The Anatomical Basis of the Motor Engram: An Extensive Overview of the Acquisition and Storage of Motor Implicit Memory

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Abstract

One of the many fascinating features of the brain is the ability to form motor habits, known as "motor memory". Following a revolutionary 1997 study, the topic of motor memory consolidation, or how the engram changes over time, began to garner significant attention, and the field has only grown since. The first objective of this review was providing an overarching synopsis of this topic's history, mainly the debate on whether motor memory consolidates and current gaps in knowledge. The second goal was to identify and provide evidence for one particular consolidation model, including acquisition and storage sites, believed to be the most well-supported. To conduct the research, Google Scholar was the main database utilized, and most articles before 1997 were eliminated. The first finding was the general mechanism of consolidation: similar to declarative memory, the motor engram after encoding transforms from an initially fragile state to a stronger one resistant to disruption. The second finding was related to the proposed acquisition sites, such as the cerebellum and prefrontal cortex. This paper contended for the former, as the cerebellum's significance in acquisition has been demonstrated through vestibulo-ocular reflex training and Pavlovian eye conditioning. This paper also identified studies that discuss long-term storage areas, such as the vestibular nuclei. Finally, existing issues like the complexity of the encoding mechanism, effects of sleep fragmentation, and the factor of age were addressed. This review contributes towards a more unified consolidation model to be used in various real-life applications, such as sports science.

Keywords: Implicit memory, Motor memory, Memory consolidation, Cerebellum, Prefrontal cortex, Vestibulo-ocular reflex, Pavlovian eye conditioning

1. Introduction

Procedural memory is the memory system that encodes, stores, and retrieves habits. It aids in the performances of tasks, and if the task is ingrained enough into the brain, the actions become almost automatic and do not require conscious oversight. This type of memory, also referred to as habit memory, consists of three types: motor, perceptual, and cognitive. However, this review will mainly focus on the motor aspect of procedural memory (motor memory). A 1997 study proposed that motor memories undergo a process similar to declarative memories, which is the conscious recollection of facts and events (Brashers-Krug et al., 1997). These types of memories undergo a process called consolidation, where the memories are transformed from an initially fragile state to a stable one. Many times, this process involves a change at the system level; for example, after a period of time, declarative memories no longer require the medial temporal lobe for reactivation and instead become dependent on the neocortex (Squire et al., 2015). This process of strengthening memories over time has been relatively well-established for declarative memory, but whether motor memory undergoes this process has been debated (Caithness et al., 2004). However, this initial 1997 study created an entirely new field to experiment with, shaping the current research direction. After the publication of

this study, numerous debates followed as the results were unable to be recreated; however, one study by Krakauer et. al (2005) addressed these concerns by explaining that anterograde interference may have caused these discrepancies. They argued that if anterograde effects were removed, the results from the original study could be replicated. Thus, from this point on, the notion that motor memory consolidates in a manner that is similar to declarative memory became relatively well-established. Next, the research direction shifted towards developing a consolidation model, of which there are two main points of focus: the site of acquisition and long-term storage. To uncover these two areas of interest, numerous studies have considered two types of associate motor learning, the vestibulo-ocular reflex and Pavlovian eyelid conditioning (Krakauer and Shadmehr, 2006). However, these studies have produced some mixed results, and the exact anatomical basis of procedural memory consolidation remains undefined. Several existing gaps in the literature that may have contributed to these mixed results, such as the factor of age, the effects of sleep disruption, and the challenge that a universal model for motor memories may not exist (Boyden et al., 2006; Dorfberger et al., 2007; Dionlagic et al., 2010).

One purpose of review articles is to compile literature on a topic in order to form connections between studies and suggest future directions of study; additionally, by reviewing all conflicting models, the most accurate and well-supported model can be identified. No such recent article in the public domain exists for motor memory consolidation; the latest review article was published by Krakauer and Shadmehr (2006), and many advancements have been made since then. Thus, one main objective of this article is to rectify this absence of an overarching resource by providing an overview on current and past literature on motor memory consolidation, including existing gaps in knowledge. Following the initial database search, many different proposed models of consolidation, such as sites of acquisition and storage, are anticipated to be uncovered. After identifying sites of acquisition and storage proposed by various researchers, another goal of this article to provide an unbiased viewpoint, based on the collective analysis of various experiments, on the most accurate model of consolidation. Motor memory is responsible for countless tasks in daily lives, and it has applications in fields such as music, dance, and several sports where repetitive, ingrained movements are emphasized. Only by compiling current knowledge and understanding future directions can the field of motor memory be elucidated. And, by clearly explaining various advancements and setbacks in this field while also pointing towards a specific consolidation model, steps will be made towards forming a more agreed-upon and well-corroborated model, which could then be utilized in its various real-world applications.

2. Materials and Methods

Google Scholar was the search engine used to find literature for this paper. Search results were mostly limited to studies after 1997, as the study of motor memory consolidation was kickstarted by the Brashers-Krug study in 1997. Studies as recent as 2020 were included as well. Initially, the key words "motor memory consolidation" were set for most of the articles, which further narrowed down the selection. However, after the initial history of motor memory was studied and analyzed, a different exclusion criteria was required. The next goal was to search for articles discussing consolidation models of motor memory, such as possible acquisition and storage sites. To identify these studies, the key words were further refined into "motor memory acquisition" and later, into "motor memory storage". Additionally, studies involving either motor sequence tasks, vestibulo-ocular reflex training, and Pavlovian eye conditioning were prioritized to develop a set baseline for accurate comparison between studies. Following this exclusion criteria, as many studies as possible were gathered and analyzed in order to obtain a large database, which allowed for an extensive coverage on past and current views on this specific topic.

3. Results

3.1 Does Motor-type Procedural Memory Consolidate?

In the past few decades, studies of both humans and animals have found that there is a certain window of time where declarative memories can be disrupted. This time-dependent disruption is a crucial part of the consolidation process in declarative memory tasks, and it mostly relies on the medial temporal lobe (Squire and Alvarez, 1995).

Since this property has only been found in explicit memory tasks, this would suggest that nondeclarative memories, such as procedural memory, do not undergo this same process. However, in 1997, a study suggesting that motor memory consolidates in a manner similar to declarative memory emerged (Brashers-Krug et al., 1997). The study involved a manipulandum that subjects used to guide a cursor to various targets. On the first day, the manipulandum produced imposing forces (task A) that perturbed the subject's movements. However, the patients compensated for this change and were eventually able to accurately guide the cursor. This study produced one major discovery: when a different pattern of forces (task B) was introduced to the patients immediately after task A, they showed negative retention of task A on day 2. This suggested that the introduction of task B right after task A training disrupted the retention of task A, and this phenomenon where later learning disrupts the memory of previously learned material is known as retrograde interference. As demonstrated by Dewar et al. (2010) and Robertson (2012), introducing interfering information such as cognitive tasks, electroconvulsive shocks, certain drug inhibitors, or transcranial

magnetic stimulation during consolidation can disrupt or even remove the strengthening of the memory. Thus, the fact that presenting task B, which was an opposing cognitive task, prevented the retention of task A is a key indicator that consolidation does occur for motor memories. Additionally, they trained the patients with task B with varying time intervals (5 minutes, 1 hour, or 4 hours) after the training of task A. They discovered that while the 5-minute and 1-hour group showed slight improvement when retested on the second day, it did not reach significant levels. Only the 4-hour group displayed a similar amount of task A retention and improvement as the control group. So, after 4 hours, the memory had consolidated (see Figure 1). This time-dependent disruption of motor memories has been recognized by other studies (Walker et al., 2003; Baraduc et al., 2004).
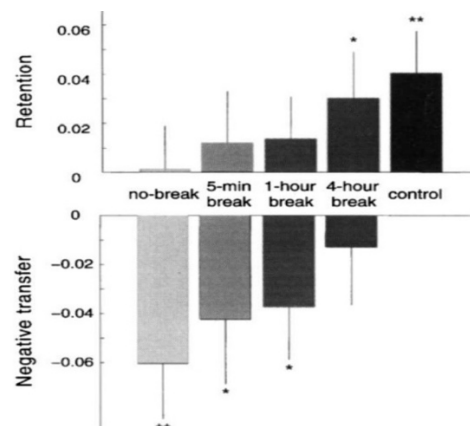

Figure 1. This figure was taken from the Brashers-Krug et al. study (1997). The graph depicts memory retention and negative transfer when task B was introduced with no break, a 5-minute break, 1-hour break, and 4-hour break after the learning of task A. Results show that the longer the break in between, negative transfer decreases while retention increases. The 4-hour break group matches the control group the best, as there appears to be no significant levels in improvement in the 5-min and 1-hour break.

However, the Brashers-Krug study was met with some initial skepticism. Attempts to recreate these results have failed. Instead, many studies have noticed a special property for visuomotor learning, which shows a flat gradient of interference. For example, Bock et al. (2001) utilized a joystick-tracking task, where the cursor was either flipped horizontally or vertically, discovering that, even with a one-month interval in between, the two tasks completely interfered with each other. Additionally, other studies, such as Goedert and Willingham (2002), showed that interference between two tasks increased as the interval increased, which is inconsistent with the properties of consolidation. Essentially, these two studies discovered that interference between two tasks remains consistent regardless of the interval between the learning sessions; this indicates that a flat gradient of interference exists, which is inconsistent with the definition of memory consolidation. To account for these discrepancies, one study suggested that anterograde interference, which is the negative impact of earlier learning on future learning, prevented the retrieval of the memories (Krakauer, 2005). The study involved examining the patient's adaptation to a 30-degree rotation and a 30-degree counter-rotation either 1 day, 2 days, or 1 week after initial training. When the relearning of the original rotation was assessed, they found that no matter the time interval in between, the two rotations still interfered with each other. In the second experiment, the researchers modified the protocol by adding "washout trials" with no rotation. This washout trial was introduced after the learning of the counter-rotation but before the assessment of the original rotation. They discovered that, when the washout trials were introduced, interference happened at 5 minutes but not 24 hours after training (see Figure 2). Additionally, a third trial where initial training was increased showed resistance to interference even at the 5-minute mark. Finally, it was concluded that the failure to recreate the original study was because "washout" trials were not applied to remove anterograde effects.
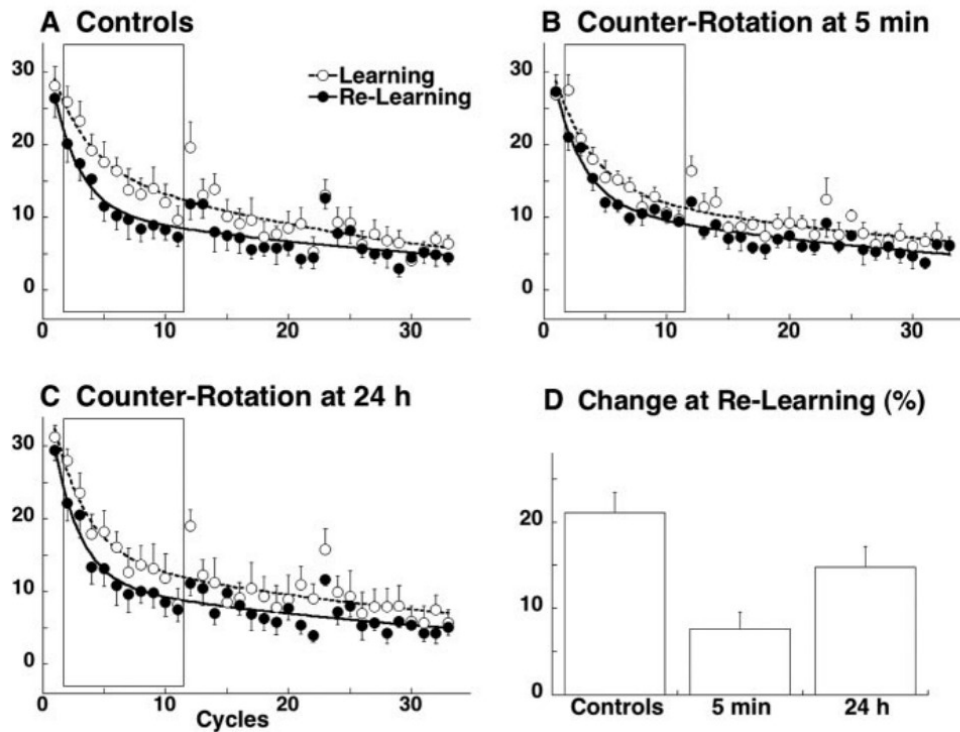
Figure 2. This graphic, which was taken from Krakauer et al. (2005), shows the effect of introducing washout trials. In the 5-minute group, a significant level of interference seems to take place; however, the 24-hour group shows only a mild level of interference, which is comparable to the control group.

3.2 The Acquisition Period of Motor Learning

Now that motor memory consolidation has been relatively well-established, the next goal was to figure out the anatomical basis of motor memory. One study suggests that the prefrontal cortex (PFC) may play a role in motor learning (Krakauer et al., 2005). Using PET scans, changes to the blood flow of the cerebral cortex (rCBF) were recorded. The novel system that the patients learned was the torque motors of a robotic arm, and the goal was to make reaching movements with the arm to hit several targets displayed on a monitor. Following practice with a disabled motor, the researchers introduced a new task where the robot produced a stationary force field named "A". During the acquisition period of force field A, increased activity in the PFC was observed. However, when the participants were retested around 5 hours after initial training, activity decreased in the PFC and increased in the premotor, posterior parietal, and anterior cerebellar cortical structures. From this, the researchers concluded that the learning of a motor skill begins in the PFC, and as training progresses, the anterior cerebellum takes on a greater role and could possibly represent the site of motor memory storage. Additionally, the results showed that several hours after practice, the motor skill becomes resistant to any interference. Therefore, a correlation was drawn between the changes in the stability of the memory; as time passes, activity in the PFC reduces while activity in the cerebellum increases. An earlier study involving PET scans has also shown that the posterior region of the cerebellum may not play a role in the early learning of this certain motor task (Grafton et al., 1992).

However, the two aforementioned studies only conducted the PET scans up to the posterior region of the cerebellum and did not take measures in the anterior cerebellum during early learning. Therefore, the cerebellum's influence as a whole in the acquisition phase cannot be ruled out. Additionally, one main function of the PFC is the temporary storage of arbitrary sensorimotor information, usually to be used in the short term (Quintana and Fuster, 1993). Thus, the PFC's contribution to the consolidation process might just be as a supplementary tool used to aid the retrieval process. If this is the case, then the PFC does not represent the area of interest, and another structure is

responsible for memory acquisition. Finally, the studies that support the PFC as the acquisition site mostly involve just one type of motor learning.

Another possible acquisition site could be the cerebellar flocculus, which resides in the posterior region of the cerebellum, as several studies attributed it as having a necessary role in motor learning. Kassardjian et al. (2005) used the glutamate antagonist cyanquixaline (CNQX), which obstructs neurotransmission in the flocculus of cats, to investigate the theory that motor memory is stored at different locations as the consolidation process advances. Their performance was measured by the vestibulo-ocular reflex (VOR), a reflex that stabilizes the eyes during head movements and whose circuitry mainly resides in the cerebellum and brainstem. The VOR is a type of motor learning, as the eye movements that stabilize the gaze in response to the head movement are encoded and strengthened until they become reflexive. Failure of the VOR to maintain this conditioned eye response (known as VOR gain) indicates a disruption in the motor neural network, as the reflexive eye movements that stabilize the gaze are no longer being made (Cohen et al., 2004). Thus, the anatomical locations of motor memory consolidation can be pinpointed by obstructing the transmission of specific areas and observing the effect it has on the VOR gain. In the study, the injection of CNQX in the cerebellar flocculus before training did not affect the initial learning of the VOR task, but it prevented the expression of short-term memory. Additionally, if floccular function was seriously damaged by the CNYX injections, it completely prevented motor learning. When CNQX was injected three days after VOR training, it had a much smaller effect on the expression of motor memory, which is consistent with the view that long-term motor memory is independent of the cerebellum. These observations could be explained if motor memory is initially encoded as a change in cerebellar synaptic transmissions, as CNQX injections block synaptic transmission in the flocculus. Additionally, the study suggests that when the flocculus is permanently inactivated 1-3 hours after acquisition, it can block the retention of a VOR gain. In contrast, another earlier study demonstrated that floccular inactivation done days after VOR training fails to block the VOR gain (Luebke and Robinson, 1994). Therefore, Kassardjian et al. (2005) hypothesized that initial learning begins in the cerebellar flocculus at the synaptic level, and as time passes, the motor memory is stabilized through neuronal changes and becomes independent of the cerebellum.

The importance of the cerebellar flocculus has also been demonstrated using Pavlovian eye conditioning (EC). The conditioned stimulus (CS) of EC is usually a tone, being shortly (100-1500 ms) followed by a puff of air to the eyes, which is an unconditioned stimulus. The puff of air elicits eyelid closure, or the conditioned response (CR). After several hundred trials, the CS will reflexively cause the CR before the air puff is produced, showing that the eye-blink response has been successfully conditioned into the brain. Like VOR training, Pavlovian eye conditioning represents a reflexive motor response, and changes made to the motor circuitry can manifest in the existence, or lack thereof, of an eyeblink response. For example, this blinking response can be extinguished in a few trials if the CS is not followed by the air puff. Yet this phenomenon, known as extinction, does not completely erase the motor memory (Robleto et al., 2004). Several studies discovered that the reacquisition of the CR after extinction is related to the plasticity in the cerebellum, and that CR is initially learned in the cerebellar cortex, which then inducts plasticity in the cerebellar nuclei (Ohyama and Mauk, 2001; Medina et al., 2001). Additionally, time also plays a role in the retention of EC. Two studies by Attwell et al. (2002) and Cooke et al. (2004) have shown that when muscimol is injected into the cerebellar cortex either 5- or 45-minutes after the first acquisition phase, the animals showed no memory retention of the EC. However, in control animals and animals that were given muscimol 90 minutes after the first acquisition phase, they retained some memory of the EC. This suggests that shortly after training, behavior relies on the cerebellar cortex, but as time passes, the memory becomes more stable and dependence on the cerebellum is removed.

Numerous studies also suggested a time-dependent role for the cerebellum. In fear conditioning, the rat's ability to recall its cue depends on the interpositus for around 4 days after training (Sacchetti et al., 2002). When that interval has passed, inactivating the interpositus has no effect on the memory. This time-dependent role of the cerebellum has also been shown in humans; Bracha et al. (2000) examined patients with cerebellar cortex lesions with two types of EC tasks: a novel task and a task that was learned before the injury. The patients were unable to learn the novel task, but they retained the response of the old task. These results extended the model to humans, showing that the cerebellum is necessary for acquisition but not for permanent storage.

3.3 The Role of Purkinje Cell Plasticity and Vestibular Nuclei

As stated in the passages above, a number of anatomical sites such as the PFC and the cerebellum have been suggested as acquisition sites for motor memory. Studies also suggest that these structures have a time-limited role in the consolidation process, and after a certain time window, the memories may not entirely depend on those structures. Initially, many studies demonstrated that the key mechanism for VOR adaptation relies on synaptic plasticity between the parallel fibers (PFs) and the Purkinje cells (PCs) in the cerebellum (Schonewille et al., 2010; Kakegawa et al., 2018). Nonetheless, some still suggest that the PF-PC synapse does not fully explain VOR learning, as growing evidence proposes that multiple sites of neural plasticity are required for VOR adaptation, such as the cerebellar cortex and the vestibular nucleus (VN) (Clopath et al., 2014; Yamazaki et al., 2015). To support this theory, Ryu et al. (2017) utilized VOR training to uncover the exact role and mechanism of intrinsic PC plasticity in motor memory consolidation. For context, many studies have suggested previously that the PC's have the highest expression of the type 1 stromal interaction molecule (STIM1), which could contribute to the intrinsic plasticity of the PC (Skibinska-Kijek et al., 2009). Specifically, STIM1 is a protein that regulates intracellular calcium levels, and the PCs rely on calcium signaling to function. If STIM1 is lost, the ability for the PCs, which are the sole output neurons of the cerebellum, to transmit information to other regions of the brain, namely the brainstem/VN, is impaired. (Hartmann et al., 2014). Thus, valuable insights on consolidation process as the memory transfers from the acquisition phase to the storage phase can be uncovered utilizing STIM1. Ryu et al. (2017) examined mice with a loss of STIM1 (STIM1^{PKO} mice) in VOR tasks and measured the VOR gain over several days. Interestingly, the STIM1^{PKO} mice showed the same capabilities for VOR learning as the control mice, and their oculomotor responses, when tested before learning, were at the same functionality as control mice. This demonstrated that STIM1^{PKO} mice still retain the ability to learn

motor skills, which confirms the idea that the cerebellar flocculus is responsible for acquisition only. To study its effect on long-term memory, the STIM1^{PKO} mice were VOR tested over the course of 4 days in 24-hour intervals. 24 hours after the first day of learning, the mice had significantly lower levels of memory retention than the control mice. After 2 more days of learning, the STIM1^{PKO} mice caught up to the control mice, but shortly forgot the newly acquired memory (Figure 4). Therefore, it was concluded that STIM1 removal significantly impairs long-term consolidation of motor memory in the VOR without impairing its acquisition. This implies that a crucial communication period between the cerebellum and the brainstem is necessary for successful long-term consolidation.

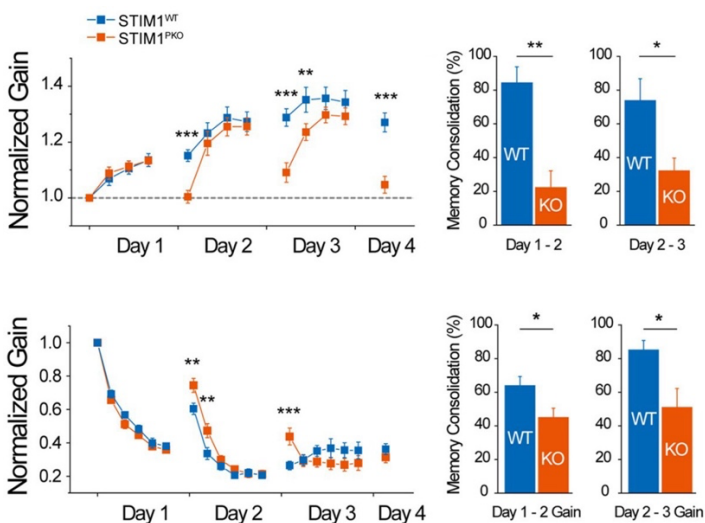Figure 4. These diagrams show the differences in control mice (STIM1WT) and STIM1 knockout mice (STIM1PKO) in VOR learning tasks. For gain-up learning protocol (top), STIM1PKO mice were initially able to keep up with the control, but as time progressed, memory retention decreased. In the gain-down learning protocol (bottom), similar results were shown, as STIM1PKO mice kept up with control mice on the first day, but lost the learned memory on the following days. Reproduced from Ryu et al. (2017).

One recent study further examined the effect of STIM1 in VOR tasks (Jang et al., 2020). This way, the researchers were able to investigate the connections between the plasticity at both the PCs and the VN, hypothesizing that if the communication between the cerebellum and VN is interrupted, consolidation will not occur. To test this theory, the researchers measured memory retention in STIM1^{PKO} mice three periods after the VOR learning task had finished: the short-term period (0.5 to 1 hour), the middle period (4 hours), and the long-term period (24 hours). They discovered that in the middle period, the amount of task information retained in the STIM1^{PKO} mice was much lower than in the

control group. In the long-term period, the STIM1^{PKO} mice showed no memory retention whatsoever. As established by the studies mentioned above, plasticity in the PCs serves as a link between two different regions of the brain, allowing information to flow from the cerebellum to the brainstem. To explain this belated loss of the motor memory in STIM1^{PKO} mice, Jang et al. (2020) claimed that by impairing PC plasticity, the connection between the cerebellum and brainstem is severed, so subsequent plasticity in the VN would not occur. This serves as direct evidence that plasticity in the VN is ultimately responsible for long-term motor memory storage, as the absence of VN plasticity leads to deficits in long-term retention.

4   Discussion

Following the relatively undisputed and well established notion that motor memory consolidates, several proposed acquisition sites, such as the prefrontal cortex and cerebellum, were outlined in this review article. However, the studies that support the prefrontal cortex present several issues, such as lack of diversity in motor training methods, the disregard of posterior cerebellum activity, and the possibility that the prefrontal cortex may just be a supplementary tool. Additionally, the cerebellum as the acquisition site was supported with several motor learning methods such as vestibulo-ocular reflex training and Pavlovian eye conditioning, making it the stronger model. Proposed storage sites included the anterior cerebellum as well as the vestibular nuclei; however, recent studies involving the type 1 stromal interaction molecule lean towards the vestibular nuclei as representing the site of long-term storage. Therefore, this article claims that the most accurate consolidation model is the initial encoding of the engram beginning in the cerebellar flocculus, possibly with the aid of sensorimotor information from the prefrontal cortex. The engram subsequently is transferred into the vestibular nuclei for long-term storage. However, several issues and limiting factors still remain.

4.1 Cerebellar plasticity – a task selective mechanism?

For example, Boyden et al. (2006) utilized VOR training to challenge the view of a universal mechanism for memory storage. Mice lacking the cal-modulin-dependent protein kinase IV (CaMKIV) were examined, as they retained normal levels of acquisition yet cannot maintain the memory. As expected, the CaMKIV knockout mice exhibited normal learning. However, when remeasured 24 hours later, the gain-up training declined while the gain-down training remained the same. These results served as direct evidence against the proposal that a universal plasticity mechanism exists for cerebellum-dependent memories. Instead, it suggests that cerebellar plasticity is a task-selective mechanism, allowing for many different methods of information encoding that adjust to the demands of a particular training condition. Thus, role of the cerebellum in motor memory consolidation might not be universal for all motor memories.

4.2 Motor learning in pre-pubescents versus adolescents

Some studies suggested that age could play a role in the speed and efficiency of the consolidation process. To investigate the role of age, Dorfberger et al. (2007) gathered 128 participants of varying ages, ranging from pre-puberty to adolescent age. The participants were split into two experiments, each being taught a finger-to-thumb opposition sequence learning task. Both groups were taught the same task and were assessed for memory retention in 24-hour blocks. However, in order to test the effect of interference, the researchers modified the procedure of the second group; they introduced a second training session, where the controls of the sequence were reversed, 2 hours after the initial session. The first group, when tested for retention of the performance gains even 6 weeks post-training, showed that age had no factor on the learning and retention of the sequence. Yet in the second group, only the adolescent group experienced a strong amount of interference, suggesting that the pre-pubescent participants were much less susceptible to interference. The researchers proposed that the susceptibility of adults to interference was not due to inferior motor skill learning, but instead the notion that adults may be more selective in terms of procedural memory consolidation.

4.3 Effects of sleep fragmentation

Additionally, some studies have researched the effect that sleep has on memory consolidation. For example, one study assessed the differences of motor learning of patients with obstructive sleep apnea (OSA) versus control patients (Djonlagic et al., 2012). Previous studies had demonstrated that OSA could lead to frequent arousals during sleep, making it an adequate model for measuring the effect that sleep fragmentation has on memory consolidation. All participants first underwent a psychomotor vigilance task (PVT) to measure their attention and reaction time, which shows direct correlation to sleep deprivation. Then, the subjects were trained with a motor sequence task (MST), and this procedure was repeated 24 hours later. Both groups showed a similar level of performance during the initial training session, suggesting that the encoding process of memory consolidation remains the same in both OSA and control patients. However, when reassessed after overnight sleep, the control group showed notably more improvement than the OSA group in the MST. Thus, the researchers concluded that sleep fragmentation has a significant negative impact on offline learning improvement.

5   Conclusion

Overall, this review article accomplished the objectives stated in the introduction. It began by outlining the history of motor memory consolidation, starting from the initial study in 1997, the debate and skepticism that followed, and the three current issues, such as the complexity of the cerebellar plasticity mechanism, the factor of age, and the effects of sleep fragmentation, that still exist in the field today. The second objective was achieved by examining several studies that consider various acquisition and storage sites. This article discovered several acquisition sites such as the prefrontal cortex and the cerebellar flocculus, and potential storage sites such as the anterior cerebellum and the vestibular nuclei were identified. Interpretation of the studies examined in this article led to the conclusion that the most accurate model is initial acquisition in the cerebellar flocculus and long-term storage in the vestibular nuclei— the prefrontal cortex may play a role as an arbitrary supplementary tool as well. By supplying evidence for this promising consolidation model, the two sites (cerebellum and vestibular nuclei) can be targeted for further exploration and optimization in their real life applications, allowing for quicker and stronger formation of motor habits. Specifically, elucidating the field of motor memory as well as pinpointing a particular consolidation model is essential, as the findings can aid in developing rehabilitation protocols in stroke patients, enhancing recovery from motor injuries in physical therapy, maximizing skill acquisition in sports, and more.

One final, fundamental limitation to the field of motor memory consolidation as a whole is that most of the existing studies utilized VOR training, Pavlovian eye conditioning, and some sort of motor sequence task to study motor memory. These models encode motor memories in ways that are easy to analyze both behaviorally and physiologically, allowing them to provide invaluable knowledge of the consolidation process. However, due to the relatively simple nature of these tasks, there still remains much room for real-life application. The motor skills used in our daily lives require much more complex and fine motor movements than a simple eyeblink or motor sequence task. Therefore, it becomes clear that there is still much more to explore in field of motor memory consolidation.

Acknowledgment

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