This has led to a more nuanced understanding of how individuals adapt their behavior, make choices, and learn from feedback (Doll et al. 2012). One specific scientific gap that these models have addressed is the dichotomy between habitual and goal-directed behavior. In model-free RL, the agent has no model of outside events and learns by caching information about the utilities of behavioral consequences in the environment (O'Doherty et al., 2017). Habitual behavior has been associated with model-free instrumental conditioning. The reward prediction error calculates the difference between expected and actual rewards, and guides decisions to increase future rewards (Gläscher, 2010). In model-based RL, however, the agent can use an internal model of events and stimuli from the external world to draw predictions about the consequence of their action. The models are built through experience. This type of learning has been associated with goal-directed behavior. In model-based learning a state prediction error (SPE) is used to capture the error in predicting behavior leading to a new state considering known transitions. From a neuroscientific perspective, model-free and model-based behavior systems appear to coexist in different corticostriatal circuits. While habitual model-free learning is associated with dopamine and the dorsolateral striatum, cognitive model-based learning is associated with the prefrontal cortex (Daw et al., 2005; Tricomi et al., 2009). Both systems learn concurrently, but they control behavior differentially. This raises the question of how the two systems compete for taking control over behavior. Given the estimates

from both systems, one explanation is the dual-process theory, where a Bayesian principle of selecting the least uncertain among the systems accounts for which system is dominant (Daw et al. 2005; Dickinson, 2012). More recently, a decision-theoretic explanation emerged, framing the selection as a cost-benefits calculation of performing model-based evaluation (Drummond & Niv, 2020). By leaning on the dual-process theory's computational model, it posits that both the model-based and model-free systems aim to optimize rewards but exhibit distinct operational advantages. Specifically, while the model-free system is quick in its responses, it struggles with flexibility when faced with new situations. In contrast, the model-based system adeptly adapts its instrumental knowledge but takes a more measured pace in decision-making. This dichotomy ensures an optimal balance between reaction time and decision accuracy, a balance that is crucial across various cognitive tasks. The brain continuously evaluates the reliability of each system. Both are rational, yet they differ in their susceptibility to situational elements that can alter decision-making. The model-based system, with its forward-planning prowess, offers a sophisticated approach to decision-making. However, it demands significant cognitive resources, often sidelining concurrent tasks. In situations demanding multitasking, the model-free reinforcement learning system takes charge, embodying habit-driven behaviors. It is worth noting that further research is necessary, as current reinforcement learning models may not fully account for the influential role of context in choosing between action and habit, and they might not explain why habits form under predictable reinforcers but not unpredictable ones (Bouton, 2021).

4.2.2.3 Instrumental Conditioning and WM. Traditional RL models may oversimplify the process of instrumental learning. A more contemporary perspective, stemming from recent research, underscores the relationship between WM and RL during instrumental learning (McDougle & Collins, 2020). It is proposed that human instrumental learning extends beyond the boundaries of learning from prediction errors, but rather encapsulates a broader spectrum of higher-level functions, such as executive functions and WM (Collins & Frank, 2012). This interplay between WM and RL is reflected by multiple brain areas, especially the prefrontal cortex, that are actively engaged in early stages of learning. Research into the coexistence of model-free and model-based systems highlight the model-based system's higher computational costs (Daw et al., 2005). Collins & Frank (2012) demonstrates that higher-level processes,

particularly capacity-limited WM with decay, play a vital role in simple learning tasks that are traditionally examined using model-free RL algorithms. They designed a new model to represent contributions of both the RL–Basal Ganglia system and the WM–prefrontal cortex system. Even when adjusting traditional algorithms, they do not fit the data as well as the proposed hybrid model. Additionally, individual differences in learning were identified, linked to genetic variance in the prefrontal and striatal mechanisms. The study found that WM’s capacity and stability distinctly influenced learning behavior, with learning being slower under greater load but achieving similar final performance levels. The impact of delay on performance, although pronounced early on, diminished over the course of learning.

It is especially important to be aware of this issue when RL models are applied for the analysis of neuroscientific findings (Collins & Frank, 2012). While RL is a robust model for specific learning behaviors, especially in controlled settings, human learning encompasses more than just stimulus-response-reward dynamics. Psychological models aiming to provide a comprehensive understanding of human behavior should incorporate other cognitive processes, like WM, attention, and emotions. NF offers a compelling example of the complexities involved in human learning. Although it can be tempting to view NF through the RL lens (see Lubianiker et al., 2022), doing so might oversimplify the process. One of the significant challenges in generalizing RL models to rt-fMRI NF learning is accounting for non-responders. Factors like motivation, emotional state, or attention can play a significant role in learning (Sitaram et al., 2016). If an individual is not motivated, even the most optimized RL-based reward might not lead to the desired outcome. While RL often conceptualizes reward in a broad sense, humans might have deeply personal and individualized notions of what constitutes a reward (Peters & Büchel, 2010). Cultural, social, and individual factors can all influence this perception. Furthermore, do positive and negative feedback operate differently in the brain, affecting feelings, motivation, and learning outcomes (Klöbl et al., 2020).

4.2.3 Neural Underpinnings of Associative Learning

Hebbian neural plasticity is suggested to be the foundation of associative learning (Sitaram et al., 2017). The concurrent or rapid consecutive activation of two synaptically joined neurons modifies the strength of the synapses binding them (Hebb, 1949). Long-term potentiation (LTP) and long-term depression (LTD) of excitatory synaptic transmission are a

basic form of synaptic plasticity. LTP occurs when a brief, high-frequency train of stimuli to a synapse causes a long-lasting increase in the amplitude of the excitatory postsynaptic potentials (EPSPs) in the postsynaptic neuron (Bliss & Lømo, 1973; Glanzman, 2010). They can be expressed at every excitatory synapse in the brain (Malenka & Bear, 2004). LTP and LTD facilitate the bidirectional adjustment of synaptic strength based on activity, positioning them as potential foundational elements for the synaptic understanding of learning and memory. Recent studies on the neurobiological correlates of learning have focused on a form of LTP called spike timing-dependent plasticity STDP. STDP is a type of synaptic plasticity that is thought to be a mechanism for learning and memory in the brain (Khacef et al., 2022). It is based on the idea that the timing of spikes between pre- and postsynaptic neurons can modify the strength of the synapse between them (Wilmes et al., 2017). Specifically, if the presynaptic neuron fires just before the postsynaptic neuron, the synapse is strengthened, while if the postsynaptic neuron fires just before the presynaptic neuron, the synapse is weakened (Wilmes et al., 2017).

NF strengthens a neural pattern that aligns with the arrival of feedback, suggesting the involvement of Hebbian plasticity in rt-fMRI NF learning (Sitaram et al., 2017). Applying STDP to learning voluntary control over one's brain activity suggests that when a desired pattern of brain activity is achieved by the individual, the timing of the neuronal spikes associated with that pattern can influence the synaptic connections between neurons. If the desired pattern is consistently followed by positive feedback or reinforcement, it can lead to strengthening of the synaptic connections associated with that pattern. This strengthening of synaptic connections can facilitate the individual's ability to reproduce the desired brain activity in subsequent trials. Conversely, if the individual fails to achieve the desired pattern or receives negative feedback, the timing of the neuronal spikes associated with that pattern can lead to weakening of the synaptic connections. This weakening of synaptic connections encourages the individual to adjust their brain activity to try to achieve the desired pattern in future attempts. Therefore, STDP provides a theoretical framework for understanding how learning occurs in rt-fMRI NF. By associating the timing of neuronal spikes with positive or negative feedback, the synaptic connections in the brain can be modified, leading to the acquisition and refinement of the desired brain activity patterns.

4.2.4.1 STDP and Feedback Contingency. The significance of timing in neuronal spikes in relation to positive or negative feedback, has been underlined in the previous section. Another key concept emerging from this is the ideal temporal contiguity in rt-fMRI NF. Temporal contiguity describes the time interval from the emergence of neural activity to the moment feedback is provided regarding that activity (Sulzer et al., 2013). Rt-fMRI being an emerging methodology, there is still debate over the optimal feedback processing (Sherlin et al., 2011; Sulzer et al., 2013). The timing of feedback, or feedback latency, determines the reinforcement schedule, which should have a notable impact on the results of instrumental conditioning. In the rt-fMRI NF setting, there is an intrinsic delay due to the delay between neural activity and the measurable BOLD signal (Oblak et al., 2017). Additional to this is the delay in acquisition and computation of the feedback signal. A pilot study by Johnson et al. (2010) with an imagery-based learning strategy showed participants generating a greater activation in the ROI when given intermittent feedback compared to continuous feedback. In a study on self-regulation efficacy, Hellrung et al. (2018) investigated the effects of either continuous or intermittent feedback on brain activity in the amygdala. Participants received instructions to engage in mental imagery centered on positive memories and feelings. Their findings indicated that intermittent feedback enhances regulation performance in contrast to the continuous feedback approach. Conversely, Emmert et al. (2017) focused on regulation performance in participants who did not receive a specific strategy instruction. Through their analysis, continuous feedback was shown to have a higher efficacy compared to intermittent feedback, especially when observed across multiple sessions. This divergence in findings highlights that the optimal feedback delay in rt-fMRI NF research remains unresolved.

A possible explanation for the advantages of intermittent feedback is the high cognitive load in continuous feedback. Attention must be divided between monitoring the feedback and applying a regulatory strategy to control brain activity. Additionally, the intrinsic delay in the hemodynamic response results in a postponed feedback delivery. As a result, participants are required to link feedback to mental events from a few seconds prior, all while processing the feedback and continuing to participate in the experimental setup (Hellrung et al., 2018). WM is tasked with retaining, reconciling, and acting upon multiple streams of data at a predictable but relentless pace. Intermittent feedback might be beneficial to WM as it offers moments of lesser

cognitive strain. Given the principles of STDP, the variability resulting from intermittent feedback can result in a broader spectrum of spike-timing intervals, thereby potentiating synapses corresponding to successful actions. STDP can capitalize on this variability to potentiate synapses that correspond to successful actions, regardless of whether the feedback arrives earlier or later than expected due to latency (Legenstein et al., 2008). With continuous feedback, the tight and constant coupling between actions and immediate feedback could potentially lead to a narrower range of spike-timing intervals. This could limit the range of STDP-induced synaptic changes, as the consistent timing might result in more synchronized spikes that follow a similar pattern, limiting the impact of STDP in adjusting synaptic weights. Therefore, intermittent feedback presentation could facilitate a broader exploration of spike-timing intervals, potentially leading to more diverse STDP-induced changes in synaptic strengths. This greater diversity may contribute to a more flexible learning process and, consequently, better regulation performance.

4.2.4.2 Basal Ganglia. Recent studies have shed light on the basal ganglia and their role in learning. Emmert, Kopel et al. (2016) found that during rt-fMRI NF, the basal ganglia are consistently active. The basal ganglia, made up of subcortical nuclei like the striatum, connect significantly with the cortex, thalamus, and limbic system (Seger, 2006; Yahya, 2020). They process extensive inputs from the cortex and thalamus, orchestrating outputs through three major pathways. Historically, the basal ganglia have been associated with motor functions (Foerde & Shohamy, 2011). However, recent insights highlight the striatum's role in various types of learning. Yahya (2020) in their extensive review, pinpointed the striatum's involvement in all conditional learning processes needing abstraction of associations. The striatum itself is divided into two primary sections in humans: the ventral and dorsal striatum, each with its unique set of functions and subregions (Ferré et al., 2010). Particularly, the dorsal striatum, comprising regions like the dorsomedial that oversees goal-directed actions and the dorsolateral which handles habitual, stimulus-driven actions, seems vital for learning instrumental actions (Peak et al., 2018; Yahya, 2020). Studies have proposed network models to understand the striatum's complex connections in the brain (Seger, 2006; Ikemoto et al., 2015; Eisinger et al. 2019) Specifically the dorsal striatum's associative region highlighted in these network models appears critical in

forming action-outcome associations, underpinning its importance in the instrumental action-outcome association domain (Balleine et al., 2007).

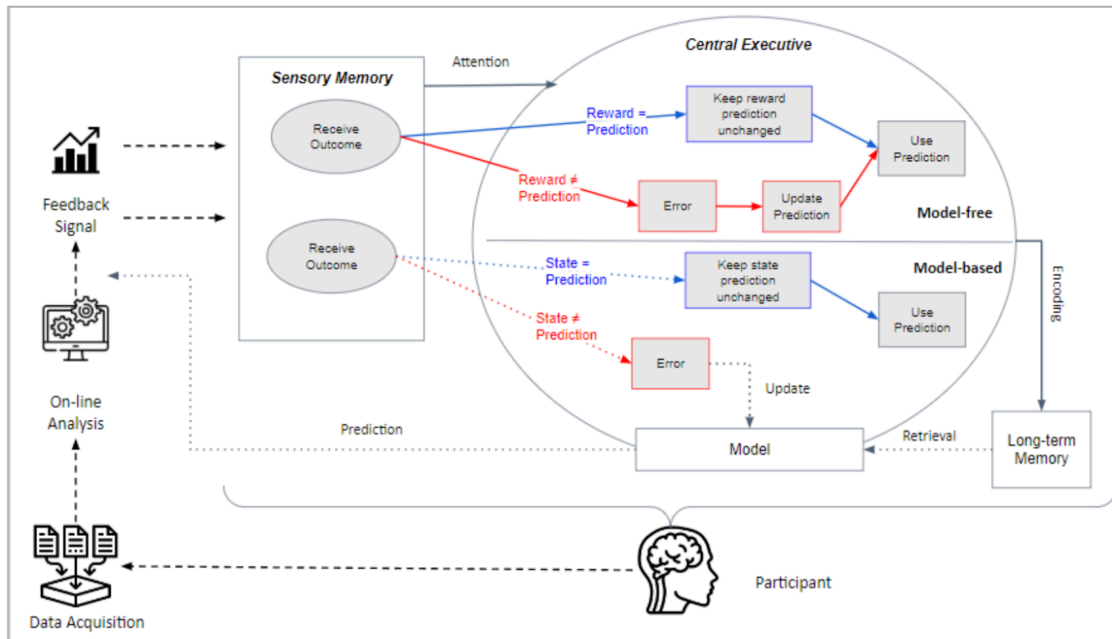
Considering this, the findings from Emmert, Kopel et al. (2016) of consistent basal ganglia activation over multiple rt-fMRI NF studies align with the basal ganglia's recognized involvement in cognitive processes, particularly instrumental learning. Therefore, when considering rt-fMRI NF, it becomes evident that the basal ganglia's activation signifies its pivotal role in learning and adjusting behaviors based on real-time feedback.

4.2.4.3 Dopamine. Dopamine's involvement in associative learning has been recognized for quite some time (Sutton & Barto, 1981). A critical component of this understanding centers around the notion of three-factor learning, which suggests that synaptic transmission gets strengthened particularly in neurons that simultaneously receive an environmental event's input and a dopaminergic input aligned with the reward prediction error (Legenstein et al., 2008). In instrumental conditioning, dopaminergic projections to the striatum can modify behavior in response to salient stimuli and contingent feedback. Dopamine release originating from the substantia nigra and ventral tegmental area, along dopaminergic pathways connecting the basal ganglia to cortical and subcortical regions, establishes associations between cues and responses (Haber, 2014). The phasic response of dopamine to an unexpected reward or better-than-expected reward seems to represent the prediction error on a neural level (Schultz, 2016). While the relationship between dopamine activity and reward remains complex, evidence suggests that phasic activity of dopamine is involved in signaling the value of rewards and driving reinforcement learning (Glimcher, 2011). Dopamine neurons exhibit changes in firing in response to unexpected rewards or reward-predictive cues, indicating their connection to the subjective value of rewards. Conversely, dopaminergic neuron firing is suppressed when expected rewards are omitted or worse than expected. As a cue reliably predicts a reward, dopamine neuron firing gradually diminishes in response to the reward and becomes more focused on the cue itself.

4.2.3 Associative Learning, WM and rt-fMRI NF

The underlying principle of self-regulation in rt-fMRI can be mapped onto the associative learning principles and the interplay between model-free and model-based

instrumental learning (Figure 8). The fundamental functional requirements crucial for effective NF learning are congruent with the fundamental components of instrumental conditioning (Caria et al., 2011; Sulzer et al., 2013; Sitaram et al., 2016). Individuals are given real-time feedback about their brain activity, allowing them to modulate or regulate certain patterns. Feedback displaying successful regulation of the ROI acts as a positive reinforcer. When individuals first begin NF training using rt-fMRI, they often rely on a trial-and-error approach (Stoeckel et al., 2014). They might not have a clear understanding or model of how their mental strategies will influence brain activity. As they receive feedback, mental strategies that produce the desired brain patterns are reinforced. Over time, these behaviors become habitual, rooted in the model-free system. An individual might not consciously consider the "why" or the mechanics; they just react based on past success. This automatic, habit-driven behavior can be likened to the role of the dorsolateral striatum, which reinforces actions that have historically led to rewarding outcomes (Daw et al., 2005). Indeed, meta-analysis of rt-fMRI showed consistent activity in the striatum during self-regulation of brain activity across studies (Emmert et al., 2016). As individuals gain more experience and understanding of how their cognitive strategies influence brain activity, they can start to anticipate the outcomes of their mental actions. They develop an internal model of the cause-and-effect relationship between cognitive strategy and brain feedback (Oblak et al., 2017). This is the realm of model-based reinforcement learning. When engaging in a NF session, they might actively employ strategies that have proven successful in the past (Klöbl et al., 2020). This conscious, forward-thinking strategy aligns with the functions of the prefrontal cortex, which is responsible for more deliberate, goal-oriented behaviors. Meta-analysis on rt-fMRI highlighted the role of the prefrontal cortex in rt-fMRI NF self-regulation (Emmert et al., 2016). A participant might start with a model-free approach, reinforcing strategies based on immediate feedback. But as they become more practiced and familiar, they may transition to a model-based approach, utilizing a mental model of the expected outcomes of their strategies. However, self-regulation via rt-fMRI is not just about choosing one system over the other. For optimal outcomes, a balance might be necessary. Relying solely on habitual reactions might lead to rigidity and lack of adaptability when faced with new or

Figure 8*Model-Free and Model-Based Instrumental Learning in rt-fMRI*

Note. This figure shows an illustrative representation of the closed-loop real-time functional magnetic resonance imaging neurofeedback (rt-fMRI NF) system and how it integrates with both model-free and model-based reinforcement learning within a participant's working memory. The closed-loop structure of the rt-fMRI NF system emphasizes the continual cycle of feedback based on brain activity. As this feedback signal is processed, it first enters the sensory memory, and with focused attention, progresses into the central executive. Within the central executive, the model-free reinforcement learning process is depicted. When the received reward from the feedback signal matches the predicted reward, the established reward prediction is utilized. If there is a mismatch, indicating a reward prediction error, this discrepancy leads to an update in the reward prediction. In the bottom part of the central executive the model-based reinforcement learning is detailed. Here, the emphasis is on the state prediction. If the actual state aligns with the predicted state, the model remains unaltered. In contrast, when the observed state deviates from the prediction, this signals a need to update the internal model, adapting to the new information.

changing feedback. Conversely, overthinking every action (model-based) can slow down the decision-making process and make it hard to react promptly to real-time feedback. Further studies are needed to delve deeper into this interplay and its implications for rt-fMRI self-regulation, ensuring a comprehensive understanding and more refined techniques in the future. Given the assumption that newly trained participants or those struggling with rt-fMRI NF rely on model-free learning, while more adept participants utilize model-based learning, future

studies could explore if this difference is reflected on a neural level, as is with the different corticostriatal circuits involved in model-free and model-based learning.

5. Factors Affecting rt-fMRI NF Learning Success

After laying the groundwork on the significance of WM and instrumental conditioning in the realm of rt-fMRI NF, it becomes crucial to explore other elements that interplay in determining the success of brain self-regulation. The rt-fMRI NF effectiveness is influenced by a range of factors. These include the individual's psychological characteristics, their natural physiological makeup, and the detailed elements found within the training protocol (Friedrich, 2014). Previous studies have explored these areas, enhancing the knowledge of their overall impact. Studies have highlighted the importance of psychological elements, especially focus and prolonged attention, in determining NF outcomes (Kadosh & Staunton, 2019). This chapter delves into these psychological aspects and later sections explore the details of training protocols and physiological influences, providing a clearer understanding of what shapes rt-fMRI learning success.

5.1 Psychological Factors

Among the many factors potentially influencing rt-fMRI NF learning success, psychological factors stand out as particularly compelling. Kadosh and Staunton's (2019) comprehensive review centers around the psychological underpinnings that shape NF learning outcomes. Their findings underscore the role of focus and sustained attention as cornerstones of NF efficacy. Furthermore, aspects such as emotional susceptibility, individual personality traits and even an individual's coping strategies come into play. This chapter will delve into findings on psychological factors influencing successful self-regulation, weaving together recent discoveries to provide a holistic picture of their role in mastering self-regulation via rt-fMRI.

5.1.1 Attention

Attention is likely to be an important psychological factor influencing rt-fMRI NF learning success. Attention was found to have the most consistent positive influence on learning and performance in NF across EEG and BCI studies (Kadosh & Staunton, 2019) and researchers suggest it has an equally important role in rt-fMRI NF learning success (Haugg et al., 2021). However, an empirical validation of these suggestions is still needed. One study in the field of

rt-fMRI NF identified a significant overlap between brain regions involved in rt-fMRI NF and the task-positive network (TPN), a set of regions activated during tasks requiring attention modulation (Chiew et al., 2012). This suggests that the expression of the TPN is positively correlated with successful NF, indicating that subject engagement in NF training is linked to attentional processes. Their results further indicated that TPN expression serves as a robust marker for NF performance, explaining a substantial portion of the performance variance, especially in right hemisphere trials. However, while this attentional effect is evident in right hemisphere trials, it does not fully explain the behavior of all good responders in left hemisphere trials, indicating the presence of other factors influencing performance.

Attention lacks a uniform definition but can be broadly categorized into two key roles in human cognition and WM: a resource and a selection mechanism (Oberauer, 2019). The resource perspective implies that attention's limited capacity must be distributed across tasks based on their demands. The more focused the attention, the better the task's efficiency. WM capacity mirrors this constrained attentional resource. Evidence largely supports the notion that attentional resources are used both for storing and processing information (Cowan et al., 2005). Translating this to rt-fMRI NF, adept allocation of attention can lead to superior self-regulation of brain activity, fostering more efficient learning. Distractions or conflicting attentional demands can potentially hinder this learning curve. Optimizing the balance of attention could enhance NF interventions. It is worth noting that some theories define attention not as a resource but a selection tool (Oberauer, 2019). In this view, attention does not determine WM's limits. Instead, WM represents a type of attention concentrated on memory representations. This means that when WM is used, a specific memory representation is chosen from a wider range of representation.

In instrumental learning, the transition of actions to habits relies heavily on the predictability of outcomes and the attention allocated to behaviors (Bouton, 2021). As behaviors become well-practiced and outcomes are consistently anticipated, the attention they command diminishes, rendering them habitual. Two predominant theories offer insights into this process. Pearce and Hall (1980) suggest that as outcomes become more predictable, attention to the associated behavior wanes. In contrast, Mackintosh (1975) postulates that attention intensifies

towards the most reliable predictor of an outcome. In the context of rt-fMRI NF, the self-regulation of brain activity can be likened to the formation of habits based on the predictability of outcomes and attention allocation. As participants become more practiced in modulating their brain activity and the feedback from the rt-fMRI becomes consistent and predictable, the cognitive effort or attention they devote to the self-regulation task might decrease. This parallels the Pearce-Hall theory: as the outcomes become more predictable through consistent feedback, the participant's attention to the self-regulation process wanes, making the act of modulation more habitual and potentially more efficient. On the other hand, drawing from Mackintosh's theory, if the feedback from the rt-fMRI is perceived as the most reliable predictor of successful brain activity modulation, then participants might intensify their attention towards it. This could mean that in sessions where the feedback is particularly salient or presented as the primary cue for success, participants may be more engaged and attentive, ensuring that the self-regulation remains goal-directed rather than habitual. Thus, in NF sessions, the balance between predictability and attention is crucial. If the goal is to make brain activity self-regulation more innate or habitual for the participant, then consistent and predictable feedback might be beneficial. However, if the aim is to keep the participant actively engaged in the process, ensuring that the feedback remains the primary and most reliable predictor of success could be more effective. Further studies aimed at understanding and leveraging the principles of attention and outcome predictability, as seen in habit formation theories, could be important in optimizing the effectiveness of rt-fMRI NF sessions and ensuring successful self-regulation of brain activity.

5.1.2 Consciousness

While basic associations can be unconsciously learned (Scott et al., 2018), it is debated whether complex forms of learning, such as instrumental conditioning, can occur without consciousness. Skora et al. (2021) demonstrate an absence of unconscious instrumental conditioning in both trace and delay conditioning experiments, underscoring the potential necessity of consciousness in adaptive behavior. Considering that rt-fMRI NF is thought to operate primarily through instrumental conditioning, these results raise important questions about the role of consciousness in the mechanisms underlying rt-fMRI NF learning. Before delving deeper into the implications of these findings for rt-fMRI NF, it is essential to establish

an understanding of consciousness and examine contemporary theories that shape our perspective on this crucial cognitive phenomenon.

Defining consciousness is challenging due to its subjective nature. Two prevailing theories address this. The *global neuronal workspace* theory posits that consciousness emerges when sensory data is broadcast across cognitive systems, facilitated by networks in the frontal and parietal lobes (Baars, 1993). The WM's limited capacity constrains our momentary consciousness (Koch, 2018). The *integrated information theory* argues that consciousness emerges in interconnected systems capable of encoding causal relationships (Tononi et al., 2016). It introduces a measure, Φ , quantifying consciousness based on system complexity. A higher Φ indicates greater consciousness. The human brain, due to its intricate connectivity, exhibits a high Φ , denoting significant consciousness. It is unclear whether consciousness and awareness are neurologically distinct. For the purpose of this thesis, consciousness and awareness are defined as conscious recognition, rendering it reportable and actionable (Block, 2007). In the rt-fMRI NF context, this awareness is essential for understanding and interpreting feedback about one's brain activity. Muñoz-Moldes and Cleeremans (2020) introduced a detailed taxonomy to categorize NF paradigms, placing particular emphasis on the role of awareness in the learning process. They define awareness as being conscious of something. Their taxonomy breaks down NF paradigms into three key dimensions: control awareness, NF awareness, and strategy awareness. Within these dimensions, they identify specific paradigms such as the *active overt cued tasks*, where participants are both aware of their control influence and are guided on NF strategies. In contrast, *active overt uncued tasks* allow participants to control feedback without knowledge of possible effective strategies, having them rely on personal strategies. In *active covert tasks* participants are aware of their active control and the presence of a feedback signal from the brain, but they remain unaware of specific strategies and unaware of the fact they receive NF. Participants are not asked to actively control, or influence brain activity and they are not aware that the feedback signal from the brain is guided by themselves. Lastly, *passive covert tasks* place participants in a position where they lack insight into the feedback dynamics and do not have any strategies. According to this taxonomy, most NF tasks can be classified as *active overt cued tasks*. Within these tasks, participants predominantly show an ability to actively modulate their brain activity, although there are always some individuals, the non-responders,

who do not exhibit this capability. Furthermore, participants in *active overt uncued tasks* can learn voluntary self-regulation without being provided an explicit strategy (Marxen et al., 2016; Sepúlveda et al., 2016; Sitaram et al., 2016). This raises the questions about the necessity of such strategies, with some researchers suggesting that providing a strategy might be superfluous (Ramot et al., 2016), or even counterproductive (Sepúlveda et al., 2016). The role of providing mental strategies will be discussed at a later point in this thesis.

Studies using *active covert tasks* indicate that rt-fMRI-based NF can succeed even without awareness of the connection between rewards and brain activities. Participants, without being aware or intentionally trying, managed to show a correlation between trained network modulations during rt-fMRI NF and subsequent changes in resting-state connectivity (Ramot et al., 2016; Ramot et al., 2017; Taschereau-Dumouchel et al., 2018). One study even showed changed brain reactions related to a cue in the early visual areas of the brain using a passive covert task (Amano et al., 2016). Further research into the role of awareness in NF hinted at a relationship between being self-aware of one's brain activity and being confident in that self-awareness, which can be seen as a form of metacognition in the realm of NF (Stirner et al., 2022). This research aimed to compare participants' subjective estimations about their brain activity with the actual recorded activity. Despite anticipating that participants would improve both in terms of regulating their brain activity and estimating it, the study did not confirm these predictions. Nevertheless, it showed a correlation between participants' subjective estimations and their actual activity in the ROI. Moreover, when participants were precise in their estimations, they displayed heightened confidence, suggesting a potential metacognitive element in rt-fMRI NF. A need for more comprehensive studies remains, particularly those that compare NF outcomes across diverse settings such as varying control awareness, NF awareness, and strategy awareness.

5.1.2.1 Neural Underpinnings: The Anterior Insular Cortex. Evidence from neuroimaging suggests that the anterior insular cortex (AIC) plays a crucial role in human awareness (Craig, 2009). The AIC separates the temporal lobe from the parietal and frontal lobes (Namkung et al., 2018). AIC activation seems to explicitly reflect awareness of interoceptive information (Critchley et al., 2004). Further studies also highlight the AIC's role for attributing actions to oneself (Farrer & Frith, 2002). One fMRI study showed that the AIC is part of a

functionally connected cognitive control network that is active when instructions or goals in a task are being converted to stimulus–response associations for proper task performance (Cole & Schneider, 2007). In a meta-analysis aimed at identifying regions involved in NF regulation, Emmert, Kopel et al. (2016), showed activation of the AIC which hints at the involvement of interoceptive cognition and self-awareness in NF regulation. The activation of the AIC in rt-fMRI NF studies may reflect several cognitive processes and functions. Various studies across different fields have consistently associated the AIC with a wide range of functions, including attention, intentions, awareness of sensations and movements, perception of visual and auditory stimuli, perception of the self-image, reliability of sensory images and subjective expectation (see Craig, 2009 for a review). Some rt-fMRI NF study with a *passive covert task* reports success in achieving the NF effect (e.g., Ramot et al., 2016). The effect was achieved, even without participants having a goal for the task. This suggests that AIC activation in rt-fMRI may be related to implicit processes involved in awareness, independent of explicit knowledge or conscious intention. The exact mechanisms through which the AIC remains active in the absence of conscious awareness are not fully understood and require further investigation.

5.1.3 Motivation

Motivation appears to play a crucial role in the self-regulation of brain activity during NF training (Kadosh & Staunton, 2019). Several studies highlight that patients with more severe symptoms show enhanced down-regulation capacities (Nicholson et al., 2016; see Weber et al., 2020 for a review on predictors of improvement in clinical symptoms in NF), possibly due to a heightened motivation to alleviate these symptoms. This notion is further supported by the observation that patients frequently participate in NF training with an aspiration to reduce clinical symptoms, whereas healthy participants often do so primarily out of general interest or for monetary gains (Haugg et al., 2021). This differential motivation is evident as patients consistently demonstrate higher ratios of successful NF runs compared to healthy participants (Skouras & Scharnowski, 2019). The superior performance observed in patients might be ascribed to stronger connectivity in specific brain regions, such as the default mode network, rendering them more receptive to NF interventions (Bassett & Khambhati, 2017). Moreover, dysfunctional brain patterns inherent in the patient populations could render them more adaptable to change, reducing the likelihood of reaching a performance ceiling. However, it is important to

note that NF performance might vary substantially across patient demographics, given that specific cognitive deficits could impact attention and, by extension, NF performance (Heeren et al., 2014). Instrumental learning offers insights that underscore the significance of motivation in learning dynamics (Lehner et al., 2017). If instrumental learning and WM fundamentally underpin the learning mechanisms of rt-fMRI, the role of motivation becomes even more evident. In a study investigating the impact of motivation on goal-directed behavioral adjustments during feedback-based learning, participants performed better in the loss condition than in the gain condition and worst in the neutral condition (Unger, 2013). This is in line with findings that show faster learning in rt-fMRI NF when positive punishment in the form of a negative NF signal is delivered to participants (Klöbl et al., 2020). Participants who were incentivized with monetary rewards displayed a heightened ability to self-regulate during rt-fMRI training in contrast to those who were not (Sepúlveda et al., 2016). Furthermore, rt-fMRI NF studies show that monetary rewards show an increase in participants' ability to self-regulate (Sepúlveda et al., 2016). This is akin to findings from instrumental conditioning studies which show higher response rates for behavior reinforced with more preferred items (Lee et al., 2010). This indicates that error avoidance and appetitive reward represent important motivational factors that could potentially enhance NF learning.

5.1.4 Personality and Emotion

Personality refers to an individual's patterns of thoughts, feelings, and behaviors (Revelle & Scherer, 2017), often encapsulated in traits like the *big five* (openness, conscientiousness, extraversion, agreeableness, and neuroticism; Costa and McCrae, 1992). Emotion, on the other hand, signifies shorter-lived feelings, reactions, or states that may be elicited by various stimuli (Revelle & Scherer, 2017). Although distinct, the two are intricately connected, with personality traits often influencing how an individual may react emotionally in certain scenarios. One study found that people with higher psychopathic traits had a reduced ability to control the insula (Sitaram et al., 2014). Another study revealed no association between intelligence and the capacity for brain activity self-regulation or NF treatment success (Karch et al., 2019). Challenges arose in modulating the nucleus accumbens for individuals with lower drive traits and monetary incentive task performance (Li et al., 2018). Participants with active pain coping strategies were more adept at using NF, resulting in reduced pain perceptions compared to those

less inclined towards active coping (Emmert et al., 2016). Such findings underscore the significance of evaluating cognitive and personality traits before starting NF. This ensures that the intervention is tailored for those who will most benefit from it. A pioneering study on emotion in rt-fMRI NF by Marxen et al. (2016) focused on using rt-fMRI NF to enable subjects to regulate the BOLD signal from their bilateral amygdala. Subjects effectively used NF to regulate their amygdala activity without being provided with a specific strategy, even in a post-training transfer run without feedback. The study found that higher levels of agreeableness were negatively correlated with regulation capacity in post-training runs without feedback. However, in another study by Scharnowski et al. (2015) potential links between mood, spatial orientation, creative imagination, and the ability to regulate brain activity were investigated but found no associations. A related study by Zotev et al. (2011) highlighted that those individuals more susceptible to anger had reduced BOLD activation in the left amygdala during training. This points to the idea that heightened emotional states, like anger, might hinder the process of learning self-regulation in rt-fMRI. Furthermore, those with traits like empathy, which involve high susceptibility or sensitivity to emotions, might find it challenging to regulate imagined emotions. The ability to recognize and label one's emotions was also shown to influence self-regulation capacities. Marxen et al. (2016) found no correlation between amygdala regulation and scores on the *difficulty identifying feelings* scale (Bagby, et al., 1994), while Zotev et al. (2011) observed that those who could better identify their feelings achieved superior regulation. This discrepancy might relate to the strategies employed during training; some strategies might demand more accurate emotion identification than others. Individual differences, both in terms of stable personality traits and emotional states, can shape how subjects engage with, respond to, and benefit from NF training. A study by Koush et al. (2017) examined control in brain networks related to emotion regulation. They found that participants who reported higher levels of anxiety prior to the study had difficulty successfully regulating their emotions. Specifically, those with higher anxiety showed less activity in the dorsomedial prefrontal cortex. This suggests that while factors like anxiety can influence success in regulating brain activity, other factors like mood may not be as impactful.

5.2 Aspects of the Training Protocol

The realm of rt-fMRI NF has seen significant advancements in the attention to the nuances of the training protocol itself. Differences in NF performance between subjects can be attributed not just to individual motivation but also to the intricacies of the experimental design. Often, clinical studies benefit from rigorous pilot studies on healthy participants, optimizing the training protocol and laying the groundwork for successful patient studies (Fede et al., 2020). To further understand the implications of these findings, subsequent sections will dissect specific factors intrinsic to the training protocol, offering insights into the optimized design of NF interventions and its promising role in clinical applications.

5.2.1 Feedback and Reward

The relationship between feedback and reward in the realm of rt-fMRI NF is pivotal for enhancing brain self-regulation, forming a cornerstone of current research aimed at optimizing this NF method. Most rt-fMRI NF studies employ activity meters, continuous lines, or graphs to convey feedback to participants (Sulzer et al., 2013). However, there have been attempts to explore alternative feedback displays (Fede et al., 2020). Studies comparing approaches to displaying NF indicated that social feedback is more effective than standard feedback (Mathiak et al., 2015). Furthermore, monetary incentives appear to play a role in learned self-regulation (Bray et al., 2007). Participants who were incentivized with monetary rewards displayed a heightened ability to self-regulate during rt-fMRI training in contrast to those who were not (Sepúlveda et al., 2016). This phenomenon could potentially be attributed to the amplification of the desired neural response, similar to prior instrumental learning observations which highlighted the augmentation of desired behaviors through increased reinforcement (Maia, 2009). In line with this, instrumental learning research has underlined the roles of both social and monetary rewards. Interestingly, while monetary, food, and social rewards seem to modulate instrumental behavior with similar intensity (Lehner et al., 2017), they each pass distinct neural pathways, governed by dedicated neural circuits (Clithero & Rangel, 2013). One plausible deduction from these findings is the superior ecological validity of social and monetary feedback in contrast to conventional visual representations like lines or graphs.

Furthermore, the modality of feedback, especially the auditory versus visual debate, has been another area of interest. Research has posited that auditory feedback through tone variations

or verbal inputs from an experimenter could potentially be more impactful than visual feedback (Harmelech et al., 2013). In fact, individuals have reported auditory feedback to be less intrusive to their mental strategies. This claim was further supported when it was observed that combining both visual and auditory feedback seemed to be inferior to solely auditory feedback. Concurrent presentation of multiple feedback signals diminishes neural response regulation (Hartwell et al., 2013). The ineffectiveness of simultaneous conditioning can be explained by findings from studies on WM, which demonstrate impaired WM capacity when attending to multiple stimuli simultaneously (Klink et al., 2014). WM capacity is akin to a limited reservoir of attentional resources. When individuals are confronted with multiple feedback signals at once, this finite capacity is divided, thereby reducing the focus and attention dedicated to any single feedback stream. Consequently, the complexity of each feedback may be overlooked or insufficiently processed, leading to a decline in the strength and precision of self-regulation. Understanding these dynamics will be crucial to harnessing the full potential of rt-fMRI NF.

5.2.2 Pre-Training

An important element impacting NF performance is the inclusion of a pre-training no-feedback run (Haugg et al., 2021). Studies incorporating this feature reported notably higher success rates in their NF sessions. This initial run, done prior to actual training, requires participants to modulate their brain signals without receiving any performance feedback. Such runs are beneficial in multiple ways: they help participants get accustomed to the NF paradigm and the scanning setup and act as a baseline for evaluating subsequent training and transfer runs. The familiarization and additional practice opportunity afforded by these runs can significantly enhance participants' performance during actual training. Additionally, they provide a baseline for comparison with subsequent NF training and transfer runs. The potential advantage of pre-training no-feedback runs is attributed to participants' enhanced familiarity with the NF setup and a supplementary opportunity to practice brain regulation strategies, ultimately facilitating improved performance.

5.2.3 Providing a Mental Strategy

Most studies provide participants with at least a general mental strategy to modulate the BOLD signal in addition to contingent feedback (Thibault et al., 2018). However, there is evidence that providing a strategy might not be necessary (Ramot et al., 2016), or even

counterproductive (Sepúlveda et al., 2016). Some researchers believe that simply relying on instrumental conditioning is enough for effective NF training, arguing that offering explicit mental strategies might impede the learning process (Sepulveda et al., 2016; further discussed in Sitaram et al., 2017). Interestingly, even without giving specific instructions, participants have reported employing their own mental strategies. This suggests that participants who are motivated either intrinsically or through external rewards, might come up with their own techniques to achieve control over their brain signals. A critical takeaway revolves around the potentially diminished role of conscious involvement in such training. While conscious mental imagery might assist, it could also inadvertently obstruct the organic, potentially more efficient, mechanisms of brain control. This mirrors the interplay of model-free and model-based behavior systems (Daw et al. 2005; Dickinson, 2012). Both aim to optimize rewards but have distinct operational advantages and susceptibilities (Drummond & Niv, 2020). A key advantage of organic mechanisms is bypassing the potential for overthinking or over-analyzing a situation. Conscious strategies can consume cognitive resources, especially if they are complex. Relying on organic mechanisms can reduce this load in the WM, allowing the brain to allocate resources elsewhere. By not providing a specific strategy, participants might naturally tap into the brain's innate capacity to recognize and reinforce patterns that lead to positive feedback. However, it is crucial to understand that this does not negate the value of conscious strategies. In some contexts, particularly novel ones or those that demand complex problem-solving, a well-devised strategy can be beneficial (Scharnowski et al., 2015). Further research could aim at discerning when to allow organic mechanisms to lead and when to employ conscious strategies.

5.3 Physiological Factors

Additional to the psychological factors and factors of the training protocol are physiological correlates, a promising candidate for understanding learning self-regulation. A previous meta-analysis examining NF studies aimed to determine if the initial activation levels in the ROI could serve as a dependable predictor of their future learning success (Haugg et al., 2020). However, this analysis did not find a consistent predictor for the effectiveness of NF, suggesting the necessity to explore more reliable alternative indicators for gauging NF learning outcomes. In an earlier rt-fMRI NF study, Scheinost et al. (2014) revealed that resting-state fMRI can predict response to training by correlating changes in anxiety control with pre-intervention

brain connectivity in the anterior prefrontal cortex. However, one limitation of this finding is the small sample size. Ninaus et al. (2013) demonstrate in their study using fMRI that a frontoparietal and cingulo-opercular network is involved in cognitive control. A subsequent meta-analysis by Emmert, Kopel et al. (2016) of various rt-fMRI NF studies supported this finding. They revealed a distinct regulation network that prominently encompasses several critical brain regions such as the anterior insula, basal ganglia, temporo-parietal area, anterior cingulate cortex, the dorsolateral prefrontal cortex, ventrolateral prefrontal cortex, and the visual association area. Among these, the anterior insula is commonly linked to interoceptive cognition and self-awareness (Critchley et al., 2004). Furthermore, the right AIC and the adjacent ventrolateral prefrontal cortex play pivotal roles in cognitive control tasks, which include motor inhibition, action updating, and reorientation by leveraging connections with the fronto-basal-ganglia. This connection might explain the observed simultaneous activation of the AIC in combination with the ventrolateral cortex and basal ganglia in some instances (Emmer, Kopel et al., 2016). In terms of learning, while the dorsomedial striatum facilitates declarative learning, the dorsoventral striatum primarily handles procedural learning (Daw et al., 2005; Balleine et al., 2007). The temporo-parietal area's activation is likely associated with integrating visual feedback, recollecting memories, and blending multisensory body-related data (Emmer, Kopel et al., 2016). Additionally, the posterior anterior cingulate cortex activation is believed to underline the motivational facets of NF, especially in the context of positive feedback rewards and the deterrence of negative feedback. Meanwhile, the dorsolateral prefrontal cortex and premotor areas are correlated with the act of imagining actions, thereby linking to the mental imagery often utilized during NF sessions. Lastly, the activation within the visual association area and temporo-occipital junction indicates a strong inclination towards visual imagery and the subsequent processing of visual feedback.

A recent study by Karch et al. (2019) investigated brain activity during the initial training session of a program for individuals trying to quit smoking. A comparison group received sham feedback. They found that participants who resumed smoking after three months had different brain activity patterns during that first session compared to those who did not relapse. Specifically, the relapse group showed more activity in dorsolateral prefrontal areas, the anterior cingulate cortex and the supplementary motor. This suggests that they might have had a harder

time controlling their cravings. Knowing these brain activity differences might help predict who will benefit most from this treatment in the short term. However, the rate of participants who managed to stay smoke-free was similar in both the real and sham feedback groups. This means there might be other factors at play in determining who successfully quits smoking, which requires further investigation. NF learning outcomes are intricately tied to a diverse array of brain regions and networks, underscoring the multifaceted nature of cognitive control and emphasizing the need for comprehensive approaches to understand and enhance rt-fMRI NF interventions.

7. Overall Summary

Contemporary learning theories in psychology offer a robust framework for comprehending self-regulation mechanisms in rt-fMRI NF. The distinction between STM and LTM elucidates the dual focus of learning models, addressing both rapid acquisition and enduring retention of self-regulation skills. This differentiation enables a comprehensive exploration of immediate learning processes and lasting transfer effects in rt-fMRI NF interventions. The WM model, a key component of STM, emerges as particularly promising for understanding learned self-regulation in rt-fMRI NF. The fundamental rt-fMRI NF loop closely aligns with the WM model, facilitating the integration of sensory input, attentional processes, and cognitive control mechanisms. Sensory information from the feedback display enters the sensory memory component of the WM model, with attention mechanisms transferring it to the WM for active maintenance and manipulation. Depending on the nature of the feedback signal, encoding may occur in the phonological loop or visuo-spatial memory. The central executive component of WM sustains attention and orchestrates cognitive control processes, enabling individuals to regulate brain activity based on the feedback signal. Moreover, the central executive can draw upon information stored in LTM to optimize self-regulation strategies.

However, applying the WM model to rt-fMRI NF presents several limitations. The complexity of the NF task and cognitive demands involved may overwhelm individuals with limited WM capacity, potentially impeding their self-regulation abilities. Moreover, individual differences in WM capacity and cognitive control abilities may influence the efficacy of NF training, emphasizing the need for personalized approaches. Interestingly, while previous research has shown impaired performance with visual interference and auditory interference in

WM tasks, it cannot fully explain the potentially more impactful auditory feedback observed in cognitive tasks like rt-fMRI NF.

Similarly, LTM models, particularly instrumental conditioning theory, provide valuable insights into how prediction errors drive adaptive behavior changes in response to feedback signals. The interplay between model-free and model-based instrumental learning principles underlies the fundamental functional requirements for effective NF learning. Participants initially rely on a trial-and-error approach, reinforcing successful mental strategies over time. This automatic, habit-driven behavior aligns with the dorsolateral striatum's role in reinforcing actions leading to rewarding outcomes. With experience, individuals develop an internal model of the cause-and-effect relationship between cognitive strategies and brain feedback, transitioning to a more deliberate, goal-oriented approach consistent with the prefrontal cortex's functions.

While psychological learning theories offer valuable insights into the mechanisms of self-regulation in rt-fMRI, their application has limitations. Firstly, these theories may oversimplify the complex cognitive processes involved in real-time NF training, potentially hindering our ability to effectively predict and optimize learning outcomes. Secondly, individual differences in cognitive abilities and psychological factors may not always be adequately accounted for, leading to variability in response to NF interventions. Additionally, the dynamic and multifaceted nature of neural responses during NF training presents challenges in fully capturing and integrating psychological constructs into predictive models of learning success. Finally, the reliance on theoretical frameworks derived from laboratory-based experiments may not fully capture the intricacies of real-world NF settings, highlighting the need for further research and refinement in this area.

In conclusion, integrating insights from psychological learning theories with neuroscientific findings enhances our understanding of self-regulation mechanisms in rt-fMRI NF. This approach informs the design of more effective interventions aimed at improving cognitive function and well-being through real-time NF training. Despite limitations, ongoing research promises to deepen our understanding and refine techniques for maximizing the potential of rt-fMRI NF in cognitive neuroscience.

8. Conclusion and Outlook

The models and research discussed in this thesis underscore the dynamic interplay between STM and LTM models, particularly focusing on WM and the principles of model-free and model-based instrumental learning in rt-fMRI NF training. While these theories offer a foundational framework for understanding self-regulation mechanisms, further research is imperative to validate and refine these concepts and to advance rt-fMRI NF techniques.

Future studies should delve deeper into the interaction between different learning mechanisms, particularly exploring how WM processes interact with LTM representations during rt-fMRI NF training. Investigating individual differences in psychological factors, such as attention, consciousness, motivation, and personality traits, could provide valuable insights into optimizing training protocols for diverse populations. Moreover, exploring if individual WM capacity parallels learning success in rt-fMRI may uncover new insights into the NF inefficacy problem and might give way for novel strategies for enhancing rt-fMRI NF effectiveness.

In conclusion, ongoing exploration and refinement of rt-fMRI NF approaches hold the promise of a more nuanced understanding of cognitive self-regulation mechanisms. By continuing to advance our understanding and techniques in this field, we can improve the practical application of rt-fMRI NF in cognitive neuroscience, ultimately leading to enhanced cognitive function and well-being for individuals across diverse populations.

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