INVESTIGATING THE DECLARATIVE AND PROCEDURAL MEMORY PROCESSES UNDERLYING ACQUISITION OF TOOL-RELATED KNOWLEDGE AND SKILLS

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Abstract

It has been proposed that the acquisition of tool-related knowledge and skills (e.g., attributes of a tool, how it is used, how it is grasped) relies on a complex set of memory processes. However, the precise memory representations of different aspects of tool knowledge are still unclear. It has also been argued that some aspects may require an interaction between the declarative and procedural memory systems. However, the nature of this interaction between both memory systems in relation to tool-related knowledge is not well understood. A series of three experiments was carried out in the current dissertation to systematically investigate the role of declarative and procedural memory in mediating complex tool knowledge and skills. In Experiment 1 participants with Parkinson’s disease (PD) showed unimpaired memory for tool attributes and tool grasping relative to controls. In addition, participants with PD showed intact motor skill learning and skilled tool use within sessions, but failed to retain proficiency of these skills after a 3-week delay. In Experiment 2, declarative encoding processes were interrupted in healthy adults by dividing attention during training. Findings showed that dividing attention during training was detrimental for subsequent memory for tool attributes as well as accurate demonstration of tool use and tool grasping. However, dividing attention did not interfere with motor skill learning. In Experiment 3, motor procedural learning among healthy adults was disrupted by limiting access to performance-based feedback during training. Results showed that recall of tool attributes and tool grasping were intact, but limited feedback was detrimental for motor skill learning and skilled tool use. Taken together, the results suggest that memory for tool attributes and tool grasping primarily relies on declarative memory which is associated with the medial temporal lobes. In contrast, findings suggest that motor skill acquisition related to complex tools is primarily supported by striatal-dependent procedural memory. Thus, these results represent a dissociation between declarative and procedural aspects of tool knowledge and skills. Findings from the current studies also provide new insights into the interaction between declarative and procedural memory. The results suggest that skilled tool use requires a cooperative interaction of both systems. The evidence also suggests that the pattern of interaction between memory systems may vary, depending on the learning context.

Keywords: declarative memory, procedural memory, memory systems, tool knowledge, motor skill acquisition, skilled tool use

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Chapter l: General Introduction

Tools enable us to perform essential everyday activities such as eating with a fork, brushing our teeth with a toothbrush, and unlocking a door with a key. Although these tasks may seem rather effortless or automatic in our daily lives, they are supported by a complex network of memory processes. Damage to any part of this network may lead to severe impairment in performing everyday activities. Yet, the specific memory representations of tool-related information are not well understood. It has been proposed that different aspects of tool knowledge and skills (e.g., function, motor skills, tool grasping) may be mediated by different types of memory. However, the relative contributions of these memory systems and their interaction in mediating tool knowledge and skills require further investigation. My dissertation had two primary objectives: (a) to identify the specific memory representations of various aspects of tool knowledge and skills; and more broadly (b) to gain a better understanding of how declarative and procedural memory systems are organized as well as how they interact with each other. I pursued these research objectives through a series of three behavioural experiments. In the following introduction, I will discuss limitations of previous research in this area, I will briefly summarize my master's thesis which provided a foundation for this dissertation, and lastly, I will provide a brief overview of each of the three experiments in this dissertation. Detailed literature reviews on specific topics can be found in subsequent chapters of individual experiments.

Association between Memory and Tools

Currently, we have little understanding of how memory supports tool knowledge and skills. Part of this limited knowledge is due to a lack of studies focusing on the role of memory in tool use. Research on neural mechanisms of tool use has predominantly focused on various action systems and motor networks affected in apraxia, a disorder of skilled actions (Goldenberg & Spatt, 2009; Goldenberg & Hagmann, 1998; Vingerhoets, 2008). Although many of these studies have commented on the involvement of memory, and the neural regions associated with memory, these issues were not the primary focus of the research. Also, the possible involvement of multiple memory systems in skilled tool use has received little or no attention. Another issue is that the few existing studies that have directly addressed memory contributions to tool use have focused on isolated aspects of tools such as tool use, tool grasping, or knowledge of tool features (Creem-Regehr & Lee, 2005; Silveri & Ciccarelli, 2009; Warrington, 1975). It is possible that there are important links between the mechanisms supporting different aspects of tools. For instance, findings related to tool grasping may have important implications for tool use. However, previous studies lack this level of integrative analysis. Thus, this area would benefit from further research focusing on the role of different memory systems across various aspects of tool knowledge and skills.

Interaction between Memory Systems

Traditional theories have divided memory into two broad systems: declarative memory and procedural memory (Squire, 2009). Declarative memory has been shown to rely on medial temporal lobe structures and is believed to mediate recollection of facts and events

(Squire, 2009). In contrast, procedural memory mediates the formation of new skills and habits and is believed to rely on a frontal-striatal network (Squire, 2009, also see Doyon et al., 2009). These two memory systems have been considered to be functionally and anatomically dissociable (Cohen & Squire, 1980; also see Knowlton, Mangels, & Squire, 1996). More recently, research has demonstrated that the declarative and procedural memory systems may interact under some circumstances (Packard & Goodman, 2013; Poldrack & Packard, 2003). For instance, there is evidence suggesting that the two memory systems interact in a cooperative manner where both systems are critically involved. There is also evidence showing that the two systems may interact in a competitive manner where one system inhibits the other system (see Foerde & Shohamy, 2011). In addition, it has been shown that one system may compensate for the other in some situations (see Moody, Bookheimer, Vanek, and Knowlton, 2004). However, the characteristics of this interaction, as well as its limitations, are not well understood. In addition, much of the recent research regarding memory interactions has been conducted with probabilistic classification learning, a computerized task involving learning of visual associations (Poldrack et al., 2001). Therefore, the use of different types of memory tasks may help to clarify the interaction between declarative and procedural memory systems.

Summary of MA Thesis

My MA thesis (Roy & Park, 2010) was arguably the first study to systematically investigate the role of different memory systems in mediating tool knowledge and skills. Specifically, I analyzed the unique contributions of declarative memory in acquiring novel tool knowledge and skills in D.A., an individual with profound hippocampal amnesia. I trained D.A., along with a group of healthy age-matched controls, to use a set of novel complex tools over three sessions. Participants were tested on their ability to recall attributes of the tools (e.g., function) as well as to demonstrate the appropriate manner of grasping and skilled tool use to command. Findings showed that D.A. learned the motor skills at the same rate as controls and retained these skills over a 3-week delay. However, he was severely impaired in his ability to recall tool attributes, demonstrate grasp to command, and demonstrate tool use to command. This pattern of results suggest that memory for tool attributes, tool grasping, and skilled tool use are at least partly dependent on declarative memory processes. In contrast, results suggest that motor skill learning associated with complex tools critically relies on intact procedural memory. It was also proposed that skilled tool use may rely on an interaction of both memory systems where the declarative system encodes critical task-related details and procedural memory guides proficient tool use. Experiments 1, 2, and 3 of the current dissertation extend these findings using similar protocols in both patient and healthy populations.

Overview of Current Experiments

Experiment 1

Previous research has shown that multiple subcortical networks (e.g., striatal, cerebellar) are involved in various procedural memory tasks (see Doyon et al., 2009). However, the specific form of procedural memory involved in mediating motor skill learning associated with tools has not been examined. In addition, previous research on motor procedural memory has largely focused on skill learning, and the role of procedural memory in supporting other aspects of tool knowledge and skills (e.g., tool grasping, tool use) has been largely unexplored. In Experiment 1, I investigated the specific contributions of the procedural memory system in mediating various aspects of tool knowledge and skills. The interaction between the declarative and procedural memory systems was also directly examined. Individuals with Parkinson's disease (PD) and age-matched controls were tested on a similar protocol as the one implemented in Roy and Park (2010). In general, it was predicted that participants with PD would show impairment on aspects of tool knowledge and skills that rely on striatally mediated procedural memory. It was also predicted that participants with PD would have unimpaired memory for aspects of tool knowledge and skills that are primarily declarative in nature (e.g., tool attributes). In other words, a double dissociation of results from my MA thesis was expected. Lastly, based on findings from my MA, it was hypothesized that skilled tool use to command would rely on a cooperative interaction of both memory systems and that participants with PD would be particularly impaired in the procedural aspect of skilled tool use (e.g., increased proficiency in using a tool). An in-depth literature review of memory mechanisms supporting motor skill learning can be found in Chapter 2.

Experiment 2

Although motor skill learning is believed to be a type of procedural memory, there is debate in the current literature regarding the role of declarative memory in motor skill learning. Some researchers argue that motor skill learning does not require declarative memory and that people can learn motor skills implicitly, without any knowledge of what was learned (Song, Howard, & Howard, 2007). However, others have argued that the declarative memory system plays a critical role in motor skill learning and may interact with the procedural memory system, particularly during early stages of learning (see Penhune & Steele, 2012). Therefore, it is unclear whether motor skill learning is supported by different memory systems and how these systems may interact. Findings from Roy and Park (2010) suggest that motor skill learning associated with complex tools does not require declarative memory, as D.A. showed unimpaired skill learning. However, it is important to note that that study was based on data from a single individual. Furthermore, other research has shown that D.A. appears to perform unexpectedly well on tasks that are believed to rely on hippocampal function, despite his extensive bilateral hippocampal damage (see Ryan, Moses, Barense, & Rosenbaum, 2013). Thus, it is unclear how results from this individual may generalize to a healthy population. In Experiment 2, a group of younger healthy adults were tested on a protocol similar to the previously mentioned studies. Half of the tools were trained under divided attention, using an auditory 1-back task, whereas the remaining tools were trained under full attention. The dual-task paradigm has been shown to be particularly detrimental for encoding new declarative information (e.g., Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000). Therefore, it was expected that aspects of tool knowledge and skills that are believed to rely on declarative memory would be negatively impacted by dividing attention during training. In contrast, aspects that do not require declarative memory would not be affected by dividing attention. Further background information on the effects of dividing attention on different types of learning can be found in Chapter 3.

Experiment 3

The role of feedback-based learning during motor skill learning associated with complex tools was investigated in Experiment 3. It has been shown that feedback-based learning critically relies on the striatum and the procedural memory system (Wilkinson et al., 2014; also see Shohamy, Myers, Kalanithi, & Gluck, 2008). It has been argued that probabilistic classification learning relies on the striatum and is a form of feedback-based learning as participants learn associations through trial-by-trial corrective feedback (Foerde et al., 2006). It could be argued that learning how to use a new tool to achieve a specific goal is also a form of feedback-based learning that relies on the striatum. If so, studying the role of feedback may provide another means of delineating the procedural and declarative components of tool knowledge and skills in healthy individuals. More specifically, by manipulating the amount of feedback provided during skill learning, it may be possible to disrupt the processes involved in striatally based procedural learning. Findings could help specify more precisely the psychological and neural processes involved in the acquisition of motor procedural skills. In Experiment 3, access to performance-based feedback during motor skill acquisition was varied across three groups of healthy younger adults using a protocol similar to the previous studies. This was done by limiting access to sensorimotor feedback from tools and their associated recipients. The impact of limited feedback on motor skill learning and subsequent memory for tool attributes, tool grasping to command, and tool use to command was explored. In general, it was expected that aspects of tool knowledge and skills that critically rely on striatally mediated procedural memory system would be impaired with limited access to feedback during training. In contrast, it was expected that limiting feedback would not impact memory for declarative aspects of tool knowledge and skills. A literature review on feedback-based learning as it relates to skill learning can be found in Chapter 4.

The following chapters present full details on each of these three experiments. A general discussion of broader implications of this research is also presented in the final chapter of this dissertation.

References

Cohen, N. J., & Squire, L. R. (1980) Preserved learning and retention of pattern-analyzing skill in amnesia: Dissociation of knowing how and knowing that. *Science, 210,* 207-210. doi:10.1126/science.7414331

Creem-Regehr, S. H., & Lee, J. N. (2005). Neural representations of graspable objects: Are tools special? *Cognitive Brain Research, 22,* 457-469. doi:10.1016/j.cogbrainres.2004.10.006

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J.,... Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research, 199,* 61-75. doi:10.1016/j.bbr.2008.11.012

Foerde, K., & Shohamy, D. (2011). The role of the basal ganglia in learning and memory: Insight from Parkinson’s disease. *Neurobiology of Learning and Memory, 96,* 624–636. doi:10.1016/j.nlm.2011.08.006

Goldenberg, G., & Hagmann, S. (1998). Tool use and mechanical problem solving in apraxia. *Neuropsychologia*, 36, 581–589. doi:10.1016/s0028-3932(97)00165-6

Goldenberg, G. & Spatt, J. (2009). The neural basis of tool use. *Brain, 132*, 1645-1655. doi: 10.3389/fpsyg.2014.00310 10.3389/fpsyg.2014.00310

Iidaka, T., Anderson, N. D., Kapur, S., Cabez, R., & Craik, F. I. M. (2000). The effect of divided attention on encoding and retrieval in episodic memory revealed by positron emission tomography. *Journal of Cognitive Neuroscience, 12*, 267–280. doi:10.1162/089892900562093

Knowlton, B. J., Mangels, J. A., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science, 273,* 1399–1402. doi:10.1126/science.273.5280.1399

Moody, T. D., Bookheimer, S. Y., Vanek, Z., & Knowlton, B. J. (2004). An implicit learning task activates the medial temporal lobe in patients with Parkinson's disease. *Behavioral Neuroscience, 118,* 438–442. doi: 10.1037/0735-7044.118.2.438

Packard, M. G., & Goodman, J. (2013). Factors that influence the relative use of multiple memory systems. *Hippocampus, 23*, 1044-1052. doi:10.1002/hipo.22178

Penhune, V. B., & Steele, C. J. (2012). Parallel contributions of cerebellar, striatal and M1 mechanisms to motor sequence learning. *Behavioural Brain Research, 226,* 579-591. doi:10.1111/j.1749-6632.2011.06434.x

Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature, 414*, 546–550. doi:10.1038/35107080

Poldrack, R., & Packard, M. G. (2003). Competition among multiple memory systems: converging evidence from animal and human brain studies. *Neuropsychologia, 41,* 245-251. doi:10.1016/s0028-3932(02)00157-4

Roy, S., & Park, N. W. (2010). Dissociating the memory systems mediating complex tool knowledge and skills. *Neuropsychologia*, *48*, 3026-3036. doi:10.1016/j.neuropsychologia.2010.06.012

Ryan, J.D., Moses, S.N., Barense, M., & Rosenbaum, R.S. (2013). Intact learning of new relations in amnesia as achieved through unitization. *Journal of Neuroscience*, *33,* 9601-9613. doi: 10.1523/JNEUROSCI.0169-13.2013

Shohamy, D., Myers, C. E., Kalanithi, J., & Gluck, M. A. (2008). Basal ganglia and dopamine contributions to probabilistic category learning. *Neuroscience & Biobehavioral Reviews, 32*, 219–236. doi:10.1016/j.neubiorev.2007.07.008

Silveri, M. C., & Ciccarelli, N. (2009). Semantic memory in object use. *Neuropsychologia*, 47, 2634-2641. doi:10.1016/j.neuropsychologia.2009.05.013

Song, S., Howard, J. H., & Howard, D. V. (2007). Implicit probabilistic sequence learning is independent of explicit awareness. *Learning & Memory*, *14*, 167-176. doi:10.1101/lm.437407

Squire, L. R. (2009). Memory and brain systems: 1969-2009. *Journal of Neuroscience*, *29*, 12711-12716. doi:10.1523/jneurosci.3575-09.2009

Warrington, E. K. (1975). The selective impairment of semantic memory. *The Quarterly Journal of Experimental Psychology*, *27*, 635-657. doi:10.1080/14640747508400525

Wilkinson, L., Tai, Y. F., Lin, C. S., Lagnado, D. A., Brooks, D. J., Piccini, P., & Jahanshahi, M. (2014). Probabilistic classification learning with corrective feedback is associated with in vivo striatal dopamine release in the ventral striatum, while learning without feedback is not. *Human Brain Mapping*, n/a–n/a. doi:10.1002/hbm.22536

Vingerhoets, G. (2008). Knowing about tools: Neural correlates of tool familiarity and experience. *NeuroImage*, 40, 1380–1391. doi:10.1016/j.neuroimage.2007.12.058

Chapter 2: Interaction of memory systems during acquisition of tool-related knowledge and skills in Parkinson's disease (Experiment 1)

Frey (2007) defines tools as "manipulable objects that are used to transform an actor's motor output into predictable mechanical actions for purposes of attaining specific goals" (p. 368). Tools can be further classified as being either *simple tools,* which amplify the movement of the upper limbs (e.g., using a stick to extend reach), or *complex tools,* which are manufactured to provide a mechanical advantage in performing a task (e.g., cutting paper with scissors; Frey, 2007; Heilman, 2002). As humans, we rely on complex tools to perform many activities of daily living (ADLs; e.g., using a fork to eat) as well as instrumental activities of daily living (IADLs; e.g., using cooking utensils to prepare a meal). In addition, we have a remarkable adaptive ability to learn how to use novel tools to perform new tasks. Thus, the ability to use both familiar and novel complex tools is essential for continued independent living. Studies have shown that the inability to perform ADLs and IADLs can have a substantial negative impact on a person's quality of life as they are not able to function independently (Foundas, Macauley, Raymer, & Maher, 1995). However, our understanding of the cognitive processes underlying complex tool use, including how we acquire tool-related knowledge and skills, is still incomplete.

Although using a complex tool (e.g., a hammer) may seem rather effortless, this act is supported by a complex set of cognitive processes. For instance, there are multiple memory processes involved in both the acquisition and retrieval of different aspects of tool-related knowledge and skills (e.g., knowing the function of the tool, how to grasp it, how to manipulate it), and it has been proposed that each of these aspects has a different memory representation (Daprati & Sirigu, 2006). It has been argued that memory for tool-specific features (e.g., a tool's function) is represented within declarative memory (Warrington & Shallice, 1984). In contrast, motor skills are believed to be primarily represented by procedural memory (learning of skills that occurs beyond awareness; Packard & Knowlton, 2002). Furthermore, it has been proposed that some aspects of tool-related knowledge and skills may rely on an interaction of both memory systems (Negri, Lunardelli, Gigli, & Rumiati, 2007; Roy & Park, 2010; Silveri & Ciccarelli, 2009). However, the specific memory representations of these different aspects of tool-related knowledge and skills are still not well understood. In addition, it is unclear how the declarative and procedural memory systems may interact in mediating tool-related knowledge and skills.

Roy and Park (2010) systematically investigated the role of declarative memory in the acquisition of various aspects of tool-related knowledge and skills. An individual with profound hippocampal amnesia, D.A., and healthy age-matched controls, were trained to use a set of novel complex tools to perform motor tasks (e.g., guide a plastic wheel down a curved path). Participants were trained to use these tools over three sessions and were tested on their ability to recall tool attributes (e.g., function of the tool, tool colour), demonstrate proper grasp of the tool, and demonstrate proper use of the tool. There was also a 3-day delay between the first two sessions and a 3-week delay between the second and third sessions. Results showed that D.A. was unimpaired in his ability to acquire motor skills associated with the novel tools, and his completion time decreased at the same rate as control participants across training trials. In contrast, he showed severe impairment in his ability to recall tool attributes compared to controls. His demonstration of tool grasping and tool use was also severely impaired. However, when the experimenter positioned the tool's recipient in the appropriate starting location, thereby providing a strong retrieval cue of the tool's use, D.A.'s tool use performance improved remarkably. Taken together, the findings from this study present a dissociation of the procedural and declarative aspects of tool-related knowledge and skills. Specifically, they suggest that motor skill acquisition is primarily mediated by the procedural memory system, whereas recall of tool features, tool grasping, and skilled tool use are at least partly mediated by the declarative system. Although these findings help to shed light on the role of declarative memory in the acquisition of tool-related knowledge and skills, the type of procedural memory and its specific contributions have not yet been directly investigated. Furthermore, possible interaction between the declarative and procedural memory systems with respect to mediation of tool-related knowledge and skills is still unclear. To address these questions, I investigated the acquisition of tool-related knowledge and skills in an experiment similar to Roy and Park (2010) in a sample of individuals with Parkinson's disease (PD) and healthy controls.

It is well established that motor procedural tasks depend on the striatal network, and people with PD have been shown to be impaired on tasks relying on the striatum

(Packard & Knowlton, 2002; Siegert, Taylor, Weatherall, & Abernethy, 2006). Findings regarding declarative memory in PD have been mixed. Hay, Moscovitch, and Levine (2002) reported that declarative memory was relatively intact in mild stages of PD, but somewhat impaired in moderate stages of PD. However, one study showed that declarative memory was intact even in a sample of PD patients with moderate disease severity (Barnes, Boubert, Harris, Lee, & David, 2003). Several studies have investigated various forms of learning in PD, and these studies will be reviewed in subsequent sections. To my knowledge, however, no studies have yet examined acquisition of tool-related knowledge and motor skills in PD. If participants with PD have impaired memory for certain aspects of tool knowledge and skills, it would suggest that these aspects rely on regions damaged in PD. This research may also provide further insights into the interaction between declarative and procedural memory systems.

Human Memory Systems

Human memory is traditionally divided into two broad systems: declarative memory and procedural memory. These two memory systems are believed to be dissociable in many respects as they have been localized to different parts of the brain and are believed to mediate different types of learning. The declarative system is believed to rely on medial temporal lobe structures including the hippocampal complex (Nadel & Moscovitch, 1997). It is involved in learning of both semantic (i.e., general knowledge) and episodic (i.e., recollection of experiences) information. This information can be acquired rapidly and is often, but not invariably, explicitly encoded and retrieved (see

Schendan, Searl, Melrose, & Stern, 2003). However, declarative memories tend to be sensitive to interference and decay over time if not rehearsed (Squire, 2009). In contrast, procedural memory, which is a form of nondeclarative memory, is involved in skill learning. Both acquisition and retrieval of skills take place implicitly, beyond conscious awareness (Squire, 2009). Unlike declarative memory, procedural memory tends to be resistant to both interference and decay (Gabrieli, Corkin, Mickel, & Growdon, 1993, but see Brashers-Krug, Shadmehr, & Bizzi, 1996). The anatomical representations of the procedural memory system are not well understood; however, the current understanding is that there are multiple forms of nondeclarative memory, some of which are mediated by various subcortical regions including cortico-cerebellar and cortico-striatal pathways (see Doyon et al., 2009; also see Knowlton & Foerde, 2008).

The declarative and procedural memory systems are functionally and anatomically distinct (Bechara et al., 1995; Cohen & Squire, 1980). In one study, Knowlton, Squire, and Mangels (1996) reported a double dissociation of the two systems. The study used a probabilistic classification learning (PCL) task in which participants learn the probability of certain outcomes (e.g., weather outcomes) based on the combination of visual cues. This form of learning is believed to occur implicitly with the support of the striatum. Declarative memory for the task was also tested using multiple choice questions about the various outcomes. Results showed that amnesic individuals with medial temporal lobe damage were impaired relative to controls in answering multiple choice questions about the task, but were unimpaired in their implicit learning of the outcomes. In contrast, people with PD, which is associated with striatal dysfunction, were impaired in their implicit learning, but were unimpaired on their multiple choice performance. Based on these findings, it appears that the medial temporal lobe and the striatum mediate different aspects of learning.

Although the declarative and procedural systems may be distinct in many respects, recent research has shown that the two systems may also interact in some circumstances (see Packard & Goodman, 2013; see also Poldrack & Packard, 2003). Much of the research on the interaction of the two systems in humans has involved PCL, described in the previous section, although other tasks have been examined as well (see Albouy, King, Maquet, & Doyon, 2013). Some studies using PCL have presented evidence of *competition* between the two memory systems in which there is an inhibitory influence of one system over the other during learning. These studies also demonstrate that it is possible to modulate which system is being engaged. For instance, it has been shown that occupying the declarative system with a secondary task leads to adoption of a procedural learning strategy during PCL (Foerde, Knowlton, & Poldrack, 2006). Other studies demonstrate a *compensatory* interaction between the two systems in which the primary system for a particular function is compromised, and the other system attempts to support the lost function. Moody, Bookheimer, Vanek, and Knowlton (2004) showed that people with PD were unimpaired on behavioural measures of a PCL task. However, neuroimaging findings revealed that the participants with PD recruited medial temporal structures during the task and essentially employed declarative memory during learning, whereas healthy controls showed activation in the striatum. Finally, the declarative and procedural memory systems may interact in a *cooperative* manner whereby both systems have essential roles in mediating performance. For instance, studies that investigated tool use have proposed that both memory systems are required for skilled tool use and that each system may have a specific role during tool use (Roy & Park, 2010; Silveri & Ciccarelli, 2009). Thus, there is strong evidence to suggest that the two memory systems share a dynamic relationship that varies according to the learning context. However, the factors that determine the nature of their interaction in a given learning situation are currently not well understood. As many existing studies have demonstrated, examining memory function in PD has been helpful in understanding the interaction between memory systems. Continued research with this population may lead to further advancement in our understanding of memory organization in the context of tool use.

Memory Representations of Tool-related Knowledge and Skills

Motor Skill Learning

It has been proposed that motor skill learning takes place over three stages (Albouy et al., 2013; Doyon, 2003; Doyon et al., 2009). First, there is an early learning phase in which rapid gains are made within session. It has been argued that this early stage is supported by a vast network of brain regions including the hippocampus and both cortico-striatal and cortico-cerebellar circuits (Albouy et al.; Schendan et al., 2003). Second, there is a consolidation phase during which the motor skill becomes resistant to decay or interference. Consolidation of skills typically requires both sleep and passage of time and is believed to be critically dependent on the striatum (Doyon et al.). Third, there is a slow learning phase during which the motor skill continues to become automatized and can be performed with very little attention. The striatum, as well as motor and parietal cortices, are all involved in the slow learning phase (Doyon et al.). Thus, regions from both declarative and procedural memory systems are believed to be involved in motor skill learning. However, the interaction and relative contributions of the two systems in motor skill learning are not well understood. Further, it has been suggested that the relative involvement of the two systems varies across the different stages of learning (e.g., greater striatal involvement during the consolidation phase; Doyon et al.).

The serial reaction time task (SRTT) is a commonly used task believed to measure implicit skill learning (Nissen & Bullemer, 1987). Studies have shown that people with PD are impaired on the SRTT, indicating that the procedural memory system, involving the striatum, has a critical role in motor sequence learning (Siegert et al., 2006). However, there is currently a debate in the literature regarding the role of the hippocampus and declarative memory in motor skill learning. One position argues that motor sequence learning is predominantly procedural and occurs independently of any explicit awareness or declarative knowledge of what is learned (Song, Howard, & Howard, 2007). Evidence for this position comes from patient studies involving individuals showing that people with Alzheimer’s disease and other diseases affecting the medial temporal lobes who were shown to be unimpaired on the SRTT (Nissen & Bullemer, 1987; Reber & Squire, 1994; Van Halteren-wan Tilborg 2007). A second position argues that the two memory systems have a competitive interaction during early stages of motor skill learning. According to this position, the hippocampus is heavily involved in early stages of skill learning, but gradually becomes deactivated as the striatum takes on a greater role in later stages (see Albouy et al., 2013). A third position argues that early stages of motor skill learning require a cooperative interaction of both declarative and procedural memory systems, where each system has a distinct role (see Penhune & Steele, 2012). Finally, it has been proposed that there may be a compensatory relationship between memory systems during motor skill learning. A recent study investigated performance of people with mild cognitive impairment (MCI) and people with PD on a motor sequence learning task shown to be mediated by the corticostriatal circuit (Gobel et al., 2013). Results suggested that two of the participants with PD may have employed a declarative strategy to learn the motor sequence as a means of compensation. This theory of compensation would suggest that in cases of damage to the procedural system, such as in individuals with PD, the declarative system may be engaged to undertake the function typically mediated by the procedural system. Overall, there is growing evidence to suggest that the declarative system has a role in motor skill learning, but its precise role and its interaction with procedural memory is still under investigation.

Skilled tool use

Skilled tool use (i.e., intentional demonstration of a tool’s use) is similar to motor skill learning in that they both involve motor expression of a skill; however, there are some key differences. During motor skill learning, the learner typically has access to external supports (e.g., trainer, manual) to scaffold skill development. In contrast, during skilled tool use, the learner must recreate the training context independently and demonstrate the motor skill that was acquired during prior training. As with motor skill acquisition, there is some controversy in the literature regarding the memory representations of skilled tool use. Some researchers argue that tool use can be mediated through sensorimotor processes (i.e., mechanical problem-solving) along with physical affordances and that declarative tool knowledge is not necessary (Gibson, 1977; Goldenberg & Spatt, 2009; Hartmann, Goldenberg, Daumüller, & Hermsdörfer, 2005). Studies have also shown that patients with semantic dementia and other declarative memory impairment are still able to use familiar tools efficiently (Negri, Lunardelli, Gigli, & Rumiati, 2007). However, another perspective argues that semantic tool knowledge is required in order to use tools efficiently in a conventional manner. Advocates of this position have argued that people with semantic dementia often have some residual semantic memory which may explain preserved tool use for familiar tools (Buxbaum, Carew, & Schwartz, 1997). This theory of residual semantic memory guiding tool use was supported by a study that found that more severe semantic memory impairment was associated with greater impairment in tool use (Silveri & Ciccarelli, 2009).

While the role of semantic memory continues to be debated, the role of procedural memory in skilled tool use has not received much focus in the literature. However, there has been the suggestion that skilled tool use may rely on a cooperative interaction of both declarative and procedural memory systems (Buxbaum et al., 1997; Negri et al., 2007; Silveri & Ciccarelli, 2009). Roy and Park (2010) proposed that declarative memory may be required for learning task-related details, whereas procedural memory supports expression of learned motor skills. However, this interaction and the specific roles of both memory systems in skilled tool use require further investigation.

Tool Grasping

Previous research has suggested that grasping a tool for the purpose of moving it versus grasping a tool for the purpose of using it rely on different cognitive mechanisms; however, there has been limited research specifically investigating the memory representations of tool grasping (Buxbaum, Kyle, Tang, & Detre, 2006). Research suggests that tool grasping has strong declarative memory involvement. In a behavioral study, Creem and Proffit (2001) showed that healthy participants were less likely to grasp familiar tools appropriately, by their handles, when they concurrently performed a semantic secondary task compared to when they performed a visuomotor secondary task. The authors concluded that grasping a tool for the purpose of using it, but not simply moving it, requires semantic knowledge about the tool. In a subsequent neuroimaging study, Creem-Regehr and Lee (2005) reported greater activation in the middle temporal gyrus and fusiform gyrus for images of familiar tools with handles compared to unfamiliar graspable shapes, suggesting that functional knowledge of tools influences neural representations associated with grasping the tool for use. Further evidence comes from the earlier described study by Roy and Park (2010) in which an amnesic individual was impaired in his grasp demonstration for novel tools after being trained to use them. Thus, previous research with both novel and familiar tools suggests that grasping a tool for the purpose of using it requires declarative knowledge of the tool. It could be argued that tool grasping involves skilled motor processes as well and therefore may involve the procedural memory system. However, it is unclear at this point whether the procedural memory system and related subcortical structures are involved in tool grasping.

Memory for Tool Features

It is generally accepted that retrieval of knowledge related to object features (e.g., function, colour) is mediated primarily by declarative memory. It has been shown that people with temporal lobe damage have difficulty remembering object-specific characteristics as this information is semantically represented (Warrington, 1975; Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000). The amnesic individual studied in Roy and Park (2010) was severely impaired in his ability to recall attributes of novel tools that he had been trained to use over several trials. Neuroimaging research with healthy individuals has also shown that remembering information about novel tools and their properties relies on neural regions associated with declarative memory (Weisberg, van Turennout, and Martin, 2007). Thus, the ability to recall properties of both familiar and novel tools appears to be primarily mediated by declarative memory.

Overview and Rationale of Experiment

Results from Roy and Park (2010), along with other existing research, suggest that intact declarative memory is necessary for the acquisition of tool attributes, tool grasping, and skilled tool use. However, the precise role of procedural memory in mediating aspects of tool-related knowledge and skills has not yet been investigated. Although it has been proposed that motor skill acquisition associated with complex tools requires procedural memory, it is unclear which form of procedural memory supports this type of learning (e.g., cortico-striatal vs. cortico-cerebellar). There is also growing evidence to suggest that, in addition to procedural memory, both motor skill acquisition and skilled tool use rely on declarative memory to a certain extent. In other words, these aspects of tool-related knowledge and skills may rely on an interaction of both memory systems. However, it is unclear what form this interaction takes (e.g., competitive, compensatory, cooperative) for different measures of tool-related knowledge and skills.

The current study was conducted as an extension to Roy and Park (2010) in order to investigate the specific role of the procedural memory system as well as the interaction of the declarative and procedural memory systems across various measures of tool-related knowledge and skills. This follow-up study investigated memory for the same aspects of tool-related knowledge and skills (i.e., motor skill acquisition, recall of tool features, tool grasping, and skilled tool use) in a sample of people with PD and healthy age-matched controls. Participants were tested over two sessions, with a 3-week delay between sessions. The following hypotheses were tested:

1. If motor skill learning associated with complex tools is mediated by a striatal form of procedural memory, participants with PD should demonstrate impairment in some aspect of motor skill learning. It has been proposed that the striatum is particularly important during retention of motor skills, but not as critical during initial learning (Doyon et al., 2009). In numerous studies, people with PD have been shown to have intact initial skill learning, but impaired long-term skill retention (Leow, Loftus, & Hammond, 2012; Marinelli et al., 2009; Mochizuki-Kawai et al., 2004). Therefore, it would be plausible to predict that participants with PD would show this same pattern of performance (i.e., intact learning within session, but impaired retention of motor skills after 3-week delay).

2. Based on previous research showing that declarative memory tends to be relatively intact in mild stages of PD, it is expected that memory for tool attributes would be unimpaired in participants with PD.

3. It was predicted that individuals with PD would be impaired in their tool grasping and skilled tool use relative to healthy controls. This prediction was based on the premise that these aspects of tool knowledge rely on an interaction of both declarative and procedural memory systems (Roy & Park, 2010).

4. It was predicted that after the 3-week delay all participants would show decreased recall of aspects of tool knowledge that are represented declaratively (e.g., function of the tool) and that the amount of decline would be equivalent for both individuals with PD and controls.

Method

Participants

A sample of 18 participants with a diagnosis of idiopathic PD and 18 healthy age-matched controls completed the study. One other participant with PD was unable to complete the study, as she was unable to follow instructions during the first session. Therefore, the session was terminated, and her data were not included in the final analyses. All participants with PD were recruited from the Sun Life Financial Movement Disorders Research Centre (MDRC) in Waterloo, Ontario, Canada. Seven control participants were recruited from the University of Waterloo's healthy older adult research participant pool, and the other 11 control participants were spouses of patients at the MDRC. A summary of participant characteristics can be found in Table 1. Participants with PD did not differ significantly from controls on any participant characteristics.

Inclusion criteria included being right-handed, fluent in English, and between the ages of 55 and 85. Exclusion criteria included a history of head injury resulting in loss of consciousness, a history of any neurological illnesses (other than PD in the patient group), psychotic symptoms (e.g., hallucinations), colour-blindness, general cognitive deterioration as evidenced by a score below 26 on the Mini-Mental State Examination (MMSE; Folstein, Folstein, & Folstein, 2010), current depression or anxiety as assessed by the Hospital Anxiety and Depression Scale (HADS; Zigmond & Snaith, 1983), and an inability to use the right hand freely due to injury or any other condition such as arthritis. In addition, participants with PD were not included if they had symptoms that would prevent them from performing the novel tool tasks including: severe tremor in the right hand, severe rigidity in the right hand or wrist which would affect the ability to manipulate small objects, or severe bradykinesia (i.e., slowed movement). These symptoms were assessed by asking patients a series of questions about their daily functioning (e.g., Does your tremor affect your ability to write? Use a hammer? Hold a toothbrush?) and by reviewing current scores from the motor section of the Unified Parkinson's Disease Rating Scale (UPDRS III; Fahn & Elton, 1987; see Table 1). Overall, participants in the current study were in the mild stages of PD disease severity (scores of ≤ 2 in UPDRS motor section).

Seventeen of the participants with PD were taking dopaminergic drugs, and they continued with their regular medication regimen throughout the study. One participant with PD was not taking any medication at all. None of the participants were taking anticholinergic drugs. Three participants with PD were also taking antidepressant medication; however, their symptoms did not meet criteria for depression or anxiety on the HADS at the time of testing. The experiment was approved by the relevant ethics review boards at York University, Wilfrid Laurier University, and University of Waterloo. Each participant provided written consent prior to participation.

Materials

Novel tools. A set of novel complex tools was constructed from K'NEX, a children's construction toy (see Figure 1). The tools were originally developed for an earlier study (Roy & Park, 2010). For the current study, a subset of nine tools was selected from the original set of 15. Of the 15 tools, these nine tools were included as they were found to be least susceptible to motor disturbance during pilot testing with a separate sample of PD patients. Each tool was designed to act on a unique object, hereafter called a recipient (e.g., small plastic wheel), in order to perform a specific function (e.g., guide a plastic wheel down a curved path). Each tool was painted a different colour, and previous research established that neither the function of the tool nor manner of grasp were apparent from physical appearance (see Roy & Park, 2010). All tools were designed to be used unimanually. Brief training videos of the tools were created to demonstrate the use of each tool. The videos also included an audio track that directed the participant's attention to specific details about the task as it was viewed (e.g., how to grasp the tool, where to position the recipient). The nine tools were divided randomly into three sets of three tools (Sets A, B, and C).

Recall test. A set of grey-scale images of the tools were used to develop a recall test of tool attributes. Three photographs of each tool were taken from three different, approximately equidistant, angles. During the recall test, participants were shown the three pictures of each tool, one tool at a time, and were asked to answer the following five questions about each tool: 1) What is the function of the tool/What is it used for? 2) What is the colour of the actual physical tool? 3) What is the recipient that the tool interacts with? 4) What is the colour of the recipient? and 5) How many recipients does the tool act on? Once the participant completed the five questions for a tool, they were not allowed to go back and review previous responses. Participants were asked to verbally provide their responses, and the experimenter recorded these responses verbatim.

Grasp-to-command test. Each tool was placed on a table in front of the participant without its associated recipient(s). In order to control for the position of the tool's handle, the tool was presented in one of three orientations. To use the analogy of a clock, if the participant was sitting at the hour-hand position of 6 o'clock, the tool handle was placed at approximately 1 o'clock, 4 o'clock, or 7 o'clock, in no predetermined order. The tool was not presented at 11 o'clock (i.e., handle furthest away from participant's right hand) to minimize discomfort and awkward hand positioning that may have interfered with scoring. The participant was instructed, "With your right hand, show me how you would grasp this tool if you were to use it. Show me the first thing that comes to mind." The participant was allowed to rotate the tool in order to make the handle more accessible. After the participant demonstrated the grasp, the participant was asked to release the tool.

Use-to-command test. After the participant demonstrated the grasp of a tool, the experimenter set up the entire task with all associated materials. The tool was positioned in front of the participant in the proper orientation for use, and the recipient(s) was placed in a small outlined square, to the left of the tool. The participant was instructed, "Again, using your right hand, I'd like you to show me how you would use the tool. Show me the first thing that comes to mind. Please let me know when you've completed the task." Participants were expected to first position the recipient in the correct starting location.

Then, they were given a limit of 90 seconds to demonstrate correct use of the tool from start to finish. Timing began when the tool made contact with the recipient and ended when either the task was completed without error or when the time limit was up. During use-to-command, participants were informed that the experimenter would not be providing them with any assistance or feedback on any aspect of their performance. Further details on the experimental materials and procedures can be found in Roy and Park (2010).

Neuropsychological Tests. A battery of standardized neuropsychological tests was administered to characterize participants with PD. This battery included the Hopkins Verbal Learning Test-Revised (HVLT-R; Benedict, Schretlen, Groninger, & Brandt, 1998), Brief Visuospatial Memory Test-Revised (BVMT-R; Benedict, 1997), Stroop Test - Victoria version (Troyer, Leach, & Strauss, 2006), Boston Naming Test (BNT; Heaton, Miller, Taylor, & Grant, 2004; Strauss, Sherman, & Strauss, 2006), Rey-Osterrieth Complex Figure Test – Copy only (ROCF; Fastenau, Denburg, Hufford, 1999; Lezak, Howieson, & Loring, 2004), Trail Making Test (Heaton et al., 2004; Strauss et al., 2006), FAS Verbal Fluency Test (Heaton et al., 2004), Animal Naming Test (Tombaugh, Kozak & Rees, 1999), selected tests from the Wechsler Adult Intelligence Scale (WAIS-IV; Wechsler, 2008), Grooved Pegboard (Lezak et al., 2004), and the Pantomime test from the Waterloo-Sunnybrook Apraxia Battery (Almeida, Black, & Roy, 2002). The Pantomime test was performed at the end of the session. The results from the Pantomime test will be reported in another related study and are therefore not presented here. The entire battery took approximately 50 minutes to complete, and it was administered on a separate day, after the two experimental sessions. Test results of individuals were combined to create a cognitive profile of the patient group (see Table 2). As a group, participants with PD performed within normal limits across all cognitive domains tested, with the majority of scores falling within one standard deviation above or below the normative mean. PD participants performed slightly above the normative mean on WAIS-IV subtests assessing working memory, perceptual reasoning, and verbal comprehension. Performance on tests of memory (HVLT-R, BVMT-R) were within normal limits. Performance on measures of executive function (Trails B–A, Stroop) were also within the normal range. Participants with PD performed within normal limits on tests of language abilities, scoring slightly above the normative mean on tests of naming and semantic fluency. Finally, there was a trend of weakness across speeded tests (e.g., Trails, Grooved Pegboard) which likely reflects generalized motor slowing associated with PD. Control participants did not undergo formal cognitive testing.

Design and Procedure

Each participant was tested individually over two 60-minute sessions (S1 and S2), three weeks apart.[1] Prior to each session, participants with PD underwent assessment of their motor symptoms (i.e., UPDRS-III) by Dr. Quincy Almeida, a kinesiologist and director of the Sun Life Financial Movement Disorders Research and Rehabilitation at

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[1] Participants with PD had one additional session, scheduled on a separate day, for neuropsychological testing.

Wilfrid Laurier University. Each session was composed of three phases: pretest, training, and post-test. The three tool sets (i.e., A, B, and C) were counterbalanced in their presentation across the three phases. Appendix A presents the experimental design and the counterbalance for the first six participants. The counterbalance was repeated two more times for the remaining 12 participants. In order to reduce fatigue for participants with PD, the number of tools trained was limited to two sets (i.e., six tools), and participants were trained twice on each tool (i.e., two trials per tool). One of the two trained sets was tested in the pretest and the other set was tested in the post-test. More specifically, the set that was trained first was presented in the post-test and the set that was trained second was presented in the pretest. The remaining untrained tool set was reserved for a single training trial at the end of S2. This design allowed for each session to fit within one hour, while still obtaining data on all measures. The implementation of this design will be outlined in the pretest, training, and post-test sections that follow.

Pretest. The pretest began with the recall test, followed by grasp-to-command and, finally, the use-to-command test, all described earlier. The pretest was conducted on only one set of the tools. The purpose of the pretest in S1 was to confirm that participants were not able to infer attributes, grasp, or use of the tools prior to formal training.

Training. After the pretest, participants were trained to use six of the tools, one at a time. In other words, they were trained on two sets of tools, one of which included the set used in the pretest. First, participants viewed the training video for the tool. During the video, the actual tool being shown in the video was positioned on a table in front of the participant in the proper orientation for use, and the recipient(s) was placed in a small outlined square to the left of the tool. Materials were positioned in the same locations in the videos as well. Participants were asked not to handle the tool while the video was playing.

Immediately after viewing the video, participants were asked to perform the task in the same manner as in the video. They were instructed to perform the task as quickly as possible, from start to finish, without making any errors, and to restart the task if they made any errors. They were given a 90-second time limit to complete one errorless trial. In order to perform the task in the same manner as shown in the video, participants first had to position the recipient in the correct location and then complete the task using the tool. Timing began when the tool made contact with the recipient and ended once an errorless (successful) trial was completed or when the time limit was up. The experimenter provided verbal feedback to participants to correct the initial grasp as well as errors during the task. Once the task was completed, or after the time limit was reached, the tool and all materials were reset to their original position and the participant was asked to perform the task again with the same tool for a second trial. Thus, participants performed two consecutive trials for each of the six tools. The order in which the tools were presented was fixed within each set; however, the order of tool sets was counterbalanced across participants.

Post-test. After completing the training phase, the post-test was administered which included the same test measures as the pretest. However, the Post-test was performed on the set of trained tools that was not used in the pretest (see Appendix A). For example, for Participant 1, the pretest was administered for Set A in S1. Then the participant was trained on Sets B and A, respectively. After training, the S1 post-test was administered on Set B. The post-test was administered on the tool set that was trained first (i.e., Set B) in order to minimize recency recall effects. In S2, a pretest was administered using Set B again, which allowed for the effect of delay to be examined for the same tools.

After the post-test in S2, participants were given one training trial with the remaining third set of tools that had not been presented earlier in the experiment (see Appendix A). The purpose of this trial with untrained tools was to confirm that improvement in performance across trials was attributable to learning of tool-specific motor skills rather than generalized improvement in ability to use similar tools.

Scoring and Statistical Analysis

The following scoring procedures were implemented for all measures in the current study. Inter-rater reliability is also presented for those measures that do not have an objective scoring system and, therefore may have required experimenter judgment. Inter-rater scores reflect the percentage of agreement between the two raters for a given measure. Further details on scoring procedures can be found in Roy and Park (2010).

Training performance for each training trial was assessed in two ways. Time to errorless (TTE) attempt measured the total time to complete the task from the start of the first attempt to the end of the first errorless attempt, and Time of errorless (TOE) attempt measured only the length of the successful attempt, from start to finish of that single attempt.(i.e., a subset of the TTE). In both scoring methods, if a participant was unable to complete the task successfully within the 90-second time limit, a maximum score of 90 seconds was recorded. The number of errors made during each task was also tallied and averaged across tools for each training trial.

Performance on the recall test was measured as the percentage of correct responses to items in each test trial. Total recall accuracy was measured as the percentage of correct items out of the total number of items. A scoring rubric was developed for the recall test which contains a set of acceptable responses for each item. This rubric is based on responses obtained from participants during initial pilot testing of the materials.

Grasp-to-command performance was scored as the percentage of correct grasp demonstrations to command in each test trial. Each correct demonstration was given one point. As described earlier, each tool has a unique functional manner of grasping that participants learn during the training phase. A second independent rater scored 30% of the data, and an inter-rater reliability score of 92.4% was obtained for grasp-to-command.

Performance on the use-to-command test can be broken down into two components, accuracy and completion time. Tool use accuracy was measured as the percentage of correct tool use demonstrations to command (e.g., whether or not a participant was able to complete the task successfully within 90 seconds), whereas completion time provided a measure of how quickly the participant was able to complete the task, in seconds. In terms of accuracy, if a participant was able to accurately demonstrate the tool's use within the 90-second time limit, the demonstration was scored as correct and one point was given. If the task was performed incorrectly, or was not completed within the 90-second time limit, the demonstration was marked as incorrect and given a score of zero. A second independent rater scored 30% of the data, and an inter-rater reliability score of 94.5% was obtained for use-to-command accuracy. Completion time for use-to-command performance was measured in the same manner as in training.

All experimental measures were analyzed using parametric statistical techniques. Analyses for each measure were divided into within-session and between-session components. Primary analyses for each measure included a two-way mixed ANOVA with group and trial as factors for the interaction and a one-way ANOVA for main effects of group and trial. All pairwise comparisons were performed using Bonferroni corrections and raw, unadjusted, *p*-values are reported.

Results

Training Completion Time

Within-session effects. There was a main effect of group showing that participants with PD were slower relative to controls overall, $F(1,34) = 8.51$, $p = .006$, $\eta^2 = .20$ (see Figure 2).[2] There was also a main effect of trial, showing that all participants became faster from T1 to T2, $F(1, 34) = 13.35$, $p = .001$, $\eta^2 = .28$, but there was no

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[2] In order to ensure that average time scores were not inflated by incomplete attempts (i.e., maximum time scores of 90 seconds) these incomplete attempts were removed before conducting analyses on completion time for both training and use-to-command.

significant interaction between group and trial, indicating that the rate of improvement across the two trials was comparable for the two groups. Slopes of improvement between T1 and T2 were calculated using linear regression for each group. Participants with PD improved at a rate of 8.67 s (*SE* = 4.60 s) between T1 and T2, whereas controls became faster at a rate of 7.43 s (*SE* = 2.68 s; see Figure 2). An independent samples *t*-test, using the means of individual slopes from T1 to T2, showed that there was no significant difference in rate between PD and control participants in S1, $t(34) = -.28$, $p = .78$, $\eta^2 = .002$.

Training performance for S2 was analyzed in the same manner as for S1. Results again showed that there was a main effect of group showing that participants with PD were slower overall compared to controls, $F(1,34) = 32.16$, $p < .001$, $\eta^2 = .48$ (see Figure 2). There was also a main effect of trial, showing that participants became faster from T3 to T4 across groups, $F(1, 34) = 36.80$, $p < .001$, $\eta^2 = .52$, but there was no significant interaction between group and trial. In S2, participants with PD became faster at a rate of 6.33 s (*SE* = 3.96 s) between T3 and T4, whereas controls became faster at the rate of 4.86 s (*SE* = 2.28 s). An independent samples *t*-test again showed no rate difference between PD and control participants, $t(17) = -.79$, $p = .43$, $\eta^2 = .018$. In summary, participants with PD were slower overall than controls in both S1 and S2. More importantly, however, both groups improved at an equal rate in both sessions.

Between-session effects. Analysis of performance after a 3-week delay revealed a significant interaction between group and trial on completion time, $F(1, 34) = 15.99$, $p <$

.001, $\eta^2 = .32$ (see Figure 2). Follow-up analyses showed that participants with PD exhibited significant slowing between T2 and T3, $t(17) = -4.57$, $p < .001$, $\eta^2 = .55$. In contrast, controls did not show significant slowing between sessions.

Trained versus untrained tools. Completion times for TI and the untrained set were analyzed and showed that there was no significant interaction between group and trial and no main effect of trial (see Figure 2). However, there was a main effect of group on completion time, $F(1, 34) = 4.64$, $p = .038$, $\eta^2 = .12$. In summary, although control participants were faster overall than participants with PD, there were no differences in completion time between T1 and untrained tools, demonstrating that skills acquired during training were tool-specific. [3]

Training Accuracy

Within session effects. In S1**,** there was no significant interaction between group and trial on the number of errors made, and there was also no main effect of group, between participants with PD (*M* = .68 errors, *SD* = .44 errors) and controls (*M* = .47 errors, *SD* = .39 errors). However, there was a main effect of trial between T1 (*M* = .71 errors, *SD* = .53 errors) and T2 (*M* = .43 errors, *SD* = .49 errors), $F(1, 34) = 8.26$, $p = .007$, $\eta^2 = .20$. In S2**,** there was no significant interaction between group and trial on the number of errors made. There was also no main effect of group between PD (*M* = .61

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[3] A similar pattern of training completion time results was obtained with TTE scores. Thus, only analyses with TOE scores are reported for both training and subsequent use-to-command analyses. TOE scores are reported as they are considered to be less biased than TTE scores. TTE scores may be influenced by variable inter-attempt factors that are unrelated to performance (e.g., time for participant to reset the task between attempts, participant pausing and reacting after making errors).

errors, *SD* = .48 errors) and controls (*M* = .34 errors, *SD* = .44 errors) and no main effect of trial between T3 (*M* = .51 errors, *SD* = .61 errors) and T4 (*M* = .53 errors, *SD* = .64 errors).

Between session effects. The effect of the 3-week delay on training accuracy was analyzed and there was no interaction between trial (T2 and T3) and group on the number of errors. There was no main effect of group between PD (*M* = .70 errors, *SD* = .54 errors) and controls (*M* = .34 errors, *SD* = .53 errors) and there was no main effect of trial between T2 (*M* = .44 errors, *SD* = .49 errors) and T3 (*M* = .51 errors, *SD* = .61 errors). In summary, the two groups did not differ in the number of errors made during training; hence, any differences obtained in completion time cannot be attributed to unexplained accuracy by group interactions.

Use-to-command Completion Time

Within-session effects. As expected, none of the participants were able to complete any of the tool tasks in S1 pretest, prior to training, resulting in a mean completion time of 90 s for both groups. Therefore, within-session analyses were not conducted for S1. An independent samples *t*-test showed that participants with PD were significantly slower than controls on S1 post-test, $t(34) = 2.11$, $p = .042$, $\eta^2 = .12$ (see Figure 3). Analysis of within-session effects in S2 found no interaction between group and trial on use-to-command completion time. However, there was a main effect of group, showing that participants with PD performed slower than controls overall, $F(1, 34) = 29.71$, $p < .001$, $\eta^2 = .47$. Also, there was a main effect of trial, showing that participants became faster from pretest to post-test in S2, $F(1, 34) = 9.48$, $p = .004$, $\eta^2 = .22$. Participants with PD became faster at a rate of 13.16 s (*SE* = 5.78 s) between pretest and post-test in S2, while controls became faster at the rate of 7.71 s (*SE* = 4.27 s). An independent samples *t*-test was conducted to compare rate of performance between participants with PD and controls for S2. No significant difference in rate was found between the two groups, $t(34) = .80$, $p = .43$, $\eta^2 = .02$.

Between-session effects. The effect of the 3-week delay on use-to-command completion time was analyzed and a significant interaction was found between group and trial, $F(1, 34) = 4.24$, $p = .047$, $\eta^2 = .11$ (see Figure 3). Follow-up analyses revealed that participants with PD showed significant slowing across the delay, $t(17) = -2.53$, $p = .021$, $\eta^2 = .27$. In contrast, controls did not show any difference in completion time between S1 post-test and S2 pretest.

Use-to-command Accuracy

Within-session effects. There was no significant interaction between group and test trial on use-to-command accuracy within S1 (see Figure 4). There was also no main effect of group. However, there was a main effect of test trial demonstrating that participants improved in their use-to-command accuracy across trials in S1, $F(1, 34) = 142.09$, $p < .001$, $\eta^2 = .81$. No significant interaction between group and test trial on use-to-command accuracy was found in S2. Also, there was no main effect of group on use-to-command accuracy within S2. However, there was a main effect of test trial, demonstrating that participants improved in use-to-command accuracy across test trials in S2, $F(1, 34) = 47.27$, $p < .001$, $\eta^2 = .58$.

Between-session effects. No significant interaction was found between group and test trial on use-to-command accuracy between sessions, and there was also no main effect of group (see Figure 4). However, there was a main effect of test trial, $F(1, 34) = 21.93$, $p < .001$, $\eta^2 = .39$, showing that use-to-command accuracy declined between S1 post-test and S2 pretest.

Recall Accuracy

Within-session effects. There was no interaction between group and test trial on recall performance within S1 (see Figure 5). Also, there was no main effect of group across the test trials. However, there was a main effect of test trial, such that recall accuracy improved significantly from pretest to post-test in S1, $F(1, 34) = 109.91$, $p < .001$, $\eta^2 = .76$. Within S2, there was again no significant interaction between group and test trial on recall accuracy (see Figure 5). However, there was a main effect of test trial, where recall accuracy improved significantly within S2, $F(1, 34) = 33.75$, $p < .001$, $\eta^2 = .50$. As in S1, recall accuracy did not differ between participants with PD and controls within S2, $F(1, 34) = .81$, $p = .38$, $\eta^2 = .023$.

Between-session effects. Analysis of the 3-week delay performance showed that there was no significant interaction between group and test trial on recall performance (see Figure 5). There was also no main effect of group and no main effect of trial. Thus, the two groups were equivalent in their recall performance as predicted, but, contrary to predictions, there was no significant decline in recall accuracy after the delay.

Grasp-to-command Accuracy

Within-session effects. There was no interaction between group and test trial on grasp-to-command accuracy and no main effect of group within S1 (see Figure 6). However, there was a significant main effect of test trial, where grasp-to-command performance improved in S1 for both groups, $F(1, 34) = 45.00$, $p < .001$, $\eta^2 = .57$. There was again no interaction between group and test trial on grasp-to-command performance and no main effect of group within S2. However, there was a significant main effect of test trial showing that grasp-to-command performance improved in S2 for both groups, $F(1, 34) = 27.88$, $p < .001$, $\eta^2 = .45$.

Between-session effects. Analysis of performance after the 3-week delay on grasp-to-command accuracy indicated no significant interaction between group and test trial and no main effect of group (see Figure 6). However, there was a main effect of trial, $F(1, 34) = 31.59$, $p < .001$, $\eta^2 = .48$, showing that grasp-to-command performance declined between S1 post-test and S2 pretest.

Discussion

Participants with PD and healthy age-matched controls were trained to use a set of novel complex tools over two sessions and were tested on their memory for various aspects of each tool’s use and its features. Previous research has shown that both declarative and procedural memory systems contribute to skilled tool use (Roy & Park, 2010). Previous research has also presented evidence of competitive, compensatory, and cooperative interaction between the declarative and procedural memory systems; however, these different forms of interaction have not yet been investigated in the domain of tool use. Thus, the aim of the current study was to directly investigate the role of procedural memory, and the nature of interaction between declarative and procedural memory, in mediating tool-related knowledge and skills in PD compared to a healthy control group.

Motor Skill Learning

Based on the assumption that motor skill acquisition associated with novel complex tools is striatally mediated, it was predicted that participants with PD would show impairment in motor skill learning relative to healthy controls. Within-session analysis indicated that although participants with PD were slower overall than controls, their performance improved at the same rate, suggesting intact skill learning. However, between-session analysis showed significant slowing over the 3-week delay in participants with PD suggesting impaired long-term retention of the motor skills. In contrast, the control participants did not show evidence of slowing over the 3-week delay and this result is consistent with findings reported in Roy and Park (2010). In other words, with generalized slowing already observed across trials, it appears that participants with PD showed additional slowing between Trials 2 and 3. It is unlikely that the additional increase in completion time across the delay can be explained by disease-related slowing alone, but rather reflects a lack of procedural skill retention due to striatal dysfunction. As previous research has shown, procedural skills are generally resistant to interference and decay (e.g., Matsuzaka, Picard, & Strick, 2006). Therefore, the current pattern of performance demonstrates that the striatal regions are not required for initial skill learning associated with use of complex tools, but appear to play a critical role in the retention of these skills. With regard to accuracy, participants performed well, with very few errors overall. There were also no group differences in the number of attempts across trials. In addition, the number of errors declined within S1, but did not decrease or increase in subsequent trials.

Regarding to the pattern of within- and between-session performance, it appears that different processes may be underlying these different stages of motor skill learning. Intact skill learning within session, but impaired skill retention between sessions, has been shown previously in individuals with PD as measured by both accuracy (Bédard & Sanes, 2011; Leow, Loftus, & Hammond, 2012; Marinelli et al., 2009) and completion time (Mochizuki-Kawai et al., 2004) on a variety of motor tasks. In terms of processes, it has been argued that the cortico-cerebellar circuit along with the hippocampus and frontal regions are primarily involved in early stages of learning and, therefore may support initial skill learning, but that the striatal system is necessary for long-term retention of motor skills after initial training (Albouy et al., 2013; Doyon et al., 2009; Mochizuki-Kawai et al., 2004).

Although the above interpretation of training results is plausible, it is worth noting that the pattern of intact learning within sessions and a decline in performance after a delay is also characteristic of a declarative pattern of learning. Thus, another interpretation of training results is that in participants with PD, declarative memory helped participants to compensate for an inefficient procedural memory system. This form of declarative memory compensation in participants with PD has been shown previously in studies using other striatally mediated tasks including PCL and motor sequence learning (Gobel et al., 2013; Moody et al., 2004). It has also been previously argued that the declarative and procedural memory systems share a competitive interaction during motor skill learning in healthy individuals (Albouy et al., 2013). Therefore, it is possible that the lack of an efficient procedural memory system, which would typically override the declarative system, led to overuse of the declarative system as a means of compensation. However, the extent to which the declarative system can effectively compensate for a dysfunctional procedural system during motor skill learning requires further investigation. Current findings would suggest that although declarative memory may be able to support initial skill learning, some aspect of performance would remain unfulfilled (e.g., retention over a delay) due to vulnerability of the declarative system to both decay and interference. In summary, training performance of participants with PD is consistent with impaired functioning of the procedural memory system, but the possibility of declarative compensation (instead or in addition) cannot be ruled out.

Skilled Tool Use

The use-to-command accuracy measure indicates whether or not a task was correctly performed, regardless of how quickly it was performed. Use-to-command accuracy of participants with PD was equivalent to that of controls. Both groups showed improved accuracy over test trials. Both groups also showed a significant decline in use-to-command accuracy after the 3-week delay. This pattern of performance is consistent with findings from Roy and Park (2010) and demonstrates that the use-to-command accuracy is heavily dependent on declarative memory.

As described, the use-to-command accuracy measure indicates whether or not a task is performed correctly, regardless of speed. In contrast, use-to-command completion time measures how quickly correctly performed tasks were completed. Results showed that within sessions, participants with PD were slower than controls; however, they improved at the same rate as controls. There was also an effect of the 3-week delay for participants with PD, but not for controls. In other words, participants with PD were significantly slower after the delay, whereas controls maintained their speed of performing the tool tasks. Thus, the pattern of use-to-command completion time within session is very similar to that of training performance. For both measures, performance reflects intact learning within sessions, but impaired retention between sessions. It should also be noted that only correct trials were included in analysis of completion time; therefore, slower completion time cannot be attributed to lower accuracy.

Based on the distinct patterns of performance, it could be proposed that use-to-command accuracy and completion time may measure distinct types of memory required for skilled tool use. For instance, based on the assumption that PD participants in the current study have intact declarative memory, but impaired procedural memory, it could be hypothesized that use-to-command accuracy depends on declarative memory whereas completion time reflects procedural memory. That is, tool use accuracy assesses whether declarative memory related to the tool task including critical contextual information (e.g., positioning of recipient) was retained, whereas tool use speed reflects procedural learning. As with motor skill learning, it is possible that skilled tool use performance in participants with PD reflects a greater reliance on declarative memory than procedural memory as a compensatory mechanism. Overall, use-to-command results are consistent with the hypothesis that skilled tool use relies on a cooperative interaction between declarative and procedural memory systems in healthy individuals. The current findings, taken together with Roy and Park (2010), suggest that both systems are necessary for proficient and accurate tool use. Although other studies have proposed that both memory systems are involved in skilled tool use, this is arguably the first study to provide direct evidence of this interaction and speculate on the differential roles of each system. However, further investigation is required to determine the specific contributions of declarative and procedural memory during skilled tool use.

Recall

It was predicted that participants with PD would be unimpaired in their recall of tool attributes relative to controls, and that both PD and control participants would show a decline in recall accuracy after a 3-week delay. As predicted, PD and control participants showed equivalent recall accuracy for tool attributes. Both groups showed evidence of learning various tool features (e.g., tool function, colours) across test trials.

Although a decline in recall accuracy was predicted after the 3-week delay for both groups, this hypothesis was not supported by the data. Neither group showed evidence of forgetting tool features after the delay. This result is inconsistent with the findings from Roy and Park (2010) in which control participants had significantly worse recall of tool attributes after a 3-week delay using the same tools. However, there are some methodological differences that may explain the lack of decline in recall accuracy in the current study. In Roy and Park (2010), participants were both trained and tested (i.e., Pretest and Post-test) on a set of 10 tools. In the current study, only six tools were trained, and three of the six were subsequently tested. Thus, it is possible that having a smaller tool set meant that participants had less information to learn and, hence, less information to forget over the delay. Although no effect of delay was found for either group, participants with PD still performed as well as controls in their recall accuracy. Unimpaired recall performance in the participants with PD is consistent with the hypothesis that knowledge of tool attributes is primarily mediated by declarative memory and neuropsychological test results showing that participants with PD were unimpaired on tests of declarative memory. These findings are also consistent with previous research showing that information about tool properties is represented within the declarative memory system and that declarative memory is relatively unimpaired in PD, at least in mild stages of the disease (Weisberg at al., 2007; Hay et al., 2002).

Tool Grasping

It was predicted that if tool grasping to command was dependent on both declarative and procedural memory systems, it would be impaired in participants with PD due to their procedural memory impairment. However, results showed that grasp-to-command performance of participants with PD was equivalent to that of controls. Both groups showed improvement over trials. In addition, both groups showed a significant decline in their grasp-to-command performance after the 3-week delay. Taken together, these results suggest that grasping a tool for use is strongly declarative in nature. These findings are also consistent with previous research showing that tool grasping for use relies on the declarative memory system (Creem & Proffit, 2001; Roy & Park, 2010). Although participants with PD were not impaired, a procedural component cannot be ruled out based on current findings. It is possible that the explicit manner of testing for tool grasping (i.e., to command) may have biased participants to use a more declarative strategy. It is also possible that precise methods of assessing grasp involving kinematic measures may reveal contributions of procedural memory in tool grasping.

Future Directions

It was proposed that the declarative memory system was more strongly activated in participants with PD compared to controls to compensate for their impaired procedural system during training and possibly use-to-command as well. The possibility of some form of compensation holds important implications for rehabilitation purposes. For instance, it may be worth exploring effects of inhibiting or limiting declarative involvement during skill learning to test the limits of this compensatory mechanism. Future research in this area would also benefit from more studies using tools and other physical objects as stimuli. The majority of existing studies investigating motor skill learning have used some form of computer-based testing. These types of tests are highly valued because of their standardization, ease of administration, and their established neural correlates. However, the use of physical tools may help to increase ecological validity and generalizability to everyday activities.

Conclusion

The current study demonstrates that declarative and procedural memory systems are both involved in learning many aspects of tool-related knowledge and skills. Although memory for tool features and tool grasping appears to be predominantly declarative, findings suggest that motor skill acquisition and skilled tool use require an interaction of both declarative and procedural memory systems. In the case of tool use, findings demonstrate a cooperative interaction in which the declarative memory system appears to be essential for encoding task-specific details, whereas the striatal-based procedural memory system is critical for the acquisition and retention of motor skills. Findings also suggest that motor skill acquisition requires an interaction of both systems. However, the precise nature of this interaction is less clear and may depend on various factors (e.g., nature of the task, measurement of performance; see Packard & Goodman, 2013). In general, the current findings suggest that striatal-based procedural memory is not required for initial stages of motor skill learning, and that this initial learning may be at least partly supported by the declarative system. However, declarative memory does not appear to be sufficient to support long-term retention of motor skills, which most likely requires striatal-based procedural memory. Current findings also raise the possibility that a declarative approach to skill learning, although not effective for all stages of learning, may be adopted by individuals with striatal damage (e.g., individuals with PD) as a means of compensation. From a clinical perspective, this compensatory tendency may have important implications for the development and modification of interventions that could improve rehabilitation programs for participants with PD.

References

Albouy, G., King, B. R., Maquet, P., & Doyon, J. (2013). Hippocampus and striatum: Dynamics and interaction during acquisition and sleep-related motor sequence memory consolidation. *Hippocampus*, *23*, 985-1004. doi:10.1002/hipo.22183

Almeida, Q. J., Black, S. E., & Roy, E. A. (2002). Screening for apraxia: A short assessment for stroke patients. *Brain and Cognition*, *48*, 253–258. doi: 10.1006/brcg.2001.1356

Barnes, J., Boubert, L., Harris, J., Lee, A., & David, A. S. (2003). Reality monitoring and visual hallucinations in Parkinson's disease. *Neuropsychologia*, 41, 565–574. doi:10.1016/s0028-3932(02)00182-3

Bechara, A., Tranel, D., Damasio, H., Adolphs, R., Rockland, C., & Damasio, A. (1995). Double dissociation of conditioning and declarative knowledge relative to the amygdala and hippocampus in humans. *Science*, *269*, 1115-1118. doi: 10.1056/NEJM199710303371801

Bédard, P., Sanes, J. N. (2011) Basal ganglia-dependent processes in recalling learned visual-motor adaptations. *Experimental Brain Research, 209*, 1–9. doi:10.1007/S00221-011-2561-Y

Benedict, R. H. B. (1997). *Brief Visuospatial Memory Test - Revised. Professional manual*. Odessa, FL: Psychological Assessment Resources.

Benedict, R. H. B., Schretlen, D., Groninger, L., & Brandt, J. (1998). The Hopkins Verbal Learning Test - Revised: Normative data and analysis of interform and test-retest reliability. *The Clinical Neuropsychologist, 12*, 43-55. doi:10.1076/clin.12.1.43.1726

Brashers-Krug, T, Shadmehr, R., Bizzi, E. (1996). Consolidation in human motor memory. *Nature, 382*, 252-255. doi:10.1038/382252a0

Buxbaum, L. J., Kyle, K.M., Tang, K., & Detre, J. M. (2006). Neural substrates of knowledge on hand postures for object grasping and functional object use: Evidence from fMRI. *Brain Research, 1117*, 175–185.

Buxbaum, L. J., Schwartz, M. F., & Carew, T. G. (1997). The role of semantic memory in object use. *Cognitive Neuropsychology, 14*, 219-254. doi: 10.1080/026432997381565

Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience, 2*, 913-919. doi:10.1038/13217

Cohen, N. J., & Squire, L. R. (1980) Preserved learning and retention of pattern-analyzing skill in amnesia: Dissociation of knowing how and knowing that. *Science, 210*, 207-210. doi:10.1126/science.7414331

Creem-Regehr, S. H., & Lee, J. N. (2005). Neural representations of graspable objects: Are tools special? *Cognitive Brain Research, 22*, 457-469. doi: 10.1016/j.cogbrainres.2004.10.006

Creem, S. H., & Proffit, D. R. (2001). Grasping objects by their handles: A necessary interaction between cognition and action. *Journal of Experimental Psychology:*

Human Perception and Performance, 27, 218-228. doi:10.1037/0096-1523.27.1.218

Daprati, E., & Sirigu, A. (2006). How we interact with objects: Learning from brain lesions. *Trends in Cognitive Sciences, 10*, 265-270. doi:10.1016/j.tics.2006.04.005

Doyon, J. (2003). Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia*, *41*, 252-262. doi:10.1016/s0028-3932(02)00158-6

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J.,... Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research*, *199*, 61-75. doi:10.1016/j.bbr.2008.11.012

Fahn, S., & Elton, R. L. (1987). Unified Parkinson's disease rating scale. In S. Fahn, C. D. Marsden, C. D., D.B. Calne, & M. Goldstein (Eds.), *Recent developments in Parkinson's disease II* (pp.153-163). Florham Park, NJ: Macmilian.

Fastenau, P. S., Denburg, N. L., & Hufford, B. J. (1999). Adult Norms for the Rey-Osterrieth Complex Figure Test and for Supplemental Recognition and Matching Trials from the Extended Complex Figure Test. *The Clinical Neuropsychologist*, *13*, 30–47. doi:10.1076/clin.13.1.30.1976

Foerde, K., Knowlton, B. J., & Poldrack, R. A. (2006). Modulation of competing memory systems by distraction. *Proceedings of the National Academy of Sciences, USA, 103*, 11778-11783. doi:10.1073/pnas.0602659103

Folstein, M., Folstein, S. and Folstein, J. (2010) The Mini-Mental State Examination: A Brief Cognitive Assessment. In M. T. Abou-Saleh, C. Katona & A. Kumar (Eds.), *Principles and Practice of Geriatric Psychiatry (3rd Edition)* (pp.145-146). Chichester, UK: John Wiley & Sons. doi: 10.1002/9780470669600.ch27

Foundas, A. L., Macauley, B. L., Raymer, A. M., & Maher, L. M. (1995). Ecological implications of limb apraxia: Evidence from mealtime behavior. *Journal of the International Neuropsychological Society, 1*, 62-66. doi:10.1017/s1355617700000114

Frey, S. H. (2007). What puts the how in where? Tool use and the divided visual streams hypothesis. *Cortex, 43,* 368-375. doi:10.1016/s0010-9452(08)70462-3

Gabrieli, J. D., Corkin, S., Mickel, S. F.,& Growdon, J. H. (1993). Intact acquisition and long-term retention of mirror-tracing skill in Alzheimer's disease and in global amnesia. *Behavioral Neuroscience, 107,* 899-910. doi: 10.1037/0894-4105.11.2.272

Gibson, J.J. (1977). The theory of affordances. In R. Shaw & J. Bransford (Eds.), *Perceiving, acting, and knowing: Toward an ecological psychology*. Hillsdale, NJ: Erlbaum.

Gobel, E. W., Blomeke, K., Zadikoff, C., Simuni, T., Weintraub, S., & Reber, P. J. (2013). Implicit perceptual-motor skill learning in mild cognitive impairment and Parkinson’s disease. *Neuropsychology, 27,* 314-321. doi: 10.1037/a0032305

Goldenberg, G. & Spatt, J. (2009). The neural basis of tool use. *Brain, 132*, 1645-1655. doi: 10.3389/fpsyg.2014.00310 10.3389/fpsyg.2014.00310

Hartmann, K., Goldenberg, G., Daumüller, M., & Hermsdörfer, J. (2005). It takes the whole brain to make a cup of coffee: The neuropsychology of naturalistic actions involving technical devices. *Neuropsychologia*, *43*, 625-637. doi: 10.1016/j.neuropsychologia.2004.07.015

Hay, J. F., Moscovitch, M., & Levine, B. (2002). Dissociating habit and recollection: evidence from Parkinson's disease, amnesia and focal lesion patients. *Neuropsychologia*, 40, 1324–1334. doi:10.1016/s0028-3932(01)00214-7

Heaton, R. K., Miller, S. W., Taylor, M. J., & Grant, I. (2004). *Revised comprehensive norms for an expanded Halstead–Reitan battery*. Odessa, FL: Psychological Assessment Resources.

Heilman, K. L. (2002). *Matter of mind.* New York: Oxford University Press. doi: 10.1093/acprof:oso/9780195144901.001.0001

Hodges, J. R., Bozeat, S., Lambon Ralph, M. A., Patterson, K., & Spatt, J. (2000). The role of conceptual knowledge in object use. Evidence from semantic dementia. *Brain*, *123* 1913–1925. doi:10.1093/brain/123.9.1913

Knowlton, B. J.., & Foerde, K**.** (2008). Neural representations of nondeclarative memories. *Current Directions in Psychological Science*, *17*, 62-67. doi: 10.1111/j.1467-8721.2008.00558.x 10.1111/j.1467-8721.2008.00558.x

Knowlton, B. J., Mangels, J. A., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science, 273,* 1399–1402. doi:10.1126/science.273.5280.1399

Leow, L., Loftus, A. M., & Hammond, G. R. (2012). Impaired savings despite intact initial learning of motor adaptation in Parkinson's disease. *Experimental Brain Research, 218*, 295-304. doi: 10.1007/s00221-012-3060-5

Lezak, M., Howieson D.B., & Loring D.W. (2004). *Neuropsychological assessment 4th Edition.* New York: Oxford University Press.

Marinelli, L., Crupi, D., Di Rocco, A., Bove, M., Eidelberg, D., Abbruzzese, G., & Ghilardi, M. F. (2009) Learning and consolidation of visuo-motor adaptation in Parkinson's disease. *Parkinsonism and Related Disorders, 15,* 6–11. doi: 10.1016/j.parkreldis.2008.02.012

Matsuzaka, Y., Picard, N., & Strick, P. L. (2006). Skill representation in the primary motor cortex after long-term practice. *Journal of Neurophysiology, 97*, 1819-1832. doi:10.1152/jn.00784.2006

Mochizuki-Kawai, H., Kawamura, M., Hasegawa, Y., Mochizuki, S., Oeda, R., Yamanaka, K., & Tagaya, H. (2004). Deficits in long-term retention of learned motor skills in patients with cortical or subcortical degeneration. *Neuropsychologia*, *42*, 1858-1863. doi:10.1016/j.neuropsychologia.2004.03.012

Moody, T. D., Bookheimer, S. Y., Vanek, Z., & Knowlton, B. J. (2004). An implicit learning task activates the medial temporal lobe in patients with Parkinson's disease. *Behavioral Neuroscience, 118,* 438–442. doi: 10.1037/0735-7044.118.2.438

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology, 7*, 217-227. doi: 10.1016/s0959-4388(97)80010-4 10.1016/s0959-4388(97)80010-4

Negri, G. A., Lunardelli, A., Gigli, G. L., & Rumiati, R. I. (2007). Degraded semanticknowledge and accurate object use. *Cortex, 43*, 376–388. doi:10.1016/s0010-9452(08)70463-5

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology, 19,* 1–32. doi:10.1016/0010-0285(87)90002-8

Packard, M. G., & Goodman, J. (2013). Factors that influence the relative use of multiple memory systems. *Hippocampus, 23,* 1044-1052. doi:10.1002/hipo.22178

Packard, M. G., & Knowlton, B. J. (2002). Learning and memory functions of the basal ganglia. *Annual Review of Neuroscience, 25,* 563-593. doi: 10.1146/annurev.neuro.25.112701.142937

Penhune, V. B., & Steele, C. J. (2012). Parallel contributions of cerebellar, striatal and M1 mechanisms to motor sequence learning. *Behavioural Brain Research, 226,* 579-591. doi:10.1111/j.1749-6632.2011.06434.x

Poldrack, R., & Packard, M. G. (2003). Competition among multiple memory systems: Converging evidence from animal and human brain studies. *Neuropsychologia*, *41*, 245-251. doi:10.1016/s0028-3932(02)00157-4

Reber, P. J., & Squire, L. R. (1994). Parallel brain systems for learning with and without awareness. *Learning & Memory, 1*, 217–229. doi: 10.1101/lm.1.4.217

Roy, S., & Park, N. W. (2010). Dissociating the memory systems mediating complex tool knowledge and skills. *Neuropsychologia*, *48*, 3026-3036. doi: 10.1016/j.neuropsychologia.2010.06.012

Schendan, H. E., Searl, M. M., Melrose, R. J., & Stern, C. E. (2003). An fMRI study of the role of the medial temporal lobe in implicit and explicit sequence learning. *Neuron*, *37*, 1013-1025. doi: 10.1016/s0896-6273(03)00123-510.1016/s0896-6273(03)00123-5

Siegert, R. J., Taylor, K. D., Weatherall, M., & Abernethy, D. A. (2006). Is implicit sequence learning impaired in Parkinson’s disease? A meta- analysis. *Neuropsychology, 20*, 490–495. doi:10.1037/0894-4105.20.4.490

Silveri, M. C., & Ciccarelli, N. (2009). Semantic memory in object use. *Neuropsychologia*, 47, 2634-2641. doi:10.1016/j.neuropsychologia.2009.05.013

Song, S., Howard, J. H., & Howard, D. V. (2007). Implicit probabilistic sequence learning is independent of explicit awareness. *Learning & Memory*, *14*, 167-176. doi:10.1101/lm.437407

Squire, L. R. (2009). Memory and brain systems: 1969-2009. *Journal of Neuroscience, 29*, 12711-12716. doi:10.1523/jneurosci.3575-09.2009

Strauss, E., Sherman, E. M. S., & Spreen, O. (2006). *A compendium of neuropsychological tests – Administration, norms and commentary (3rd Edition).* Oxford: Oxford University Press.

Tombaugh, T.N., Kozak, J., & Rees, L. (1999). Normative data stratified by age and education for two measures of verbal fluency: FAS and animal naming. *Archives of Clinical Neuropsychology*, *14*, 167–177. doi:10.1016/s0887-6177(97)00095-4

Troyer, A. K., Leach, L., & Strauss, E. (2006). Aging and response inhbition: Normative data for the Victoria Stroop Test. *Aging, Neuropsychology, and Cognition, 13*, 20-35. doi: 10.1080/13825589096818710.1080/138255890968187

van Halteren-van Tilborg, I. A. D. A., Scherder, E. J. A., & Hulstijn, W. (2007). Motor-skill learning in Alzheimer's disease: A review with an eye to the clinical practice. *Neuropsychology Review, 17,* 203–212. doi:10.1007/s11065-007-9030-1

Warrington, E. K. (1975). The selective impairment of semantic memory. *The Quarterly Journal of Experimental Psychology*, *27,* 635-657. doi:10.1080/14640747508400525

Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain, 107*, 829–854. doi:10.1093/brain/107.3.829

Wechsler, D. (2008). *Wechsler Adult Intelligence Scale–Fourth Edition*. San Antonio, TX: Pearson.

Weisberg, J., van Turennout, & Martin, A. (2007). A neural system for learning about object function. *Cerebral Cortex, 17,* 513-521. doi:10.1093/cercor/bhj176

Zigmond, A. S., & Snaith, R. P. (1983). The Hospital Anxiety and Depression Scale. *Acta Psychiatrica Scandinavica*, *67*, 361-370. doi:10.1037/t03589-000

Table 1

Participant Characteristics

	PD (n = 18)	CON (n = 18)	*t*-value	*p*-value
Variable	M (SD)	M (SD)		
Age (years)	67.3 (6.6)	70.8 (6.8)	-1.57	.13
Education (years)	14.8 (2.7)	14.5 (3.6)	.28	.78
Sex (M/F)	10/8			
MMSE (max = 30)	28.2 (1.4)	28.8 (1.0)	-1.63	.11
HADS – Total (max = 42)	9.8 (6.4)	7.2 (6.2)	1.22	.23
HADS – Depression (max = 21)	4.3 (3.1)	2.6 (3.5)	1.51	.14
HADS – Anxiety (max = 21)	5.5 (3.6)	4.6 (3.6)	.76	.46
Onset (years)	4.6 (3.4)			
UPDRS motor section				
Session 1	24.9 (6.7)			
Session 2	23.2 (6.3)			
Side affected (L/R/B)	10/7/1			
LED (mg/day)	516.7 (168.7)			

PD, Parkinson's disease; CON, Controls; MMSE, Mini-mental State Examination; HADS, Hospital Anxiety and Depression Scale; UPDRS, Unified Parkinson's Disease Rating Scale (higher scores reflect greater motor impairment); L/R/B, Left/Right/Both; LED, levodopa-equivalent dose.

Table 2

Neuropsychological Test Performance of PD Participants

Neuropsychological Test	Mean Score	Mean z-scores (SD)[a]
WAIS-IV (selected subtests)		
Digit Span (SS)	10	.074 (.63)
Matrix Reasoning (SS)	10	.16 (.90)
Information (SS)	11	.41 (.93)
HVLT-R		
Total Recall (T-score)	47	-.28 (.96)
Delayed Recall (/12)	8.50	-.22 (1.0)
Percent Retained (%)	86.28	.00 (1.0)
BVMT-R		
Total Recall (T-score)	48	-.20 (1.2)
Delayed Recall (/12)	8.11	.00 (1.1)
Percent Retained (%)	91.42	.06 (.5)
ROCF - Copy (/36)	29.94	-.12 (1.3)
Trail Making Test		
Part A (in seconds)	39.79	-.38 (.7)
Part B (in seconds)	106.79	-.63 (1.1)
Part B-A (in seconds)	67.00	-.04 (.9)
Stroop Test (Victoria version)		
Dots (in seconds)	12.39	.06 (.9)
Words (in seconds)	16.33	.10 (.8)
Colour-Word (in seconds)	28.94	.31 (1.1)
Phonemic fluency – FAS (total words)	43.67	.28 (.9)
Semantic fluency		
Animals (total words)	20.39	.53 (1.2)
Supermarket (total words)	21.83	.00 (1.0)
Boston Naming Test (/30)	28.83	.62 (.7)
Grooved Pegboard		
Dominant hand (in seconds)	96.60	-.83 (.90)
Non-dominant hand (in seconds)	114.90	-1.08(.90)

WAIS-IV = Wechsler Adult Intelligence Scale – Fourth Edition; HVLT-R = Hopkins Verbal Learning Test – Revised; BVMT-R = Brief Visuospatial Memory Test – Revised; ROCF = Rey Osterrieth Complex Figure.

[a] Raw scores on each test were first scored according to appropriate normative data for each participant and were then converted to z-scores. Mean z-scores represent group averages of these z-scores.

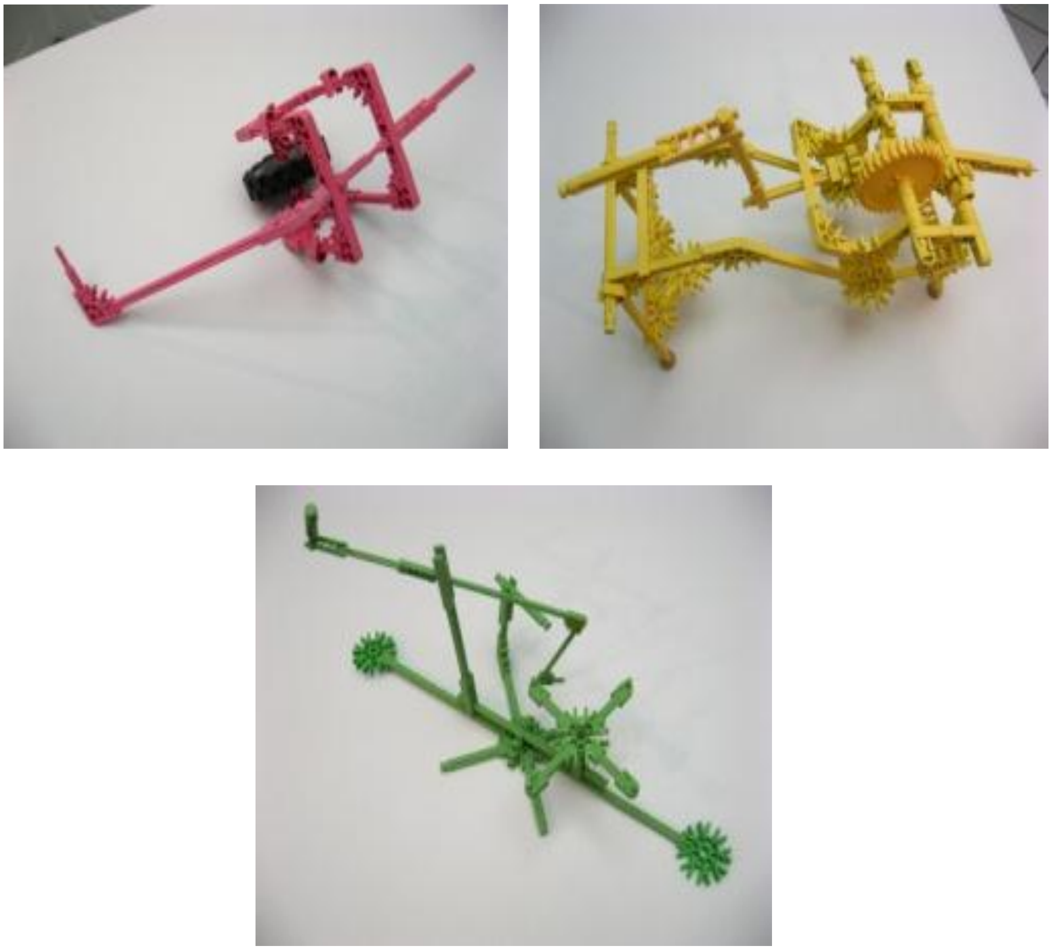

Figure 1. Examples of novel tools developed for this research.

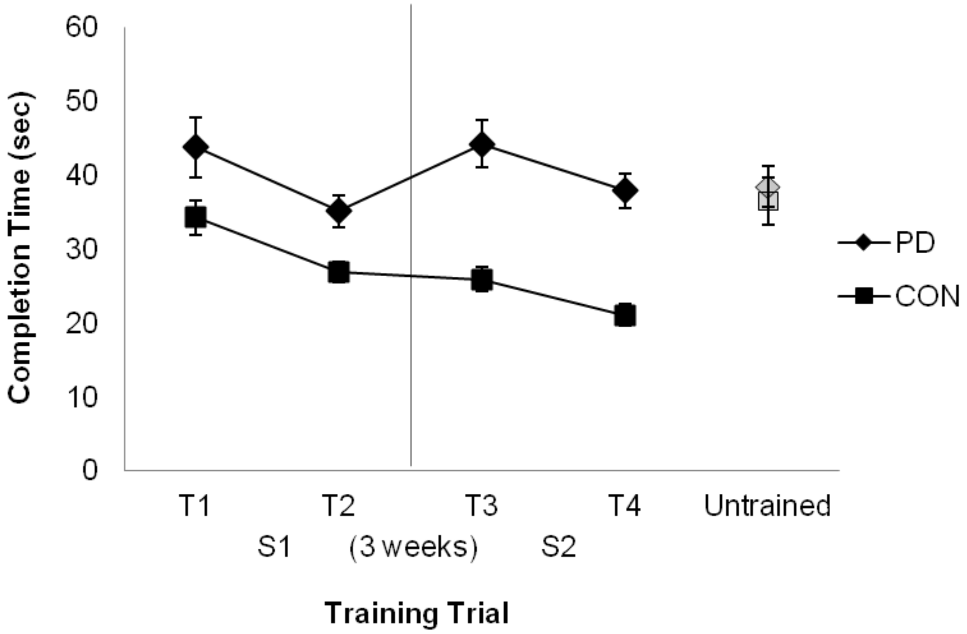

Figure 2. Mean completion time (+/- SE) across training trials (T1, T2, T3, T4, and Untrained) in Sessions 1 and 2 (S1, S2) for PD and control participants.

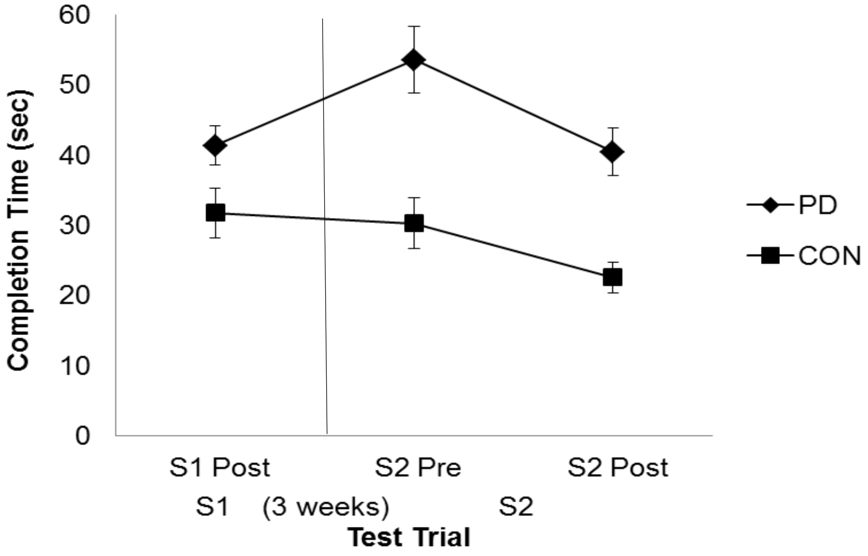

Figure 3. Mean completion time during use-to-command (+/- SE) across test trials (S1 Post-test, S2 Pretest, and S2 Post-test) in Sessions 1 and 2 (S1, S2) for PD participants and controls.

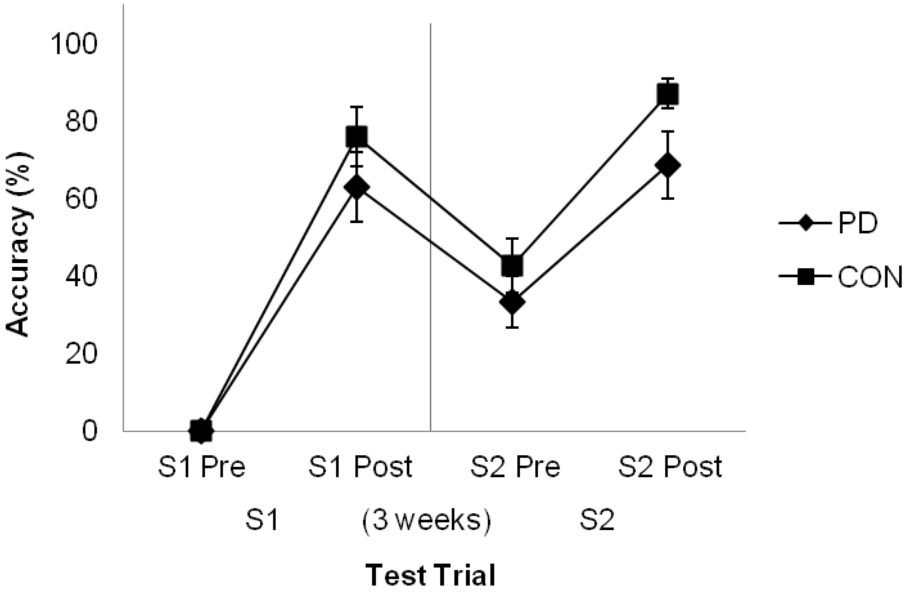

Figure 4. Percentage of correct use-to-command demonstrations (+/- SE) across test trials (S1 Pretest, S1 Post-test, S2 Pretest, and S2 Post-test) in Sessions 1 and 2 (S1, S2) for PD participants and controls.

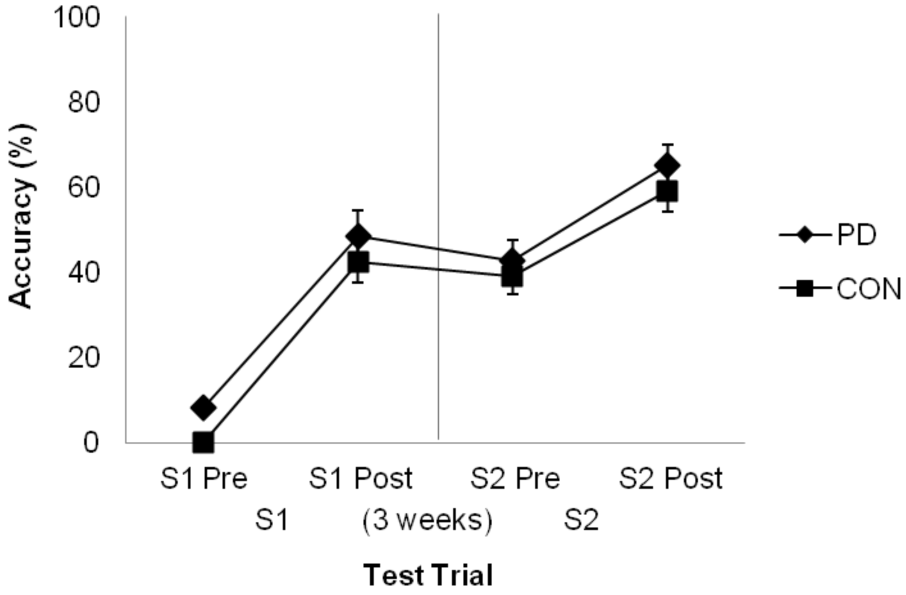

Figure 5. Percentage of correct responses (+/- SE) for recall items across test trials (S1 Pretest, S1 Post-test, S2 Pretest, and S2 Post-test) in Sessions 1 and 2 (S1, S2) for PD participants and controls.

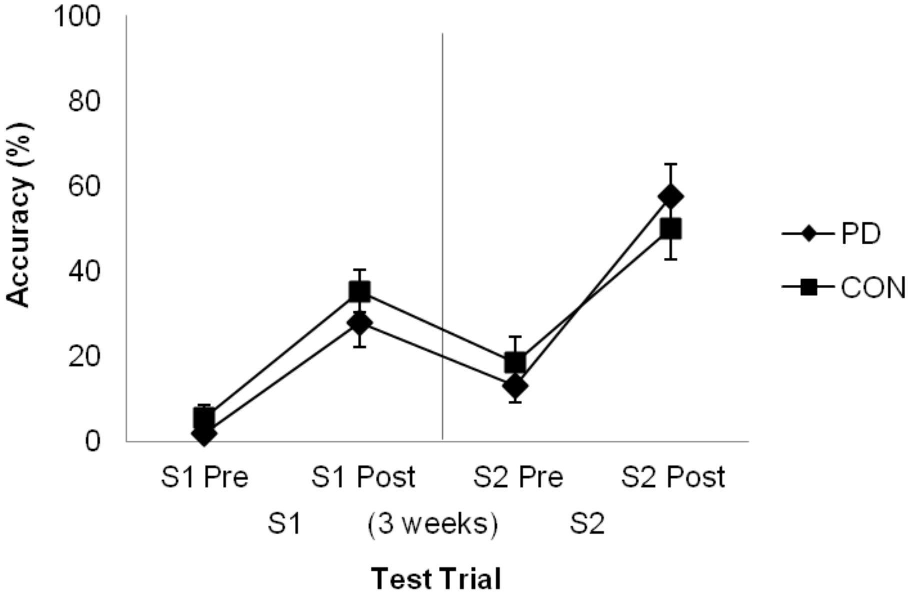

Figure 6. Percentage of correct grasp-to-command demonstrations (+/- SE) across test trials (S1 Pretest, S1 Post-test, S2 Pretest, and S2 Post-test) in Sessions 1 and 2 (S1, S2) for PD participants and controls.

Chapter 3: Using divided attention to investigate the interaction of declarative and procedural memory in mediating tool-related knowledge and skills (Experiment 2)

As humans, we have developed customized tools for almost every function in our lives whether it is to shave with a razor, flip an egg with a spatula, or cut paper with scissors. These manufactured tools, which are designed to provide a mechanical advantage in interacting with action recipients, are referred to as *complex tools*. *Simple tools*, in contrast, only amplify the movement of upper limbs (e.g., extending reach with a stick; Frey, 2007; Heilman, 2002). We learn how to use various complex tools throughout our lives and become heavily dependent on them to perform daily activities. Thus, the ability to use such tools is critical for independent living. However, as a result of certain neurological conditions, people are often left unable to use tools that they may have used proficiently in the past. In some cases, these individuals may also be unable to learn how to use new tools to perform new functions. These devastating impairments can impact one's ability to live independently, and it has been shown that a lack of independent living is associated with poor quality of life (Foundas, Macauley, Raymer, & Maher, 1995). Yet we do not have a clear understanding of how people learn to use novel tools and how different aspects of tool-related knowledge and skills are represented in the brain. For instance, it has been proposed that multiple memory systems are involved in learning various aspects of tool-related information and that these memory systems may interact in mediating some aspects of tool use (Daprati & Sirigu, 2006; Roy & Park, 2010; Silveri & Ciccarelli, 2009). However, there is still some debate about the specific memory representations of different components of tool use. Furthermore, we are still discovering how different memory systems are organized and how they function, both independently and interactively (e.g., Albouy, King, Maquet, & Doyon, 2013; Packard & Goodman, 2013). Further investigation in this area would deepen our understanding of human memory organization and would also assist in rehabilitative efforts of various tool-related deficits.

The current experiment was conducted as an extension to two previous patient studies that investigated the memory representations of complex tool-related knowledge and skills (Roy & Park, 2010; Roy, Park, Roy, & Almeida, in press). Findings from these two patient studies suggest that memory for tool attributes and tool grasping is primarily declarative, whereas motor skill acquisition and skilled tool use may rely on an interaction of both declarative and procedural memory systems. However, the nature of these interactions and the relative contribution of each memory system are still unclear. Furthermore, findings in these previous studies are based on performance of individuals with damage to particular memory systems (i.e., amnesia, PD). Thus, it is unclear how tool-related knowledge and skills are represented in healthy, cognitively unimpaired, individuals and whether these representations are consistent with earlier patient studies. The current study investigated memory for tool knowledge and skills in a healthy population using a divided attention paradigm as a means of selectively interfering with declarative encoding processes. A brief review of human memory systems, memory representations of tool-related knowledge and skills, and effects of divided attention on memory is provided below, followed by an overview of the current study.

Human Memory Systems

It is generally accepted that memory is not a unitary construct, but that there are multiple memory systems represented in different parts of the brain (see Squire, 2009). The most common distinction is made between declarative memory and procedural memory. Declarative memory includes knowledge that can be consciously retrieved, including both semantic (i.e., general knowledge) and episodic (i.e., recollection of personal experiences) memory (Squire, 2009). Declarative memory is believed to rely on the medial temporal lobes, including the hippocampus and related structures (Squire, 2009). Procedural memory, in contrast, is a form of nondeclarative memory that is involved in incremental learning of motor skills and cognitive habits (Squire, 2009). Procedural learning is believed to take place implicitly, without demands for attentional resources (Reber, 1993). It is also believed that the frontal-striatal system plays a critical role in supporting procedural memory; however, other brain regions, such as the cerebellum, have also been implicated (see see Doyon et al., 2009; Penhune & Steele, 2012; also see Shohamy, Myers, Kalanithi, & Gluck, 2008). Thus, declarative and procedural memory systems appear to be anatomically and functionally dissociable (see Knowlton, Mangels, & Squire, 1996).

Although early memory research tended to investigate each memory system in isolation based on the assumption that they are distinct, a growing body of research suggests that the two systems are connected and may function interactively. For instance, studies have provided evidence for a *cooperative* interaction, a *competitive* interaction, and a *compensatory* interaction between the two systems. It has been proposed that the two systems are cooperative, or complementary, in that they are both required, but each system has a different role in supporting performance (McLelland, McNaughton, and O'Reilly, 1995). For instance, it has been proposed that the declarative system is equipped to rapidly learn new information, but that this information tends to be sensitive to interference and decay. On the other hand, the procedural system is a slow learning system, but the information tends to be resistant to interference and decay (Gabrieli, Corkin, Mickel, & Growdon, 1993; but see Brashers-Krug, Shadmehr, & Bizzi, 1996). Thus, the two systems may support learning of different aspects of the same task (McLelland et al., 1995).

Evidence of a competitive relationship between declarative and procedural memory can be found in the domain of motor skill acquisition. It has been argued that whereas motor skill acquisition is primarily mediated by procedural memory, the declarative memory system may interfere with procedural learning in early stages of learning. Brown and Robertson (2007) showed that when motor skill learning was immediately followed by a declarative memory task, offline procedural learning of the motor skill was enhanced. Thus, in some circumstances, the two systems may compete, such that one system interferes with the functioning of the other system.

In a compensatory interaction, the system that typically mediates performance is compromised, and the other system is recruited to support performance. In research with probabilistic classification learning, a task considered to be learned implicitly, a compensatory interaction was found in participants with Parkinson's disease (PD; Moody, Bookheimer, Vanek, & Knowlton, 2004). Participants with PD were able to perform the probabilistic classification learning task as well as controls; however, neuroimaging results showed that controls recruited the striatum for task performance, whereas PD participants recruited medial temporal lobe structures. Thus, the concept of two fully independent memory systems may no longer be accurate, and recent research suggests that the nature of interaction between the two systems actually varies across different domains and forms of learning (for a review, see Foerde & Shohamy, 2011).

Memory Representations of Tool-related Knowledge and Skills

Learning how to use a novel complex tool requires one to learn several bits of information and skills related to the tool (e.g., knowledge of its function, how it is grasped, motor skill associated with its use). It has been argued that different components of tool-related knowledge and skills may be represented within different memory systems. For instance, previous research suggests that information about tools and their properties depend on regions associated with declarative memory (Roy & Park, 2010, Warrington & Shallice, 1984; Weisberg, van Turennout, and Martin, 2007). Individuals with medial temporal lobe damage are impaired in their memory for object-specific information (Warrington, 1975; Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000). The declarative memory system has also been shown to be critical in mediating tool grasping for use (Creem-Regehr & Lee, 2005; Creem & Proffitt, 2001). In Roy and Park (2010), an amnesic individual who was trained to use a set of novel complex tools was severely impaired in his ability to recall the proper manner of grasping for these tools when subsequently tested.

In contrast to memory for tool attributes and tool grasping, which have been shown to rely on declarative memory, it is generally accepted that motor skill learning relies primarily on the procedural memory system. It is believed that the basal ganglia and related structures, particularly the striatum, play a critical role in supporting motor skill acquisition and retention (Doyon et al., 2009). Disease of these brain regions has been associated with impaired procedural memory. For example, people with Parkinson's disease are impaired on procedural memory tasks such as probabilistic classification learning and motor sequence learning (Knowlton et al., 1996; Siegert, Taylor, Weatherall, & Abernethy, 2006). However, there is some debate about the role of declarative memory in motor skill learning. Some have argued that motor skill learning may involve a competitive interaction of declarative and procedural memory. In this interaction, declarative memory competes with procedural memory during early stages of motor skill learning and creates a naturally occurring impediment in learning. Similarly, when the declarative system is disengaged from the process, motor skill learning is enhanced (Brown & Robertson, 2007).

Others have argued that declarative memory has a necessary role in early stages of motor skill learning and that a cooperative interaction of both systems is required (see Penhune & Steele, 2012). There is also evidence of a compensatory interaction in which the declarative system may become more involved in supporting motor skill learning when the procedural system is compromised (Gobel et al., 2013). Thus, although procedural memory may have the primary role in mediating motor skill learning, declarative memory may be involved in some capacity during learning. The precise nature of this interaction between the two memory systems, however, is unclear.

Lastly, it has been proposed that skilled tool use (i.e., intentional tool use) also relies on an interaction of both declarative and procedural memory systems (Negri, Lunardelli, Gigli, & Rumiati, 2007; Roy & Park, 2010; Silveri & Ciccarelli, 2009). However, this interaction had not been directly investigated until recently. In Roy & Park (2010), an amnesic individual, D.A., showed unimpaired motor skill acquisition associated with novel complex tools, but was unable to demonstrate the use of these tools to command. Yet, when the tool's recipient (i.e., the object that the tool acts on) was positioned in its starting location (i.e., appropriate location for task execution) by the experimenter, his ability to use the tools improved remarkably. This finding suggests that although D.A. was able to learn the motor skill associated with a tool's use, he could not demonstrate the tool's use to command because he could not retrieve declarative knowledge related to the tool's use (e.g., recipient placement). Thus, it was argued that declarative memory is critical for remembering contextual information related to the task, whereas procedural memory is critical for skilled enactment of the motor skill. Individuals with PD were tested in a similar experiment in which they were trained to use a set of novel complex tools and were subsequently tested on their ability to demonstrate tool use to command (Experiment 1). Results showed that participants with PD had no difficulty in performing components of the tasks accurately; however, unlike healthy controls, they did not maintain their speed of task completion after a 3-week delay. Based on these previous patient studies, it could be argued that skilled tool use relies on a cooperative interaction of both declarative and procedural memory systems. More precisely, it could be argued that declarative memory guides accurate tool use involving recall of task-related details (e.g., recipient placement, sequence of steps) and that procedural memory mediates skilled demonstration of tool use.

Effects of Dividing Attention on Memory

The dual-task paradigm, also known as the divided attention paradigm, is a classic behavioural technique used to study the effects of distraction on memory performance. In the typical experimental procedure, participants perform a primary memory task (e.g., list learning) and a secondary attention-demanding distracter task (e.g., tone counting) concurrently. Performance of the primary task under both divided and full attention conditions are then compared to assess consequences of dividing attention.

Effects of Dividing Attention on Declarative Memory

The general consensus in the literature is that declarative memory requires attentional resources and that dividing attention can have a negative effect on both encoding and retrieval of declarative knowledge (Fernandes & Moscovitch, 2013). Furthermore, numerous studies have shown that dividing attention during encoding is more detrimental than dividing attention during retrieval or performance (Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Naveh-Benjamin, Craik, Gavrilescu, & Anderson, 2000; Naveh-Benjamin, Kilb, & Fisher, 2006). It is believed that both primary and secondary tasks compete for common attentional resources, which disrupts encoding of new associations into declarative memory. Medial temporal lobe structures, along with regions in the prefrontal cortex, are involved during encoding (Chun & Turk-Browne, 2007). In contrast, retrieval processes of the primary task are believed to have minimal demands for attention, and therefore, are less affected by dividing attention at this stage (Anderson, Iidaka, Cabeza, Kapur, McIntosh, & Craik, 2000). The majority of research investigating effects of divided attention on declarative memory involves learning of verbal stimuli (e.g., list learning). Few studies have examined the effects of divided attention on memory for skilled actions or knowledge related to tools. Research in our lab has studied the effects of divided attention on learning of novel naturalistic actions (NNAs) which are arts and crafts type of tasks involving use of everyday objects to create an end product (e.g., building a mock volcano using a plastic bottle, baking soda, and other objects). It has been argued that learning of the steps associated with performing an NNA requires declarative memory, and dividing attention during encoding is more detrimental to NNA accuracy than dividing attention during performance (Gold & Park, 2008).

Effects of Dividing Attention on Procedural Memory

The effects of divided attention on procedural memory are not well understood at this point, and findings on the attentional demands of procedural learning have been mixed. Early researchers in this area showed a decrement in motor sequence learning under divided attention and attributed this impairment to a lack of sufficient attentional resources (Nissen & Bullemer, 1987). This argument was subsequently challenged, and it was proposed that it is not learning per se that is affected by dividing attention; rather, performance, or behavioural expression, of the learned skill is affected. It was demonstrated that when a skill trained under divided attention was subsequently trained under full attention, performance was equivalent for both full and divided attention conditions (Frensch, Lin, & Buchner, 1998). Although the serial reaction time task (SRTT) is perhaps the most widely used primary task in these studies, studies using other procedural learning tasks, such as pursuit rotor and probabilistic classification learning tasks, have shown that performance, and not learning, was affected by dividing attention (Eysenck & Thompson, 1966; Foerde, Poldrack, & Knowlton, 2007).

In some circumstances, dividing attention may actually enhance motor learning. It has been suggested that features of the secondary task influence whether motor sequence learning will be impaired or enhanced. For instance, one study showed that participants retained a perceptual-motor task better under difficult rather than easy dual-task conditions (Roche et al., 2007). The authors argued that the more difficult secondary task mobilized greater attentional resources. Motor sequence learning may also be enhanced when the secondary task is similar in nature to the primary task. Findings from one study suggested that when the primary and secondary tasks draw on common cognitive processes, skill learning is enhanced, whereas when they rely on different cognitive processes, skill learning is impaired (Goh, Sullivan, Gordon, Wulf, & Winstein, 2012). Thus, the effects of dividing attention on procedural memory are complex and warrant further study, especially given the lack of research with tool-related skilled actions.

Overview

The current experiment was conducted as an extension of two previous studies (Roy & Park, 2010; Experiment 1). As described earlier, it has been proposed that memory for tool features is primarily mediated by declarative memory processes, and motor skill learning is primarily dependent on procedural memory. It has also been suggested that motor skill learning and skilled tool use may rely on an interaction of both memory systems. Specifically, it was argued that skilled tool use relies on a cooperative interaction of both declarative and procedural memory systems. With respect to motor skill learning, the degree to which declarative memory is involved requires further investigation. Dividing attention is believed to selectively disrupt encoding of new information into declarative memory. Therefore, this behavioural technique may be useful in determining whether or not encoding of declarative task knowledge is critical during motor skill learning with complex tools. To my knowledge, no previous studies have directly investigated the effect of dividing attention on learning of motor skills and knowledge associated with complex tools. Findings regarding memory representations of other aspects of tool knowledge and skills (i.e., tool features, skilled tool use) were largely consistent across the two earlier studies; however, it is important to note that these previous findings are based on patient performance. As such, the degree of generalizability to a healthy population is not known. Thus, if converging evidence were obtained in a healthy population, it would provide additional support of the proposed roles of declarative and procedural memory in mediating tool-related knowledge and skills.

The current study investigated the nature of interaction between declarative and procedural memory on tool-related knowledge and skills with the use of a dual-task paradigm. Healthy younger adults were trained to use a set of novel complex tools and were subsequently tested on their memory for tool features (e.g., function, colour), tool grasping, and skilled tool use to command. Some of the tools were trained under divided attention as a means of disrupting encoding of declarative information related to tools and their uses. In general, it was expected that divided attention during training would be detrimental for memory of any aspect of tool-related knowledge that relied on declarative memory, but that there would be no impact on aspects supported primarily by procedural memory. Four hypotheses were tested in the current study:

1. Motor skill learning is believed to be a form of procedural memory and should therefore not be impaired by dividing attention and restricting declarative encoding processes. In other words, motor skill acquisition does not require cooperation between both memory systems. Specifically, it was hypothesized that the rate of motor skill

learning associated with complex tools, as assessed by training completion time, would not differ between full and divided attention conditions. Based on findings from Roy and Park (2010), it is reasonable to believe that declarative memory is not required for motor skill learning. However, given the lack of consensus among previous studies, it is possible that motor skill learning may suffer if encoding of task knowledge is disrupted by dividing attention which would be reflective of a cooperative interaction of memory systems. It is also possible that motor skill learning involves a competitive interaction between declarative and procedural memory. If so, it would be expected that skill learning would be faster in the divided attention condition compared to full attention.

2. Recall of tool features should be impaired for tools that were trained under divided compared to full attention. This hypothesis is based on research showing that dividing attention is detrimental to learning of declarative information (e.g., Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000).

3. Demonstration of tool grasping should be impaired for tools trained under divided compared to full attention based on research showing that tool grasping has a strong declarative component (Creem & Proffit, 2001; Roy & Park, 2010).

4. Tool use accuracy should be impaired for tools trained under divided compared to full attention, but there should be no difference in completion time between attention conditions. This hypothesis is based on the previous findings suggesting that skilled tool use relies on a cooperative interaction of both memory systems, such that declarative

memory mediates recall of knowledge related to using a tool and procedural memory mediates motor efficiency of tool use.

Method

Participants

Thirty-two younger adults (22 females, 10 males) between the ages of 18 and 33 years (*M* = 23.81 years, *SD* = 3.88 years) participated in the current study. Participants were recruited and tested at York University in Toronto, Canada. They were recruited through the York University undergraduate research pool and through flyers posted in various locations on campus. Participants from the research pool were granted course credits for their participation, and participants who responded to flyers were offered a nominal amount of monetary compensation. All participants were required to be right-handed, fluent in spoken and written English (learned English by age 5), and have at least 12 years of education. Exclusion criteria included colour-blindness, past head injury resulting in loss of consciousness, and any psychological, neurological, or serious medical illness that could potentially affect cognition or motor performance. The experiment was approved by the ethics review board at York University, and each participant provided written consent prior to participation.

Materials

Novel tools. Twelve novel complex tools were constructed from K’NEX, a commercial children’s construction toy (see Figure 1). These twelve tools were divided into four sets of three tools each (Sets A, B, C and D). The tools used in the current study were a subset of 15 tools that were developed by Roy and Park (2010). Each tool was designed to perform a specific function by interacting with a unique action recipient (e.g., guide a wheel down a curved path). Tools were designed to be used unimanually, with the right hand, and each tool task involved a distinct motor skill. As demonstrated in Roy and Park (2010), the tools were designed in such a manner that their function, manner of use, and manner of grasping could not be determined from physical appearance. Each tool was painted a different solid colour. A set of tests was also developed to assess memory for various aspects of the tools (e.g., knowledge of the tool's function, manner of grasp). Further details on these materials can be found in Roy and Park (2010) and also in Experiment 1 above.

Recall test. A set of grey-scale images of the tools was used to develop a recall test of tool attributes. Three photographs of each tool were taken from three different, approximately equidistant, angles. During the recall test, participants were shown the three pictures of each tool, one tool at a time, and were asked to answer the following five questions about each tool: 1) What is the function of the tool/What is it used for? 2) What is the colour of the actual physical tool? 3) What is the recipient that the tool interacts with? 4) What is the colour of the recipient? and 5) How many recipients does the tool act on? Once the participant completed the five questions for a tool, they were not allowed to go back and review previous responses. Participants were asked to verbally provide their responses, which the experimenter recorded verbatim.

Grasp-to-command test. Each tool was placed on the table in front of the participant without its associated recipient(s). In order to control for the position of the tool's handle, the tool was presented in one of three orientations. To use the analogy of a clock, if the participant were sitting at the hour-hand position of 6 o'clock, the tool handle was placed at approximately 1 o'clock, 4 o'clock, or 7 o'clock, in no predetermined order. The tool was not presented at 11 o'clock (furthest away from participant's right hand) to minimize discomfort and awkward hand positioning that may have interfered with scoring. The participant was instructed, "With your right hand, show me how you would grasp this tool if you were to use it. Show me the first thing that comes to mind." The participant was allowed to rotate the tool in order to make the handle more accessible. After the participant demonstrated the grasp, the participant was asked to release the tool.

Use-to-command test. After the participant demonstrated the grasp of a tool, the experimenter set up the entire task with all associated materials. The tool was positioned in front of the participant in the proper orientation for use, and the recipient(s) was placed in a small outlined square, to the left of the tool. The participant was instructed, "Again, using your right hand, I'd like you to show me how you would use the tool. Show me the first thing that comes to mind. Please let me know when you've completed the task." Participants were expected to first position the recipient in the correct starting location. Then, they were given a limit of 60 seconds to demonstrate correct use of the tool from start to finish. Timing began when the tool made contact with the recipient and ended when either the task was completed without error or when the time limit was up.

N-back task. An auditory n-back task was created (see Dobbs & Rule, 1989). The n-back task was chosen as a secondary task as it has been shown to draw on working memory and attentional processes (Owen, McMillan, Laird, & Bullmore, 2005). In this n-back task, an audio file of spoken numbers was played on a laptop. During pilot testing, it was determined that a 1-back task, presented at a 2-second rate (i.e., one number every two seconds) was sufficiently challenging without overwhelming participants. In the task, participants were told to repeat out loud the number that preceded the last number they heard. For example, for the sequence, "5......6......2....," after hearing "6," the participant would say "5." In total, ten 1-back files were created, each with a different, random, sequence of numbers. One of these files was 20 seconds in length and was used as a practice file. The other nine files were each five minutes in length and were used during training of tool tasks.

Design and Procedure

Each participant was tested individually in a single session lasting approximately 90 minutes. The session was composed of two phases: training and test. Half of the tools were trained under full attention (FA) as in the traditional manner of performing the tasks (see Roy & Park, 2010), and the other half were trained under divided attention (DA). Thus, each participant was trained in both FA and DA conditions. Participants were trained to use all 12 tools (i.e., all four sets), one tool at a time. As an example, as shown in Appendix B, Participant 1 was trained on sets A and B under FA and on sets C and D under DA. Out of the two sets in each attention condition, one set (e.g., Set A) was trained over four consecutive trials (i.e., T1, T2, T3, and the probe trial) to provide a measure of training performance. The other tool set (e.g., Set B) served as the test set and was trained on a single trial.[1] The combination of attention conditions and tool sets resulted in four training conditions (i.e., FA – training test, FA – test set, DA – training set, and DA – test set). The order of these training conditions was fully counterbalanced across participants. It should be noted that all components of the test phase were conducted under full attention for all participants (see Appendix B for experimental design).

Training

At the start of the session, participants were given instructions for the 1-back task and were given a brief practice trial with a 20-second 1-back file. Errors were corrected and, if necessary, instructions were repeated to ensure that participants fully understood the task. After the practice trial, one of the other eight 1-back files was played at random, and the participant performed the 1-back task for the first 60 seconds of the clip. This 60-second trial served as the pretraining measure of performance on the 1-back task.

After measuring pretraining performance on the 1-back task, participants were trained on the tool tasks. Before beginning with the 12 experimental tools, participants

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[1] During pilot testing, it was found that four consecutive training trials countered the effects of dividing attention on the subsequent recall test. The effects of dividing attention appeared to diminish after repeated exposure to tool attributes over trials. For this reason, tools presented in the test phase were only given a single training trial.

were given two practice training trials, one for each attention condition, with two different tools. These tools had no similarity to the 12 experimental tools (e.g., different colours, functions, manner of grasp). Before proceeding to the experimental training trials, it was ensured that participants understood all instructions, and clarification was provided if necessary. During training of a tool task, participants were told that they would have up to 60 seconds to try and perform each tool task as quickly as possible, without making any errors, and that they should restart the task if they make an error.

Before training with each tool, a cardboard divider was placed on the table to hide the tool and its associated recipient(s) from the participant's view. However, a small section of the divider in front of the participant's right hand was cut out. The participant's right hand came through this small space and rested on the table throughout the duration of the training phase. On the other side of the divider, the experimenter placed the tool into the participant's right hand and positioned the participant's fingers in the correct configuration for use. Thus, participants could feel the tool but could not yet see it. Participants were instructed to keep their grasp of the tool until they had completed training with that particular tool. Once the participant's hand was positioned on the tool, the experimenter verbally described the type of errors that could be made in the task which would require the participant to restart the task (e.g., "In this task, if the recipient falls off the tool onto the table, the task has to be restarted"). However, these descriptions did not provide any specific information about the tool's use or its features. Although these details are normally provided in the tool videos, the videos were muted for this experiment to prevent auditory interference with the 1-back task.

After receiving instructions about potential task errors, participants viewed the associated training video, with the tool and its recipient(s) hidden from view. Participants were instructed not to maneuver the tool, or try to perform the task, while the video was playing. Immediately after the video finished playing, the experimenter removed the divider and gestured for the participant to begin the task. Timing began when the tool made contact with the recipient and ended once an errorless trial was completed, or when the 60-second time limit was up. Once the participant had completed training with a tool, the experimenter removed it from the table, placed the cardboard divider back on the table, and positioned the next tool into the participant's right hand.

In the DA condition, the secondary task was started immediately prior to the training video, before the divider was removed. Participants were encouraged to do their best on both the 1-back task and the tool task, but to treat the 1-back task as the more important task in order to draw attention away from the tool task. A different 1-back set was selected for each of the six tools in the DA condition. For the training set, in which tools were trained over four consecutive trials, the 1-back task was turned off after Trial 3, and the probe trial was then performed under full attention. For the test set, in which tools were trained on a single trial, the 1-back task was turned off once the trial was completed and all materials related to the tool were removed from the participant's view.

The experimenter did not provide any verbal feedback to participants during training in order to limit interference in the DA condition. However, participants were instructed beforehand that the experimenter would tap on the desk if the participant made an error and did not restart. This gesture would signal the participant to start over. Also, participants were informed before the introduction of each tool whether it would be trained under FA or DA and whether it would be trained over four trials or one trial.

After completing training of the 12 tools, all participants performed the 1-back task on its own to assess post-training performance. The remaining 1-back file was played, and participants performed the task during the first 60 seconds of the file. After performing the 1-back task, participants were given a 3-minute break during which they worked on a dinosaur word search as a distracter task. The purpose of this distracter task was to give the participant a brief break from the experiment and to keep them engaged with a pleasant but unrelated task.

Test. After completing the training phase, the test phase was administered, which included the recall, grasp-to-command, and use-to-command test measures. Only tools that were given a single training trial (i.e., test set) during training were included in the test phase. Thus, three tools from the FA condition and three tools from the DA condition were included in the test (see Appendix B).

Scoring and Statistical Analyses

The following scoring procedures were implemented for all measures. Inter-rater reliability is also presented for measures that do not have an objective scoring system and therefore may have required experimenter judgment. Inter-rater scores reflect the percentage of agreement between the two raters for a given measure. Further details on scoring procedures can be found in Roy and Park (2010).

Training performance for each training trial was assessed in two ways. Time to errorless (TTE) attempt measured the total time to complete the task from the start of the first attempt to the end of the first errorless attempt, and Time of errorless (TOE) attempt measured only the length of the successful attempt, from start to finish of that single attempt. In both scoring methods, if a participant was unable to complete the task successfully within the 60-second time limit, a maximum score of 60 seconds was recorded. The number of errors made during each task was also tallied and averaged across tools for each training trial.

Performance on the recall test was measured as the percentage of correct responses to items in each test trial. Recall items were divided into two conceptual categories, *functional associative* and *perceptual*. This classification is based on earlier research by Warrington and Shallice (1984) that distinguished between functional associative and perceptual features of living and nonliving objects. This classification was also used to report detailed results on recall data in Roy and Park (2010). The functional associative category included functionally relevant tool features including function of the tool and the identity of the recipient on which it performs the function. In contrast, perceptual recall items referred to incidental physical attributes such as tool colour, recipient colour, and number of recipients. A scoring rubric was developed for the recall test which contains a set of acceptable responses for each item. This rubric is based on responses obtained from participants during initial pilot testing of the materials.

Grasp-to-command performance was scored as the percentage of correct grasp demonstrations to command in each test trial. Each correct demonstration was given one point. As described earlier, each tool has a unique functional manner of grasping that participants learn during the training phase. A second independent rater scored 30% of the data and an inter-rater reliability score of 94.9% was obtained for grasp-to-command.

Performance on the use-to-command test can be broken down into two components, accuracy and completion time. Tool use accuracy was measured as the percentage of correct tool use demonstrations to command (e.g., whether or not a participant was able to complete the task successfully within 60 seconds), whereas completion time provided a measure of how quickly the participant was able to complete the task, in seconds. In terms of accuracy, if a participant was able to accurately demonstrate the tool's use within the 60-second time limit, the demonstration was scored as correct and one point was given. If the task was performed incorrectly, or was not completed within the 60-second time limit, the demonstration was marked as incorrect and a score of zero was given. A second independent rater scored 30% of the data, and an inter-rater reliability score of 98.3% was obtained for use-to-command accuracy. Completion time for use-to-command performance was measured in the same manner as in training.

Parametric statistics were used to analyze all measures of performance. Analysis of motor skill acquisition was based on tools trained over four trials during training. Analysis of all other measures including recall of tool attributes, grasp-to-command, and use-to-command was based on tools trained on a single trial (i.e., the test set). All pairwise comparisons were performed using Bonferroni correction and raw, unadjusted, *p*-values are reported.

Results

Baseline Performance

To ensure that tool attributes, proper manner of grasping, and proper manner of use could not be inferred by either appearance or handling of the tools, a brief baseline study was conducted prior to the current experiment. Baseline performance of all measures were obtained from a separate sample of 20 younger adults (8 males, 12 females) between the ages of 18 and 26 years (*M* = 20.6 years, *SD* = 2.56 years). As expected, participants were unable to accurately demonstrate any of these attributes of skills associated with the tools (see Table 1.). Thus, improved performance in the current study can be attributed to learning that occurred during the training phase.

Training

Completion Time. Figure 2 shows average completion time across training trials (T1, T2, T3) for tools trained under DA and FA, using TOE scores. Trials in which participants did not complete the task (i.e., maximum time scores) were removed before conducting analyses to prevent inflation of scores. A one-way within-subjects ANOVA showed that overall completion time was also slower for tools in the DA condition than in the FA condition, $F(1, 31) = 5.78$, $p = .022$, $\eta^2 = .16$. Linear regression analysis was conducted using the slopes of individuals across T1, T2, and T3 for tools trained under DA and FA conditions. Participants became significantly faster in using tools in the FA condition at a rate of 3.39 s per trial ($SE = .88$ s), $R^2 = .14$, $F(1, 94) = 14.87$, $p < .001$, with a y-intercept of 24.02 s ($SE = 1.90$ s). They became significantly faster in using tools in the DA condition at a rate of 4.22 s ($SE = 1.11$ s) per training trial, $R^2 = .13$, $F(1, 94) = 14.39$, $p < .001$, with a y-intercept of 31.10 s ($SE = 2.40$ s). The rates of completion time for tools trained under DA ($M = -4.22$ s, $SD = 3.51$ s) and FA ($M = -3.38$ s, $SD = 3.05$ s) did not differ, $t(31) = .97$, $p = .34$, $\eta^2 = .03$. In summary, participants were slower overall in the DA condition compared to the FA condition; however, the rate of learning was equivalent in the two conditions.

As described earlier, the purpose of the probe trial was to distinguish between effects of divided attention on performance versus learning. A paired samples *t*-test on the probe trial completion time showed no difference between tools trained under FA ($M = 15.21$ s, $SD = 6.43$ s) and tools trained under DA ($M = 16.68$ s, $SD = 5.26$ s), $t(31) = -.91$, $p = .37$, $\eta^2 = .03$. Thus, although dividing attention slowed performance in the DA condition in T1, T2, and T3, it did not affect learning of the motor skills.[1]

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[1] A similar pattern of training completion time results was obtained with TTE scores. Thus, only analyses with TOE scores are reported for both training and subsequent use-to-command analyses.

Training

Accuracy. A two-way repeated-measures ANOVA with attention condition (FA vs. DA) and trial (T1, T2, and T3) as within-subject factors showed no significant interaction on error production. There was also no main effect of attention condition on overall error production across trials. However, there was a main effect of trial, showing that participants made fewer errors across trials (T1: *M* = 1.01 errors, *SD* = .71 errors; T2: *M* = .64 errors, *SD* = .66 errors; T3: *M* = .67 errors, *SD* = .69 errors), F(2, 62) = 5.64, *p* = .006, η^2 = .15. Pairwise comparisons showed that the average number of errors was significantly higher in T1 compared to both T2, *t*(31) = 2.93, *p* = .006, η^2 = .22 and T3, *t*(31) = 3.93, $p < .001$, η^2 = .33. Average number of errors did not differ between T2 and T3. Error analysis for the probe trial, which was conducted in a separate paired-samples *t*-test, showed that the average number of errors in the probe trial was significantly higher in the DA condition (*M* = .76 errors, *SD* = .80 errors), than in the FA condition (*M* = .36 errors, *SD* = .58 errors), *t*(31) = -2.22, *p* = .034, η^2 = .14. In summary, although there was no significant difference in completion times between the two attention conditions in the probe trial, participants made more errors in the DA than in the FA condition.

N-back Task. A paired-samples *t*-test was conducted to compare pretraining (*M* = 98.89%, *SD* = 2.86%) and post-training (*M* = 97.56%, *SD* = 3.98%) accuracy on the 1-back task. Accuracy did not differ between the two time points, *t*(31) = 1.92, *p* = .07, η^2 = .11. A paired–samples *t*-test was also conducted to compare the average 1-back percent accuracy performed during DA (i.e., T1, T2, and T3; *M* = 73.50%, *SD* = 11.49%) and during FA (i.e., pre and post tests; $M = 98.23\%$, $SD = 2.85\%$). Accuracy on the 1-back task was significantly lower during DA than during FA, $t(31) = 13.04$, $p < .001$, $\eta^2 = .85$. Lastly, a repeated-measures ANOVA showed that 1-back accuracy improved across 1-back training trials, $F(2, 62) = 7.57$, $p = .001$, $\eta^2 = .20$.

Use-to-command

Accuracy. A paired-samples *t*-test showed that use-to-command accuracy was significantly worse for tools trained under DA relative to FA conditions, $t(31) = 3.69$, $p = .001$, $\eta^2 = .31$ (see Figure 3).

Completion Time. As with the training analyses, maximum time scores were removed before conducting analyses on use-to-command completion time. There was no significant difference in use-to-command completion time between tools trained under FA and DA, $t(31) = -.21$, $p = .83$, $\eta^2 = .001$ (see Figure 3). In summary, although use-to-command accuracy was worse for tools trained under DA relative to FA, when looking only at correctly performed use-to-command attempts, there is no effect of dividing attention on completion time.

Recall Accuracy

A two-way repeated measures ANOVA was conducted with attention (FA vs. DA) and recall category (functional associative vs. perceptual) as factors and percentage accuracy as the dependent variable (see Figure 4). There was no significant interaction between attention condition and recall category on accuracy. However, there was a main effect of attention condition showing lower overall recall accuracy for tools trained under

DA compared to FA, $F(1, 31) = 8.78$, $p = .006$, $\eta^2 = .22$. There was also a main effect of recall category showing that participants had higher recall accuracy for functional associative details about tools than perceptual details, $F(1, 31) = 185.34$, $p < .001$, $\eta^2 = .86$.

Grasp-to-command

Grasp-to-command accuracy for tools trained in the two attention conditions was analyzed using a paired samples *t*-test. Grasp-to-command demonstration was significantly worse for tools trained under DA ($M = 11.46\%$, $SD = 21.77\%$) than tools trained under FA ($M = 35.42\%$, $SD = 31.61\%$), $t(31) = 3.47$, $p = .002$, $\eta^2 = .28$.

Discussion

The current study investigated the contributions of declarative and procedural memory in mediating various aspects of tool-related knowledge and skills. Participants were trained to use a set of novel complex tools under full or divided attention and were subsequently tested on their recall for various aspects related to these tools (e.g., tool attributes, tool grasping, and tool use). In general, it was expected that dividing attention during training would be detrimental for any aspects of tool-related knowledge dependent on declarative memory. Components of tool-related knowledge and skills that do not rely on declarative memory were expected to be unaffected by dividing attention during training. Overall, current findings obtained with healthy adults provide converging evidence for results of previous patient studies in support of differential memory representations of tool knowledge and skills, as discussed below.

Motor Skill Learning

It was hypothesized that motor skill learning is primarily mediated by procedural memory processes and, therefore, would not be negatively affected by dividing attention with a secondary auditory 1-back task. Results showed that, aside from overall slowing, there was no effect of dividing attention on rate of motor skill learning across training trials. There was also no difference in completion time between DA and FA conditions in the probe trial, when the secondary task was removed. These findings are consistent with previous research showing that performance but not learning is affected by dividing attention (Frensch, Lin, & Buchner, 1998; also see Kantak & Winstein, 2012). This result is also consistent with previous research suggesting that motor skill acquisition is primarily mediated by the procedural memory system and that it does not require declarative memory or attentional resources (Gabrieli et al., 1993; Roy & Park, 2010; Song, Howard, & Howard, 2007). Thus, motor skill learning associated with complex tools does not appear to rely on a cooperative interaction of both memory systems.

However, analysis of error patterns does raise the possibility of a competitive, or inhibitory, role of declarative memory during procedural motor skill learning. Participants made more errors in the probe trial for tools trained under DA compared to FA. It is possible that in the DA condition participants had adopted a procedural learning strategy during the first three trials, but then attempted to perform the tasks consciously, drawing on episodic memory of the task, in the probe trial. Previous studies have shown that introducing a secondary task can enhance motor skill learning (Goh et al., 2012; Roche et al., 2007). In the current study, although performance was not enhanced by dividing attention, removal of the secondary task in the DA condition was associated with a higher number of errors than in the FA condition. This pattern of performance is consistent with previous research showing that putting accuracy of experienced golfers was less accurate under full attention than divided attention (Beilock, 2002). Therefore, current findings suggest that declarative and procedural memory systems may compete during motor skill learning, such that declarative memory and associated attentional processes can disrupt procedural skill learning. Findings also demonstrate the importance of investigating different aspects of performance (e.g., speed, accuracy) in order to thoroughly assess the impact of dividing attention on performance.

Skilled Tool Use

Skilled tool use was broken down into two components: accuracy and completion time. The accuracy measure assessed whether or not a tool was used correctly within the time limit, regardless of how quickly the participant performed the task. In contrast, completion time assessed how quickly participants were able to perform tool tasks. It was hypothesized that skilled tool use relies on a cooperative interaction of both declarative and procedural memory systems. This hypothesis is based on previous studies showing that disruption of either declarative or procedural memory leads to impaired skilled tool use (Roy & Park, 2010; Experiment 1). More specifically, it has been proposed that declarative memory may be required for encoding of task-related details (e.g., recipient placement, sequence of steps) required for accurate tool use, whereas procedural memory mediates motor adeptness of tool use (i.e., completion time). Consistent with these predictions, participants showed lower tool use accuracy for tools trained under DA compared to FA. In addition, tool use completion time was unaffected by dividing attention during training. Thus, current findings provide evidence of a cooperative interaction of memory systems in skilled tool use in a healthy population. Taken together with training data, current findings suggest that motor skill acquisition primarily relies on procedural memory, and may be disrupted by involvement of declarative memory, whereas skilled tool use requires involvement of both memory systems. Therefore, although motor skill acquisition and skilled tool use essentially involve performance of the same task, the role of different memory systems varies across these two aspects of tool-related skilled action.

Recall

It was predicted that dividing attention during training would negatively affect accuracy on a subsequent memory test of tool attributes. Results showed that total recall of tool attributes was significantly lower for tools trained under DA versus FA. Tool attributes were divided into two categories, functional associative and perceptual. The same pattern was found for both functional associative (i.e., tool function and recipient identity) and perceptual (i.e., tool colour, recipient colour, number of recipients) attributes. The results for recall of functional associative tool attributes are particularly informative. Taken together with results from training, these results suggest that although participants were able to acquire motor skills under divided attention during training, they did not acquire declarative knowledge related to the tasks they had performed (e.g., function of the tool). This pattern is consistent with previous research showing that although participants showed intact implicit learning under divided attention, they lacked explicit knowledge of what they had learned (Foerde, Knowlton, & Poldrack, 2006; Foerde et al., 2007). Thus, current findings provide converging evidence of the proposed dissociation between declarative and procedural components of tool-related knowledge and skills. Memory for tool attributes is negatively affected by dividing attention during encoding and therefore is highly characteristic of declarative memory. In addition, current results demonstrate that motor skill acquisition can take place implicitly, without encoding functionally relevant tool knowledge, as is characteristic of procedural memory.

Tool Grasping

As predicted, tool grasping was significantly lower for tools trained under DA relative to FA. This finding is consistent with previous research showing that grasping a tool for the purpose of using it requires declarative memory about the tool's use (Creem & Proffit, 2001; Roy & Park, 2010). However, grasping accuracy for tools in the FA condition was much lower than expected (only 35%). This pattern of poor grasping accuracy even in the FA condition suggests that tool grasping has a strong declarative representation that requires extensive repetition.

Overall, the current experiment conducted with healthy adults provides converging evidence to support findings from two previous patient studies (Roy & Park, 2010; Experiment 1). Taken together, findings suggest that the contribution of declarative and procedural memory systems varies across different aspects of tool knowledge and skills. Furthermore, although motor skill acquisition and skilled tool use both appear to rely on an interaction of declarative and procedural memory, they rely on different forms of memory interaction (i.e., competitive, cooperative). Thus, the current study provides a novel approach to studying organization of memory systems in the context of tool use and contributes to existing research which has predominantly used computer-based tasks.

Limitations and Future Directions

Although the current study proposes that specific memory systems play a primary role in mediating different aspects of tool-related knowledge and skills, no argument for "process-pure" measures are being made (Jacoby, 1991). Multiple memory systems and cognitive processes are likely involved in the acquisition of all aspects of tool-related knowledge and skills. For instance, although the current study specifically focuses on declarative long-term memory, the role of working memory was not directly assessed. Likewise, although the current study focuses on procedural memory, other forms of nondeclarative memory (i.e., perceptual, cerebellar) are also likely involved in learning of motor skills. Lastly, this area of inquiry would benefit from future research investigating the characteristics of different secondary tasks and their impact on motor skill learning.

Conclusion

The current study, taken together with previous research, provides evidence of both dissociation and interaction of the declarative and procedural memory systems with respect to tool-related knowledge and skills. Specifically, the results indicate that memory for tool attributes and tool grasping involves strong declarative representations. In addition, findings demonstrate that a cooperative interaction between declarative and procedural memory is required to support accurate and efficient skilled tool use. Lastly, findings suggest that motor skill acquisition may be primarily mediated by the procedural memory system, although declarative memory may play an inhibitory role during learning, thereby suggesting a competitive interaction of the two memory systems. Thus, the current study provides new insights into the memory representations of motor skill acquisition in healthy individuals and also extends on previous research on the relative contributions of declarative and procedural memory systems across different aspects of tool-related knowledge and skills.

References

Anderson, N. D., Iidaka, T., Cabeza, R., Kapur, S., McIntosh, A. R., & Craik, F. I. M. (2000). The effects of divided attention on encoding- and retrieval-related brain activity: a pet study of younger and older adults. *Journal of Cognitive Neuroscience, 12*, 775–792. doi:10.1162/089892900562598

Albouy, G., King, B. R., Maquet, P., & Doyon, J. (2013). Hippocampus and striatum: Dynamics and interaction during acquisition and sleep-related motor sequence memory consolidation. *Hippocampus*, *23*, 985-1004. doi:10.1002/hipo.22183

Beilock, S. L., Carr, T. H., MacMahon, C., & Starkes, J. L. (2002). When paying attention becomes counterproductive: Impact of divided versus skill-focused attention on novice and experienced performance of sensorimotor skills. *Journal of Experimental Psychology: Applied, 8*, 6–16. doi:10.1037/1076-898x.8.1.6

Brashers-Krug, T, Shadmehr, R., Bizzi, E. (1996). Consolidation in human motor memory. *Nature, 382*, 252-255. doi:10.1038/382252a0

Brown, R. M., & Robertson, E. M. (2007). Inducing motor skill improvements with a declarative task. *Nature Neuroscience, 10*, 148–149. doi:10.1038/nn1836

Chun, M. M., & Turk-Browne, N. B. (2007). Interactions between attention and memory. *Current Opinion in Neurobiology, 17*, 177–184. doi:10.1016/j.conb.2007.03.005

Creem-Regehr, S. H., & Lee, J. N. (2005). Neural representations of graspable objects: Are tools special? *Cognitive Brain Research, 22*, 457-469. doi:10.1016/j.cogbrainres.2004.10.006

Creem, S. H., & Proffit, D. R. (2001). Grasping objects by their handles: A necessary interaction between cognition and action. *Journal of Experimental Psychology: Human Perception and Performance, 27*, 218-228. doi:10.1037/0096-1523.27.1.218

Daprati, E., & Sirigu, A. (2006). How we interact with objects: learning from brain lesions. *Trends in Cognitive Sciences, 10*, 265-270. doi:10.1016/j.tics.2006.04.005

Dobbs, A. R., & Rule, B. G. (1989). Adult age differences in working memory. *Psychology and Aging, 4*, 500–503. doi:10.1037/0882-7974.4.4.500

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J.,... Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research, 199*, 61-75. doi:10.1016/j.bbr.2008.11.012

Eysenck, H. J., & Thompson, W. (1966). The effects of distraction on pursuit rotor learning, performance and reminiscence. *British Journal of Psychology, 57*, 99-106. doi:10.1111/j.2044-8295.1966.tb01009.x

Fernandes, M. A., & Moscovitch, M. (2013). *Divided Attention and Memory*. Encyclopedia of the Mind. doi:10.4135/9781452257044.n98

Foerde, K., Knowlton, B. J., & Poldrack, R. A. (2006). Modulation of competing memory systems by distraction. *Proceedings of the National Academy of Sciences, USA, 103*, 11778-11783. doi:10.1073/pnas.0602659103

Foerde, K., Poldrack, R. A., & Knowlton, B. J. (2007). Secondary-task effects on classification learning. *Memory & Cognition, 35*, 864–874. doi:10.3758/bf03193461

Foerde, K., & Shohamy, D. (2011). The role of the basal ganglia in learning and memory: Insight from Parkinson's disease. *Neurobiology of Learning and Memory, 96*, 624–636. doi:10.1016/j.nlm.2011.08.006

Foundas, A. L., Macauley, B. L., Raymer, A. M., & Maher, L. M. (1995). Ecological implications of limb apraxia: Evidence from mealtime behavior. *Journal of the International Neuropsychological Society, 1*, 62-66. doi:10.1017/s1355617700000114

Frensch, P. A., Lin, J., & Buchner, A. (1998). Learning versus behavioral expression of the learned: The effects of a secondary tone-counting task on implicit learning in the serial reaction task. *Psychological Research, 61*, 83–98. doi:10.1007/s004260050015

Frey, S. H. (2007). What puts the how in where? Tool use and the divided visual streams hypothesis. *Cortex, 43*, 368-375. doi:10.1016/s0010-9452(08)70462-3

Gabrieli, J. D., Corkin, S., Mickel, S. F.,& Growdon, J. H. (1993). Intact acquisition and long-term retention of mirror-tracing skill in Alzheimer's disease and in global amnesia. *Behavioral Neuroscience, 107*, 899-910. doi: 10.1037/08944105.11.2.272

Gobel, E. W., Blomeke, K., Zadikoff, C., Simuni, T., Weintraub, S., & Reber, P. J. (2013). Implicit perceptual-motor skill learning in mild cognitive impairment and Parkinson's disease. *Neuropsychology, 27*, 314-321. doi: 10.1037/a0032305

Goh, H.-T., Sullivan, K. J., Gordon, J., Wulf, G., & Winstein, C. J. (2012). Dual-task practice enhances motor learning: a preliminary investigation. *Experimental Brain Research, 222*, 201–210. doi:10.1007/s00221-012-3206-5

Gold, D. A., & Park, N. W. (2008). The effects of dividing attention on the encoding and performance of novel naturalistic actions. *Psychological Research Psychologische Forschung, 73*, 336–349. doi:10.1007/s00426-008-0148-4

Heilman, K. L. (2002). *Matter of mind.* New York: Oxford University Press. doi: 10.1093/acprof:oso/9780195144901.001.0001

Hodges, J. R., Bozeat, S., Lambon Ralph, M. A., Patterson, K., & Spatt, J. (2000). The role of conceptual knowledge in object use. Evidence from semantic dementia. *Brain, 123* 1913–1925. doi:10.1093/brain/123.9.1913

Iidaka, T., Anderson, N. D., Kapur, S., Cabez, R., & Craik, F. I. M. (2000). The Effect of divided attention on encoding and retrieval in episodic memory revealed by positron emission tomography. *Journal of Cognitive Neuroscience, 12*, 267–280. doi:10.1162/089892900562093

Jacoby, L. L. (1991). A process dissociation framework: separating automatic from intentional uses of memory, *Journal of Memory and Language, 30*, 513-541. doi:10.1016/0749-596x(91)90025-f

Kantak, S. S., & Winstein, C. J. (2012). Learning–performance distinction and memory processes for motor skills: A focused review and perspective. *Behavioural Brain Research, 228*, 219–231. doi:10.1016/j.bbr.2011.11.028

Knowlton, B. J., Mangels, J. A., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science, 273,* 1399–1402. doi:10.1126/science.273.5280.1399

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory, *Psychological Review, 102*, 419-457. doi:10.1037/0033-295x.102.3.419

Moody, T. D., Bookheimer, S. Y., Vanek, Z., & Knowlton, B. J. (2004). An implicit learning task activates medial temporal lobe in patients with Parkinson's disease. *Behavioral Neuroscience, 118,* 438–442. doi: 10.1037/0735-7044.118.2.438

Naveh-Benjamin, M., Craik, F. I. M., Gavrilescu, D., & Anderson, N. D. (2000). Asymmetry between encoding and retrieval processes: Evidence from divided attention and a calibration analysis. *Memory & Cognition, 28*, 965–976. doi:10.3758/bf03209344

Naveh-Benjamin, M., Kilb, A., & Fisher, T. (2006). Concurrent task effects on memory encoding and retrieval: Further support for an asymmetry. *Memory & Cognition, 34,* 90–101. doi:10.3758/bf03193389

Negri, G. A., Lunardelli, A., Gigli, G. L., & Rumiati, R. I. (2007). Degraded semanticknowledge and accurate object use. *Cortex, 43*, 376–388. doi:10.1016/s0010-9452(08)70463-5

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology, 19*, 1–32. doi:10.1016/0010-0285(87)90002-8

Owen, A. M., McMillan, K. M., Laird, A. R. & Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping*, 25**,** 46–59. doi:10.1002/hbm.20131

Packard, M. G., & Goodman, J. (2013). Factors that influence the relative use of multiple memory systems. *Hippocampus, 23*, 1044-1052. doi:10.1002/hipo.22178

Penhune, V. B., & Steele, C. J. (2012). Parallel contributions of cerebellar, striatal and M1 mechanisms to motor sequence learning. *Behavioural Brain Research, 226*, 579-591. doi:10.1111/j.1749-6632.2011.06434.x

Reber, A. S. (1993). *Implicit learning and tacit knowledge: an essay on the cognitive unconscious*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780195106589.001.0001

Roche, R. A. P., Commins, S., Agnew, F., Cassidy, S., Corapi, K., Leibbrand, S., … O’Mara, S. M. (2007). Concurrent task performance enhances low-level visuomotor learning. *Perception & Psychophysics, 69*, 513–522. doi:10.3758/bf03193908

Roy, S., & Park, N. W. (2010). Dissociating the memory systems mediating complex tool knowledge and skills. *Neuropsychologia*, *48*, 3026-3036. doi: 10.1016/j.neuropsychologia.2010.06.012

Roy, S., Park, N.W., Roy, E.A., & Almeida, Q. J. (in press). Interaction of memory systems during acquisition of tool knowledge and skills in Parkinson's disease. *Neuropsychologia.*

Shohamy, D., Myers, C. E., Kalanithi, J., & Gluck, M. A. (2008). Basal ganglia and dopamine contributions to probabilistic category learning. *Neuroscience & Biobehavioral Reviews, 32*, 219–236. doi:10.1016/j.neubiorev.2007.07.008

Siegert, R. J., Taylor, K. D., Weatherall, M., & Abernethy, D. A. (2006). Is implicit sequence learning impaired in Parkinson's disease? A meta- analysis. *Neuropsychology, 20,* 490–495. doi:10.1037/0894-4105.20.4.490

Silveri, M. C., & Ciccarelli, N. (2009). Semantic memory in object use. *Neuropsychologia*, *47,* 2634-2641. doi:10.1016/j.neuropsychologia.2009.05.013

Song, S., Howard, J. H., & Howard, D. V. (2007). Implicit probabilistic sequence learning is independent of explicit awareness. *Learning & Memory*, *14,* 167-176. doi:10.1101/lm.437407

Squire, L. R. (2009). Memory and brain systems: 1969-2009. *Journal of Neuroscience, 29,* 12711-12716. doi:10.1523/jneurosci.3575-09.2009

Warrington, E. K. (1975). The selective impairment of semantic memory. *The Quarterly Journal of Experimental Psychology*, *27*, 635-657. doi:10.1080/14640747508400525

Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments, *Brain, 107*, 829–854. doi:10.1093/brain/107.3.829

Weisberg, J., van Turennout, & Martin, A. (2007). A neural system for learning about object function. *Cerebral Cortex, 17*, 513-521. doi:10.1093/cercor/bhj176

Table 1

Baseline Performance on Test Measures

Test Measure	M	SD
Total recall (%)	2.92	3.10
Grasp-to-command (%)	2.50	5.47
Use-to-command		
Accuracy (%)	0.00	0.00
Completion time (seconds)	60.00	0.00

Figure 1. Example of novel complex tools used in the current experiment.

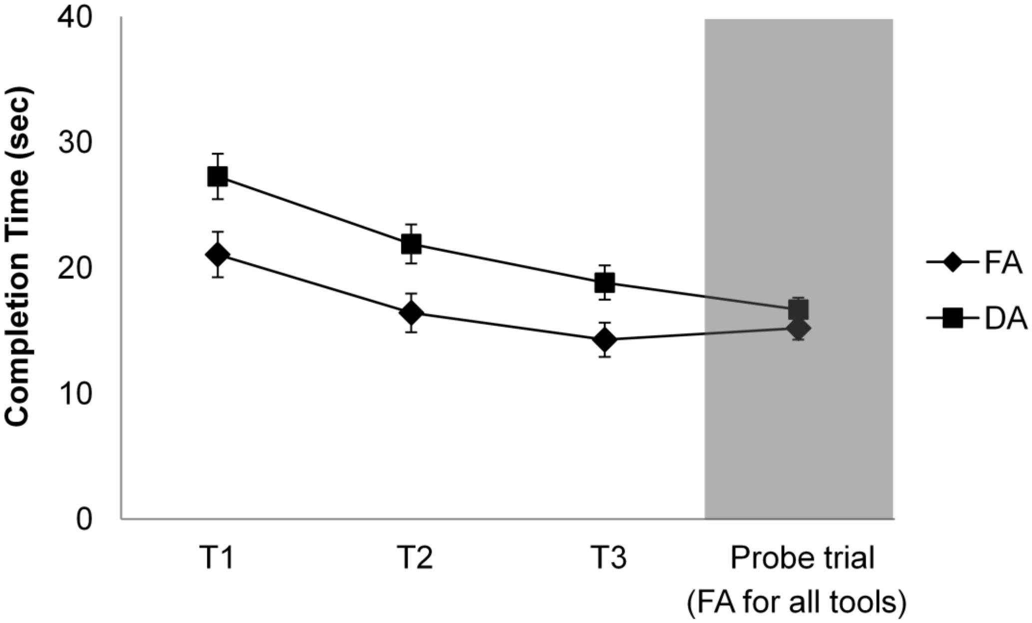

Figure 2. Mean completion time (+/- SE) across training trials (T1, T2, T3, T4, and Probe trial) for tools trained under full attention (FA) and divided attention (DA).

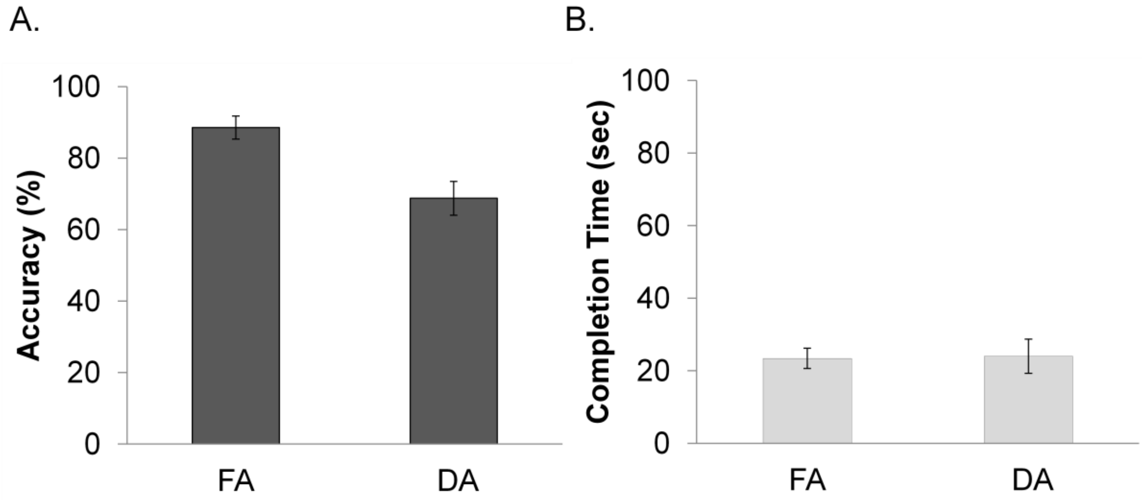

Figure 3. Use-to-command accuracy (A.) and completion time (B.) in the test phase for tools trained under DA and FA. A. Percentage of correct use-to-command demonstrations (+/- SE). B. Mean completion time of correct use-to-command demonstrations (+/- SE).

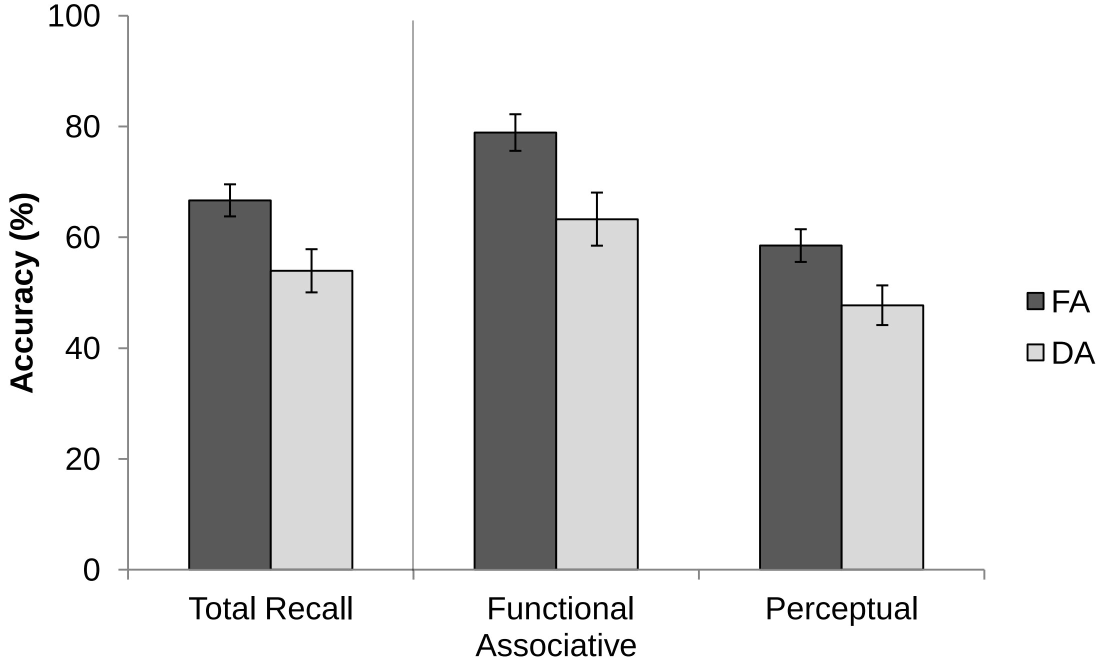

Figure 4. Percentage of correct responses (+/- SE) for recall of test items for tools trained under full attention (FA) and divided attention (DA).

Chapter 4: Effects of diminished performance-based feedback on declarative and procedural tool-related knowledge and skills (Experiment 3)

Humans rely on complex tools to perform everyday activities such as cooking and grooming. Unlike *simple* tools (i.e., objects that amplify movements of the upper limbs), *complex* tools are manufactured to provide a mechanical advantage in performing a specific function (e.g., bottle opener; Frey, 2004). Over time, we develop expertise in using complex tools and our interactions with them become part of our daily routines. However, the process by which we acquire information and skills related to these complex tools is not well understood. Specifically, it is unclear how various aspects of tool-related knowledge and skills are represented within different memory systems. It has been proposed that different components of tool-related knowledge and skills may have a different memory representation (Daprati & Sirigu, 2006; Roy & Park, 2010). For instance, it has been argued that memory for tool features (e.g., colour) are mediated by the declarative memory system, whereas motor skills associated with using the tool are supported primarily by the procedural memory system (Gabrieli, Corkin, Mickel, & Growden, 1993; Roy & Park, 2010). In some circumstances, declarative and procedural memory systems may interact in mediating skilled tool-related actions (Experiment 1; Silveri & Ciccarelli, 2009). In addition to having clinical significance, this area of research is also important in understanding the general organization of different memory systems and how they interact with each other.

Previous research suggests that declarative and procedural memory systems interact in supporting performance on a number of different tasks (Packard & Goodman, 2013; Roy, Park, Roy, & Almeida, in press). It has also been proposed that the relative contribution of different memory systems may shift according to various factors of the learning context. The current study investigated how limiting access to performance-based feedback affects memory for declarative and procedural aspects of tool-related knowledge and skills. As will be discussed, feedback-based learning is believed to be dependent on the striatum, a key structure involved in procedural learning, and procedural learning is enhanced when feedback is available (Foerde, Knowlton, & Poldrack, 2006; Lam, Wachter, Globas, Karnath, & Luft, 2013). Thus, in the current study, the amount of available feedback during initial motor skill acquisition was manipulated, and subsequent memory for tool features, tool grasping, and skilled tool use was assessed. In the following, a brief review of human memory systems will be provided along with our current understand of how tool-related knowledge and skills are organized within different memory systems. This will be followed by a discussion of the memory representations of feedback-based learning. Lastly, an overview of the current study will be provided.

Human Memory

It is generally agreed that memory is not a unitary construct. One view, referred to as the multiple memory systems (MMS) theory (Squire, 2009; also see Poldrack & Foerde, 2008) holds that there are multiple memory systems, each supporting a different type of learning. Proponents of this theory have attempted to distinguish between the different types of memory and identify brain regions supporting each type of learning. Traditionally, memory has been categorized as being either declarative or procedural. Declarative memory encompasses recollection of both semantic (i.e., general knowledge and facts) and episodic (i.e., events and experiences) information (Squire, 2009). Declarative memory is believed to rely on the hippocampus and other medial temporal lobe structures (see Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006). In contrast, procedural memory—a form of nondeclarative memory—mediates formation of skills and habits. Striatal and cerebellar networks are implicated in various forms of skill-based learning (see Doyon et al., 2009). It has been argued that the striatum is particularly involved in mediating the acquisition of skills and habits, especially when learning is based on feedback or reinforcement (Foerde et al., 2006; Foerde, Race, Verfaellie, & Shohamy, 2013).

Numerous studies have shown that the declarative and procedural memory systems are functionally and anatomically distinct (e.g., Knowlton, Mangels, & Squire, 1996; Cohen & Squire, 1980). However, evidence also suggests that the two systems may interact in some circumstances (see Poldrack & Packard, 2003). Studies have provided evidence of various forms of interaction between the two memory systems including competitive, compensatory, and cooperative interactions (Foerde et al., 2006; Moody, Bookheimer, Vanek, & Knowlton, 2004; Poldrack et al., 2001; Roy & Park, 2010; Silveri & Ciccarelli, 2009). It is likely that the nature of the interaction varies depending on the learning context and the type of information being learned.

Memory Representations of Tool-related Knowledge and Skills

Learning how to use a novel complex tool requires one to learn several bits of information and skills related to the tool (e.g., knowledge of its function, how it is grasped, motor skill associated with its use). It has been argued that different components of tool-related knowledge and skills may rely on different types of memory. For instance, previous research suggests that information about tools and their properties relies on the declarative memory system (Roy & Park, 2010, Warrington & Shallice, 1984; also see Weisberg, van Turennout, and Martin, 2007). Individuals with medial temporal lobe damage have been shown to be impaired in their memory for object-specific information (Warrington, 1975; Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000). Declarative memory has also been shown to be critical in mediating tool grasping for use (Creem & Proffitt, 2001). In Roy and Park (2010), an amnesic individual was trained to use a set of novel complex tools, and he was found to be severely impaired in his ability to demonstrate the proper manner of grasping for these tools when subsequently tested. Although previous research suggests that tool grasping heavily relies on declarative memory, the role of procedural memory in tool grasping has not been well studied.

In contrast to memory for tool attributes and tool grasping, each of which has been shown to be heavily dependent on declarative memory, it is generally accepted that motor skill learning primarily relies on the procedural memory system; moreover, it has been proposed that the basal ganglia and related structures, particularly the striatum, play a critical role in supporting motor skill acquisition (Doyon et al., 2009). Disease of these brain regions has been associated with impaired procedural memory. For example, people with PD have been shown to be impaired in motor sequence learning (Siegert, Taylor, Weatherall, & Abernethy, 2006). However, there is some debate about the role of declarative memory in motor skill learning. For instance, it has been argued that motor skill learning does not require awareness of learning and does not rely on declarative memory at all (Song, Howard, & Howard, 2007). Alternatively, it has also been proposed that the two memory systems may interact in mediating motor skill learning. Studies have provided evidence of cooperative, competitive, and compensatory interactions between the two memory systems during motor skill learning (Brown & Robertson, 2007; Experiment 1; also see Penhune & Steele, 2012). However, the conditions and factors that determine the nature of this interaction require further investigation.

Lastly, it has been proposed that skilled tool use (i.e., intentional tool use) relies on an interaction of both declarative and procedural memory systems (Negri, Lunardelli, Gigli, & Rumiati, 2007; Roy & Park, 2010; Silveri & Ciccarelli, 2009). This interaction had not been directly investigated until recently. In Roy & Park (2010), an amnesic individual, D.A., showed unimpaired motor skill acquisition associated with novel complex tools, but was unable to demonstrate the use of these tools to command. However, when the tool’s recipient (i.e., object tool acts on) was positioned in its starting location (e.g., placing a nail against a wall before using a hammer) by the experimenter, his ability to use the tools improved remarkably. This finding suggests that although D.A. was able to learn the motor skill associated with a tool's use, he could not demonstrate the tool's use to command because he could not retrieve declarative knowledge related to the tool's use (e.g., recipient placement). Thus, it was argued that declarative memory is critical for remembering contextual information related to the task while procedural memory is critical for proficient motor performance of the skill.

Individuals with PD were tested in a similar experiment in which they were trained to use a set of novel complex tools and were subsequently tested on their ability to demonstrate tool use to command (Experiment 1). Participants with PD showed equivalent tool use accuracy (e.g., positioning of recipient, steps of task), relative to controls. In addition, participants with PD showed an equivalent rate of improvement in completion time for skilled tool use relative to controls, within sessions. However, they failed to maintain their proficiency of skilled tool use (i.e., speed) across a 3-week delay. In other words, while tool use accuracy was intact in participants with PD, they demonstrated some impairment in maintaining their level of skilled performance. It should be noted that this lack of efficiency could not be fully attributed to general slowing associated with the disease. Based on the findings from these two patient studies which suggest that different memory mechanisms underlie tool use accuracy and speed, it could be argued that skilled tool use relies on a cooperative interaction of both declarative and procedural memory systems. More precisely, it could be argued that declarative memory guides accurate tool use involving recall of task-related details (e.g., recipient placement, sequence of steps) while procedural memory mediates skilled demonstration of tool use.

Feedback-based learning

It has been proposed that the striatum plays a critical role in establishing contingencies between motor output (response) and sensory input (feedback) so as to refine the parameters of the motor output to achieve a desired outcome (Thirkettle, Walton, Shah, Gurney, Redgrave, & Staffordd, 2013; also see Shohamy, Myers, Kalanithi, & Gluck, 2008). Thus, feedback-based learning is a process of continuous adjustment of behaviour guided by sensory input. It has also been proposed that feedback-based learning is primarily mediated by the procedural memory system, whereas observational learning is primarily mediated by the declarative memory system (Foerde et al., 2006). Evidence of this distinction has been reported with the "weather prediction task," a classic probabilistic classification learning task in which participants learn the probability of certain outcomes (e.g., weather outcomes) based on the combination of cues. This form of learning is believed to occur implicitly with the support of the striatum (Poldrack et al., 2001).

Researchers have developed two versions of the weather prediction task, a feedback version and an observation version (Poldrack et al., 2001). In the feedback version, participants receive corrective feedback after each response. In the observation version, they are explicitly presented with the correct association that is to be learned, and no response is required. In a neuroimaging study of healthy participants, researchers found greater striatal activation in the feedback version than in the observation version (Poldrack et al., 2001). In a subsequent study, people with PD, who typically have striatal damage, were impaired in the feedback version of the task but were unimpaired on the observation version (Shohamy, Myers, Onlaor, & Gluck, 2004).

People with Huntington's disease, who typically have procedural memory impairment due to brain damage primarily involving the caudate nuclei, are also impaired in feedback-based probabilistic classification learning (Holl, Wilkinson, Tabrizi, Painold, & Jahanshahi, 2012). These findings suggest that feedback-based learning is primarily mediated by the procedural memory system and that the striatum plays a critical role in this type of learning. It is believed that positive performance feedback is followed by a burst of dopamine which serves to reinforce the response and promote learning, whereas negative feedback is followed by a dip in dopamine (see Frank, 2005). One study showed that increasing dopamine levels pharmacologically in healthy participants also led to improved feedback-based learning (de Vries, Ulte, Zwitserlood, Szymanski & Knecht, 2010). Thus, the dopaminergic activity in the striatum is believed to underlie the mechanism of feedback-based learning (Wilkinson et al., 2014).

The vast majority of studies that have investigated feedback-based learned have used tasks involving single-response behaviours (i.e., trial-by-trial learning). For instance, in animal research, the animal makes a single response and is either rewarded or punished (e.g., press a lever and receive a food pellet or a shock). In humans, feedback-based learning has been studied with probabilistic classification learning in which the actor makes a computer response and receives trial-by-trial corrective feedback (see Poldrack et al, 2001). Thus, previous studies have primarily focused on contingencies between a single response (e.g., button press) and outcome (e.g., correct or incorrect). However, it is possible that feedback-based learning is also involved in other forms of skill learning, which requires the actor to learn a sequence of actions or responses. For instance, when learning how to tie shoelaces, each step can be considered a response, and successful completion of each step can be considered positive feedback as it takes the actor closer to the desired final outcome.

Similarly, learning a new motor skill associated with using a tool involves learning of several steps that ultimately leads to successful tool use (e.g., mastering the steps involved in knitting). Thus, it could be proposed that feedback-based learning is critical in motor skill acquisition associated with tools. If so, one would expect that minimizing availability of feedback would be detrimental for skill learning. The link between motor skill learning and feedback-based learning has not yet been explored. Research in this area would provide a more specific understanding of how the procedural memory system, including the striatum, contributes to motor skill learning and would also expand on the current understanding of different forms of feedback-based learning.

Overview

The current study was conducted as an extension to previous research investigating memory representations of tool-related knowledge and skills (Roy & Park, 2010; Experiment 2). These previous studies proposed that knowledge of a tool's specific attributes, such as its function, and its physical features are represented primarily by the declarative memory system. In contrast, motor skill acquisition related to complex novel tools appears to be primarily mediated by the procedural memory system. These existing studies also suggest that skilled tool use relies on a cooperative interaction of both declarative and procedural memory systems. However, there are some limitations to this earlier research. For instance, in Experiment 1, I presented evidence of impaired motor skill acquisition in participants with PD, which suggests that motor skill acquisition is striatally mediated. However, it is possible that general motor impairment, even if minimal, may have contributed to impaired performance of participants with PD.

In addition, the population of individuals with PD is known to be clinically heterogenous, and findings often differ from sample to sample, even on the same task (see Muslimovic, Post, Speelman, & Schmand, 2007). Thus, the memory representations of motor skill acquisition and other procedural aspects of tool knowledge and skills would benefit from converging evidence in a healthy population. As described earlier, it has been argued that feedback-based learning relies on the striatum (Foerde et al., 2006). It could be argued that motor skill learning associated with complex tools is a form of feedback-based learning and therefore relies on the striatum. The current study aims to study the effects of feedback-based learning on acquisition of tool knowledge and skills as a means of identifying components that rely on striatally based procedural memory. Results of this study will also help to further delineate the roles of declarative and procedural memory in mediating various components of tool-related knowledge and skills.

In the current study, the amount of performance-based feedback was varied across three groups of healthy younger adults. The three conditions differed in the amount of access to performance-based feedback during training. It was expected that interfering with access to feedback would be detrimental to aspects of tool-related knowledge and skills that rely on striatally mediated procedural memory. Aspects relying on declarative memory, however, were not expected to be affected by feedback manipulation. Based on these general expectations, the following specific hypotheses were developed:

1. Completion time should decrease as performance-based feedback increases across training conditions (i.e., more feedback associated with faster performance).

2. There should be no difference in recall of tool features across the three training conditions.

3. In terms of tool grasping, numerous studies have shown that grasping a tool for the purpose of using it relies on declarative memory (Roy & Park, 2010; Creem & Proffit, 2001; Experiment 2 above). However, the contribution of the procedural memory system has not been well studied. Based on the hypothesis that tool grasping relies, at least partly, on procedural memory, accuracy of tool grasping should decrease as access to feedback during training decreases (i.e., more feedback associated with higher grasping accuracy).

4. It has been proposed that declarative memory is required to use a tool accurately, whereas procedural memory is required to use a tool skillfully (Experiment 1; Roy & Park, 2010). Thus, tool use completion time, but not accuracy, should be negatively affected by decreased performance-related feedback during training.

Method

Participants

Forty-five younger adults (26 females, 19 males) aged between 18 and 30 years (*M* = 21.53 years, *SD* = 3.31 years) participated in the current study. Participants were recruited and tested at York University in Toronto, Canada. They were recruited either through the York University undergraduate research pool or through flyers posted in various locations on campus. Participants from the research pool were granted course credit for their participation and participants who responded to the flyers were offered a nominal amount of monetary compensation. All participants were required to be right-handed, fluent in both spoken and written English (English as first language or learned English by age 5), and have at least 12 years of education. Exclusion criteria included colour-blindness, past head injury resulting in loss of consciousness, and any psychological, neurological, or serious medical illness that could potentially affect cognitive or motor functioning. The experiment was approved by the Ethics Review Board at York University, and each participant provided written consent prior to participation.

Materials

Novel tools. Twelve novel complex tools were constructed from K'NEX, a commercial children's construction toy (see Figure 1). The tools used in the current study were a subset of 15 tools that were originally developed for a similar study by Roy and Park (2010). Each tool was designed to perform a specific function by interacting with a unique action recipient (e.g., guide a wheel down a curved path). Tools were designed to be used unimanually, with the right hand, and each tool task involved a distinct motor skill. As demonstrated in Roy and Park (2010), the tools were designed in such a manner that their function, manner of use, and manner of grasping could not be determined from physical appearance. Each tool was also painted a different solid colour. A set of tests were also developed to assess memory for various aspects of the tools (e.g., knowledge of the tool's function, manner of grasp). Further details on these materials can be found in Roy and Park (2010).

Recall test. A set of grey-scale images of the tools were used to develop a recall test of tool attributes. Three photographs of each tool were taken from three different, approximately equidistant, angles. During the recall test, participants were shown the three pictures of each tool, one tool at a time, and were asked to answer the following five questions about each tool: 1) What is the function of the tool/What is it used for? 2) What is the colour of the actual physical tool? 3) What is the recipient that the tool interacts with? 4) What is the colour of the recipient? and 5) How many recipients does the tool act on? Once the participant completed the five questions for a tool, they were not allowed to go back and review previous responses. Participants were asked to verbally provide their responses, which the experimenter recorded verbatim.

Grasp-to-command test. Each tool was placed on the table in front of the participant without its associated recipient(s). In order to control for the position of the tool's handle, the tool was presented in one of three orientations. To use the analogy of a clock, if the participant were sitting at the hour-hand position of 6 o'clock, the tool handle was placed at approximately 1 o'clock, 4 o'clock, or 7 o'clock, in no predetermined order. The tool was not presented at 11 o'clock (furthest away from participant's right hand) to minimize discomfort and awkward hand positioning that may have interfered with scoring. The participant was instructed, "With your right hand, show me how you would grasp this tool if you were to use it. Show me the first thing that comes to mind." The participant was allowed to rotate the tool in order to make the handle more accessible. After the participant demonstrated the grasp, the participant was asked to release the tool.

Use-to-command test. After the participant demonstrated the grasp of a tool, the experimenter set up the entire task with all associated materials. The tool was positioned in front of the participant in the proper orientation for use and the recipient(s) was placed in a small outlined square, next to the tool. The participant was instructed, "Again, using your right hand, I'd like you to show me how you would use the tool. Show me the first thing that comes to mind. Please let me know when you've completed the task." Participants were expected to first position the recipient in the correct starting location.

Then, they were given a limit of 60 seconds to demonstrate correct use of the tool from start to finish. Timing began when the tool made contact with the recipient and ended when either the task was completed without error or when the time limit was up. During use-to-command, participants were informed that the experimenter would not be providing them with any assistance or feedback on any aspect of their performance. Further details on the experimental materials and procedures can be found in Roy and Park (2010).

Design and Procedure

Each participant was tested individually in a single session lasting approximately 60 minutes. The session was composed of two phases: training and test. The study was developed using a between-subjects design with three separate training groups: “perform with recipient” (PWR), “perform no recipient” (PNR), and “observation” (OBS). The three groups varied in the degree of access to performance-based feedback during training. Specifically, participants in the PWR group performed the tasks in the traditional manner, physically interacting with both the tool and its recipients (see Roy & Park, 2010). Participants in the PNR group physically interacted with the tool to perform the task, but without the recipient(s). Lastly, participants in the OBS group only observed the tasks being performed. Further details about each condition will be provided in the following section. Each participant was randomly assigned to one of the three training groups, with a total of 15 participants per condition. The 12 novel tools were divided into two sets of six tools – Set A (tools 1 – 6) and Set B (tools 7 – 12). The order of tool sets in both training and test phases was counterbalanced such that the two tool sets appeared in various positions of the counterbalancing sequence approximately an equal number of times, and counterbalancing was identical for all groups. However, the order of tool presentation within each set remained constant. As an example, as shown in Appendix C, a given participant in each of the three groups was first trained on Set A and then on Set B. Training was then followed by the test phase, administered only on Set A. Participants who were trained on Set B first, were also tested on Set B in the test phase. Thus, the test phase included only the tool set that was presented first during training in an effort to minimize recency effects of the second set (i.e., participants tend to remember the last few tools better than tools presented earlier).

Training

Participants were trained to use all 12 tools (i.e., Sets A and B), one tool at a time (see Appendix C for an outline of the procedure). In the PWR group, participants watched the associated video demonstration for each tool task before physical training with the tool. The tool and associated recipients were positioned on a table in front of the participant; however, the participant was instructed not to touch any of the materials while the video was playing (see Roy & Park, 2010, for further details about tool videos). Following the video, participants were instructed to perform the task as they had seen it performed in the video. They were told that they would have up to 60 seconds to perform the task as quickly as possible, without making any errors, and that they should restart the task if they make an error. After completing the task without error, or once the 60-second time limit was up, the experimenter reset the task and the participant performed the same task two more times, for a total of three consecutive training trials per tool (T1, T2, and T3). During training, the experimenter provided feedback if necessary (e.g., correcting grasp, instructing participants to restart the task if they failed to do so on their own).

Training for the PNR group was similar to that of the PWR group with a few differences in the procedure. As in the PWR group, participants in the PNR group first viewed each video demonstration, before making physical contact with the tool. After each video, participants in the PNR group performed the tool task as well; however, they were instructed to perform the tool tasks without their associated recipients in Trials 1 and 2. Recipients were placed on the table to the left of the tool so that they could be seen, but participants were instructed to only pretend to interact with the recipients while performing the task. This would be analogous to holding a nonexistent nail against a wall and performing the gesture of hammering it into the wall while holding the actual hammer. Thus, participants still made physical contact with the tool and manipulated it in the appropriate manner for use.

In addition, for participants in the PNR group, the video was replayed two more times after the initial video demonstration so that participants could perform the task alongside the video during Trials 1 and 2. The videos were replayed during performance to ensure that participants were manipulating the tools correctly, as they essentially imitated the gestures as they saw them in the video. This procedure also standardized exposure time to each tool across participants, which prevented participants from rushing through the gestures. Trial 3 in the PNR group was administered in the same manner as in the PWR group. In other words, in Trial 3 for each tool, participants in the PNR group performed the task with the recipient, but without the video. As in the PWR group, they were also instructed to perform the task as quickly as possible without making any errors in Trial 3. Also, although participants did not perform the tool tasks with the recipients in Trials 1 and 2, the experimenter still corrected grasping errors and any other task errors.

Participants in the OBS group viewed each video demonstration three times in a row (i.e., once for the initial video demonstration and once each for Trials 1 and 2). Thus, they only observed performance of the tool tasks for Trials 1 and 2, without enacting the tasks themselves. While they were watching the videos, the tools and associated recipients were on the table in front of them. Participants were able to look at the materials while they watched the videos; however, they did not make physical contact with any of the materials until Trial 3. After watching the video three times, participants performed the task in Trial 3, with the all materials. Thus, Trial 3 was identical in administration for all three groups and followed procedure of the PWR group. After the training phase, participants were given a brief 3-minute break during which they were given a dinosaur word search to work on. The purpose of the word search was to engage the participant in an unrelated task and distract them from the experimental procedure.

Test. After completing the training phase, all participants were tested on recall, grasp-to-command, and use-to-command. As described earlier, only the first training set was included in the test phase. For example, if a participant was trained on Set A and then Set B, only the six tools from Set A were included in the subsequent test phase (see Appendix C).

Scoring and Statistical Analyses

The following scoring procedures were implemented for all measures in the current study. Inter-rater reliability is also presented for those measures which do not have an objective scoring system and therefore may have required experimenter judgment. Inter-rater scores reflect the percentage of agreement between the two raters for a given measure. Further details on scoring procedures can be found in Roy and Park (2010).

Training performance for each training trial was assessed in two ways. Time to errorless (TTE) attempt measured the total time to complete the task from the start of the first attempt to the end of the first errorless attempt, and time of errorless (TOE) attempt measured only the length of the successful attempt, from start to finish of that single attempt. In both scoring methods, if a participant was unable to complete the task successfully within the 60-second time limit, a maximum score of 60 seconds was recorded. The number of errors (i.e., attempts) made during each task was also tallied and averaged across tools for each training trial.

Performance on the recall test was measured as the percentage of correct responses to items in each test trial. Total recall accuracy was measured as the percentage of correct items out of the total number of items. Recall items were also divided into two conceptual categories, *functional associative* and *perceptual*. This classification is based on earlier research by Warrington and Shallice (1984) which distinguished between functional associative and perceptual features of living and nonliving objects. This classification was also used to report detailed results on recall data in Roy and Park (2010). The functional associative category includes functionally relevant tool features including function of the tool and the identity of the recipient on which it performs the function. In contrast, perceptual recall items refer to incidental physical attributes including tool colour, recipient colour, and number of recipients. A scoring rubric was developed for the recall test which contains a set of acceptable responses for each item. This rubric is based on responses obtained from participants during initial pilot testing of the materials.

Grasp-to-command performance was scored as the percentage of correct grasp demonstrations to command in each test trial. Each correct demonstration was given one point. As described earlier, each tool has a unique functional manner of grasping that participants learn during the training phase. A second independent rater scored 30% of the data and an inter-rater reliability score of 93.2% was obtained for grasp-to-command.

Performance on the use-to-command test can be broken down into two components, accuracy and completion time. Tool use accuracy was measured as the percentage of correct tool use demonstrations to command (e.g., whether or not a participant was able to complete the task successfully within 60 seconds) while completion time provided a measure of how quickly the participant was able to complete the task, in seconds. In terms of accuracy, if a participant was able to accurately demonstrate the tool’s use within the 60 second time limit, the demonstration was scored as correct, and one point was given. If the task was performed incorrectly, or was not completed within the 60 second time limit, the demonstration was scored as incorrect. A second independent rater scored 30% of the data and an inter-rater reliability score of 96.6% was obtained for use-to-command accuracy. Completion time for use-to-command performance was measured in the same manner as in training.

Statistical analyses for all experimental phases and relevant test measures are presented in the following Results section. All pairwise comparisons were performed using Bonferroni correction and raw, unadjusted, *p*-values are reported.

Results

Training

Completion Time. Figure 2 shows average completion time (i.e., time of errorless attempt) across training trials (T1, T2, and T3) for tools trained in PWR, PNR, and OBS conditions. Incomplete trials (i.e., maximum time scores) were removed before analyzing training data. Note that only participants in the PWR condition have performance scores for T1 and T2. Linear regression analysis showed that participants in the PWR condition became significantly faster in using tools across T1, T2, and T3 at a rate of 2.49 s per trial (*SE* = .63 s), $R^2 = .27$, $F(1, 43) = 15.54$, $p < .001$, with a y-intercept of 23.69 s (*SE* = 1.37 s).

A one-way ANOVA compared PWR, PNR, and OBS conditions on their T3 completion time and found a significant overall difference, $F(2, 42) = 19.21$, $p < .001$, η^2

= .48. Pairwise comparisons revealed that participants in the PWR condition were significantly faster than participants in the PNR condition, t(28) = -3.65, *p* = .001, η^2 = .32. Participants in the PWR condition were also faster than participants in the OBS condition, *t*(28) = -6.01, *p* < .001, η^2 = .56. Lastly, participants in the PNR condition were significantly faster than participants in the OBS condition, *t*(28) = 2.69, *p* = .012, η^2 = .21. In summary, both PWR and PNR completion time was faster than OBS completion time in T3, and PWR completion time was faster than PNR completion time.

Two independent samples *t*-tests were conducted to see if there were any differences in completion time between T1 in the PWR condition and T3 in the PNR and OBS conditions. There was no significant difference in completion time between T1 in the PWR condition and T3 in the PNR condition. There was also no significant difference in completion time between T1 in the PWR condition and T3 in the OBS condition. These results suggest that T3 performance in both PNR and OBS conditions was statistically equivalent to that of T1 in the PWR condition. [1]

Accuracy. A repeated-measures ANOVA, showed that the number of errors decreased across training trials (T1, T2, and T3) in the PWR group, F(2, 28) = 5.18, p = .012, η^2 = .27. Pairwise comparisons showed a significant decrease in errors between T1 (*M* = .86 errors, *SD* = .30 errors) and T3 (*M* = .58 errors, *SD* = .33 errors), *t*(14) = 3.035, *p* = .009, η^2 = .40. Average number of errors in T2 (*M* = .83 errors, *SD* = .44 errors) did

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[1] A similar pattern of training completion time results was obtained with TTE scores. Thus, only analyses with TOE scores are reported for both training and subsequent use-to-command analyses.

not differ significantly from T1 or T3. A one-way ANOVA showed a significant difference in average number of errors in T3 across all three groups (PWR, PNR, and OBS), $F(2, 42) = 3.31$, $p = .046$, , $\eta^2 = .14$. However, follow-up comparisons, did not show any significant difference in errors between PWR ($M = .58$ errors, $SD = .33$ errors), PNR ($M = .85$ errors, $SD = .33$ errors), and OBS ($M = .83$ errors, $SD = .28$ errors) conditions.

Use-to-command

Accuracy. A one-way ANOVA compared the three training conditions (PWR, PNR, and OBS) on their use-to-command accuracy. There was a significant overall effect of training condition on use-to-command accuracy, $F(2, 42) = 8.11$, $p = .001$, $\eta^2 = .28$ (see Figure 3). Pairwise comparisons found that use-to-command accuracy was higher in the PWR condition than in the OBS condition, $t(28) = 3.54$, $p = .001$, $\eta^2 = .31$. Use-to-command accuracy of the PNR condition was also higher than in the OBS condition, $t(28) = -2.40$, $p = .023$, $\eta^2 = .17$. However, there was no significant difference in use-to-command accuracy between the PWR and PNR conditions. In summary, both PWR and PNR training conditions had higher subsequent use-to-command accuracy than did the OBS condition; however, PWR and PNR conditions did not differ in their use-to-command accuracy.

Completion Time. A one-way ANOVA compared the three training conditions (PWR, PNR, and OBS) on their use-to-command completion time using TOE scores. As in the training analyses, all maximum time scores were removed before conducting analyses on completion time. There was a significant overall effect of training condition on use-to-command completion time, $F(2, 42) = 7.54$, $p = .002$, $\eta^2 = .26$ (see Figure 3). Pairwise comparisons found that use-to-command completion time was faster for the PWR condition than the OBS condition, $t(28) = -3.93$, $p = .001$, $\eta^2 = .36$. Use-to-command completion time of the PNR condition was also faster than the OBS condition, $t(28) = 2.36$, $p = .026$, $\eta^2 = .17$. However, as with use-to-command accuracy, there was no significant difference in completion time between the PWR and PNR conditions.

Recall Accuracy

A two-way mixed ANOVA was conducted to compare recall accuracy of the three training conditions (PWR, PNR, and OBS) across the two categories of recall items (functional associative vs. perceptual). There was no significant interaction between training condition and recall category (see Figure 4). There was also no main effect of training condition on total recall accuracy. However, there was a main effect of recall category showing that participants had better recall accuracy for functional associative tool features than for perceptual details, $F(1, 42) = 65.10$, $p < .001$, $\eta^2 = .61$.

Grasp-to-command

A one-way ANOVA compared the three training conditions (PWR, PNR, and OBS) on their grasp-to-command accuracy. There was no significant difference in grasping accuracy between PWR ($M = 53.3\%$, $SD = 26.87\%$), PNR ($M = 56.67\%$, $SD = 20.70\%$), and OBS ($M = 38.89\%$, $SD = 29.32\%$) conditions.

Discussion

In the current study the effects of diminished feedback during skill learning and subsequent effects on memory for tool-related knowledge and skills were explored. Previous studies have shown that feedback-based learning relies on striatal-dependent procedural memory (e.g., Foerde et al., 2006). Therefore, the role of feedback-based learning was examined as a way of delineating the procedural and declarative components of tool knowledge and skills. The interaction of procedural and declarative components was further investigated. In general, it was anticipated that reduced feedback during training would be detrimental for all procedural aspects of tool-related knowledge and skills, but would not affect elements supported primarily by declarative memory.

Motor Skill Learning

It was predicted that limiting access to performance-based feedback during training would be detrimental to motor skill learning. More specifically, it was predicted that average completion time on Trial 3 would increase as access to feedback was minimized across training conditions (i.e., OBS > PNR > PWR). Results supported these predictions for training performance. These findings support the hypothesis that motor skill acquisition associated with complex tools is a form of feedback-based learning. It could be argued that performing a tool task with the physical recipient provides critical feedback information that is necessary for optimal skill learning (e.g., how much strength to apply, how far to rotate the tool). In other words, the presence of the physical recipient during learning allows for refinement of the skill. The overall pattern of training performance also provides further support for the argument that motor skill acquisition relies on striatally-mediated procedural memory and is consistent with findings obtained with individuals with PD in Experiment 1.

Considering that performance feedback was varied by limiting physical interaction with the tool and associated objects, it could be argued that tactile interaction with the tool is necessary to learn its use and that observation alone is not sufficient to develop expertise in using a complex tool. This finding is consistent with studies showing that action-based learning is superior to learning based on pure observation (Shea, Wright, Wulf, & Whitacre, 2000). However, it is inconsistent with some studies showing that observational learning can be just as effective as action-based learning (Osman, 2008). It could also be argued that observation-based learning biases the participant to a more declarative approach to skill learning. Although a declarative approach may be effective in mediating some forms of skill learning (see Moody et al., 2004), action-based learning may be necessary for other types of tasks, such as those involving skilled motor movements.

Skilled Tool Use

Skilled tool use performance was broken down into two components: accuracy and completion time. The accuracy measure assessed whether or not a tool was used correctly within the time limit during use-to-command, regardless of how quickly the participant performed the task. In contrast, completion time assessed how quickly participants were able to perform tool tasks, for correct attempts. This division was implemented in earlier studies based on the hypothesis that accuracy and speed of tool use relied on different memory systems. Based on the findings of Experiment 1, it was proposed that tool use accuracy (e.g., performing all steps in proper sequence, recipient positioning) is declaratively represented whereas tool use speed (i.e., completion time) is an indication of procedural memory. Thus, it was hypothesized that skilled tool use relies on a cooperative interaction of both memory systems and that each system mediates a different component of skilled tool use.

In terms of tool use completion time, it has been proposed that this component of tool use is represented primarily by the procedural memory system and therefore would be negatively affected by reduced feedback during initial training. It was predicted that completion time during use-to-command would be slower for conditions in which performance feedback was reduced during initial training of the motor skill. This hypothesis was partially supported. Both PWR and PNR groups were faster than the OBS group during use-to-command; however, there was no difference between PWR and PNR groups.

Slower completion time in the OBS group may be a result of compromised procedural learning during training, as hypothesized. It is also possible that observation-based learning during training biased participants in the OBS group to employ declarative memory in both skill acquisition and skilled tool use which may not have been as efficient as engaging the procedural memory system. Faster completion time for both PWR and PNR relative to OBS is consistent with training results and supports the argument that tool use speed is a reflection of procedural learning. However, it is unclear why there was no difference between PWR and PNR groups, as the groups differed during training. One possible explanation is that participants in the PNR group had acquired the skill to a certain degree during Trials 1 and 2 in training and that the single trial with the recipient (i.e., Trial 3) served as a highly effective learning trial. In other words, they had learned the motor skill through physical enactment with the tool alone during Trials 1 and 2, but were able to further refine their movements once the recipient was introduced in Trial 3.

With respect to tool use accuracy, it was hypothesized that the declarative memory system mediated this aspect of tool use. It was predicted that level of feedback during motor skill acquisition would not impact tool use accuracy during use-to-command and that all three groups would be equivalent (i.e., PWR = PNR = OBS). Accuracy did not differ between PWR and PNR which is consistent with predictions; lack of feedback did not affect ability to learn task-related details in PNR condition. However, OBS condition was significantly less accurate than both PWR and PNR conditions. Thus, predictions were only partly supported. Nonetheless, the finding of lower tool use accuracy in the OBS condition raises some interesting possibilities. One potential explanation for this result may be that physical enactment of the task facilitates encoding of task-related details (e.g., sequence of steps). Although it has been proposed that tool use accuracy is highly declarative, it is possible there is some added benefit of performing the task. This explanation is consistent with previous research showing that people tend to have better memory for action phrases and details related to objects if they have physically performed actions using the objects (Engelkamp, Zimmer, Mohr, & Sellen, 1994; Karantzoulis, Rich, & Mangels, 2006; Morady & Humphreys, 2009). It could also be argued that due to the lack of physical performance, participants in the OBS group were less engaged during training, leading to poor skilled tool use performance overall. However, equivalent performance for both recall and tool grasping accuracy across groups, suggests that participants in the OBS were fully engaged during training.

Recall

It was predicted that recall accuracy for tool features would not differ between training conditions. It has been shown that memory for object-specific features is mediated by the declarative memory system and thus relies on medial temporal lobe structures (Roy & Park, 2010; Warrington & Shallice, 1984; Weisberg et al., 2007). Results showed that recall for functional associative and perceptual elements did not differ among the three training conditions. Overall, however, participants showed better recall for functional associative tool features than perceptual details. These results suggest that tool features (e.g. tool's function, colour) can be learned without physical interaction with the tool and can be learned through observation alone. This pattern of findings also suggests that people tend to encode information related to a tool's use more readily than arbitrary physical attributes.

Tool Grasping

Previous research suggests that tool grasping for use is at least partly mediated by the declarative memory system (Creem & Proffit, 2001; Roy & Park, 2010). It has been suggested that the procedural memory system may also be involved in tool grasping; however, this has not yet been demonstrated. In the current study, it was predicted that if the procedural memory system is involved in learning a tool's grasp, tool grasping for use would be negatively affected by diminished performance feedback during training (i.e., PWR > PNR > OBS). This prediction was not supported as grasp-to-command performance did not differ significantly across the three training conditions. However, there is an evident trend in the data showing that grasping accuracy was lower in the OBS condition than in the PWR and PNR conditions. Thus, it is still unclear whether tool grasping can be learned using a declarative approach (through observation alone) or if the nonsignificant results reflects a lack of statistical power. It could be argued that the method by which grasping accuracy is measured in the current line of studies is not very precise. Although it takes into account gross configuration of the hand and fingers, there are many other details associated with measuring grasp that were not assessed. Thus, inconclusive findings may also be related to the lack of specificity in methodology for measuring tool grasping.

Limitations and Future Directions

The current study has some limitations that may be addressed in future research. For instance, it can be argued that motor skill acquisition involves naturally occurring feedback, rather than the preprogrammed, trial-by-trial, corrective feedback as in other tasks (e.g., probabilistic classification learning). However, the specific characteristics of the type of feedback involved in motor skill learning with tools is unclear (e.g., internal vs. external, positive vs. negative, sensorimotor vs. visual). A clear definition of feedback associated with motor skill learning will allow more precise investigation of its impact on skill learning. In addition, while the current study focused on the role of the striatum in supporting feedback-based learning, it has been suggested that the medial temporal lobes may also be involved in feedback-based learning, especially when feedback is provided after a delay (Foerde et al., 2013). Future research may help to identify ways in which feedback can be used to modulate involvement of different memory systems.

Conclusion

The current experiment investigated the effects of limiting performance-based feedback on motor skill acquisition and subsequent memory for tool features, tool grasping, and skilled tool use. Processes involved in striatal-based procedural memory were behaviourally disrupted by restricting feedback during motor skill learning in healthy, cognitively unimpaired, individuals. Overall, results provided converging evidence to support findings obtained with individuals with PD in Experiment 1. More specifically, results suggest that motor skill acquisition associated with complex tools relies on performance-based feedback and that limiting this feedback is detrimental to skill learning and subsequent skilled tool use. The striatum has been implicated in different forms of feedback-based learning (e.g., probabilistic classification learning).

However, the current study provides evidence to suggest that motor skill learning associated with complex tools is also a form of feedback-based learning that relies on the striatum. Current findings are also consistent with previous research showing that memory for tool attributes is primarily mediated by declarative memory processes. Lastly, findings support the proposed cooperative interaction of both memory systems during skilled tool use. Thus, the current study corroborates previous patient studies and also highlights the role of feedback-based learning in acquisition of tool knowledge and skills in healthy individuals.

References

Brown, R. M., & Robertson, E. M. (2007). Inducing motor skill improvements with a declarative task. *Nature Neuroscience*, *10*, 148–149. doi:10.1038/nn1836

Cohen, N., & Squire, L. (1980). Preserved learning and retention of pattern-analyzing skill in amnesia: dissociation of knowing how and knowing that. *Science, 210,* 207–210. doi:10.1126/science.7414331

Creem, S. H., & Proffit, D. R. (2001). Grasping objects by their handles: A necessary interaction between cognition and action. *Journal of Experimental Psychology: Human Perception and Performance, 27*, 218-228. doi:10.1037/00961523.27.1.218

Daprati, E., & Sirigu, A. (2006). How we interact with objects: learning from brain lesions. *Trends in Cognitive Sciences, 10*, 265-270. doi:10.1016/j.tics.2006.04.005

De Vries, M. H., Ulte, C., Zwitserlood, P., Szymanski, B., & Knecht, S. (2010). Increasing dopamine levels in the brain improves feedback-based procedural learning in healthy participants: An artificial-grammar-learning experiment. *Neuropsychologia, 48,* 3193–3197. doi:10.1016/j.neuropsychologia.2010.06.024

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J.,... Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research, 199*, 61-75. doi:10.1016/j.bbr.2008.11.012

Engelkamp, J., Zimmer, H. D., Mohr, G., & Sellen, O. (1994). Memory of self-performed tasks: Self-performing during recognition. *Memory and Cognition, 22,* 34–39. doi:10.3758/bf03202759

Foerde, K., Knowlton, B. J., & Poldrack, R. A. (2006). Modulation of competing memory systems by distraction. *Proceedings of the National Academy of Sciences, USA, 103*, 11778-11783. doi:10.1073/pnas.0602659103

Foerde, K., Race, E., Verfaellie, M., & Shohamy, D. (2013). A role for the medial temporal lobe in feedback-driven learning: evidence from amnesia. *Journal of Neuroscience, 33*, 5698–5704. doi:10.1523/jneurosci.5217-12.2013

Frank, M. J. (2005). Dynamic Dopamine Modulation in the Basal Ganglia: A neurocomputational account of cognitive deficits in medicated and nonmedicated parkinsonism. Journal of Cognitive Neuroscience, 17, 51–72. doi:10.1162/0898929052880093

Frey, S. H. (2007). What puts the how in where? Tool use and the divided visual streams hypothesis. *Cortex, 43*, 368-375. doi:10.1016/s0010-9452(08)70462-3

Gabrieli, J. D., Corkin, S., Mickel, S. F.,& Growdon, J. H. (1993). Intact acquisition and long-term retention of mirror-tracing skill in Alzheimer's disease and in global amnesia. *Behavioral Neuroscience, 107*, 899-910. doi: 10.1037/0894-4105.11.2.272

Hodges, J. R., Bozeat, S., Lambon Ralph, M. A., Patterson, K., & Spatt, J. (2000). The role of conceptual knowledge in object use. Evidence from semantic dementia. *Brain, 123,* 1913–1925. doi:10.1093/brain/123.9.1913

Holl, A. K., Wilkinson, L., Tabrizi, S. J., Painold, A., & Jahanshahi, M. (2012). Probabilistic classification learning with corrective feedback is selectively impaired in early Huntington's disease—Evidence for the role of the striatum in learning with feedback. *Neuropsychologia, 50*, 2176–2186. doi: 10.1016/j.neuropsychologia.2012.05.021

Karantzoulis, S., Rich, J. B., & Mangels, J. A. (2006). Subject-performed tasks improve associative learning in amnestic mild cognitive impairment. *Journal of International Neuropsychological Society, 12,* 493-501. doi: 10.1017/s1355617706060632

Knowlton, B. J., Mangels, J. A., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science, 273,* 1399–1402. doi:10.1126/science.273.5280.1399

Lam, J. M., Wächter, T., Globas, C., Karnath, H.-O., & Luft, A. R. (2013). Predictive value and reward in implicit classification learning. *Human Brain Mapping*, 34, 176–185. doi:10.1002/hbm.21431

Moody, T. D., Bookheimer, S. Y., Vanek, Z., & Knowlton, B. J. (2004). An implicit learning task activates medial temporal lobe in patients with Parkinson's disease. *Behavioral Neuroscience, 118,* 438–442. doi: 10.1037/0735-7044.118.2.438

Morady, K., & Humphreys, G. W. (2009). Real object use facilitates object recognition in semantic agnosia. *Neurocase*, 15, 135–144. doi:10.1080/13554790802680321

Moscovitch, M., Nadel, L., Winocur, G., Gilboa, A., & Rosenbaum, R. S. (2006). The cognitive neuroscience of remote episodic, semantic and spatial memory. *Current Opinion in Neurobiology, 16*, 179–190. doi:10.1016/j.conb.2006.03.013

Muslimovic, D., Post, B., Speelman, J. D., & Schmand, B. (2007). Motor procedural learning in Parkinson's disease. *Brain, 130*, 2887-2897. doi: 10.1093/brain/awm211

Negri, G. A., Lunardelli, A., Gigli, G. L., & Rumiati, R. I. (2007). Degraded semanticknowledge and accurate object use. *Cortex*, *43*, 376–388.

Osman, M. (2008). Observation can be as effective as action in problem solving. *Cognitive Science*, *32*, 162-183. doi:10.1080/03640210701703683

Packard, M. G., & Goodman, J. (2013). Factors that influence the relative use of multiple memory systems. *Hippocampus, 23,* 1044-1052. doi:10.1002/hipo.22178

Penhune, V. B., & Steele, C. J. (2012). Parallel contributions of cerebellar, striatal and M1 mechanisms to motor sequence learning. *Behavioural Brain Research, 226,* 579-591. doi:10.1111/j.1749-6632.2011.06434.x

Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature, 414,* 546–550. doi:10.1038/35107080

Poldrack, R. A., & Foerde, K. (2008). Category learning and the memory systems debate. *Neuroscience & Biobehavioral Reviews, 32*, 197–205. doi: 10.1016/j.neubiorev.2007.07.007

Poldrack, R. A., & Packard, M. G. (2003). Competition among multiple memory systems: converging evidence from animal and human brain studies. *Neuropsychologia, 41*, 245–251. doi:10.1016/s0028-3932(02)00157-4

Roy, S., & Park, N. W. (2010). Dissociating the memory systems mediating complex tool knowledge and skills. *Neuropsychologia*, *48*, 3026-3036. doi: 10.1016/j.neuropsychologia.2010.06.012

Roy, S., Park, N.W., Roy, E.A., & Almeida, Q. J. (in press). Interaction of memory systems during acquisition of tool knowledge and skills in Parkinson’s disease. *Neuropsychologia*.

Shea, C. H., Wright, D. L., Wulf, G., & Whitacre, C. (2000). Physical and observational practice afford unique learning opportunities. *Journal of Motor Behavior, 32*, 27–36. doi:10.1080/00222890009601357

Shohamy, D., Myers, C. E., Kalanithi, J., & Gluck, M. A. (2008). Basal ganglia and dopamine contributions to probabilistic category learning. *Neuroscience and Biobehavioral Reviews, 32*, 219–236. doi:10.1016/j.neubiorev.2007.07.008

Shohamy, D., Myers, C. E., Onlaor, S., & Gluck, M. A. (2004). Role of the basal ganglia in category learning: how do patients with parkinson's disease learn? *Behavioral Neuroscience, 118*, 676-686. doi: 10.1037/0735-7044.118.4.676

Siegert, R. J., Taylor, K. D., Weatherall, M., & Abernethy, D. A. (2006). Is implicit sequence learning impaired in Parkinson's disease? A meta- analysis. *Neuropsychology, 20,* 490–495. doi:10.1037/0894-4105.20.4.490

Silveri, M. C., & Ciccarelli, N. (2009). Semantic memory in object use. *Neuropsychologia, 47,* 2634-2641. doi:10.1016/j.neuropsychologia.2009.05.013

Song, S., Howard, J. H., & Howard, D. V. (2007). Implicit probabilistic sequence learning is independent of explicit awareness. *Learning & Memory, 14*, 167–176. doi:10.1101/lm.437407

Squire, L. R. (2009). Memory and brain systems: 1969-2009. *Journal of Neuroscience, 29*, 12711-12716. doi:10.1523/jneurosci.3575-09.2009

Thirkettle, M., Walton, T., Shah, A., Gurney, K., Redgrave, P., & Stafford, T. (2013). The path to learning: Action acquisition is impaired when visual reinforcement signals must first access cortex. *Behavioural Brain Research, 243*, 267–272. doi:10.1016/j.bbr.2013.01.023

Warrington, E. K. (1975). The selective impairment of semantic memory. *The Quarterly Journal of Experimental Psychology*, *27,* 635-657. doi:10.1080/14640747508400525

Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments, *Brain, 107*, 829–854. doi:10.1093/brain/107.3.829

Weisberg, J., van Turennout, & Martin, A. (2007). A neural system for learning about object function. *Cerebral Cortex, 17,* 513-521. doi:10.1093/cercor/bhj176

Wilkinson, L., Tai, Y. F., Lin, C. S., Lagnado, D. A., Brooks, D. J., Piccini, P., & Jahanshahi, M. (2014). Probabilistic classification learning with corrective feedback is associated with in vivo striatal dopamine release in the ventral striatum, while learning without feedback is not. *Human Brain Mapping*, n/a–n/a. doi:10.1002/hbm.22536

Figure 1. Images of novel complex tools used in the current experiments.

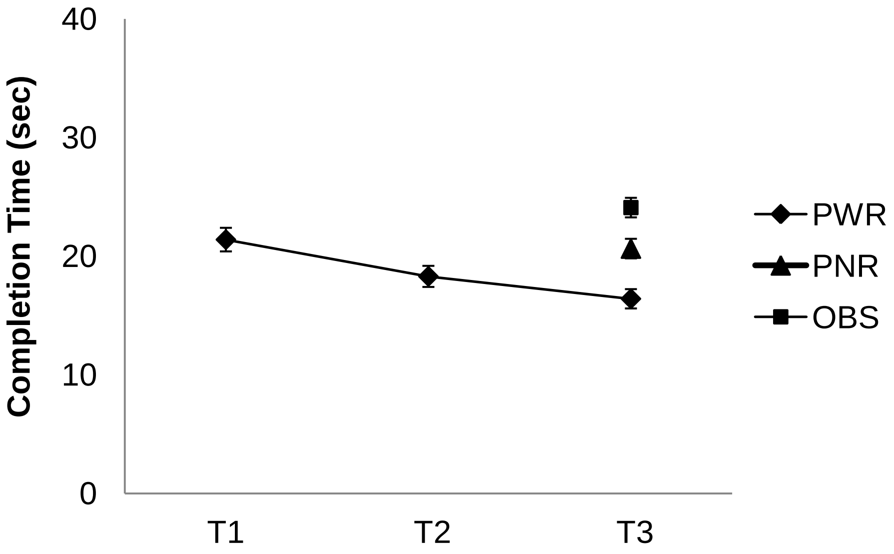

Figure 2. Mean completion time (+/- SE) across training trials (T1, T2, and T3) for participants in all three groups: perform with recipient (PWR), perform no recipient (PNR), and observation (OBS).

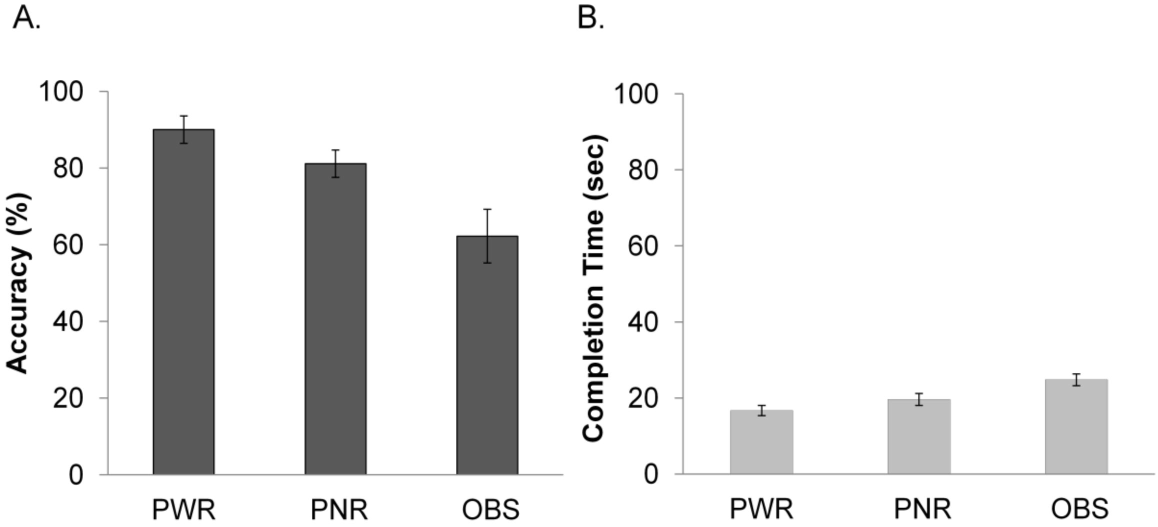

Figure 3. Use-to-command accuracy (A.) and completion time (B.) in the test phase for PWR, PNR, and OBS training conditions. A. Percentage of correct use-to-command demonstrations (+/- SE). B. Mean completion time of correct use-to-command demonstrations (+/- SE).

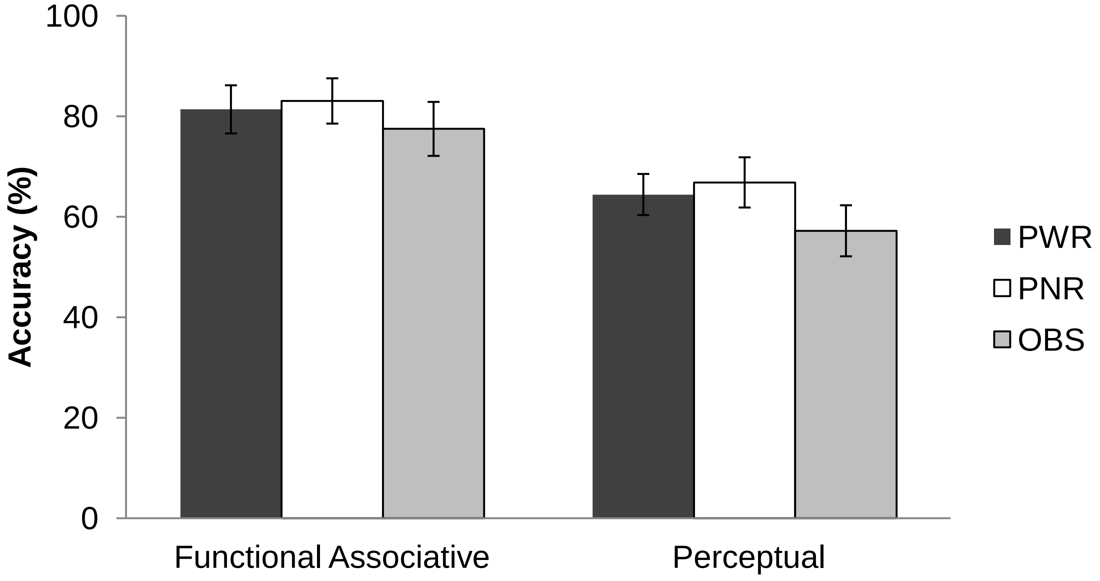

Figure 4. Percentage of correct responses (+/- SE) for both functional associative and perceptual recall items for all three groups: perform with recipient (PWR), perform no recipient (PNR), and observation (OBS).

Chapter 5: General Discussion

The objective of the current dissertation was to gain a better understanding of how various aspects of tool-related knowledge and skills are mediated by declarative and procedural memory systems. This research also aimed to better understand the functions and boundaries of these memory systems as well as how they interact with each other. Three separate experiments were carried out to pursue these common research goals through various behavioural manipulations as well as by studying performance of a patient population. In Experiment 1, I examined acquisition of tool knowledge and skills in individuals with PD. In Experiment 2, I investigated effects of dividing attention on acquisition of tool knowledge and skills in healthy adults. Lastly, In Experiment 3, I studied the effects of diminished performance-based feedback on acquisition of tool knowledge and skills in healthy adults. Through these experiments, the current dissertation has made significant contributions to the understanding of how striatal-dependent procedural memory is critically involved in motor skill acquisition and skilled tool use, how declarative and procedural aspects of tool knowledge and skills can be delineated by considering involvement of frontal/attentional resources, and more broadly, how different memory systems function, both independently and interactively.

Contributions of Striatal-Dependent Procedural Memory

Previous research has shown that various forms of skill learning (e.g., motor sequence learning, probabilistic classification learning) rely on a striatal-dependent form of procedural memory (Doyon et al., 2009; Poldrack et al., 2001). However, to my knowledge, the precise role and type of procedural memory involved in acquiring tool-related motor skills had not been previously identified. In Experiment 1, performance of a patient group (i.e., PD) with striatal dysfunction was examined to determine whether or not skilled actions associated with complex tools were also mediated by a striatal form of procedural memory versus other forms of procedural memory (e.g., cerebellar). Although participants with PD learned motor skills and demonstrated tool use at the same rate as controls within sessions, they were unable to retain these skills after a 3-week delay. This result demonstrates that the striatum is involved in mediating long-term retention of motor skills and tool use associated with complex tools and extends similar findings with other forms of motor learning (see Doyon et al., 2009; see also Mochizuki-Kawai et al., 2004). Findings from Experiment 3 demonstrated the importance of motor procedural memory through performance-based feedback during learning in a healthy population and provided converging evidence of findings from Experiment 1. More specifically, results showed that limited performance-based feedback was detrimental to motor skill learning and subsequent speed of skilled tool use. Furthermore, findings from Experiment 3 suggest that skilled tool use and motor skill learning rely on a form of feedback that must be generated through physical enactment of the task. Thus, the current dissertation provides a better understanding of how striatal-based procedural memory is involved in motor skill acquisition and skilled tool use associated with complex novel tools.

Involvement of Frontal/Attentional System in Acquiring Tool Knowledge and Skills

It has been proposed that declarative and procedural memory differ in their sensitivity to distraction and requirement of frontal/attention processes. For instance, it is generally accepted that frontal/attentional processes are required for encoding of new declarative knowledge (Chun & Turk-Browne, 2007; but see Schendan, Searl, Melrose, & Stern, 2003). However, the requirement of frontal/attentional resources during formation of new procedural memories is less clear and findings based on a variety of tasks have been mixed (Nissen & Bullemer, 1987; Foerde, Poldrack, & Knowlton, 2007; Goh, Sullivan, Gordon, Wulf, & Winstein, 2012).

Findings from Experiment 2 showed that recall of tool features (e.g., function, colour) was impaired when encoding of this information was disrupted under divided attention compared to full attention. This finding is consistent with previous research showing that information about tools and their properties is represented in brain regions associated with declarative memory (Roy & Park, 2010; Weisberg, van Turennout, and Martin, 2007). Although the memory representations of object features have been studied in great detail and it is well established that declarative memory supports learning of this information, the memory mechanisms supporting tool grasping and tool use have received little attention. Results from Experiment 2 suggest that these skilled components of tools are also heavily dependent on declarative memory, which is a unique contribution of this work.

In terms of procedural aspects of tool knowledge and skills, findings from Experiment 2 provide compelling evidence that disrupting frontal/attentional processes does not interfere with motor skill learning associated with complex tools, but can negatively affect accuracy of tool use. For instance, results showed that motor skill learning under divided attention was equivalent to learning under full attention. However, subsequent demonstration of tool use was less accurate for tools trained under divided relative to full attention. Thus, limiting attentional resources may not impact learning of the motor skill, but may affect encoding of critical task-related details required for subsequent tool use demonstration. These results from Experiment 2 provide further evidence that motor skill learning and skilled tool use rely on different memory processes despite the two measures being very similar in nature. In summary, studying the involvement of frontal/attentional processes can help to delineate declarative and procedural aspects of tool knowledge and skills.

Dissociation and Interaction of Memory Systems

Early memory research has shown that declarative and procedural memory systems are distinct and that they mediate different types of learning (Cohen & Squire, 1980; Knowlton, Mangels, & Squire, 1996). There is also evidence of different forms of interactions between the two memory systems (Packard & Goodman, 2013; Poldrack & Packard, 2003). Furthermore, it has been shown that the nature of interaction (e.g., cooperative, competitive, or compensatory) can be modulated by altering the learning context (Foerde, Knowlton, & Poldrack, 2006; Foerde, Race, Verfaellie, & Shohamy, 2013; Packard & Goodman, 2013). Findings from the three experiments in the current dissertation provide evidence of both dissociation and interaction between memory systems in the context of acquiring tool knowledge and skills.

Evidence of dissociation between declarative and procedural memory can be found in all three of the current experiments. Results for motor skill acquisition and recall of tool attributes are particularly informative. In Experiment 1, participants with PD, who typically have procedural memory impairment, were shown to have impaired motor skill retention but unimpaired recall of tool attributes, relative to controls. A similar pattern of dissociation was found in Experiment 3 where processes involved in procedural memory were disrupted by limiting performance-based feedback during training. In this experiment, limited feedback during training was detrimental for motor skill learning, but did not have any impact on subsequent recall of tool attributes. In Experiment 2, the opposite pattern of dissociation was found. Encoding of declarative information was selectively disrupted by dividing attention of participants during training. Results showed that recall of tool attributes was impaired, whereas motor skill acquisition was unaffected. It is worth noting that these results are similar to those obtained in Roy & Park (2010) in which an amnesic individual also showed intact motor skill learning but impaired recall of tool attributes, relative to controls. Results from the current experiments, along with Roy & Park (2010), present evidence of a double dissociation in which motor skill learning is primarily supported by procedural memory whereas memory for tool attributes is primarily dependent on declarative memory.

Along with evidence of dissociation, the current dissertation also presents evidence of interaction between declarative and procedural memory. In each experiment, a specific memory system was compromised, either through behavioural manipulation or as a result of a neurological disorder. Skilled tool use performance was particularly valuable in studying the interaction between memory systems. Findings showed that disruption of either system was associated with impaired tool use across all experiments, suggesting that both declarative and procedural systems are involved in skilled tool use. In other words, some aspect of skilled tool use was impaired in each of the three experiments. Examination of tool use accuracy and completion time provided further insights into the specific contributions of each memory system to skilled tool use. Results from Experiment 2 showed that when declarative memory is compromised, tool use accuracy, but not speed, is negatively affected. Conversely, results from Experiment 1 showed that when procedural memory is compromised, retention of tool use as measured by completion time is impaired, whereas tool use accuracy is relatively intact. Thus, findings from these experiments suggest that skilled tool use is mediated by a cooperative interaction of both memory systems with each system having a unique and necessary role in supporting tool use. Based on the pattern of results obtained, it could be proposed that declarative memory is involved in learning task-related details (e.g., sequence of steps, positioning of objects) critical for accurate demonstration of tool use, whereas procedural memory is required for motor expertise associated with using a tool.

Although findings from the current research provide strong support for a cooperative interaction between declarative and procedural memory in skilled tool use, there is also evidence of other forms of interaction in the context of motor skill learning. It has been argued that motor skill learning is primarily mediated by the procedural memory system; however, results from Experiments 1 and 2 raise the possibility of competitive and compensatory interactions. For instance, in Experiment 1, the pattern of motor skill learning exhibited by participants with PD (i.e., intact learning within session but impaired retention after a delay), is characteristic of a declarative pattern of learning. Thus, some mechanism of declarative compensation may underlie skill learning performance of participants with PD. Declarative compensation for impaired procedural memory has been reported in previous research on skill learning with individuals with PD (Gobel et al., 2013). However, it is important to note that although declarative memory may have partly compensated for compromised procedural memory, retention of motor skills was still impaired, suggesting that there is a cost of procedural memory impairment. In terms of a competitive interaction, results from Experiment 2 showed that dividing attention during training did not affect motor skill learning in terms of completion time. However, analysis of errors showed that removal of the secondary task in the divided attention condition was associated with a higher number of errors than the full attention condition. This result suggests that participants may have attempted to perform the tool tasks in a conscious manner, drawing on declarative memory of the task when these cognitive resources became available. This shift to a declarative approach appears to have interfered with procedural skill learning. This type of competitive interaction has been shown in previous studies involving motor skills related to sports (e.g., Beilock, 2002).

In summary, the current dissertation provides evidence of a dynamic relationship between declarative and procedural memory that appears to be adaptable to the given learning context. This flexible interaction between memory systems has important clinical implications, not only for action-related memory impairment, but for memory impairment in general. These findings also advance our understanding of how memory systems interact and suggest that they function in a more flexible manner than was previously believed.

Advantages of Using Tools as Experimental Stimuli

The current research has expanded on existing research in the areas of tool use and interacting memory systems. However, it is important to note several distinguishing factors of the current experiments compared to previous studies in this field. For instance, existing studies have predominantly carried out research using computer-based tasks that involve learning of various associations (e.g., probabilistic classification learning). Although these types of tasks have their significant advantages (e.g., ease of administration , minimal motor involvement), it could be argued that the use of tool tasks used in the current research has greater ecological validity and real-life functioning. As such, they may have greater clinical significance for rehabilitation. In addition to limited clinical relevance of existing research, the majority of previous studies using tools have focused on specific elements of tool-related knowledge and skills (e.g., studying tool grasping in isolation). In contrast, the current research investigated the different aspects of tool knowledge and skills in a comprehensive and integrative manner, by combining all elements (e.g., motor skill learning, memory for tool attributes, tool grasping, and skilled tool use). A further advantage of investigating tools is that some aspects of tool knowledge and skills require both declarative and procedural memory which provides an opportunity to examine the interaction between these two systems in a single task.

Future Directions

As mentioned, the use of complex tools as experimental stimuli provides a closer link to everyday living situations than computerized tasks. Therefore, the current research may have important clinical implications with respect to rehabilitation of memory disorders. Current and previous research has demonstrated that declarative and procedural memory systems may interact in a flexible manner (Packard & Goodman, 2013; Foerde et al., 2013). Future research could begin to apply this knowledge to clinical populations with various memory impairments. For instance, it may be possible to behaviourally bias activation of memory systems in favour of an individual’s preserved memory functions to support performance. Alternatively, it may be the case that individuals with PD rely on their declarative memory system too heavily. This may result in impaired performance, as declarative memory system may not be equipped to support functions of the procedural memory system. Therefore, limiting use of inefficient compensatory approaches and exercising use of compromised abilities may improve performance. This set of future studies may not only reveal potential clinical benefits of behavioural manipulations, but would also advance our understanding of factors that influence the relative activation of different memory systems and help to clarify the relation between the two memory systems. This area of research may also benefit from neuroimaging studies in which the shifting interactions between memory systems could be investigated from a neuroanatomical perspective to complement behavioural findings.

Conclusion

Taken together, the three experiments in the current dissertation provide a comprehensive and cohesive set of findings. They present evidence showing that different aspects of knowledge and skills associated with complex tools are mediated by different memory systems. They also present evidence showing that declarative and procedural memory interact in supporting some aspects of tool knowledge and skills. Thus, the current research has greatly enhanced our understanding of how memory systems interact in mediating complex tool knowledge and skills. By studying complex tools, this research also presents a novel approach to examining the organization of memory systems and has bridged the domains of memory and tool use. It is hoped that future research will continue to build on this link between memory and tool use to broaden our understanding in both these areas.

References

Beilock, S. L., Carr, T. H., MacMahon, C., & Starkes, J. L. (2002). When paying attention becomes counterproductive: Impact of divided versus skill-focused attention on novice and experienced performance of sensorimotor skills. *Journal of Experimental Psychology: Applied, 8,* 6–16. doi:10.1037/1076-898x.8.1.6

Chun, M. M., & Turk-Browne, N. B. (2007). Interactions between attention and memory. *Current Opinion in Neurobiology, 17,* 177–184. doi:10.1016/j.conb.2007.03.005

Cohen, N. J., & Squire, L. R. (1980) Preserved learning and retention of pattern-analyzing skill in amnesia: Dissociation of knowing how and knowing that. *Science, 210*, 207-210. doi:10.1126/science.7414331

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J.,... Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research, 199*, 61-75. doi:10.1016/j.bbr.2008.11.012

Foerde, K., Knowlton, B. J., & Poldrack, R. A. (2006). Modulation of competing memory systems by distraction. *Proceedings of the National Academy of Sciences, USA, 103*, 11778-11783. doi:10.1073/pnas.0602659103

Foerde, K., Poldrack, R. A., & Knowlton, B. J. (2007). Secondary-task effects on classification learning. *Memory & Cognition, 35*, 864–874. doi:10.3758/bf03193461

Foerde, K., Race, E., Verfaellie, M., & Shohamy, D. (2013). A role for the medial temporal lobe in feedback-driven learning: evidence from amnesia. *Journal of Neuroscience, 33*, 5698–5704. doi:10.1523/jneurosci.5217-12.2013

Gobel, E. W., Blomeke, K., Zadikoff, C., Simuni, T., Weintraub, S., & Reber, P. J. (2013). Implicit perceptual-motor skill learning in mild cognitive impairment and Parkinson’s disease. *Neuropsychology, 27*, 314-321. doi: 10.1037/a0032305

Goh, H.-T., Sullivan, K. J., Gordon, J., Wulf, G., & Winstein, C. J. (2012). Dual-task practice enhances motor learning: a preliminary investigation. *Experimental Brain Research*, *222*, 201–210. doi:10.1007/s00221-012-3206-5

Knowlton, B. J., Mangels, J. A., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science, 273,* 1399–1402. doi:10.1126/science.273.5280.1399

Mochizuki-Kawai, H., Kawamura, M., Hasegawa, Y., Mochizuki, S., Oeda, R., Yamanaka, K., & Tagaya, H. (2004). Deficits in long-term retention of learned motor skills in patients with cortical or subcortical degeneration. *Neuropsychologia*, *42*, 1858-1863. doi:10.1016/j.neuropsychologia.2004.03.012

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology*, *19,* 1–32. doi:10.1016/0010-0285(87)90002-8

Packard, M. G., & Goodman, J. (2013). Factors that influence the relative use of multiple memory systems. *Hippocampus, 23*, 1044-1052. doi:10.1002/hipo.22178

Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature*, *414*, 546–550. doi:10.1038/35107080

Poldrack, R. A., & Packard, M. G. (2003). Competition among multiple memory systems: converging evidence from animal and human brain studies. *Neuropsychologia*, *41*, 245–251. doi:10.1016/s0028-3932(02)00157-4

Roy, S., & Park, N. W. (2010). Dissociating the memory systems mediating complex tool knowledge and skills. *Neuropsychologia*, *48*, 3026-3036. doi: 10.1016/j.neuropsychologia.2010.06.012

Schendan, H. E., Searl, M. M., Melrose, R. J., & Stern, C. E. (2003). An fMRI study of the role of the medial temporal lobe in implicit and explicit sequence learning. *Neuron*, *37*, 1013-1025. doi: 10.1016/s0896-6273(03)00123-5

Weisberg, J., van Turennout, & Martin, A. (2007). A neural system for learning about object function. *Cerebral Cortex, 17,* 513-521. doi:10.1093/cercor/bhj176

Appendix A

Experiment 1 design

	Session 1				**Session 2**				
Participant	Pretest	Training		Post-test	Pretest	Training		Post-test	Untrained
1	A	B	A	B	B	A	B	A	C
2	B	A	B	A	A	B	A	B	C
3	B	C	B	C	C	B	C	B	A
4	C	B	C	B	B	C	B	C	A
5	C	A	C	A	A	C	A	C	B
6	A	C	A	C	C	A	C	A	B

3-week delay

Appendix B

Experiment 2 design

1-back Pretraining	Training	1-back Post-training	Break	Test

		Trial 1	Trial 2	Trial 3	Probe Trial (Full Attention)
FA	Set A	tool 1 tool 2 tool 3	tool 1 tool 2 tool 3	tool 1 tool 2 tool 3	tool 1 tool 2 tool 3
	Set B	tool 4 tool 5 tool 6 } Test set			
DA	Set C	tool 7 tool 8 tool 9	tool 7 tool 8 tool 9	tool 7 tool 8 tool 9	tool 7 tool 8 tool 9
	Set D	tool 10 tool 11 tool 12 } Test set			

Appendix C

Experiment 3 design

		Training				**Test**
Group	Set Order	Observe video	Trial 1	Trial 2	Trial 3	
PWR	A Tool 1 . . B . Tool 12	observe video	perform with recipient but no video	perform with recipient but no video	perform with recipient	Set A
PNR	A Tool 1 . . B . Tool 12	observe video	perform no recipient and observe video	perform no recipient and observe video		Set A
OBS	A Tool 1 . . B . Tool 12	observe video	observe video	observe video		Set A