

**THE EFFECTS OF ACQUISITION AND TEST CONDITIONS ON
DECLARATIVE AND MOTOR-PROCEDURAL MEMORY FOR COMPLEX
TOOLS**

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Abstract

Previous research revealed that the acquisition and retention of various tool properties (e.g., recalling information about a tool's attributes, performing tool-related motor actions, demonstrating a tool's correct use) requires complex cognitive processes, including declarative and motor-procedural memory. Though certain properties may rely more heavily on one type of memory than another, evidence indicates that various aspects of tool use may be mediated by an interaction between both memory systems. Given the possibility of flexible interactions between declarative and motor-procedural memory, this dissertation examined the effects of acquisition and test conditions on learning and retention of different tool properties, and the relative contributions of underlying memory processes. In Experiment 1, participants with Parkinson's disease (PD) (who had impaired striatal processing and motor-procedural memory but intact declarative memory), as well as healthy controls, demonstrated that completing additional, massed practice trials enhanced motor acquisition performance and overall learning across sessions. However, retention differed between the two groups: healthy controls, but not PD participants, retained their motor performance across 1-day and 3-week delays. Additional practice also resulted in superior recall of tool attributes across participants, indicating enhanced declarative memory with a greater number of training trials. In Experiment 2, the effects of practice schedules were examined in a sample of healthy adults. Findings demonstrated support for the spacing effect, such that compared to massed practice (i.e., consecutive trials), spaced practice improved test performance on

all tool properties after a 3-week delay, indicating enhanced declarative and motor-procedural memory. The interaction between spacing and learning type (i.e., observation vs. practice) was examined in Experiment 3. Results showed that for tool properties mediated primarily by declarative memory, spacing effects were observed after a 3-week delay at test, regardless of whether participants observed or physically practiced the task during acquisition. However, for properties that were heavily mediated by motor-procedural memory, there were no spacing effects with observational learning. These findings demonstrated that underlying memory system must be considered when assessing spacing effects, such that the learning method must successfully engage the underlying memory system in order for spacing to be effective. Taken together, my pattern of results across studies revealed that both declarative and motor-procedural memory likely contributed to performance across various tool properties. However, the manipulation of key acquisition parameters affected how these two memory systems facilitated performance, which ultimately impacted performance after a 3-week delay. Retention findings also demonstrated that test conditions may influence the contributions of declarative and motor-procedural memory. Together these experiments provide further insights about cognitive processes underlying tool use, as well as about flexible interactions between memory systems.

Keywords: declarative memory, motor-procedural memory, memory interactions, complex tools, motor acquisition and retention, skilled tool use

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Chapter 1: General Introduction

Complex tools enable individuals to efficiently achieve goals by transforming motor output into advantageous mechanical actions (e.g., using scissors to cut paper) (Frey, 2007). In daily life, humans effortlessly use tools, but the cognitive functions involved are not well understood. Currently, debate exists about whether successful tool use requires memory processes. It has been argued that tool use can be achieved solely through technical reasoning based on a tool's affordances (Osiurak, 2014; Osiurak & Badets, 2016). Other researchers have proposed that tool use requires a variety of neurocognitive processes, including sensory-motor memories (Buxbaum, 2017; Roy & Park, 2018). Research from my lab has closely examined the role of declarative and motor-procedural memory in various tool properties, and how these forms of memory interact to facilitate performance (Fernandes, Park, & Almeida, 2017; Roy, 2014; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy, Park, Roy, & Almeida, 2015). Though there is some existing evidence for interacting relationships between different types of memory during tool use, this topic warrants further investigation as it could lead to theoretical and clinical implications for tool use, and memory systems more generally.

The primary objective of my dissertation was to critically examine how a variety of acquisition and test conditions affected acquisition and long-term retention of various properties of complex tools. In my dissertation, I defined acquisition as performance that accompanies or immediately follows practice, and retention as performance after a delay of at least 24 hours. The overall goals of this research were to: (a) develop a better understanding of the different memory processes required for tool use; (b) further theoretical knowledge about the flexible interactions between declarative and motor-procedural memory; and (c) determine the effect of different

acquisition and test conditions on learning and retaining different tool properties that rely on declarative and motor-procedural memory. I was particularly interested in identifying which acquisition and test conditions led to different performance patterns for tool properties that were mediated primarily by declarative versus motor-procedural memory. Tools in themselves are a valuable resource to investigate the interplay of memory systems because previous research has shown that these memory systems are required for different aspects of tool use (Fernandes et al., 2017; Roy, 2014; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy et al., 2015).

These research objectives were investigated through three behavioural experiments. In the following General Introduction, I provide a brief overview of declarative and non-declarative memory systems and discuss their role in tool properties. Then I briefly describe the different acquisition conditions that will be used in my dissertation, and highlight research findings that are particularly relevant to my dissertation. Then an outline of my three experiments is presented. More detailed and comprehensive information related to each topic are subsequently discussed in chapters for each experiment.

Overview of Human Memory Systems

Memory can be broadly divided into declarative and nondeclarative memory. Nondeclarative memory encompasses various types of learning that can occur without awareness, including procedural memory, which is required for skill learning. Motor-procedural memory, in particular, is important for performing motor actions, and relies largely on cortico-cerebellar and cortico-striatal networks (Doyon, Penhune, & Ungerleider, 2003). In contrast, declarative memory encompasses both episodic (i.e., personal events) and semantic (i.e., general) information¹. Episodic memory and the retrieval of new events relies heavily on processing from

¹ Declarative memory has also been divided into fact-based and event learning (Squire & Zola-Morgan, 1991).

the hippocampal complex (Moscovitch et al., 2005; Tulving, 1985), whereas semantic memory is mediated by complex neural networks, including the posterior temporal cortex (Binder & Desai, 2011; Kalénine & Buxbaum, 2016). Although there are important distinctions between episodic and semantic memory, throughout my dissertation, I intentionally use the broader term of declarative memory because my experiments were not designed to differentiate between these two subtypes of declarative memory.

Key functional differences exist between declarative and procedural memory. For instance, declarative memories can be flexible, are rapidly acquired, and are susceptible to forgetting due to decay over time or interference (Ellenbogen, Payne, & Stickgold, 2006; Squire, Knowlton, & Musen, 1993; Tulving, 1985), whereas procedural memories tend to be less flexible, are learned gradually, and are more robust to forgetting (Albouy, King, Maquet, & Doyon, 2013; Gabrieli, Corkin, Mickel, & Growdon, 1993). Additionally, feedback can have differential effects on these systems; declarative learning can occur in the context of observational learning or delayed feedback, whereas procedural processing tends to require immediate, trial-by-trial feedback (Foerde, Race, Verfaellie, & Shohamy, 2013; Schmitt-Eliassen, Ferstl, Wiesner, Deuschl, & Witt, 2007).

Declarative and procedural memory were traditionally viewed as independent forms of memory that were mediated by different neural regions. Early research based on patient studies showed that individuals with different neural damage demonstrated a double dissociation with memory ability. For example, people with amnesia due to hippocampal damage had impaired declarative memory but intact procedural memory, whereas individuals with Parkinson's disease (PD) due to striatal dysfunction showed the opposite pattern of performance (Knowlton, Mangels, & Squire, 1996). More recently, research showed that these two types of memory can

interact in a variety of ways (Poldrack & Rodriguez, 2004). With *cooperative* interactions, both declarative and procedural memory are simultaneously required to mediate performance (Brown, Ross, Tobyne, & Stern, 2012; Ferbinteanu, 2016; Sadeh, Shohamy, Levy, Reggev, & Maril, 2011). Alternatively, memory systems can have *competitive* interactions, where one system may have an inhibitory effect on the other system (Albouy et al., 2008; Brown & Robertson, 2007; Foerde & Shohamy, 2011; Packard & Goodman, 2013; Poldrack & Packard, 2003). Within a competitive relationship, *compensatory* interactions may also occur where the dysfunction of a competing system can result in greater use of the preserved system. For instance, compensatory relationships have been reported in individuals with PD who have striatal dysfunction; when performing tasks that typically require procedural learning, people with PD may instead rely more on relatively intact hippocampal processing and declarative memory (Foerde, Braun, & Shohamy, 2013; Gobel et al., 2013). Additionally, within competitive relationships, the manipulation of various factors, such as the temporal sequence of training, reinforcement parameters, and timing of feedback, may alter how these systems interact, potentially affecting the relative contributions of declarative and procedural memory (Packard & Goodman, 2013).

Memory Systems in Tool Use

Research examining praxis and apraxia revealed that complex tool use relies on a range of skills and knowledge (Boronat et al., 2005; Buxbaum & Saffran, 2002; Stanley & Krakauer, 2013). It has been argued that humans use a tool's perceptual characteristics and technical reasoning to infer its function (Goldenberg, 2013; Osiurak & Badets, 2016). However, other research has shown that the left inferior parietal lobe plays a critical role through manipulation knowledge that likely requires some form of semantic memory (Buxbaum, 2017; Tarhan, Watson, & Buxbaum, 2015). In addition, there is substantial evidence that declarative and motor-

procedural memory are also important. For instance, the ability to recall information about a tool's attributes relies primarily on declarative memory (Hodges, Bozeat, Ralph, Patterson, & Spatt, 2000; Johnson-Frey, 2004), whereas action sequences, which are acquired when learning how to use a tool, are mediated heavily by motor-procedural memory (Corkin, 1968; Eslinger & Damasio, 1986; Gobel et al., 2013; Willingham & Koroshetz, 1993).

Previous work from my lab systematically investigated how declarative and motor-procedural memory mediate novel tool use. In an initial study, Roy and Park (2010) investigated tool use in D.A., an individual with amnesia due to hippocampal damage. Results revealed that when compared to healthy controls, D.A. was impaired in recall of tool attributes (e.g., color and function of tool), tool grasping and skilled tool use (i.e., demonstrating a tool's use on command), suggesting that these aspects of tool use rely to some extent on declarative memory. However, D.A. was unimpaired in performing tool-related actions with practice; he became faster at using the tools within a session, and demonstrated retention after a 3-day and 3-week delay, suggesting that this aspect of performance was heavily mediated by motor-procedural memory.

Building on these findings, a further study examined tool use in PD (Roy et al., 2015). This patient group was selected because individuals with PD have striatal dysfunction, resulting in well-documented procedural memory impairments (Clark, Lum, & Ullman, 2014; Packard & Knowlton, 2002; Siegert, Taylor, Weatherall, & Abernethy, 2006). Findings from Roy et al. (2015) showed that compared to controls, PD participants demonstrated the opposite pattern of performance than D.A., namely, intact recall of tool attributes, but impairments in some aspects motor performance. Specifically, individuals with PD exhibited intact within-session motor learning (i.e., tool use became faster over Training trials), but performance was not retained after

three weeks. These findings provided further support that both declarative and motor-procedural memory are required for tool use, and may interact for some aspects. For instance, the authors proposed that due to impaired motor-procedural memory, PD participants may have compensated by relying on declarative memory, or an intact processing from the hippocampal complex, when learning to perform the actions associated with the tool. As a result, within a session they were able to acquire motor actions, but could not retain performance because their declarative memory declined over the 3-week delay. This possibility is notable because it suggests that the contributions of the two memory systems in tool use may have important implications for performance, especially regarding long-term retention.

The notion of memory interactions within tool use lends itself to the possibility that under certain circumstances, the relative contributions of declarative and motor-procedural memory may vary. Building on the findings from Roy et al. (2015), Fernandes et al. (2017) assessed whether more extensive practice (i.e., Training trials), distributed over multiple days, ameliorated the observed motor retention deficit in PD. In this design, PD participants and healthy controls completed four sessions, spaced one day, one week and three weeks apart, and during each session, they completed two Training trials for each tool, increasing the number of trials used by Roy et al. (2015). The study's objective was supported by research proposing that declarative and motor-procedural memory interact during motor learning. For instance, early learning has been shown to be associated more with hippocampal activation and declarative memory, whereas after practice, later learning has been associated with decreased hippocampal activation and increased striatal activation associated with procedural memory (Albouy et al., 2013; Doyon & Benali, 2005; Doyon, Gabbitov, Vahdat, Lungu, & Boutin, 2018). Individuals with PD, though, may be unable or

slower to engage procedural processing (Shohamy, Myers, Kalanithi, & Gluck, 2008; Wilkinson & Jahanshahi, 2007; Wilkinson, Khan, & Jahanshahi, 2009).

The results from Fernandes et al. (2017) demonstrated that compared to controls, PD participants exhibited intact within-session learning of the actions associated with the tools and demonstrated overall improvement across four sessions, but they still had retention impairments. These deficits were hypothesized to reflect 1) impaired consolidation of striatally-mediated memories and/or 2) compensatory processes whereby PD participants relied more on declarative memory, which is more susceptible to forgetting than procedural memory, during motor learning. Though this study was useful in examining the effects of practice on tool-related motors in PD, the ability to draw conclusions from the experiment was impacted by methodological limitation. Namely, the effects of additional practice were confounded by increasing delays, such that as participants completed more Training trials, the delay length also increased. Despite this limitation, the study still provided further evidence that with certain populations and/or acquisition conditions, the underlying memory processes supporting performance may vary.

As previously stated, the goal of my PhD dissertation was to further investigate how declarative and motor-procedural memory mediate various aspects of tool use. Specifically, I was interested in examining how different acquisition and test conditions may affect performance on tool measures primarily mediated by different memory systems, or alter the interactions between them. In doing so, I hoped to contribute to knowledge about the dynamic relationships between memory systems, which may also result in practical recommendations about structuring the learning environment to enhance performance. To achieve this broader research objective, I conducted a series of three behavioral experiments, each of which focused on a critical aspect of learning that was hypothesized to affect motor-procedural and/or

declarative memory required in tool use. Expanding on Fernandes et al. (2017), Experiment 1, further assessed the effects of extensive, massed practice in PD, a patient population with known procedural memory impairments. Experiments 2 and 3 then investigated how other behavioural techniques could improve acquisition and/or retention performance by enhancing memory systems in healthy adults; Experiment 2 assessed how the practice schedule (i.e., spacing of Training trials) impacted performance, and Experiment 3 further investigated these findings by exploring the interaction between Training schedules and type of learning.

Overview of Current Experiments

Experiment 1.

Research from Roy et al. (2015) initially demonstrated that in tool use, individuals with PD showed preserved within-session motor learning, but had impaired retention after three weeks, and Fernandes et al. (2017) showed that receiving additional practice improved some aspects of performance. Experiment 1 built upon these findings, but implemented a design that allowed for a more critical examination of how more practice may have affected performance on various tool properties, and the interactions between memory systems that underlie performance. Specifically, I wanted to determine if more Training trials completed in massed succession during one session improved short-term (1-day) and long-term (3-week) retention in individuals with PD and healthy adults. It was possible that people with PD require more opportunities to practice a task to move from more declaratively-mediated learning to procedural learning (Shohamy et al., 2008). In addition, recent research has proposed that in healthy, older adults, massed practice may increase striatal activation during acquisition and delayed retention when performing a motor action (Pauwels et al., 2018).

Based on the assumption that individuals with PD are impaired in procedural processing

that is striatally-mediated, but have relatively intact declarative memory in early stages (Davidson, Anaki, Saint-Cyr, Chow, & Moscovitch, 2006), the following general hypotheses were proposed. In both PD and control participants, I predicted that more practice would result in better performance on tasks with a large declarative memory component (e.g., recall of tool attributes) (Fernandes et al., 2017; Roy et al., 2015). Regarding motor performance, I hypothesized that controls would retain performance across delays, and more practice would result in better within-session and overall motor learning (Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015). However, it was unclear whether more practice would result in improved or unimpaired retention in PD participants. It was possible that with more learning trials, PD participants could engage procedural learning (Shohamy et al., 2008). Alternatively, it could be argued that with more practice, the learner also has greater exposure to the task, likely resulting in better declarative memory, which could benefit PD participants if a compensatory mechanism was used during motor performance. By carefully examining performance patterns across different motor learning stages, populations and tool measures, I also aimed to differentiate between these two potential mechanisms.

Overview of Experiments 2 and 3.

Experiments 2 and 3 focused on manipulating specific acquisition conditions that were hypothesized to impact motor-procedural and/or declarative memory traces, ultimately improving certain tool-related abilities. As subsequently discussed, Experiment 2 altered the distribution of Training trials within a session and compared the effects of massed versus spaced practice (i.e., examined the spacing effect). Experiment 3 then determined how the Training schedule interacted with different forms of learning to influence the contributions of these memory systems.

The spacing effect.

One potential method to improve tool-related memory in healthy adults was to alter the schedule of Training trials during the acquisition period. Though past studies from my lab (Fernandes et al., 2017; Roy, 2014; Roy & Park, 2010, 2016; Roy et al., 2015), and Experiment 1, used massed or consecutive trials, there is strong evidence to suggest that memory performance could be enhanced with the use of a spaced schedule (i.e., distributed so intervening information is presented between two acquisition trials). This well-documented finding of superior retention with the use of spaced than massed trials is commonly known as the spacing effect in the verbal literature (for a review see Cepeda, Pashler, Vul, Wixted, & Rohrer, 2006). Similarly, motor studies have typically reported that when compared to massed practice, spaced or random practice resulted in poorer within-session acquisition, but superior retention after a delay, and this finding has been typically referred to as the contextual interference effect (see Merbah & Meulemans, 2011 for a review). Though these phenomena have been studied independently in the verbal and motor literatures, there are some notable commonalities between proposed theoretical mechanisms. For instance, some theories propose that spaced trials produce superior retention performance because the learner has opportunities to retrieve or reconstruct the to-be-remembered information during the acquisition phase itself (i.e., Study-phase Retrieval Hypothesis in verbal literature; Action-Plan Reconstruction Hypothesis in motor literature) (Lee & Magill, 1983; Maddox, 2016; Thios & D'Agostino, 1976). Conversely, other theories emphasize more elaborative encoding with spaced or random trials (i.e., Encoding Variability Hypothesis in verbal literature; Elaboration Hypothesis in motor literature) (Maddox, 2016; Melton, 1970; Shea & Morgan, 1979). Regardless though of specific mechanisms, theories from the verbal and motor learning studies predict that spacing Training trials within a session would

enhance both declarative and motor-procedural memory. To my knowledge though, to date, there has yet to be a study that concurrently examined the effects of spacing on different memory systems within a single experiment.

Experiment 2.

The overall goal of Experiment 2 was to assess how the distribution of Training trials affected performance on various abilities required for novel tool use during acquisition (Session 1) and retention (i.e., after a 3-week delay in Session 2). By comparing findings across tool measures that were primarily mediated by different memory systems, I was interested in potentially identifying more specific mechanisms underlying the spacing effect in motor performance. For instance, it was unclear whether spaced trials were beneficial because they improved visual processing associated with a specific task, or whether spacing enhanced motor and action planning (Pauwels et al., 2018). In terms of predictions, I hypothesized that compared to massed trials, spaced practice would result in better retention for recall of tool attributes, which was primarily mediated by declarative memory. Within recall performance, I also was interested in assessing the type of knowledge that was enhanced with spacing. In particular, as discussed in Chapter 3, determining whether spacing improved functional/associative and/or perceptual information would allow for a more nuanced understanding of the type of declarative knowledge that may be enhanced with spacing. In terms of motor performance, which was primarily mediated by motor-procedural memory, I also predicted that spaced practice would result in superior retention performance than massed practice. Such findings would demonstrate that spacing can concurrently enhance both declarative and motor-procedural memory, leading to considerable practical implications.

The testing effect and performance-based feedback.

An additional factor that can affect the acquisition and retention of new knowledge and skills is the type of learning that individuals engage in. Though the main focus of Experiment 2 evaluated the spacing effect, results could have been impacted by the fact that participants physically practiced the tool task during the acquisition phase. Although practice trials are commonly used for motor learning, there are two important considerations that could impact interpretation of findings. First, in verbal learning studies, the act of generating a response during the acquisition phase has been extensively examined, and is referred to as the testing effect. Here, it has been shown that testing one's memory by requiring the learner to provide a response during acquisition typically produced better retention performance than restudying information (Roediger III & Butler, 2011; Roediger III & Karpicke, 2006a). Second, previous research from my lab (Roy, 2014) demonstrated that the degree of performance-based feedback available during acquisition was important for subsequent memory performance for some tool properties. In one condition, participants performed the task and interacted with the tool (practice learning) during training, and in a second condition, they only viewed the task being performed (observational learning). Motor performance was higher in the practice condition, whereas there was no difference between the two conditions for recall of tool attributes (Roy & Park, 2010). These findings suggested that performance-based feedback was only critical for motor-procedural learning, consistent with other studies demonstrating a benefit of action-based learning over observational learning on some procedurally-mediated tasks (Shea, Wright, Wulf, & Whitacre, 2000).

Experiment 3.

Given the potential impact of physically practicing the task on performance, interpretation of findings related to the spacing effect in Experiment 2 may have also been

affected by the employed learning method. Thus, Experiment 3 investigated the interaction between learning type (observation vs. physical practice) with Training schedule (massed vs. spaced) during acquisition (Session 1) and retention (Session 2). Overall, I wanted to determine if performance-based feedback was necessary for the spacing effect to occur in tool attributes that were primarily mediated by different memory systems. There is strong evidence to suggest that enhanced cognitive processing is associated with spaced trials (Maddox & Balota, 2015; Merbah & Meulemans, 2011), but the role of feedback in the spacing effect had yet to be investigated. Thus, it was unclear whether the spacing effect would exist for motor actions if the learner was restricted from receiving performance-based feedback during learning. Based on the assumption that declarative memory does not require performance-based feedback, but procedural learning does, my main hypotheses were that the spacing effect would be observed with perform and observational learning for recall of tool attributes, as this measure relies heavily on declarative memory (Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015). In contrast, for motor performance, it seemed likely that the spacing effect would only be exhibited with practice, as observation would not be effective for motor learning. I also predicted that regardless of Training schedule across tool measures, practice would be associated with superior performance because compared to observation, practice learning involves response generation and performance-based feedback, which has been shown to improve both declarative and motor-procedural memory (Roediger III & Butler, 2011; Roediger III & Karpicke, 2006a, 2006b; Roy, 2014).

The subsequent chapters provide full details for these three experiments, which are then followed by a General Discussion that synthesizes findings across experiments and discusses broader theoretical, clinical and practical implications.

Chapter 2: The effects of extensive, massed practice on tool-related memory in healthy adults and individuals with Parkinson's disease (Experiment 1)

Parkinson's disease (PD) is a neurodegenerative disorder caused by the loss of nigrostriatal dopaminergic neurons (Dauer & Przedborski, 2003). Although it is primarily characterized by motor symptoms, such as bradykinesia, tremor, rigidity, postural instability and gait disability (Rodriguez-Oroz et al., 2009), cognitive impairments are often present even in individuals without dementia (Dubois & Pillon, 1996; Kehagia, Barker, & Robbins, 2010). Cognitive deficits typically reflect fronto-striatal dysfunction, with declines in executive functioning and some aspects of memory (Aarsland et al., 2017; Lewis, Dove, Robbins, Barker, & Owen, 2003; Owen et al., 1992). With memory specifically, past research demonstrated that individuals with PD exhibited impaired procedural memory (i.e., habit or skill-based learning) (Squire, 1992a), both on tasks that required a skilled motor response (Heremans et al., 2016; Krebs, Hogan, Hening, Adamovich, & Poizner, 2001; Smiley-Oyen, Lowry, & Emerson, 2006) and those that did not (Shohamy et al., 2008; Wilkinson et al., 2009). In contrast, in early stages of the disease, declarative memory (i.e., consciously accessible information) may remain relatively intact (Knowlton et al., 1996; Robbins & Cools, 2014), though certain aspects may still be negatively affected (Beyer et al., 2013; Cohn, Giannoylis, De Belder, Saint-Cyr, & McAndrews, 2016; Cohn, Moscovitch, & Davidson, 2010; Elgh et al., 2009). For instance, past studies have observed hippocampal atrophy and/or dysfunction in individuals with PD, which was associated with poorer declarative memory performance (Beyer et al., 2013; Cohn et al., 2016; Pereira et al., 2013). It has also been proposed that a subset of people of PD can have Lewy body pathology in temporal and parietal regions, which may be predictive of eventual

development of PD dementia (PDD) (Williams-Gray, Foltynie, Brayne, Robbins, & Barker, 2007; Williams-Gray et al., 2013).

With procedural memory impairments, individuals with PD have exhibited deficits in motor-procedural attributes of complex tools (i.e., objects that transform motor output and provide a mechanical advantage when acting on a recipient object) (Frey, 2007). Roy et al. (2015) initially showed that when learning how to use novel tools, PD participants had preserved acquisition of motor actions. However, unlike healthy controls, PD motor performance was not retained after a 3-week delay. In a follow-up study, more extensive practice (i.e., Training trials), distributed over multiple days, somewhat aided motor performance, such that individuals with PD demonstrated overall improvement within and across four sessions, though they still exhibited retention impairments relative to healthy controls (Fernandes et al., 2017). Building upon these findings, the current study continued to investigate how additional training affected memory for various tool attributes; I was mainly interested in determining how more massed Training trials completed within one session affected within-session motor learning, short-term (1 day) and long-term (3 week) retention, as well as overall improvement across sessions in healthy adults and individuals with PD. Using knowledge about the interactions of memory systems, my goal was to determine how additional, massed practice may impact the relative contributions of different memory systems during the various stages of tool-related motor learning.

Memory Systems Required for Complex Tool Use

Human memory is comprised of functionally and anatomically dissociable systems, and there is a well-established distinction between declarative memory and nondeclarative memory. Declarative memory refers to consciously retrievable knowledge, and includes both semantic and

episodic information. Semantic memory refers to general world knowledge, and relies on complex cortical networks (Binder & Desai, 2011; Wiggs, Weisberg, & Martin, 1998), and the posterior temporal cortex may be particularly important for tool-related information (Kalénine & Buxbaum, 2016). Episodic memory, on the other hand, involves recollecting personal events and experiences that are specific to a time and place (Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012), and requires a network of neural regions including the hippocampus (Moscovitch et al., 2005). In contrast, nondeclarative memory refers to many forms of learning where acquisition and retrieval occurs implicitly (Squire, 1992b). Motor-procedural memory in particular is necessary for motor learning, and is heavily mediated by cortico-cerebellar and cortico-striatal pathways (Doyon et al., 2009; Doyon et al., 2018).

Initially, declarative and motor-procedural memory systems were viewed as functionally independent (Squire et al., 1993), but more recent research has shown that they can interact in a variety of ways. With *cooperative* interactions, both systems contribute to performance, and may differentially support various aspects of a task (McClelland, McNaughton, & O'reilly, 1995b; Sadeh et al., 2011). Memory systems can also function *competitively*, which occurs when activation in one may inhibit activity in another system (Packard & Goodman, 2013). Within competitive relationships, *compensatory* interactions can also occur, such that when the memory system that typically supports performance becomes impaired, a preserved system may be recruited to enable performance (Gobel et al., 2013; Packard & Goodman, 2013).

Past research from my lab demonstrated that both declarative and motor-procedural memory are required for complex tool use, and the relative contributions of each system depends on the tool property that is being tested. For instance, recalling information about a tool's function or appearance seems to rely primarily on declarative memory, whereas performing tool-

related motor actions mainly requires motor-procedural processing. In contrast, skilled tool use, which involves demonstrating a tool's use when given a verbal command after a delay, likely requires both memory systems, such that one must first recall how to use the tool (i.e., accuracy requires declarative memory), and then carry out the motor action itself (i.e., motor performance requires motor-procedural memory) (Fernandes et al., 2017; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy et al., 2015). These distinctions were first established in a patient study that examined novel tool use in D.A, an individual with a severe declarative memory deficit due to hippocampal amnesia (Roy & Park, 2010). Compared to controls, D.A. was impaired in recalling information about a tool's attributes after a 3-day and 3-week delay, though his ability to acquire and retain tool-related motor actions after both delays was preserved. A subsequent study by Roy et al. (2015) then revealed the opposite performance pattern in individuals with PD, a patient group that was selected because of their previously documented procedural memory impairments due to striatal dysfunction (Harrington, Haaland, Yeo, & Marder, 1990; Knowlton et al., 1996; Krebs et al., 2001; Mochizuki-Kawai, 2008). Results from Roy et al. (2015) demonstrated that PD participants had intact recall of tool attributes. They also exhibited preserved motor learning during each session, but unlike healthy controls, performance was not retained after three weeks.

Taken together, these results suggested that for motor performance in particular, motor-procedural memory deficits in PD compromised retention, while within-session acquisition remained intact (Roy et al., 2015). These differences in motor performance are notable, and potentially reflect the neural and cognitive processes that primarily mediate performance during these separate motor learning phases. When learning sequential motor actions, it has been previously proposed that motor learning involves: 1) a fast, early learning phase, mediated by hippocampus, where considerable improvement occurs initially, 2) a consolidation stage where

motor actions become resistant to decay or interference, and 3) a slower, later learning phase, mediated by the striatum, where smaller improvements are obtained over time (Albouy et al., 2013; Doyon et al., 2003). Consistent with this framework, studies have shown that individuals with PD have difficulty achieving motor automaticity, which reflects the end stages of motor learning (Wu, Chan, & Hallett, 2010; Wu & Hallett, 2005; Wu, Hallett, & Chan, 2015), whereas acquisition tends to be relatively well preserved (for a review see Nieuwboer, Rochester, Müncks, & Swinnen, 2009). Thus, deficits in tool-related motor retention could have been due to an inability of individuals with PD to effectively engage striatal processing during later learning.

How Might Practice Affect Memory Representations of Motor Learning?

One possible approach to ameliorate this motor retention impairment in PD is through the use of more extensive practice. Past research showed that with motor sequence learning in healthy younger adults, patterns of neural activation varied as a function of practice, such that as participants completed more practice trials, striatal activation increased, while hippocampal activation decreased (Albouy et al., 2013; Albouy et al., 2008). In addition, the flexibility of hippocampal and striatal systems was observed in a recent functional magnetic resonance imaging (fMRI) study by Pauwels et al. (2018), which assessed the effects of practice schedules on a bimanual visuomotor task. Most relevant to the current study, massed practice (i.e., consecutive trials) was correlated with neural activation in areas associated with motor automaticity, such as sensorimotor-related regions during acquisition and the striatum during delayed retention. However, random practice (i.e., trials completed in random order) was correlated more with visual processing areas. The authors hypothesized that with random practice, the participants had to pay more attention to each task's visual features as they were constantly switching from practicing one task to another. However, with massed training,

participants were able to practice one task-specific motor action at a time, resulting in greater automatization.

Thus, in healthy adults, massed practice and increasing the number of Training trials appears to bias greater use of striatal processing. These findings may also extend to PD, as some authors have proposed that individuals with mild-moderate PD may not have an absolute loss of striatal learning, but rather have an inefficient system that requires more practice to be engaged. For example, Shohamy et al. (2004) examined performance of individuals with PD and healthy controls during probabilistic classification learning using the weather prediction task. In this task, participants implicitly learn the probability of certain weather outcomes by receiving immediate trial-by-trial feedback, and learning typically relies on striatally-mediated procedural memory (Knowlton et al., 1996). Results from Shohamy et al. (2004) indicated that PD participants were impaired on the task during later training trials, but not during early trials. A subsequent study using computational modelling then revealed that after extensive amounts of practice, PD performance was comparable to the control group (Shohamy et al., 2008). The authors argued that due to striatal dysfunction, PD might result in a generalized slowing in procedural learning, so PD participants might require more opportunities to practice a task to engage striatal processes.

Alternatively, it is possible that more practice could benefit individuals with PD because it may support a compensatory mechanism during learning. The notion of compensatory interactions in PD has been previously proposed, such that due to striatal dysfunction and procedural memory impairments, individuals with PD may instead rely more heavily on relatively-preserved declarative memory and hippocampal processing (Gobel et al., 2013; Moody, Bookheimer, Vanek, & Knowlton, 2004). Research has also demonstrated that learning

conditions can be structured to bias the use of a certain memory system, which can have important implications for PD performance. For instance, Foerde and Shohamy (2011) demonstrated that slightly delaying trial-by-trial feedback in the weather prediction task shifted learning from the striatum to the hippocampus. Critically, individuals with PD were only impaired in the striatally-mediated immediate feedback condition, and not the hippocampally-mediated delayed feedback version. A follow-up study then revealed that although PD participants exhibited impaired task performance with immediate feedback, they had better declarative memory for the visual cues given during training (Foerde, Braun, et al., 2013). These results supported a competitive relationship between the two memory systems, such that in PD, when procedural memory was impaired, declarative memory was enhanced. In addition, a key manipulation in the training environment affected how these two memory systems mediated performance; the deficit in PD performance was ameliorated by delaying feedback, allowing for hippocampal processing to support learning. Building on such findings, it seems possible that more, massed practice could support a similar compensatory mechanism during tool-related motor learning. Specifically, additional practice would provide the learner with greater exposure to the task, potentially enhancing declarative memory and supporting motor performance in PD.

Following-up on the previously discussed findings from Roy et al. (2015), who initially investigated tool use in PD, I recently examined the effects of more extensive practice on various tool properties in PD and a matched sample of healthy controls. In this study, I determined whether completing more Training trials, distributed over multiple days, aided motor retention deficits in PD (Fernandes et al., 2017). Participants completed four sessions, that were spaced one day, one week and three weeks apart. During each session, for each tool they were administered two Training trials, which resulted in more Training trials than used by Roy et al.

(2015). Results indicated that for motor performance, compared to controls, PD participants exhibited intact within-session acquisition and demonstrated overall improvement across four sessions, though they still exhibited retention deficits after 1-week and 3-week delays.

Conversely, PD participants showed preserved recall of tool attributes, and completion of more Training trials resulted in higher declarative memory performance. These findings supported the use of more practice in PD, as benefits were found with respect to declarative recall and some aspects of motor performance. However, results were impacted by a limitation in the design: the effects of receiving more practice were confounded by increasing delays (i.e., as participants completed more Training trials, the length of delay also increased). This methodological factor somewhat limited my ability to carefully examine the cognitive processes that practice impacted during acquisition and retention phases of motor learning. Additionally, it is possible that massed practice completed within a one session could be more beneficial to participants' motor performance. For instance, striatal processing may be even further enhanced if participants completed extensive, massed practice within a single session, instead of spacing out training trials over multiple days (Pauwels et al., 2018).

Overview of Experiment 1

In this experiment, I examined the effects of massed practice completed within one session, and I also implemented a design that clearly separated the acquisition period in which participants received more practice from retention periods. In Session 1 (S1), PD participants and healthy age and education matched controls completed Training trials to learn how to use novel complex tools. I employed a within-session manipulation, such that for half of the tools, participants completed two successive Training trials, reflecting the traditional training procedure used (Roy et al., 2015), and the other half of the tools received five successive

Training trials, allowing for additional practice. I was primarily interested in examining motor performance, and wanted to determine how additional, massed Training trials affected within-session acquisition during S1, retention after 1-day and 3-week delays, and overall learning across sessions. I examined recall of tool attributes as my main measure of declarative memory, and skilled tool use was also assessed, as this attribute seems to require cooperative interactions from both memory systems (Fernandes et al., 2017; Roy, 2014; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy et al., 2015).

Based on the assumption that individuals with PD are impaired on motor-procedural processing that is striatally-mediated, but have relatively intact declarative memory in the early stages (Robbins & Cools, 2014), the following hypotheses were proposed. In both PD and control participants, more practice would result in superior declarative memory (i.e., recall performance). In terms of motor performance, I first wanted to determine how more, massed practice affected performance in healthy controls. Based on past research, which showed that increasing practice resulted in greater striatal activity (Albouy et al., 2013; Albouy et al., 2008), and massed training in particular may further bias the use of striatal processing (Pauwels et al., 2018), I predicted that for controls, additional Training trials would result in better within-session learning and overall motor performance. Practice with a motor action has been shown to be important for motor learning and automaticity (Doyon et al., 2018; Guadagnoli & Lee, 2004), so I hypothesized that increasing the number of massed Training trials would benefit performance. More generally, I also expected controls to demonstrate the typical pattern associated with motor learning, with large initial gains, followed by smaller improvements over time, and performance would be retained across delays (Albouy et al., 2013; Doyon et al., 2009; Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015).

For PD participants, I hypothesized that more, massed practice would result in greater learning during S1, which is consistent with past studies demonstrating relatively intact acquisition in PD (Fernandes et al., 2017; Nieuwboer et al., 2009; Roy et al., 2015). However, it was unclear whether additional practice would result in improved or unimpaired retention in PD participants. On one hand, it was possible that with more Training trials, PD participants might be able to engage striatally-mediated procedural learning (Shohamy et al., 2008). If motor-procedural learning supported performance, I expected PD participants to demonstrate unimpaired retention across delays, as procedural memory tends to be robust to forgetting (Gabrieli et al., 1993), and this result has been consistently observed with healthy adults (Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015). Conversely, it was also possible that PD participants could use a compensatory mechanism, where they could rely on relatively preserved hippocampally-mediated declarative memory to support motor learning (Foerde, Braun, et al., 2013; Gobel et al., 2013; Moody et al., 2004). If so, more practice could enhance declarative memory because participants had greater exposure to the task. However, if this type of compensation occurred, it seemed likely that motor retention might still be impaired after delays because declarative memory generally tends to decline over time (Ellenbogen et al., 2006; Mitchell, Brown, & Murphy, 1990), and previous research from my lab has demonstrated forgetting on tool-related declarative memory after delays (Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015).

Method

Participants

Eighteen participants with a diagnosis of idiopathic PD and 18 healthy age and education-matched controls completed the study. PD participants were recruited from the Sun Life Financial Movement Disorders Research Centre (MDRC), affiliated with Wilfred Laurier

University in Waterloo, Ontario. Control participants were recruited through a research participant pool at York University in Toronto, Ontario, and through local advertising.

All participants were required to be fluent in English, right-handed, and between 50 and 85 years old. Exclusion criteria were: reported colour-blindness, a history of serious head injury, a history of neurological illness (other than PD in the patient group), general cognitive deterioration demonstrated by a score less than 26 on the Mini-Mental State Examination (MMSE) (Folstein, Folstein, & McHugh, 1975), and current anxiety or depression, measured by the Hospital Anxiety and Depression Scale (HADS) (Zigmond & Snaith, 1983). Additionally, individuals with PD were not enrolled in the study if they had severe bradykinesia, severe rigidity in the right wrist or hand, severe tremor in the right hand, or severe tremor in the left hand, affecting ability to use the right hand. Participants were excluded if they received scores of 4 (“severe”) for these symptoms on the Unified Parkinson’s Disease Rating Scale (UPDRS III) (Fahn, 1987). Participants also answered questions about daily functioning prior to participation. As shown in Table 1, the groups did not significantly differ on any participant characteristic.

All PD participants were taking dopaminergic drugs; they remained on their regular medication throughout the study and were tested during an optimally medicated state (for mean dosage, see Table 1). The study was approved by the relevant ethics review boards, and participants provided written consent prior to participation.

Materials

Novel tools. Eight novel complex tools were used in the study (see Figure 1). The tools were constructed from a children’s building toy, K’NEX, and were similar to those developed by Roy & Park (2010). Each tool had a unique appearance and function, and was designed so that its function and grasp could not be inferred from its physical attributes (see Fernandes et al.,

2017 for more details). The tools were designed to be grasped unimanually, and performed a particular task by acting on an object, known as the recipient. For instance, one of the tools pushed a die (the recipient) down a path, and another tool picked up two rings and placed them in a designated area. The tools were randomly divided into two sets (Set A and B) with an equal number of tools.

Instructional videos. Each tool had a video associated with it that was approximately 30 seconds in duration. The videos played on a laptop and featured a demonstration of the task with audio instructions.

Recall test. A cued Recall test assessed memory for tool attributes. For each tool, participants viewed three grey-scale photographs of the tool taken from different angles, and gave verbal response to five questions. Three questions measured functional/associative knowledge (i.e., the function of the tool, the recipient of the tool, the number of recipients used in a task). Two question assessed perceptual information (i.e., the colour of the tool, the colour of the recipient(s)) (Roy & Park, 2010, 2016; Warrington & Shallice, 1984). The experimenter recorded each response.

Use-to-command test. The Use-to-command test assessed skilled tool use. The experimenter placed the tool and its associated materials in front of the participant, such that the tool was in its correct starting location, but the associated recipient(s) were placed in a designated, neutral location. Participants were then asked to demonstrate the tool's correct use, and to inform the experimenter once they finished the task. They had 90 seconds to complete one errorless attempt, and timing began once the tool made contact with the recipient. During the test, participants did not receive any verbal feedback on their performance.

Neuropsychological tests. All participants completed a battery of standardized neuropsychological tests. The battery consisted of the Brief Visuospatial Memory Test Revised (BVMT-R) (Benedict, 1997), Hopkins Verbal Learning Test-Revised (HVLT-R) (Benedict, Schretlen, Groninger, & Brandt, 1998), Stroop test -Victoria version (Troyer, Leach, & Strauss, 2006), Boston Naming Test (BNT) (Goodglass, Kaplan, & Weintraub, 1983), Rey-Osterrieth Complex Figure Test (ROCF) (Osterrieth, 1944), FAS Verbal Fluency Test (Heaton, Miller, Taylor, & Grant, 2004), Animal Naming Test (Tombaugh, Kozak, & Rees, 1999), Trail Making Test (Reitan & Wolfson, 1985), selected tests from the Wechsler Adult Intelligence Scale (WAIS-IV) (Wechsler, 2008), and Grooved-Pegboard test (Matthews & Klove, 1964). For each group, test results for participants were combined to create an overall cognitive profile for PD and control participants. As shown in Table 2, performance between the groups did not significantly differ on any measures, except the Grooved Pegboard Test, which primarily assesses manual dexterity and motor speed (Strauss, Sherman, & Spreen, 2006). In addition, none of the PD participants met criteria for mild cognitive impairment (MCI) based on level 2 criteria from the Movement Disorder Society Task Force using cutoff scores of 1.5 SD below normative data (Litvan et al., 2012).

Design and Procedure

As illustrated in Figure 2, participants were individually tested over three sessions (S1, S2, S3), spaced one day and three weeks apart, respectively. Participants also completed neuropsychological testing in a separate 60-minute session.

S1. During Training, participants first watched the instructional video, and were then immediately asked to complete the task with the tool in exactly the same way as it had been demonstrated. Participants were instructed to complete the task as quickly as possible without

making any errors, and had to restart if an error was made. They were given verbal feedback during Training trials, and had 90 seconds to complete one errorless trial. Once the first Training trial was completed without error or 90 seconds had elapsed, participants were immediately instructed to correctly demonstrate the tool's use a second time. Critically, the number of Training trials was a within-subjects manipulation: half of the tools (e.g., Set A) were practiced twice in a row ("2-trial condition") and the other half of the tools (e.g., Set B) were practiced 5 times in a row ("5-trial condition"). The order of tools within Set A and Set B was fixed, but counterbalancing across participants ensured that each tool set was in each Training condition an equal number of times.

S2. One day later during S2, to assess retention of motor actions, participants first completed two Training trials for all eight tools, where they watched the instructional video and demonstrated a tool's correct use twice in a row. They then completed a Post-test, consisting of the Use-to-command test. The purpose of the Post-test was to assess skilled tool use after completing Training trials, as well as to have a comparison point when assessing retention in S3. Recall was not assessed because I was concerned that there would be ceiling effects in the 5-trial condition.

S3. Three weeks later during S3, participants first completed a Pre-test consisting of a Recall test and Use-to-command test. They then completed two Training trials, followed by a Post-test where they completed the Use-to-command task again, which allowed for examination of within-session changes for skilled tool use.

Scoring and Statistical Analyses

During Training, motor performance was measured as the amount of time required to successfully complete one errorless attempt (i.e., Training Time). Timing began once the tool

made contact with the recipient. If the task was not completed during a 90-second time limit, participants received the maximum score of 90 seconds. The number of attempts was also documented, which included the number of attempts that were made before completing one errorless trial, as well as the attempt of the successful trial.

Recall was measured as the percentage of accurate responses in each trial on the Recall test, where participants received one point for a correct answer and zero points for an incorrect answer. A scoring rubric of correct responses, developed from previous pilot testing, and used in a previous study (Fernandes et al., 2017) was used to score Recall Accuracy.

Use-to-command performance was measured as Accuracy and Time. Accuracy was assessed as the percentage of accurate tool demonstrations, where participants received one point if the task was performed successfully within the time limit. A second rater independently scored 25% of the data, and inter-rater reliability was 96.76% (calculated as percentage of agreement). Similar to scoring during Training trials, Use-to-command Time reflected how quickly participants successfully completed one errorless trial. If participants could not accurately use a tool within the time limit, they received the maximum time score of 90 seconds.

Parametric statistical techniques were used to assess performance across all experimental measures². All follow-up analyses (i.e., simple effects and pairwise comparisons) were completed using Bonferroni corrections, and unless otherwise indicated, unadjusted *p*-values are reported. In addition, incomplete attempts were removed before conducting Training and Use-to-command Time analyses, so that that average time scores were not inflated by incomplete attempts (i.e., maximum time scores of 90 seconds). For Training and Use-to-command Time, I

² I also performed correlational analyses between the experimental measures and neuropsychological test scores to examine if there was a significant relationship between various tool properties and standardized cognitive performance. Results did not demonstrate significant or consistent associations, so I did not report these results.

also examined total completion time, which measured the total time required to complete the task, from the beginning of the first attempt to the end of the errorless attempt. As similar patterns of performance were observed for both completion time measures, I only reported results for time of errorless attempt.

Results

Training Time

Description of completion time performance during Training.

Figure 3 shows performance during Training measured as the mean completion time for the two groups (PDs vs. HCs) and number of Training trials (two vs. five). As expected, PD participants were slower than HCs, likely due to bradykinesia. More importantly, group differences emerged for patterns of learning and forgetting. In terms of within-session acquisition, both groups improved during S1, and greater gains were observed when participants completed five training trials. However, after a 1-day and 3-week delay, PD participants exhibited forgetting, whereas HCs retained their performance. In terms of overall improvement, performance in the last trial (T9) was faster than the first trial (T1), although this effect was attenuated in individuals with PD. Critically though, for both groups, participants improved more when they completed additional trials, demonstrating the beneficial effects of receiving more practice.

Within-session acquisition.

To assess whether performance improved within each session, difference scores were calculated as the change in completion time from the first Training trial to the last Training trial in each session. In order to analyze performance for all four conditions, scores were calculated for differences in completion time from T1 to T5 (S1, 5-trial condition), T1 to T2 (S1, 2-trial

condition), T6 to T7 (S2, both trial conditions) and T8 to T9 (S3, both trial conditions). Positive difference scores indicated learning, or improved performance within a session.

A 3-way mixed-design ANOVA assessed performance using two within-subjects factors (session and number of trials) and one between-subjects factor (group). Most critically, there was a significant 3-way interaction between session, number of trials, and group, $F(2, 68) = 5.25, p = .008, \eta^2 = .13$, suggesting that effect of two and five trials differed across sessions, and this interaction varied for PD and HC participants. To follow-up, simple interaction effects evaluated the interaction between group and number of trials at each level of session (i.e., S1, S2, S3).

For each session, a 2-way mixed-design ANOVA compared the 2-trial and 5-trial condition in PD and HC participants. Corrections for multiple comparisons were not made due to a priori hypotheses on performance patterns. In S1, there was a significant interaction between group and number of trials, $F(1, 34) = 5.66, p = .002, \eta^2 = .14$. Follow-up simple effect analyses showed that there were no group difference when completing two trials, but there was trend for PD participants to show less learning than HCs in the 5-trial condition, $F(1, 34) = 3.85, p = .058, \eta^2 = .10$. There was also a significant overall effect of number of trials, $F(1, 34) = 55.81, p < .001, \eta^2 = .62$, such that more Training trials resulted in greater learning for both groups.

In S2, there was no significant interaction between number of trials and group. However, there was a main effect of number of trials, $F(1, 34) = 10.73, p = .002, \eta^2 = .24$, indicating greater learning for tools trained under two trials in S1. There was also a main effect of group, $F(1, 34) = 18.02, p < .001, \eta^2 = .35$, where the PD group showed more learning than HCs. In S3, there was no significant interaction or main effect of number of trials, but there was a significant main effect of group, $F(1, 34) = 45.48, p < .001, \eta^2 = .57$, showing that PD participants improved more within the session than HCs.

In summary, in S1 both groups showed greater improvement when they completed more Training trials; however, PD participants showed a trend of less learning than HCs in the 5-trial condition. In S2, participants showed greater learning for tools trained under the 2-trial condition in S1, likely because they had more opportunity to improve due to reduced learning in the first session. Additionally, in both S2 and S3, PD participants exhibited more learning than controls, likely due to forgetting between sessions (described below).

Overall learning.

To determine whether participants exhibited overall improvement across the three sessions, a difference score was calculated for the change in completion time from the first training trial (T1) to the last training trial (T9). A 2-way mixed-design ANOVA compared 2-trial and 5-trial condition within each group. There was a significant effect of group, $F(1, 34) = 5.41$, $p = .026$, $\eta^2 = .14$; overall, PD participants showed less learning than HCs. However, there was no significant interaction, but a main effect of number of trials, $F(1, 34) = 11.20$, $p = .002$, $\eta^2 = .25$, showing that both groups improved more when they completed additional trials. Thus, both HCs and PD participants benefited from receiving more massed practice, though overall learning in the PD group was attenuated.

Forgetting.

To determine whether participants retained their improved motor performance from the previous session, a difference score was created to assess between-session forgetting. The dependent variable was calculated as the difference in Training Time from the first trial in one session and the last trial in the preceding session. That is, scores were calculated for the differences in completion time from T2 to T6 (1-day delay for 2-trial condition), T5 to T6 (1-day

delay for 5-trial condition) and T7 to T8 (3-week delay, both trial conditions). Negative scores indicated forgetting, or slower completion time after the delay.

A 3-way mixed-design ANOVA assessed forgetting for the number of trials, group and session (S2, S3). There was only a significant overall effect of group, $F(1, 34) = 47.45, p < .001, \eta^2 = .58$, as PD participants exhibited more forgetting than HCs. With the lack of other significant main effects or interactions, these findings suggest that overall PD participants retained less than controls, as HCs retained their performance between delays and PD participants did not. However, for PDs, the amount of forgetting did not differ in terms of the durations of the delay (i.e., S2 vs. S3), or amount of practice.

Despite showing impaired forgetting relative to HCs, I also assessed if individuals with PD showed *any* evidence of retention (i.e., improved performance from T1) after the two delays. A difference score was calculated, such that motor performance from T1 was compared to the first trial after a delay (i.e., T6 for S2 and T8 for S3), whereby positive scores indicated improvement from the first trial. For the PD group only, one-sample t-tests were used to compare this difference score to 0 (i.e., a difference score indicating no improvement from T1). Results showed that PD participants demonstrated significant improvement from T1 in the 5-trial condition after a one day, $t(17) = 5.36, p < .001, d = 1.26$, and there was a trend toward some retention after three weeks, $t(17) = 3.53, p = .052, d = 0.49$, though this finding did not reach statistical significance with a Bonferroni correction. For 2-trial learning, significant improvement from T1 was only observed after a 3-week delay, $t(17) = 3.05, p = .007, d = 0.72$. Taken together, these findings indicated that although PD participants exhibited more forgetting than HCs, they still demonstrated partial retention after delays, as shown by improved performance from the first training trial.

Number of Attempts.

A 3-way mixed-design ANOVA examined the mean number of attempts made by PD and HC participants in the 2-trial and 5-trial conditions during the first and last training trial in each session (i.e., T1, T2 for 2-trial condition/T5 for 5-trial condition, T6, T7, T8, T9). There was only a significant main effect of trial, $F(1, 34) = 16.71, p < .001, \eta^2 = .33$, demonstrating that overall, the number of attempts tended to decrease across trials: T1: $M = 1.50, SD = 0.66$; T2/T5: $M = 1.12, SD = 0.18$; T6: $M = 1.09, SD = 0.36$; T7: $M = 1.05, SD = 0.06$; T8: $M = 1.09, SD = 0.12$, T6: $M = 1.06, SD = 0.24$. However, attempts did not differ between PD and HC participants or the number training trials.

Recall Accuracy

A 3-way mixed ANOVA with group, number of trials and information type (functional/associative vs. perceptual) as factors examined Recall performance after the 3-week delay. There was a main effect of information type, $F(1,34) = 459.43, p < .001, \eta^2 = .93$, such that overall, accuracy was higher for functional/associative than perceptual information (see Figure 4). There was also a main effect of number of trials, $F(1,34) = 10.89, p = .002, \eta^2 = .24$, demonstrating that overall, that five trials resulted in higher Recall accuracy than two trials³. However, there were no significant interactions or main effect of group, indicating that both groups similarly benefited from completing more Training trials, and accuracy performance did not differ between PD participants and HCs.

Use-to-Command

Two 3-way mixed ANOVAs with group, number of trials and test trial (S2 posttest, S3 pretest, S3 posttest) as factors examined UTC performance (Accuracy and Time).

³ A similar pattern of results was obtained when functional/associative and perceptual information were analyzed together.

Use-to-Command accuracy.

There was a significant interaction between number of Training trials and test trial, $F(2,68) = 9.70, p < .001, \eta^2 = .22$ (see Figure 5). Simple effects analyses demonstrated that accuracy was higher for the 5-trial condition than the 2-trial condition in S3 pre-test, $F(1,34) = 15.66, p < .001, \eta^2 = .32$, but performance did not significantly differ in S2 posttest and S3 posttest (see Figure 5). There was also a main effect of test trial, $F(2,68) = 137.69, p < .001, \eta^2 = .80$. Follow-up post hoc comparisons showed that accuracy was higher in S2 post-test than S3 pre-test ($p < .001$), demonstrating that performance declined over the 3-week delay. Accuracy was also higher in the S3 post-test than the S3 pre-test ($p < .001$), indicating improvement within the session. There was no significant main effect of group, showing that UTC accuracy did not differ between PD participants and HCs. In summary, Use-to-Command accuracy was comparable between groups; performance declined after a 3-week delay, but in the S3 pre-test, accuracy was higher for tools that were trained under the 5-trial condition.

Use-to-Command time.

There was a main effect of test trial, $F(2,68) = 6.38, p = .003, \eta^2 = .16$ (see Figure 6). Follow-up analyses showed that S3 post-test completion time was significantly faster than in the S3 pre-test ($p = .005$), demonstrating within-session improvement. There was also a main effect of group, $F(1,34) = 9.36, p = .004, \eta^2 = .22$, indicating that overall PD participants were slower than controls (likely due to bradykinesia) (see Figure 6). However, no differences were observed during the S2 post-test or S3 pre-test, or between the 2-trial and 5-trial conditions.

Discussion

Experiment 1 examined the effects of additional, massed practice on the acquisition, retention, and overall learning of tool-related motor performance in healthy adults and

individuals with PD. During S1, participants completed two Training trials for half of the tools and five Training trials for the other half. Retention and additional within-session motor learning was then assessed in S2 (1-day delay) and S3 (3-week delay). Results generally showed that more practice in S1 resulted in greater improvement for both groups. However, after both delays, controls retained their motor performance, whereas PD participants did not, regardless of the amount of practice. Despite these retention deficits, PD participants still showed greater overall improvement in the 5-trial than 2-trial condition, although learning was attenuated when compared to HCs. In contrast to these differences with motor performance, both groups had similar Recall performance, with superior accuracy for tools trained under the 5-trial than 2-trial condition. Below I provide a more detailed description of the findings, and discuss theoretical implications from the pattern of results.

Motor Performance

The primary goal of this experiment was to assess how more extensive, massed practice affected tool-related motor acquisition and retention in HCs and PD participants. Previous research has demonstrated that with increasing practice, striatal processing increased in healthy adults (Albouy et al., 2013; Albouy et al., 2008), and massed practice trials, in particular, might further enhance striatal processing (Pauwels et al., 2018). However, it was unclear how additional practice completed within one session would affect PD performance due to their striatal dysfunction. By examining within-session acquisition, retention and overall learning, I wanted to determine if more practice benefited any aspects of performance, and an examination of performance patterns allowed me to speculate about potential cognitive and neural mechanisms.

In HCs, more massed, practice resulted in superior acquisition during S1, as participants made greater gains after completing five than two Training trials. Additional practice also enhanced overall learning, as controls exhibited greater improvements from the first to the last training trial with the 5-trial condition. HCs also retained their performance after 1-day and 3-week delays. In contrast, individuals with PD displayed key differences during certain aspects of performance. Similar to controls, during S1, PD participants showed greater learning after completing five than two trials. However, compared to HCs, there was a trend towards less learning in the 5-trial condition, suggesting that with more, massed practice, PD participants' initial acquisition was somewhat attenuated. Total improvement across sessions was also greater with additional practice, though overall learning was mitigated in PD, irrespective of the amount of practice. For retention, relative to HCs, PD participants exhibited impairments after 1-day and 3-week delays. Likely because of these retention deficits, during S2 and S3, PD participants made greater within-session gains than controls. In addition, results showed that overall, the number of attempts decreased across Training trials, suggesting that there was not a speed-accuracy trade-off (i.e., participants' faster completion times were not due to an increase in errors or attempts).

Taken together, these findings indicate that additional practice benefited both healthy adults and individuals with PD, though the underlying mechanisms may differ. In HCs, increasing the number of massed, Training trials enhanced motor learning, possibly because it further biased the use of striatal processing. Pauwels et al. (2018) recently demonstrated that completing massed, as opposed to random, practice resulted in greater neural activation in areas typically associated with motor learning and automaticity, which included the striatum after a delay. Although I do not have direct evidence for such processing in the current study, my

behavioural results for controls reflect the expected performance pattern associated with striatally-mediated motor learning; during initial acquisition, large gains were made, followed by smaller improvements as automaticity was gradually achieved (Albouy et al., 2013; Marinelli, Quartarone, Hallett, Frazzitta, & Ghilardi, 2017). Moreover, a lack of forgetting after delays is consistent with properties of motor-procedural memory (Gabrieli et al., 1993), and replicates retention findings from past studies from my lab (Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015). Furthermore, as subsequently discussed, individuals with PD exhibited motor impairments after delays, further suggesting that motor-procedural memory and striatal processing are required to retain tool-related motor actions.

While more, massed practice may have resulted in greater striatal processing in healthy adults, PD performance suggests it may have instead biased the use of relatively preserved hippocampally-mediated declarative memory. First, though additional practice was associated with greater improvement during S1, when compared to HCs, learning under the 5-trial condition was somewhat mitigated in PD. This finding may reflect difficulty with achieving automatization that is typically associated with striatal activation (Wu et al., 2010; Wu & Hallett, 2005; Wu et al., 2015), and is consistent with some studies that have observed slower learning rates in PD (Michel, Benninger, Dietz, & van Hedel, 2009; Smiley-Oyen et al., 2006). Furthermore, PD participants appeared to improve overall because they made large within-session gains, but did not retain performance across delays. This performance pattern in individuals with PD is quite reliable, and has been previously obtained in past studies using complex tools; PD participants have consistently demonstrated preserved acquisition within sessions, yet have impaired retention after 1-week (Fernandes et al., 2017) and 3-week delays (Fernandes et al., 2017; Roy et al., 2015). Beyond tool use, other studies have also reported similar findings with relatively

intact acquisition and retention deficits across a variety of motor tasks (Doyon et al., 1998; Heremans et al., 2016; Mochizuki-Kawai et al., 2004; Pendt, Reuter, & Müller, 2011).

PD performance could reflect hippocampal processing, which supports early and fast learning, where considerable improvement occurs early, and not striatal learning, which is typically associated with smaller improvements as practice increases (Albouy et al., 2013; Doyon & Benali, 2005; Doyon et al., 2018). In addition, after delays, PD participants had impaired motor retention, and unlike motor-procedural memory, declarative memory tends to decline over time (Ellenbogen et al., 2006; Squire, 1992b). While considering the possibility of hippocampal compensation, it should be noted that the current sample of PD participants did not demonstrate declarative memory impairments on both neuropsychological testing and Recall performance. However, it is possible that my measures were not sensitive to potential hippocampal dysfunction and deficits in declarative memory; some studies have demonstrated declarative memory impairments in individuals with PD (Beyer et al., 2013; Camicioli et al., 2009), including performance on a Associative Reinstatement Memory task, which has been shown to be a sensitive measure of hippocampal memory function (Cohn et al., 2016). Nonetheless, in general, motor-procedural memory is likely more disproportionately affected than declarative memory in PD. Thus, even if declarative memory was somewhat affected in my sample of PD participants, it still could have still potentially supported performance (i.e., hippocampal function was less dysfunctional than striatal processing).

The notion of compensatory interactions in PD has been supported by previous research suggesting that when acquiring skills that are normally striatally-mediated, individuals with PD might instead rely on the hippocampus. In an earlier study, Moody et al. (2004) reported that during probabilistic classification learning, PD participants exhibited intact learning at the

behavioral level. However, unlike controls, individuals with PD recruited medial temporal structures, which likely reflected the use of declarative memory to complete the task. A similar compensation mechanism was shown using implicit learning in a perceptual-motor sequencing task, Serial Reaction Time (SRT), where some PD participants appeared to employ a compensatory declarative strategy to successfully complete the task (Gobel et al., 2013). In my study, a compensatory relationship potentially enabled individuals with PD to acquire novel motor actions, and exhibit overall improvements across a 3-week period.

Despite the evidence for the use of declarative memory and hippocampal processing in PD, I cannot definitively rule out some striatal involvement as well. Though PD participants had retention deficits relative to controls, there was some evidence for partial retention after delays. That is, compared to T1, PD participants demonstrated improved performance on the first Training trial after the delays (i.e., T6 for S2 and T8 for S3). This overall finding was relatively weak though, as it was not consistently demonstrated across practice conditions and delays (i.e., statistical significance only achieved after 1-day delay for 5-trial condition and 3-week delay for 2-trial condition). This lack of consistency may reflect PD participants' limited or diminished capacity to engage striatal processing.

In addition to these main results, I observed a novel finding, which differed from my previous study that examined the effects practice on tool use in PD. In my initial study (Fernandes et al., 2017), I found that when only completing two Training trials during S1, after a 1-day delay, PD participants exhibited intact retention relative to controls. However, in the current study, PD retention was impaired after a 1-day delay. It is possible that a methodological difference between the studies contributed to these conflicting findings. Namely, in this study, participants completed "mixed" trials, such that they received two Training trials for some tools

and five trials for others. It is possible that because participants were unaware of the Training schedule, for a given tool they may have not known how many Training trials they were going to complete. As such, if they were employing declarative processes during Training, they may have less deeply encoded the task if they were anticipating additional practice trials, which could have resulted in poorer retention (Craik, 2002; Craik & Lockhart, 1972). It is also possible though that given small sample sizes and the heterogeneity of PD, a potential sampling error could have contributed to discrepant findings.

Recall

Recall Accuracy was assessed as my primary measure of declarative memory (Fernandes et al., 2017; Roy & Park, 2010, 2016; Roy et al., 2015). As hypothesized, results showed no performance differences between HCs and PD participants, which is consistent with past studies that have demonstrated unimpaired Recall performance in PD (Fernandes et al., 2017; Roy et al., 2015). Both groups had higher accuracy for functional/associative than perceptual information, replicating previous findings from my lab (Roy, 2014; Roy & Park, 2010, 2016). Superior memory for functional associative than perceptual attributes may have been observed because this information is more meaningful to the task at hand (e.g., participants attend more to the purpose of the tool, as opposed to details about its physical appearance) (Ventura, Morais, & Kolinsky, 2005; Warrington & Shallice, 1984). In terms of practice effects, participants had superior accuracy for tools that were trained under the 5-trial than 2-trial condition. The notion that repeated exposure can improve declarative learning is well established (Eichenbaum, 2004), and as initially shown by Fernandes et al. (2017), the current findings demonstrated that increasing the amount of practice enhanced tool-related declarative memory. Taken together,

Recall results provide evidence for intact declarative memory in my sample of PD participants, and also indicate that additional, massed practice enhances such knowledge.

Skilled Tool Use

I also examined the effects of additional practice on skilled tool use, which requires participants to demonstrate a tool's use from memory after a delay period, and likely requires cooperative interactions from both memory systems (Roy, 2014; Roy & Park, 2010, 2016; Roy et al., 2015). With Use-to-Command Accuracy, no differences were observed between HCs and PD participants, supporting previous findings on skilled tool use in PD (Roy et al., 2015). For both groups, accuracy declined after three weeks, which was expected because previous research showed that this aspect of performance largely required declarative memory (Roy, 2014; Roy et al., 2015). In the S3 pre-test, which assesses memory after a delay, performance was superior for tools trained under the 5-trial condition. Thus, as with Recall, accuracy with skilled tool use was enhanced by receiving additional practice. For Use-to-command Time, which assessed how quickly participants performed the successful task, PD participants were slower than HCs overall. Slower completion times likely reflect bradykinesia, and has been demonstrated in past research (Fernandes et al., 2017; Roy et al., 2015). Most critically though, during the Use-to-command tests, there were no differences between the 2-trial and 5-trial conditions, indicating that more practice did not affect the motor-procedural aspect of skilled tool use.

It is possible that additional Training trials only enhanced the component of skilled tool use that was primarily mediated by declarative memory. That is, greater exposure allowed participants to better recall information required to successfully complete the task when tested after a delay. However, once they accessed this declarative knowledge, and carried out the motor itself, the benefits of additional practice were diminished. Alternatively, a limitation in the

measure could have also impacted findings. Use-to-command Time only included tools that were accurately demonstrated. Unlike Training, where participants often successfully complete the task, Use-to-command Accuracy tends to be lower, and fewer tools comprise the Time score. As completion times vary across participants and different tools, it is difficult to make comparisons across experimental conditions.

Memory Interactions in Tool Use

The pattern of results across PD participants and HCs demonstrated that complex tool use requires multiple cognitive processes, and the relative contributions of declarative and motor-procedural memory appear to depend on a number of key factors. Though certain tool attributes may typically be primarily mediated by one memory system, my study suggests that both types of memory may be able to flexibly contribute to performance, whereby participant characteristics and acquisition and test conditions might bias the use of a certain memory system. For instance, in terms of tool-related motor actions, in healthy adults, performance seems to mainly require motor-procedural memory that is striatally mediated (Fernandes et al., 2017; Roy et al., 2015). Nonetheless, based on PD performance, hippocampally-mediated declarative memory may also be able to support performance. The possibility that both memory systems have the ability to mediate performance is supported by a competitive relationship between declarative and procedural memory. With this type of interaction, multiple memory systems can be activated simultaneously, though increasing activation in one system can decrease activity in the other, causing the relative contributions to vary (Poldrack & Packard, 2003). Critically, certain factors can influence this interaction, such as the use of compensation in patient populations (Jones, 2017; Klöppel et al., 2015; Stern, 2012), including individuals with PD (Carbon, Reetz, Ghilardi, Dhawan, & Eidelberg, 2010; Gobel et al., 2013; Marinelli et al., 2017; Moody et al., 2004).

With competitive relationships, the manipulation of certain training and test conditions has also been shown to affect the relative contributions of declarative and procedural memory, ranging from attention during encoding (Foerde, Knowlton, & Poldrack, 2006), visual cues present in the learning environment (Chang & Gold, 2004), and level of emotional arousal (Kim, Lee, Han, & Packard, 2001) (for a review see Packard & Goodman, 2013). In the current study, increasing the number of massed training trials may have increased striatal processing during motor learning in healthy adults, which is consistent with past research suggesting that more practice with motor tasks may result in greater proceduralization (Albouy et al., 2013; Albouy et al., 2008; Pauwels et al., 2018). In contrast, increased practice may have potentially enhanced the use of declarative memory in PD participants.

Additionally, test conditions themselves likely influenced the underlying cognitive and neural systems that were required for performance. For example, I assessed motor performance during Training and the Use-to-command test. There was a key difference between these tasks, such that in the former, participants viewed a Training video immediately before using the tool, and in the latter, they demonstrated the tool's use from memory. Thus, it could be argued that compared to the Use-to-command test, motor performance during Training relies more heavily on motor-procedural memory because participants do not need to first retrieve declarative knowledge about how to use a tool. Interestingly, PD participants exhibited intact performance on the skilled tool use task, likely due to their preserved declarative memory. The notion that Use-to-command performance relies critically on declarative memory is consistent with past findings demonstrating impaired skilled tool use in a hippocampal amnesic, D.A., who could not recall how to use a tool from memory (i.e., Use-to-command Accuracy was at floor), and thus he could not perform the motor associated with a particular tool (Roy & Park, 2010). Moreover, the

finding that skilled tool use requires both declarative and motor-procedural memory may extend to motor skills more generally. Stanley and Krakauer (2013) have argued that in addition to procedural aspects, motor skills require knowledge of facts (what I refer to as declarative memory) (see also Krakauer & Carmichael, 2017). From a practical perspective, this distinction between Training and Use-to-command motor performance may be particularly important. Although Training performance is useful because it may represent a “purer” measure of motor-procedurally mediated motor actions, the Use-to-command task may be more applicable to real world functioning. For instance, oftentimes people use a tool after periods of non-use where they first must recall declarative knowledge about how to use a tool (e.g., function, grasp, placement of recipient object).

Limitations and Future Directions

The current study demonstrated the beneficial effects of additional, massed practice on various tool properties in healthy adults and individuals with PD. However, it is important to acknowledge limitations that could be addressed in future research. First, although I speculated about potential cognitive and neural mechanisms mediating performance, my behavioural results cannot provide decisive conclusions about underlying neural mechanisms. Moreover, the type of training I employed could have impacted the findings, such that participants physically practiced the motor actions during each training trial. It could be argued that practice trials require participants to generate a response, which is similar to the testing effect that has been extensively examined in the verbal literature (i.e., taking a test rather than restudying information results in superior retention) (Roediger III & Butler, 2011; Roediger III & Karpicke, 2006b). It is possible that not only did the number of training trials affect performance, but the act of practicing the task may have also affected subsequent memory. Thus, the training method employed could be

examined, especially considering that observation has been found to be effective in some tasks for individuals with PD (Abbruzzese, Marchese, Avanzino, & Pelosin, 2016; Agosta et al., 2017; Caligiore, Mustile, Spalletta, & Baldassarre, 2017), and it is currently unclear how observational learning would affect memory systems required for tool use in PD.

My results also showed that more, massed practice benefitted motor performance of PD participants, possibly because it biased the greater use of declarative memory. An alternative approach to Training could be to employ a schedule that further biases the use of declarative processes, potentially facilitating the use of such compensation in PD. One possible method could be the use of a random Training schedule (e.g., ACB CBA) (Brady, 2004; Magill & Hall, 1990), or spaced trials, whereby two training trials are separated by intervening information or time (Cepeda et al., 2006; Greene, 1989). The previously discussed study from Pauwels et al. (2018) not only revealed that massed practice resulted in greater neural activity in areas associated with automaticity, but findings also demonstrated that a random schedule increased activation in visual processing areas. The authors hypothesized that the use of random trials caused participants to be more attentive to the task's visual features, so it seems possible that compared to massed practice, a random schedule could enhance tool-related declarative memory. This possibility of differential memory enhancements with massed and spaced training was subsequently investigated in Experiments 2 and 3.

Conclusion

There are various attributes related to tool use, and the relative contributions of declarative and motor-procedural may vary depending on a number of important factors. Here I demonstrated that increasing the number of massed training trials improved motor performance in healthy adults and individuals with PD, though performance patterns across groups somewhat

differed. Most critically, while additional practice enhanced motor-procedural memory likely mediated by striatal regions in HCs, it may have facilitated a compensatory mechanism in PD through biasing the use of declarative memory. From a theoretical perspective, my study provides support for flexible interactions between memory systems during tool use, which in turn may have important clinical implications. Although individuals with PD have impaired striatal processing, this dysfunction does not necessarily result in an inability to learn novel motor actions. Though individuals with PD may not fully retain motor performance over time, the current study showed that overall improvement can be achieved, as well as enhanced with additional practice.

Table 1.

Participant Characteristics

Variable	PD (n = 18)		HC (n = 18)		p-value ^a
	M	SD	M	SD	
Age	67.7	9.9	68.2	9.5	.88
Education (years)	14.8	3.3	14.6	4.3	.86
Sex (M/F)	12/6		12/6		
MMSE (/30)	28.7	1.2	28.9	1.1	.67
HADS (/42)	8.9	2.3	8.3	1.9	.40
HADS-anxiety (/21)	4.5	1.4	4.3	1.4	.72
HADS-depression (/21)	4.4	1.7	3.9	1.7	.43
Years Since Diagnosis	6.4	3.8			
UPDRS motor section	19.8	8.3			
Side Affected (L/R/B)	8/7/3				
LED (mg/day)	665.03	394.49			

PD, Parkinson's disease; HC, Healthy Controls; MMSE, Mini-mental State Examination; HADS, Hospital Anxiety and Depression Scale; UPDRS, Unified Parkinson's Disease Rating Scale; L/R/B, Left/Right/Both; LED, levodopa-equivalent dose.

^aIndependent samples t-tests comparing the PD to HC group were conducted to obtain p-values.

Table 2.

Neuropsychological Tests Standardized z-scores^a

Neuropsychological Test	PD M (SD)	HC M (SD)	p- value ^b
<i>WAIS-IV (selected subtests)</i>			
Digit Span	.17 (.65)	.18 (.64)	.63
Matrix Reasoning	.19 (.69)	.26 (.54)	.11
Information	.15 (.51)	.08 (.66)	.10
<i>HVLT-R</i>			
Total Recall (T1-T3)	-.28 (1.08)	.29 (.64)	.07
Delayed Recall	-.27 (.99)	.13 (.62)	.17
Percent Retained	-.12 (.95)	-.07 (.42)	.85
Recognition Discrimination	.10 (1.14)	.18 (.51)	.79
<i>BVMT-R</i>			
Total Recall (T1-T3)	.31 (.70)	.15 (.47)	.41
Delayed Recall	.56 (.80)	.14 (.65)	.09
<i>Trail Making Test</i>			
Part A	-.39 (.67)	-.09 (.77)	.10
Part B	-.18 (.68)	-.11 (.78)	.79
B-A	-.14 (.92)	.04 (.89)	.57
<i>Stroop Test (Victoria version)</i>			
Dots	-.07 (.68)	-.10 (.66)	.88
Words	-.15 (.60)	.01 (.64)	.44
Colour Words	.18 (.64)	.13 (.66)	.85
<i>Phonemic fluency</i>	-.19 (.63)	.18 (.68)	.09
<i>Semantic fluency</i>			
Animals	.20 (1.48)	.39 (1.12)	.68
Supermarket	.18 (.80)	.22 (.73)	.86
<i>Boston Naming Test</i>	.29 (.62)	.39 (.79)	.70
<i>ROCF Copy</i>	-.03 (.52)	.20 (.45)	.17
<i>Grooved Pegboard</i>			
Dominant hand	-1.93 (.70)	.37 (.61)	<.001
Non-dominant hand	-1.81 (.98)	-.04 (.56)	<.001

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.

^aScores represent mean z-scores across participants for each cognitive test. Raw scores on each test were first scored according to appropriate normative data for each participant and were then converted to z-scores.

^bIndependent samples t-tests comparing the PD to HC group were conducted to obtain p-values.

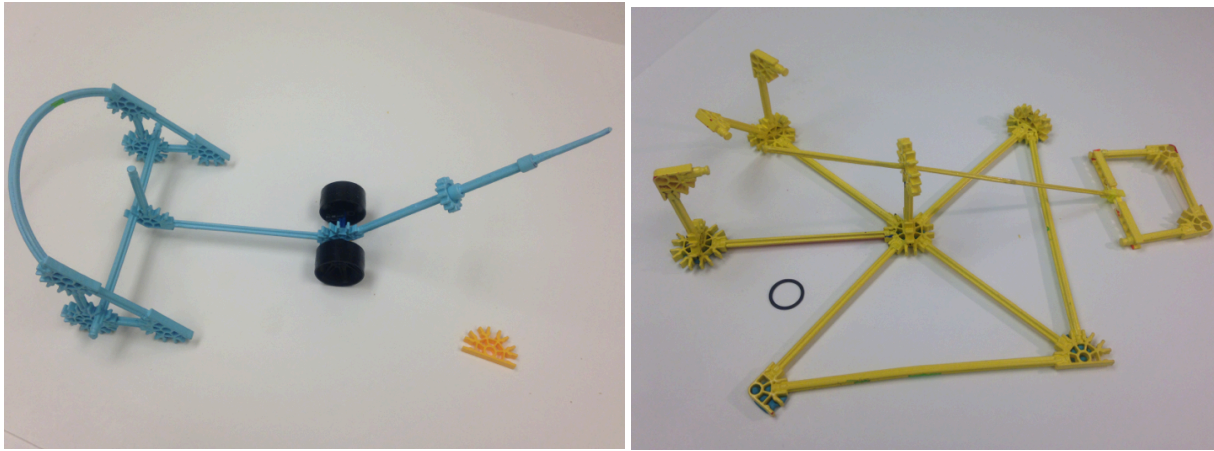


Figure 1. Examples of tools and their associated recipients



Session 1		Session 2		Session 3			
Training Trials		Training Trials	Use-to-command Post-test	Recall Pre-Test	Use-to-command Pre-test	Training Trials	Use-to-command Post-test
2-trial Condition -4 tools -2 trials per tool	5-trial Condition -4 tools -5 trials per tool	-8 tools -2 trials per tool	-8 tools	-8 tools	-8 tools	-8 tools -2 trials per tool	-8 tools
 1 Day		 3 Weeks					

Figure 2. Design of Experiment 1

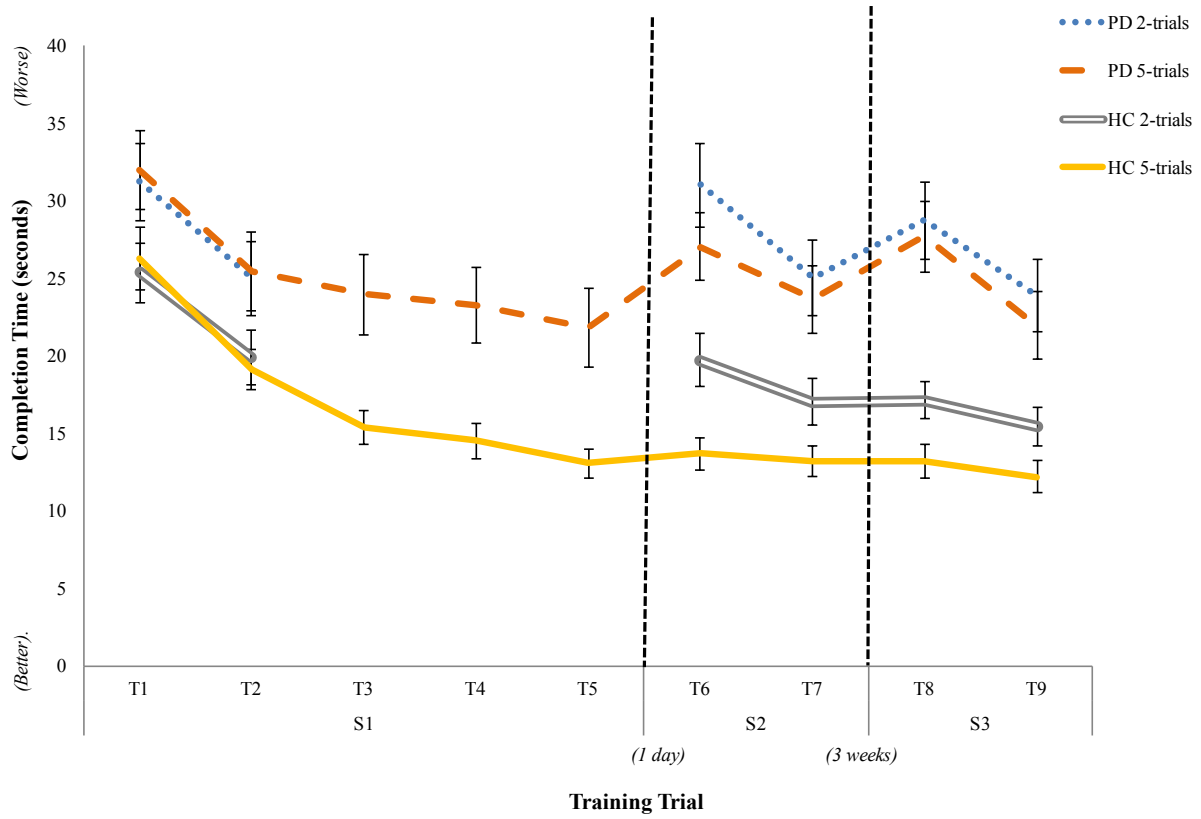


Figure 3. Mean completion time (+/- SE) across Training trials.

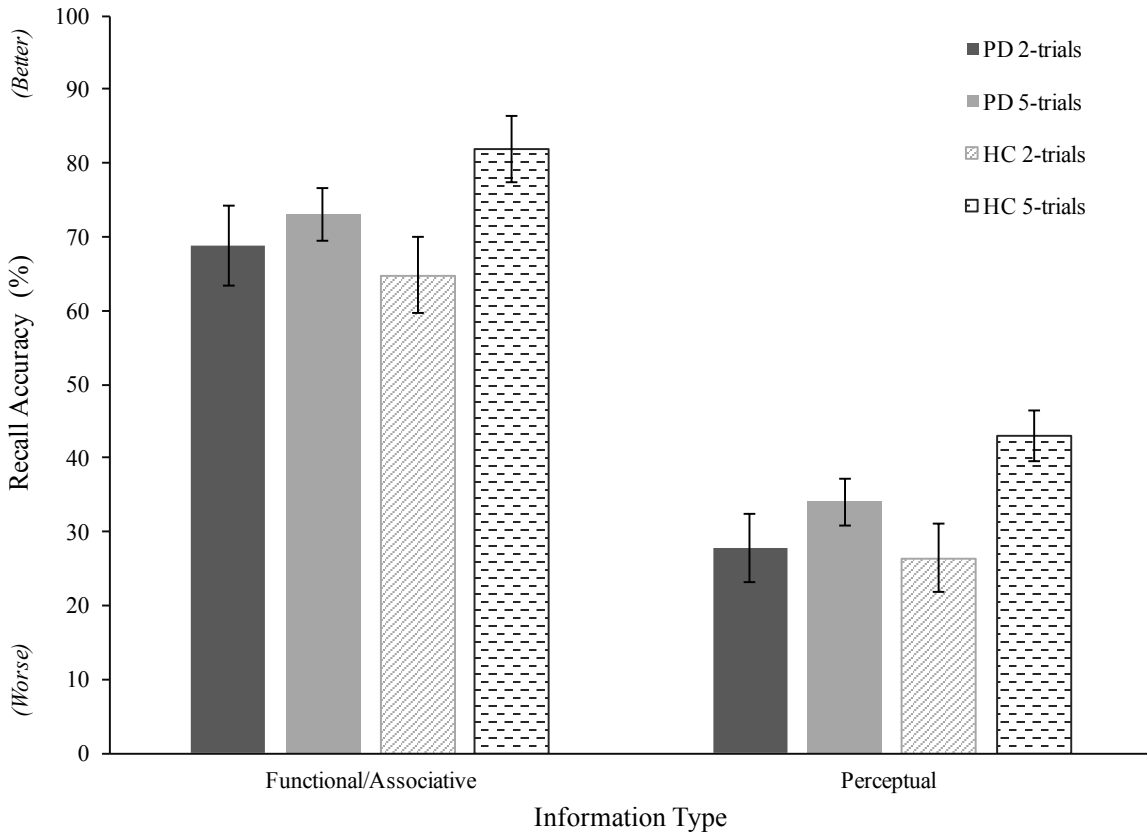


Figure 4. Percentage of correct responses (+/- SE) for Recall test items assessing functional/association and perceptual information for each group and acquisition condition.

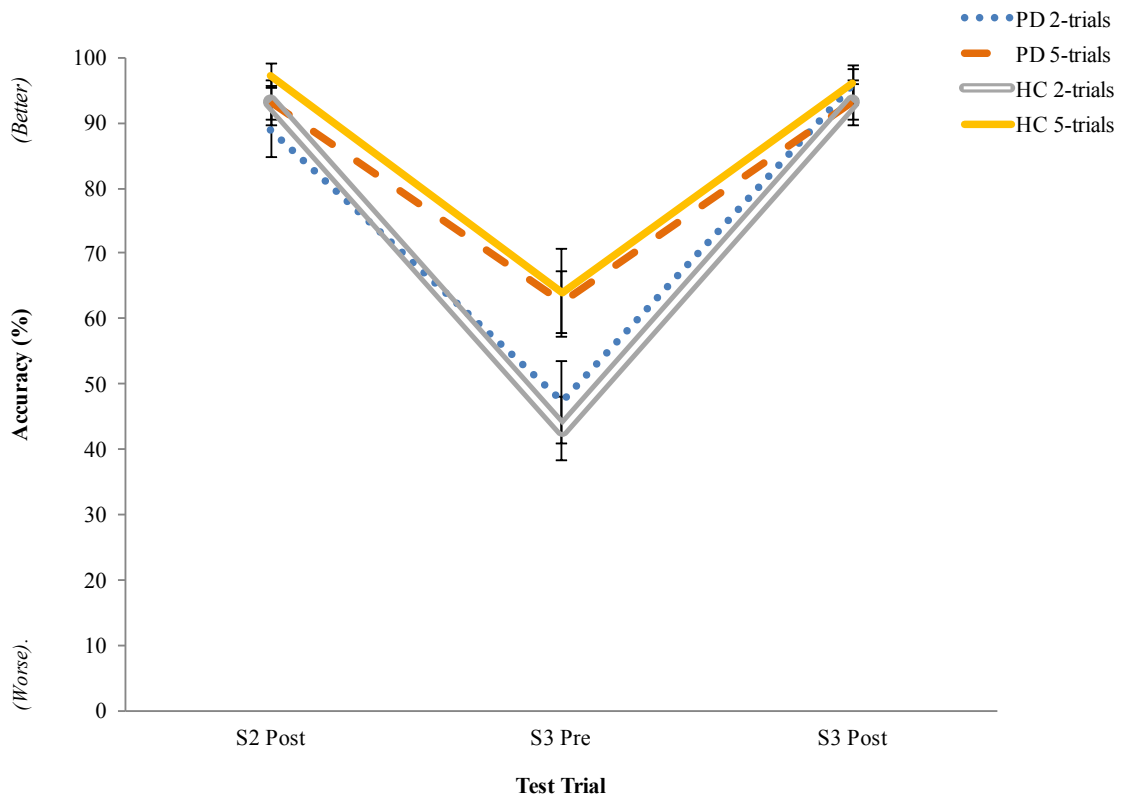


Figure 5. Percentage of correct demonstrations for Use-to-command (+/- SE) for each group and acquisition condition.

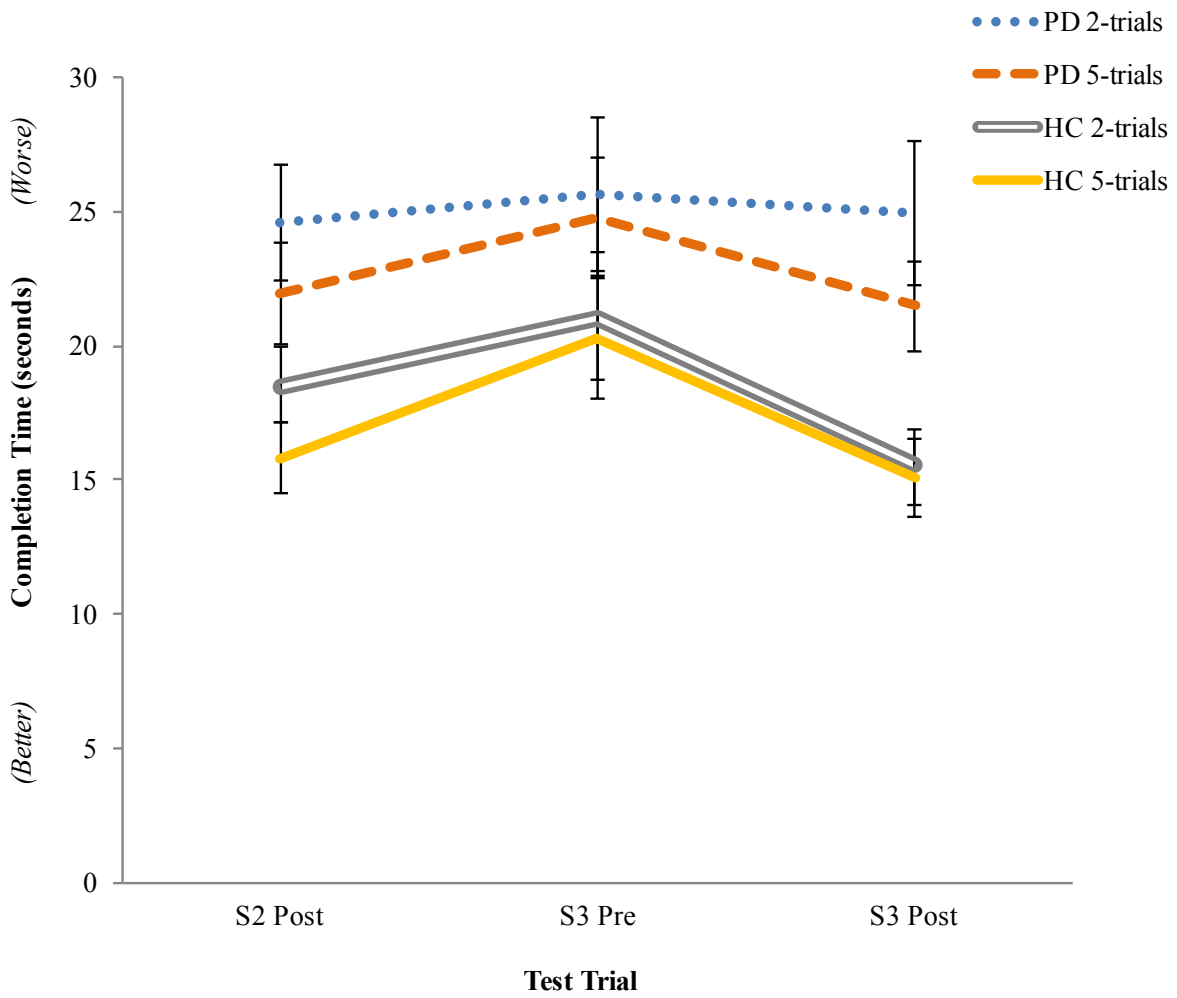


Figure 6. Mean Use-to-command Time (+/- SE) for each group and acquisition condition.

Chapter 3: How does the spacing effect impact memory systems required for tool-related knowledge and skills? (Experiment 2)

Individuals rely on tools to efficiently complete numerous tasks. Complex tools transform one's motor output in a way that provides a mechanical benefit when trying to achieve a specific goal (e.g., using a hammer) (Frey, 2007). As a result of its multifaceted nature, tool use may require various cognitive abilities, including technical reasoning (Goldenberg, 2013; Osiurak & Badets, 2016), semantic knowledge (Kalénine & Buxbaum, 2016) and sensory-motor memories (Buxbaum, 2017). Previous work from my lab has examined the role of declarative and motor-procedural memory in mediating various tool-related properties to better understand how these systems may independently or interactively enable performance (Roy & Park, 2010; Roy et al., 2015). More recent findings have demonstrated that certain types of training differentially affect various aspects of tool use after a delay (Fernandes et al., 2017; Roy, 2014; Roy & Park, 2016). The current study further examined this topic by investigating two distinct training conditions that I hypothesized would affect memory systems underlying various aspects of tool use. Experiment 2 first determined how spacing (i.e., the distribution of training trials within a session) affected memory for different tool-related properties, and Experiment 3 then assessed how spacing interacted with the type of learning used (observation versus physical practice). These two factors were investigated because, as will be discussed, spacing and learning method may have differential effects on the acquisition and retention of tool properties mediated primarily by motor-procedural versus declarative memory. A careful examination of these effects will further our understanding of tool-related cognitive processes and may also have practical implications.

In the Introduction of Experiment 2, I provide a brief review of human memory systems and their role in tool use, followed by a discussion about how the spacing of training trials may affect declarative and motor-procedural memory in the context of complex tools, leading to an overview of the experiment. Following from the results and brief discussion of Experiment 2, I present a follow-up experiment (Experiment 3) where I examined the role of feedback-based learning on the spacing effect. After a brief discussion of the findings from Experiment 3, I examine the implications of both experiments.

Memory Systems and Complex Tool Use

Human memory is not unitary in nature, but is instead comprised of multiple memory systems that are functionally and neurally distinct (Squire, 2009; Squire & Zola-Morgan, 1991). Declarative memory encompasses episodic information (i.e., experiences and events), which is primarily mediated by the hippocampal complex and related structures (Moscovitch et al., 2005; Squire, 2009; Tulving, 1985), as well as semantic information (i.e., general knowledge). Semantic memory is mediated by a variety of neocortical regions that differ depending on the nature of the stimulus being encoded (Binder & Desai, 2011; Martin & Chao, 2001). For instance, learning information about tools appears to rely heavily on the left posterior temporal cortex (Kalénine & Buxbaum, 2016). In contrast, nondeclarative memory refers to several different types of learning that can occur without awareness. Of particular relevance to the current study, motor-procedural memory, a type of nondeclarative memory, is necessary for motor learning, and is mediated subcortically by cortico-cerebellar and cortico-striatal networks (Doyon et al., 2018; Doyon et al., 2003). Once motor-procedural memories are acquired, they tend to be quite robust to forgetting (Albouy et al., 2013; Gabrieli et al., 1993). In contrast,

declarative memories can be rapidly acquired, but are more susceptible to forgetting due to interference or decay (Ellenbogen et al., 2006; Squire, 1992a; Tulving, 1985).

Although declarative and motor-procedural memory systems were initially thought to be independent of each other, more recent research has demonstrated that they can interact. For example, through *cooperative* interactions, multiple memory systems may simultaneously mediate performance without competing with each other (Sadeh et al., 2011; Wimmer & Shohamy, 2012). In contrast, during *competitive interactions*, one system can inhibit activation of the other system (Albouy et al., 2012; Packard & Goodman, 2013; Poldrack et al., 2001); this type of relationship also includes *compensatory* interactions, which may occur when the dysfunction of a competing system results in greater use of the preserved system (Packard & Goodman, 2013). It has also been shown that the manipulation of various factors (e.g., temporal sequence of training, timing of feedback) might bias the relative contributions of declarative and procedural memory during task performance (Foerde, Braun, et al., 2013; Packard & Goodman, 2013).

As tools are multifaceted, successful use involves the acquisition and retention of various properties, which are primarily mediated by different memory systems. For instance, knowledge about a tool's attributes (e.g., function, physical appearance) has been shown to largely be mediated by declarative memory, whereas performing tool-related motor actions during a training period relies heavily on motor-procedural memory (Daprati & Sirigu, 2006; Fernandes et al., 2017; Roy & Park, 2010, 2016; Roy et al., 2015; Warrington & Shallice, 1984). This dissociation is supported from studies that examined novel tool use in two patient populations: 1) an individual with amnesia, who had impaired declarative memory due to hippocampal damage, and 2) individuals with Parkinson's disease (PD), who had impaired motor-procedural memory

resulting from striatal dysfunction. Overall, these different types of patients showed opposite performance patterns. Namely, compared to healthy controls, the amnesic individual was impaired in recalling information about a tool's attributes, but showed intact motor performance. That is, he became faster at using the tools within a session, and demonstrated preserved retention after three days and three weeks (Roy & Park, 2010). In contrast, compared to healthy controls, individuals with PD showed intact recall of tool attributes, but were impaired in some aspects of motor performance; they exhibited intact within-session performance (i.e., tool use became faster over Training trials), but performance was not retained after three weeks (Roy et al., 2015). In addition, a third measure assessed skilled tool use, which required individuals to demonstrate a tool's use after a delay. Findings suggested that this measure may involve a cooperative interaction of both systems, in which declarative memory may be required to recall how to accurately use a specific tool, whereas motor-procedural memory is needed to carry out the motor action itself (Fernandes et al., 2017; Roy & Park, 2010, 2016; Roy et al., 2015).

Though one memory system may predominantly mediate a certain component of tool use, it is important to note that acquisition and retention of tool properties likely do not purely reflect a single process (Jacoby, 1991). For instance, motor performance may mainly require motor-procedural memory and striatal processing, but it is possible that hippocampally-mediated declarative memory also contributes to performance (Albouy et al., 2013), and certain training conditions may affect the relative contributions of these memory systems. Past research has posited that inclusion of extra training trials within and across sessions (Experiment 1; Fernandes et al., 2017) possibly resulted in greater use of compensatory interactions with motor performance in individuals with PD who had impaired motor-procedural memory, such that greater exposure to the task may have resulted in more preserved declarative processing. To

further investigate how declarative and motor-procedural memory may contribute to tool use, I examined a potentially robust training manipulation, the spacing effect.

The Spacing Effect

When an individual learns knowledge or skills, the distribution of training trials within the acquisition period can have large effects on retention (i.e., test performance after a delay). For instance, trials can be spaced (i.e., time or intervening information is placed between two trials) or massed (i.e., completed consecutively). Within the verbal learning literature, the well-studied and documented spacing effect refers to the finding that spaced study trials tend to result in superior retention performance compared to massed trials (Cepeda et al., 2006; Greene, 1989). A similar phenomenon has also been separately documented in the motor literature, but it is typically referred to as the contextual interference effect. Here, compared to a blocked practice schedule (e.g., AAA BBB), a random practice schedule (e.g., ACB CBA) tends to enhance performance after a delay, although it may impair acquisition (Brady, 1998; Magill & Hall, 1990; Merbah & Meulemans, 2011; Shea & Morgan, 1979; Simon & Bjork, 2001). This distinction between acquisition and retention is notable because many studies have demonstrated that contextual interference effects only occur after a sufficient delay, whereas acquisition findings are less consistent (Lee & Genovese, 1988; Leite, Ugrinowitsch, Carvalho, & Benda, 2013; Lin, Wu, Udompholkul, & Knowlton, 2010; Merbah & Meulemans, 2011; Shea & Morgan, 1979; Spittle, McNeil, & Mesagno, 2012).

For the most part, studies that have examined the spacing effect have largely used verbal stimuli (though see Donovan & Radosevich, 1999; Wiseheart, D'Souza, & Chae, 2017), whereas contextual interference studies have typically assessed acquisition and retention of motor actions (Brady, 1998, 2004; Magill & Hall, 1990; Wright et al., 2016). These two literatures have often

not cited each other (though see Schmidt & Bjork, 1992; Soderstrom & Bjork, 2015). In spite of the relative independence of these literatures, theoretical accounts for the spacing effect and contextual interference effect overlap, as some theories propose similar general processes for enhanced retention. On one hand, there are theories that emphasize greater encoding of task details with spaced trials. For instance, the encoding variability account from the verbal literature proposes that the context at encoding is more likely to vary as trials are spaced. A greater number of unique environmental cues during encoding creates more retrieval routes and increases the probability of retrieval success at test (Maddox, 2016; Melton, 1970). Similarly, for motor learning, the elaboration hypothesis proposes that with blocked practice, the learner mainly engages in “intratask” processing, where there is little comparison to other tasks. However, with random practice, multiple tasks are held in working memory at one time, resulting in “intertask” processing (i.e., comparing and contrasting tasks), which aids in encoding a more elaborate or distinct memory trace (Shea & Morgan, 1979). Conversely, other theories focus heavily on retrieval or reconstruction processes. The study-phase retrieval hypothesis (verbal theory) states that spaced trials are beneficial because they allow the learner to retrieve the to-be-remembered information during the acquisition phase itself, and each successful retrieval strengthens the existing memory trace (Delaney, Verkoeijen, & Spirgel, 2010; Maddox, 2016; Maddox & Balota, 2015; Thios & D'Agostino, 1976). Likewise, the action-plan reconstruction hypothesis (motor theory) proposes that with random practice, the plan for each motor action must be reconstructed during each trial because it is “forgotten” when an interfering skill is learned, which bolsters the long-term memory trace (Lee & Magill, 1983). Thus, although there seems to be general agreement that the mnemonic benefit of spaced trials is likely due to some kind of

enhanced cognitive processing during acquisition (i.e., elaboration vs. retrieval), more precise mechanisms are still debated.

Recent research has investigated these two general notions by using functional magnetic resonance imaging (fMRI) to examine neural activation under different training schedules. Pauwels et al. (2018) observed different patterns of neural activity in healthy adults for blocked and random practice of a bimanual visuomotor task. Overall, results showed that blocked practice resulted in greater activity in areas that were more reflective of movement automaticity (i.e., sensorimotor-related brain regions during acquisition and striatum during retention). However, random practice resulted in greater neural activity in areas required for visual processing, which was heavily required for carrying out the experimental task. They hypothesized that random practice created a richer training context, causing the learner to be more attentive to the task's visual features; the authors speculated that this finding may have been more suggestive of inter-task or elaborative processing, supporting the elaboration account, as opposed to the action-plan reconstruction hypothesis, which emphasizes motor and action planning. To further understand specific memory enhancements that may occur with spacing, I examined the spacing effect in tool use. As complex tools require both declarative and motor-procedural memory, I was particularly interested in determining how spacing affected these different memory systems. Such comparisons could potentially clarify what particular aspects of memory are enhanced with spacing.

Overview of Experiment 2

The current experiment investigated how the spacing of training trials affected memory for various properties required for novel tool use in healthy adults. During the acquisition phase in Session 1 (S1), participants completed massed and spaced practice trials. Retention was

assessed after a 3-week delay in Session 2 (S2) where I tested participants' memory for various tool-related tasks. As I was interested in examining the spacing effect in declaratively- and motor-procedurally-mediated aspects of tool use, my primary measures were motor performance during Training (motor-procedural measure), and recall of tool attributes (declarative measure). Of secondary interest, I also assessed performance on skilled tool use (i.e., demonstrating a tool's use from memory when verbally commanded), which was hypothesized to require both memory systems (Roy & Park, 2010, 2016; Roy et al., 2015).

Prior studies examining memory for novel tools have only used massed practice trials, but based on the previously reviewed studies, I predicted that retention of tool-related properties would improve with spaced practice. I separately assessed motor performance during acquisition and retention, as previous research showed that spacing can differentially impact these distinct stages of motor learning. My primary prediction was that after a 3-week delay, spaced practice would result in superior motor performance compared to massed practice, based on typical results from past studies (Brady, 1998; Magill & Hall, 1990; Merbah & Meulemans, 2011). However, I was less certain about acquisition performance in S1 because previous findings have been mixed.

I also examined recall performance, as this measure primarily requires declarative memory. Overall, I hypothesized that retention would be superior with spaced than massed practice, as this finding reflects the typical spacing effect reported in verbal learning studies (Carpenter, Cepeda, Rohrer, Kang, & Pashler, 2012; Cepeda et al., 2006; Greene, 1989). Within recall, I tested recall of both functional-associative (e.g., the purpose of the tool) and perceptual (e.g., colour of the tool) attributes. If spacing differentially affected these types of information, it could have potential implications for more specific cognitive mechanisms involved in the

spacing effect in motor actions. For example, if spaced practice resulted in superior perceptual recall, this finding could lend support to the idea that with motor actions, spacing may enhance the visual processing of the various tasks, which is consistent with the elaboration hypothesis (Shea & Morgan, 1979; Shea & Zimny, 1983), as suggested by Pauwels et al. (2018).

Finally, of secondary interest, I predicted a spacing effect for skilled tool use. This ability likely requires both memory systems, and I hypothesized that compared to massed practice, spaced practice would enhance performance.

Method

Participants

Thirty-two adults (23 females, 9 males) aged between 18 and 26 years ($M = 20.55$, $SD = 2.14$) were recruited from York University in Toronto, Ontario, and received course credit for their participation. Inclusion criteria were right-handedness, a minimum of 12 years of education and fluency in English (i.e., native language is English, or learned English before age 10). Participants were excluded from the study if they reported color-blindness, a previous head injury resulting in loss of consciousness or a history of a neurological, psychological or medical disorder that could impact cognitive or motor abilities. The experiment was approved by the Ethics Review Board at York University, and all participants provided written consent prior to participation.

Materials

Novel Tools. Thirteen novel complex tools were used in the study (see Figure 1). The tools were constructed from a children's building toy, K'NEX, and were from the same tool set developed by Fernandes et al. (2017). Tools were grasped unimanually, and performed a specific task by acting on an object, known as the recipient (e.g., moving a ring to three pegs). Each tool

had a unique appearance, colour, and function, and pilot testing demonstrated that the tool's function and grasp could not be inferred from its physical attributes.

Instructional Videos. Each tool had an instructional video that provided a visual demonstration and audio instructions to explain its correct use. The videos were approximately 30 seconds in duration, and were played on a laptop.

Recall Test. A cued Recall test was used to assess knowledge of tool attributes and function. The retrieval cue for each tool consisted of three grey-scale photographs of the tool alone, taken from different angles, which were presented on one page. For each cue, participants gave verbal responses to five questions. Three questions assessed functional-associative knowledge: 1) What is the function of the tool? 2) What is the recipient of the tool? 3) How many recipients does the tool act on? Two questions assessed perceptual information: 4) What is the colour of the tool? and 5) What is the colour of the recipient? This categorization was based on previous distinctions made by Warrington and Shallice (1984) for perceptual and functional-associative features of living and non-living things, and was used in previous studies (Roy & Park, 2010, 2016). During the test, each response was recorded by the experimenter.

Use-to-command Test. The Use-to-command test was a measure of skilled tool use, such that participants were verbally instructed to demonstrate the correct use of the tool without the aid of the instructional video. During the test, the experimenter placed the tool and its associated materials (e.g., the recipient) in front of the participant. The participant was then asked to demonstrate the tool's use, and to inform the experimenter once the task was completed. The experimenter placed the tools in their correct starting location, but the associated recipients were placed in a neutral location. Thus, to accurately complete the task, the recipient first had to be placed in the correct starting location. There was a 60-second time limit to complete one

errorless attempt, and timing began once the tool made contact with the recipient. Participants did not receive any feedback on their performance. Further details on the experimental materials and procedures can be found in Fernandes et al. (2017).

Design and Procedure

Participants were tested individually during two sessions (S1 and S2), spaced three weeks apart (refer to Figure 2 for a detailed design of the study). During S1 participants completed the acquisition phase, and there was a within-subjects manipulation regarding the spacing of Training trials. S2 assessed retention through a test portion followed by an additional Training trial (described below).

The 12 tools were randomly divided into two equal tool sets (Set A and B). As subsequently described, the thirteenth tool was only included to aid in Training schedule during S1, and was not included in S2, or in any of the data analyses. Tool sets were counterbalanced across participants such that 1) each tool set was assigned to each Training schedule an equal number of times and 2) there were two different orders of administration for the entire tool set, ensuring that the average position of each tool in the sequence of administration was equal. Additionally, the number of positions between second training trials and the start of the retention test (see Cepeda et al., 2006; Green, Weston, Wiseheart, & Rosenbaum, 2014) did not significantly differ across conditions⁴.

Session 1 (Acquisition).

Training Trials. Participants completed two Training trials (T1, T2) for all 13 tools. For each tool, participants first watched the instructional video. As the video played, the tool and its

¹ The mean number of items between the second Training trial and the beginning of the retention test for tools in the massed ($M = 12.00$, $SD = 2.27$) and distributed training ($M = 11.00$, $SD = 1.06$) conditions did not significantly differ, $t(7) = .98$, $p = .361$

associated recipients were positioned in front of the participant, though they were instructed not to touch any materials. After completion of the video, participants were then required to grasp and then use the tool in the same way as in the video, and to complete the task as quickly as possible while minimizing errors. Timing of the Training trial began once the tool made contact with the recipient, and participants had 60 seconds to complete one errorless attempt. During this time, the experimenter provided feedback if any errors were not immediately self-corrected by the participant (e.g., incorrect grasp, sequence or recipient placement), and they were asked to start over.

Six of the tools (e.g., Set A) were trained under the massed practice condition, whereby participants first viewed the instructional video, and were immediately required to demonstrate the correct use of the tool twice in a row. The other six tools (e.g., Set B) were trained under the spaced practice condition. In this condition, participants watched the instructional video and immediately after, completed one Training trial (T1). In order to distribute or space the second trial (T2), participants then completed massed practice for another tool before completing trial 2 for a spaced practice tool (see Figure 3 for an example of the Training schedule). The thirteenth tool was trained under the massed practice condition, and was required so that there were enough interfering trials for tools in spaced practice.

Delay

Following S1, there was a 3-week delay in order to assess retention.

Session 2 (Retention).

Test. S2 began with the Recall test, which assessed knowledge of tool attributes for all 12 tools. Participants then completed the Use-to-command test, which measured their ability to accurately demonstrate each tool's use from memory.

Training Trial (T3). After the test portion, participants completed one final Training trial (T3) to assess motor retention. As in S1, participants first viewed the instructional video and were then immediately asked to perform the task in exactly the same way as in the video.

Scoring and Statistical Analyses

Similar measures and scoring procedures were used as in previous studies (Fernandes et al., 2017; Roy & Park, 2010, 2016; Roy et al. 2015). During practice trials, motor performance was measured as Training Time, which was the time of errorless attempt (i.e., the duration of the single, successful attempt completed with the 60-second time limit). Timing began at the first attempt and ended when the first errorless attempt was demonstrated. If the task could not be successfully completed within the time limit, participants received the maximum score of 60 seconds. The number of attempts was also recorded, which included the successful attempt, as well as the number of errors that were made prior to successfully performing one errorless trial.

For the Recall test, performance was measured as the percentage of accurate responses to the items in each trial. Participants received one point for each correct answer and zero points for an incorrect answer. A scoring rubric, developed in a previous study (Fernandes et al., 2017), was used to score Recall performance.

Use-to-command performance was assessed by accuracy and time. Accuracy was measured as the percentage of accurate tool demonstrations. One point was awarded if the task was performed successfully within the 60-second time limit. A second independent rater scored approximately 30% of the data, and inter-rater reliability was 93.42% (calculated as percentage of agreement). Similar to scoring for the training trials, Use-to-command Time was measured as the time of errorless attempt, which reflected how quickly participants performed the task.

I analyzed all experimental measures with parametric statistical techniques. All pairwise comparisons were performed using Bonferroni corrections and raw, unadjusted p-values are reported. In addition, to ensure that average time scores were not inflated by incomplete attempts (i.e., maximum time scores of 60 seconds), incomplete attempts were removed before conducting analyses on completion times for both Training and Use-to-command. For both completion time measures, performance was also assessed as time to errorless attempt, which was the total time taken to successfully complete the task from the beginning of the first attempt to the end of the errorless attempt. Similar performance patterns were obtained with both time measures, so I only reported the time of errorless attempt.

Results

Training Time.

For motor performance during Training, a 2-way within-subjects ANOVA with Training trial (T1, T2, T3) and Training schedule (massed vs. spaced) as factors was conducted. There was a significant main effect of trial, $F(2, 62) = 59.22, p < .001, \eta^2 = .66$, showing that Training Time became faster across the three trials ($p < .001$ for all post-hoc comparisons) (see Figure 4). There was also a significant main effect of schedule, $F(1, 62) = 10.42, p = .003, \eta^2 = .25$, demonstrating better performance for tools practiced with spaced than massed schedules. Though the interaction was not significant, I conducted follow-up paired t-tests comparing the two Training schedules at each trial due to my hypotheses that spacing would improve performance after a 3-week delay. There was not a significant difference between massed and spaced training in T1 or T2, but as predicted, in T3, tools practiced under spaced schedules were significantly faster than those completed with massed practice, $t(31) = 3.10, p = .004, d = .54$. Taken together, these results indicated a benefit of spaced practice; though performance did not differ during

acquisition in S1, spaced practice resulted in better retention performance after a 3-week delay (T3).

Training Number of Attempts.

A 2-way within-subjects ANOVA examined the mean number of attempts during Training for the massed and spaced practice conditions across the three trials. There was only a significant main effect of trial, $F(2, 62) = 11.57, p < .001, \eta^2 = .27$, whereby participants made fewer attempts in T2 and T3 compared to T1 ($p = .001$ for both post-hoc comparisons) (T1: $M = 1.70, SD = 0.51$; T2: $M = 1.40, SD = 0.28$; T3: $M = 1.35, SD = 0.28$).

Though the main effect of schedule was not significant, indicating that overall the number of attempts did not differ between massed and spaced practice, I conducted a paired t-test at T2. I specifically examined this trial to verify that participants did not make more errors for tools trained under spaced practice ($M = 1.43, SD = 0.45$) than massed practice ($M = 1.38, SD = 0.40$), possibly reflecting interference or forgetting after T1, $t(31) = 0.43, p = .673$.

Recall Accuracy

A 2-way within-subjects ANOVA with Training schedule (massed vs. spaced) and information type (functional/associative vs. perceptual) as factors was conducted (see Figure 5). There was a main effect of information type, $F(1, 31) = 22.54, p < .001, \eta^2 = .42$, demonstrating that overall, Recall Accuracy was higher for functional-associative information than perceptual information. More critically, there was a main effect of Training schedule, whereby tools trained with spaced practice had higher perceptual and functional-associative recall than those trained under massed practice, $F(1, 31) = 51.10, p < .001, \eta^2 = .62$.

Use-to-command Accuracy

Paired t-tests revealed that Use-to-command Accuracy was significantly higher for tools trained under spaced than massed practice, $t(31) = 3.80, p = .001, d = 0.67$ (see Figure 6).

Use-to-command Time

Paired t-tests indicated that there was not a significant difference in Use-to-command Time between massed and spaced practice, $t(31) = 1.29, p = .207, d = 0.23$ (see Figure 7).

Experiment 2 Discussion

Experiment 2 examined the spacing effect in novel complex tools to better understand the impact it may have on declarative and motor-procedural memory. During acquisition in S1, participants completed Training trials under massed and spaced practice, and retention for various tool-related attributes (i.e., Training Time, Recall Accuracy and Use-to-command Accuracy and Time) was evaluated three weeks later in S2. Consistent with the general findings from studies examining spacing and contextual interference effects and my hypotheses, results showed that compared to a massed schedule, spaced practice resulted in superior retention across all tool measures.

Motor Performance

Based on past research examining the contextual interference effect, I predicted that compared to massed practice, spaced practice would result in superior retention after a 3-week delay, though I was less certain about acquisition performance. Overall, my results demonstrated motor learning, as Training Time improved across trials regardless of the practice schedule (i.e., from T1 to T2 to T3). More importantly though, a spaced schedule produced better retention in S2. However, during acquisition in S1, there were no differences between massed and spaced practice. Enhanced long-term retention with spaced trials is consistent with typical results from contextual interference studies (Magill & Hall, 1990; Merbah & Meulemans, 2011). However,

acquisition performance has been shown to vary across studies, and thus, there does not seem to be a well-established performance pattern. My observed performance differences across various learning stages highlight the importance of clearly distinguishing between acquisition and retention for motor performance (Kantak & Winstein, 2012; Schmidt & Bjork, 1992), particularly when assessing the spacing effect.

Recall

As predicted, Recall Accuracy was higher for tools trained under spaced than massed practice when tested in S2. This finding is consistent with verbal learning studies that have demonstrated the spacing effect across a wide range of verbal tasks (Carpenter et al., 2012; Janiszewski, Noel, & Sawyer, 2003) and populations (Balota, Duchek, Sergent-Marshall, & Roediger III, 2006; Green et al., 2014; Kim, Saberi, Wiseheart, & Rosenbaum, 2018) and shows further support that spaced trials heighten retention in abilities that principally require declarative memory.

Within Recall Accuracy, I separately assessed performance for functional-associative and perceptual knowledge; this distinction enabled me to examine the type of information that spacing benefitted. Overall, Recall Accuracy was higher for functional-associative than perceptual information. This finding is consistent with previous research demonstrating that this information type tends to be more readily recalled, possibly because with the nature of my task, the functional properties of a tool are more important than its appearance (Roy, 2014; Roy & Park, 2010, 2016). More critically though, a spacing effect was found for Recall Accuracy of both types of information. In particular, the fact that spacing enhanced recall of a tool's perceptual information supports the idea that spacing may enhance the visual processing of the tool task during encoding. This result potentially provides support for the elaboration hypothesis

from the contextual interference effect literature, which places a greater emphasis on more distinctive or elaborative sensory processes (Pauwels et al., 2018; Shea & Morgan, 1979; Shea & Zimny, 1983), not regions associated with the planning and execution of a motor (Lee & Magill, 1983).

Skilled Tool Use

As secondary measures, I also evaluated skilled tool use in my Use-to-command task by measuring Accuracy and Time, which are primarily mediated by declarative and motor-procedural memory, respectively (Fernandes et al., 2017; Roy & Park, 2010, 2016; Roy et al., 2015). I found clear evidence for superior Use-to-command Accuracy with spaced trials, further supporting enhancement of declarative memory with the spaced trials. However, there were no differences between massed and spaced practice with Use-to-command Time. Thus, it is possible that spacing may not benefit the motor-procedural aspect of skilled tool use, or it may reflect limitations in the measure itself (discussed in more detail in the General Discussion for Experiments 2 and 3).

Summary and Follow-Up Experiment

The current experiment demonstrated strong support for the spacing effect in complex tool use, as spaced practice enhanced retention for various tool-related skills. Though the powerful effects of spacing have been long established within the verbal and motor learning fields, my experiment was able to closely evaluate the spacing effect in two different memory systems simultaneously. Findings showed that spaced practice trials benefitted performance measures that were primarily mediated by declarative or motor-procedural memory.

It is important to note that in the current experiment, participants physically practiced the tool tasks during Training. That is, regardless of whether Training was completed with massed or

spaced practice, during each trial learners were required to generate a response. Thus, in addition to spacing, the act of practicing the task itself may have benefitted memory performance. This acquisition method is standard in the motor literature. However, in verbal learning studies, the production of a response during acquisition is separately examined and known as the testing effect (Roediger III & Butler, 2011; Roediger III & Karpicke, 2006a). Additionally, in a previous study, my lab demonstrated that physically practicing a task and receiving performance-based feedback during acquisition was important for some tool-related properties, as pure observation was not effective for motor learning (Roy, 2014). Thus, it could be argued that in Experiment 2, I did not evaluate a “pure” spacing effect. As a result, I conducted a follow-up experiment (Experiment 3) to more carefully examining the separate contributions of spacing (massed versus spaced) and learning method (practice versus observation) on retention of different tool properties.

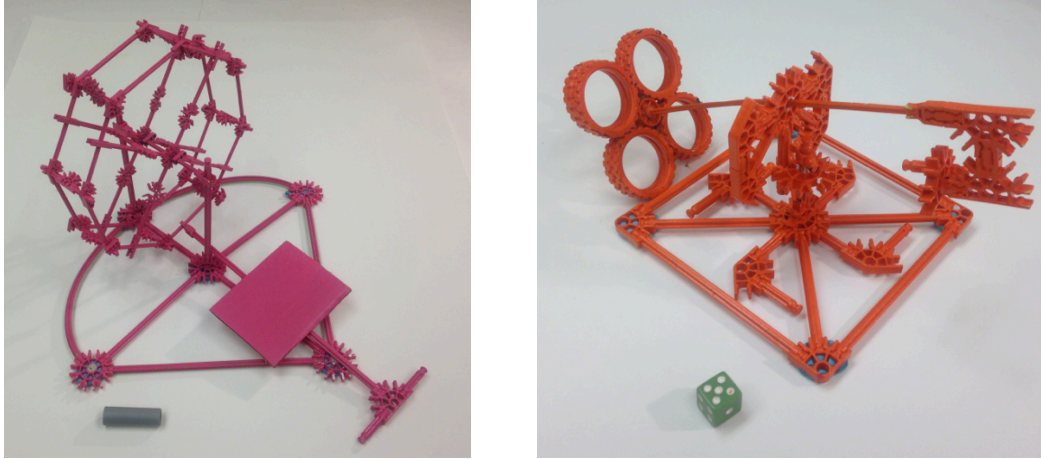


Figure 1. Examples of tools and their associated recipients

Session 1	3-Week Delay	Session 2		
Training (T1, T2)		Recall Test	Use-to-Command Test	Training (T3)
2 training trials per tool -6 tools (spaced practice trials) -6 tools (massed practice trials)		12 tools	12 tools	12 tools

Figure 2. Design of Experiment 2

Tool #	2	1	1	2	4	3	3	4
Training Trial	T1	T1	T2	T2	T1	T1	T2	T2
Condition	Spaced	Massed	Massed	Spaced	Spaced	Massed	Massed	Spaced

Figure 3. For Experiment 2, an example of the training trial schedule in S1 using four tools. In this case, Tools 1 and 3 (Set A) are in the massed practice condition. Tools 2 and 4 (Set B) are in the spaced practice condition.

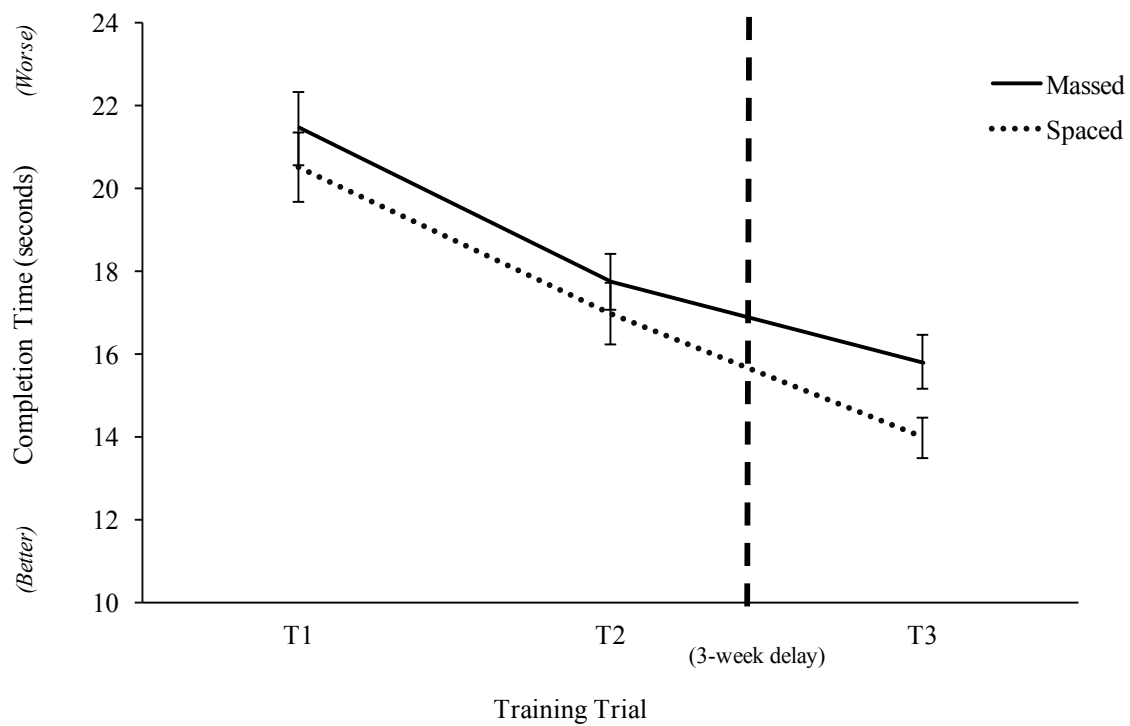


Figure 4. Mean completion time (+/- SE) for massed and spaced practice across Training trials.

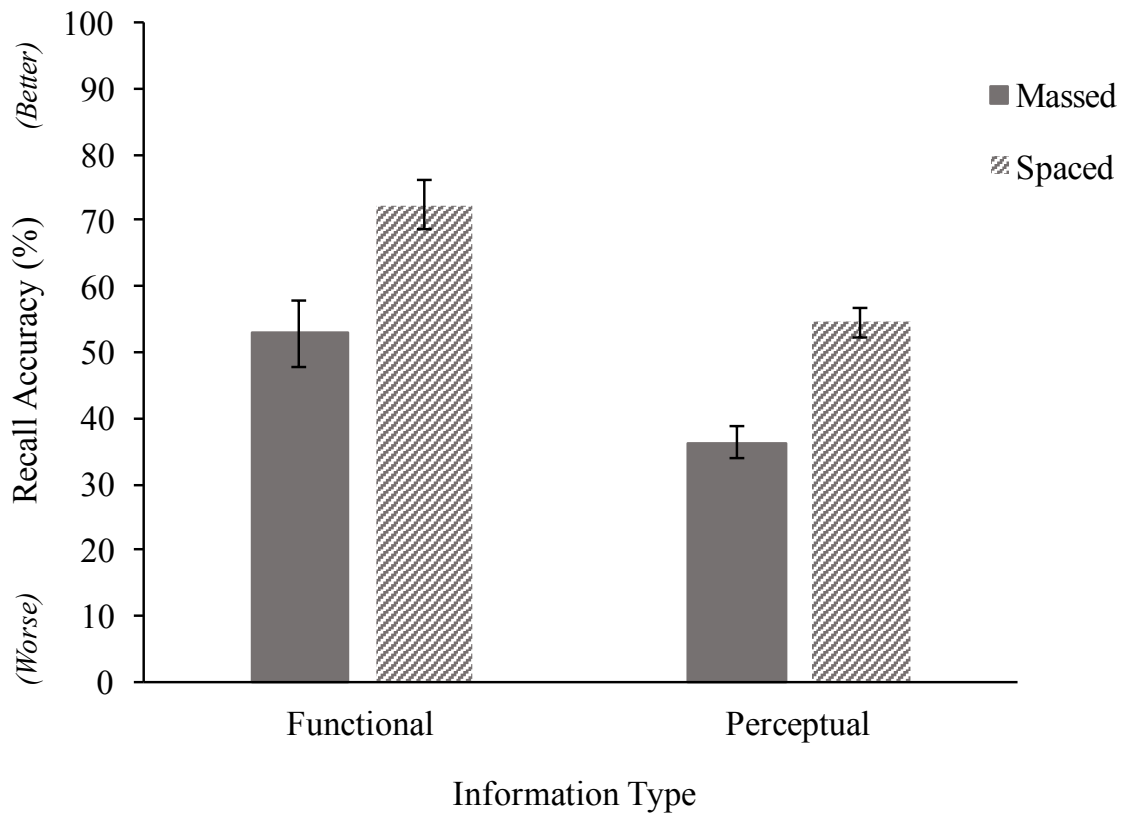


Figure 5. Percentage of correct responses (+/- SE) for Recall test items assessing functional and perceptual information for massed and spaced practice in S2 (i.e., retention after a 3-week delay)

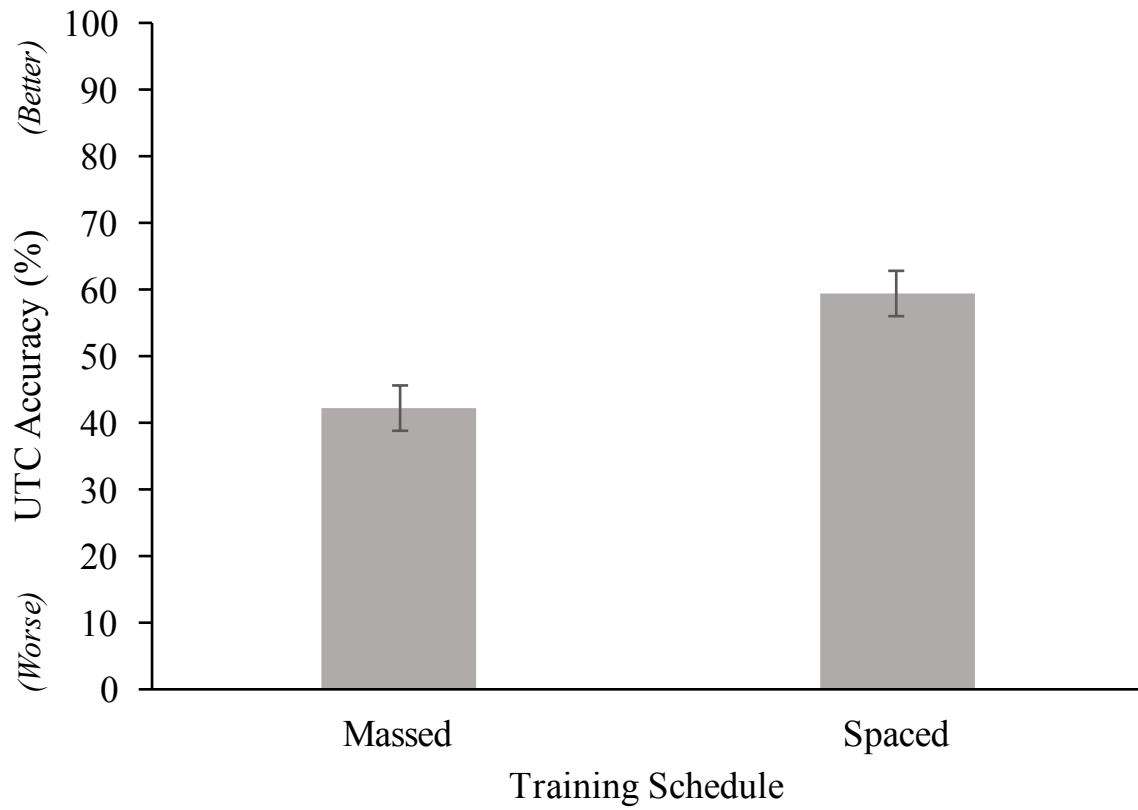


Figure 6. Percentage of correct demonstrations for Use-to-command (+/- SE) for massed and spaced practice in S2 (i.e., retention).

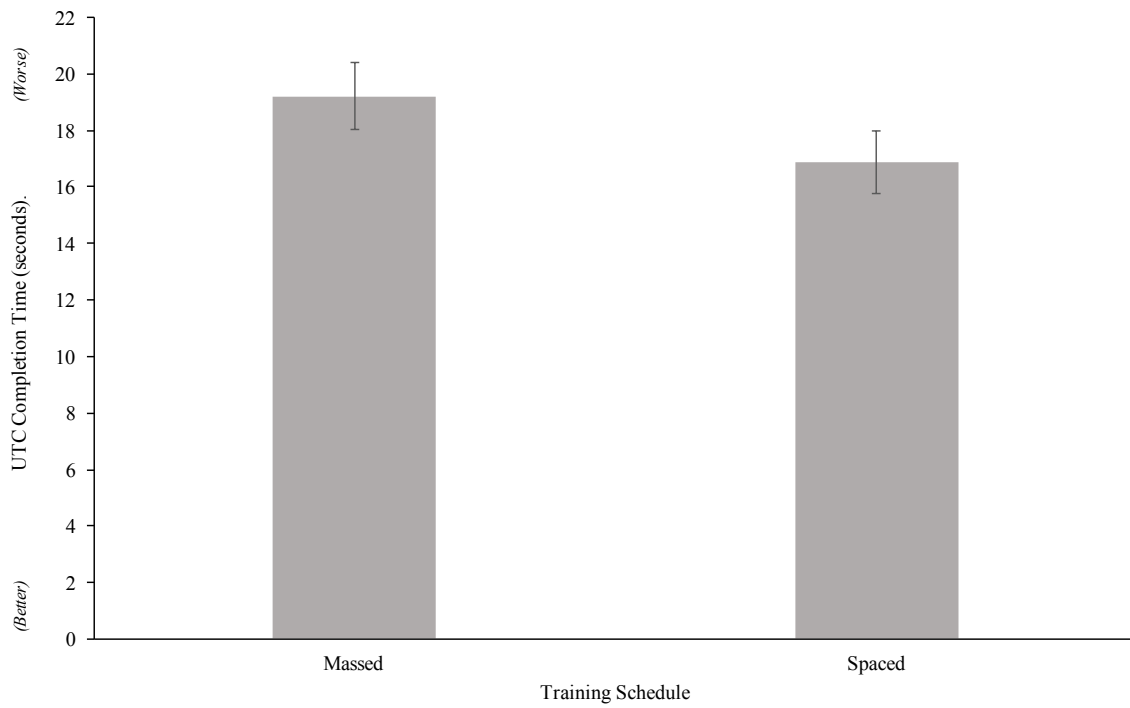


Figure 7. Mean completion time during Use-to-command (+/- SE) for massed and spaced practice in S2 (i.e., retention).

Chapter 4: Differential effects of practice and observation on the spacing effect in complex tool use

To more critically examine cognitive processes contributing to spacing effects, I assessed how spacing interacted with the type of learning used during acquisition. I focused on learning type because previous research suggested that different learning methods engage different memory systems. In addition to using practice trials (as in Experiment 2), I added observational learning, which is similar to passive study trials that have been commonly used in verbal spacing effect studies. As will be discussed, practice, but not observation, improved acquisition of motor actions when using massed training (Roy, 2014). In the current experiment, I assessed how practice and observational learning impacted spacing effects, and I was most interested in comparing retention of difference aspects of complex tools that were primarily mediated by different memory systems. This comparison was critical, as it allowed me to investigate whether spacing effects involve different cognitive processes, associated with distinct neural regions.

In the next section, I describe why the underlying memory system of a particular tool property should be considered when assessing spacing effects. I then highlight how practice and observation may engage different memory processes. Next, I relate types of learning to another well-known concept, the testing effect, and consider its possible implications for spacing.

Finally, I provide an overview of Experiment 3.

Memory Systems and the Spacing Effect

As discussed in Experiment 2, patient studies (i.e., individual with amnesia and PD participants) (Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015), demonstrated that different tool properties may be primarily encoded and retained by distinct memory systems and neural areas. For instance, recalling information about a tool's attributes mainly relies on

declarative memory mediated by complex neural areas including the hippocampal complex, and performing a tool-related motor actions relies heavily on motor-procedural memory mediated by the striatum. Considering these well-established cognitive and neural distinctions, tools can be used to further investigate how the distinct properties of declarative and motor-procedural memory might result in different patterns of retention, especially within the spacing effect.

Experiment 2 examined spacing using only practice trials where participants physically interacted with the tool to complete a task. Though this type of learning is typically used to investigate motor learning (Blandin, Proteau, & Alain, 1994; Roy, 2014; Wulf & Shea, 2002), it also introduces additional factors that could contribute to my understanding of the cognitive mechanisms mediating the spacing effect. In particular, performing the task during training involves performance-based feedback and a self-generated response, both of which have been shown to impact memory performance (Roediger III & Karpicke, 2006a; Roy, 2014). Subsequently, I consider how these two factors could potentially impact motor-procedural and declarative memory, and the possible implications for the spacing effect.

Feedback-based learning.

Declarative and procedural memory have different properties, which can impact how new knowledge, skills or actions are acquired and retained. For instance, individuals can rapidly acquire declarative knowledge through various means (e.g., actively studying, testing oneself, passively acquiring new information) (Eichenbaum, 2000; Squire, 1992a, 2009). In contrast, with procedural learning, acquisition typically occurs gradually and relies on trial-by-trial feedback, such that the learner continuously adjusts their motor-output response based on sensory inputs containing feedback (De Vries, Ute, Zwitserlood, Szymanski, & Knecht, 2010; Shohamy, 2011; Shohamy et al., 2008; Thirkettle et al., 2013).

Evidence for this distinction stems from a seminal study by Knowlton et al. (1996) that investigated habit learning, a form of procedural learning, which involves gradual and incremental learning of stimulus–response associations, but does not require a skilled motor response. In a commonly-used probabilistic learning task used to investigate habit learning, the “weather prediction” task, participants learned to predict the weather outcomes (i.e., sun or rain) based on the presentation of several cues and trial-by-trial probabilistic feedback about the outcome. The study showed that individuals with PD and striatal dysfunction were impaired at probabilistic (i.e., habit) learning, yet had intact declarative memory for information about the cues shown and the training phase itself. In contrast, individuals with amnesia due to medial temporal lobe damage showed the opposite performance pattern, where they had preserved probabilistic learning, but impaired declarative knowledge (Knowlton et al., 1996).

Subsequent research further examined two versions of the weather prediction task: 1) the traditional feedback version where participants were given corrective feedback each time they gave a response (i.e., “procedural emphasis”), and 2) a novel observation version where participants did not make a response, but were instead explicitly told the correct answer (i.e., “declarative emphasis”). A neuroimaging study showed that the feedback version was associated with greater striatal activation, whereas the observation version resulted in greater activity in the medial temporal lobes (Poldrack et al., 2001). A behavioural study then demonstrated that compared to healthy controls, participants with PD were impaired in the feedback version, but not in the observational version (Shohamy et al., 2004). Taken together, these findings highlighted that the type of learning method used during acquisition can bias the use of one memory system over the other. Here, feedback-based learning resulted in greater use of

procedural memory mediated by the striatum, whereas observational learning relied more heavily on declarative memory mediated by the medial temporal lobes.

Though the majority of studies on feedback-based learning and procedural memory have paired a single response with an outcome (e.g., habit memory in probabilistic learning task), it has been previously argued that these principles may extend to tool use (Roy, 2014). For example, when acquiring tool-related actions, individuals perform a series of actions in a correct sequence, and as each movement is performed, they receive sensory-motor feedback. In other words, though more complex than single action-outcome associations, motor performance in tool use may rely on similar processes: after each movement, the learner receives sensory feedback about the just-performed action, and adjusts their motor outputs, thereby resulting in motor-procedural learning.

A previous study from Roy (2014) specifically examined how limiting performance-based feedback affected tool use across various measures. Most relevant to the current experiment, during acquisition, healthy adults completed training trials under one of two conditions. During the practice learning condition, participants physically interacted with the tool and its recipient(s) to complete the task (i.e., high degree of feedback). In the observational learning condition, participants watched the task being performed, but did not physically interact with the tool or its recipients (i.e., low degree of feedback). After completing two massed training trials, performance was assessed with an immediate test. As hypothesized, results showed that limiting performance-based feedback hindered motor performance (i.e., Training Time was faster for practice than observation). However, there were no group differences in Recall Accuracy, suggesting that immediate recall of this information was not affected by learning type. Together these findings showed that performance-based feedback was only

necessary for motor-procedural (i.e., motor performance), but not declarative memory (i.e., Recall) when memory was assessed on an immediate test. It is not certain, however, that similar results would have been observed if memory was tested after a longer delay because different patterns of memory performance have been frequently observed on immediate versus delayed tests (Kantak & Winstein, 2012; Roediger III & Karpicke, 2006b).

Taken together, there is strong evidence showing that feedback may be a critical factor for procedural learning, which includes acquiring and performing tool-related motors. However, practice trials also have some remarkable similarities to another phenomenon, the testing effect in the verbal learning literature. In the following section, I discuss how practice trials not only provide performance-based feedback, which is necessary for procedural processing, but the act of generating a response itself can also improve memory, where enhancements may extend to declarative processes.

The Testing Effect.

The act of recalling information during acquisition (i.e., taking a “test”), rather than restudying it (i.e., seeing or hearing information that was previously presented) can be a powerful strategy to bolster retention. The testing effect has been demonstrated on a wide-range of declaratively-mediated verbal memory tasks, such as list-learning (Rowland, Littrell-Baez, Sensenig, & DeLosh, 2014; Zaromb & Roediger, 2010), prose passages (Roediger III & Karpicke, 2006b), and paired associates (Carpenter, Pashler, & Vul, 2006; Toppino & Cohen, 2009), as well as visuospatial tasks (Carpenter & Pashler, 2007; Kang, 2010). According to the Retrieval and Desirable Difficulties Hypotheses testing recall during acquisition is advantageous because an individual must actively retrieve information while learning, which may increase the number retrieval routes or create a more elaborative memory trace (Bjork, 1988, 1994; Gardiner,

Craik, & Bleasdale, 1973) (for a review of theories see Roediger III & Karpicke, 2006a).

Consistent with these hypotheses, some studies have highlighted the importance of the retention interval when assessing performance (Roediger III & Karpicke, 2006b; Thompson, Wenger, & Bartling, 1978; Wenger, Thompson, & Bartling, 1980; Wheeler, Ewers, & Buonanno, 2003). As with spacing effects, testing may require greater cognitive demands during acquisition which may initially hinder performance, but it has been proposed that this enhanced processing ultimately improves long-term retention (Carpenter, Pashler, Wixted, & Vul, 2008; Karpicke & Roediger, 2008; Toppino & Cohen, 2009).

Although the distinction between study and test trials comes from verbal studies, it also may be relevant to observational versus practice learning used in motor studies. In both study and observational learning methods, the learner is simply re-presented with the to-be-learned material. In contrast, with test and practice trials, the individual must retrieve task-related information from memory to produce a response. The parallels are noteworthy because the type of learning used during acquisition may have important consequences on subsequent memory traces.

Overview of Experiment 3

Like Experiment 2, Experiment 3 examined the spacing effect in tool use, while adding a second condition: learning type (practice and observation). I predicted that these two conditions might differentially affect Recall Accuracy and motor performance during Training because practice involves performance-based feedback and response generation, whereas observation does not. In turn, I also thought that these learning types might impact the effectiveness of spacing for some aspects of tool use. During S1, two variables, Training schedule (massed vs. spaced) and learning type (practice vs. observation) were combined to create four acquisition

conditions: massed practice, spaced practice, massed observation and spaced observation.

Retention for motor performance (i.e., Training Time), Recall and skilled tool use (i.e., Use-to-Command) was then assessed in S2 after a 3-week delay.

Overall, I hypothesized that observational learning would principally engage declarative memory, whereas practice would engage both motor-procedural memory and declarative memory based on findings from probabilistic learning (Knowlton et al., 1996; Poldrack et al., 2001; Shohamy et al., 2004) and tool use (Roy, 2014). Based on this differential engagement, I then developed more specific and separate predictions for my two primary outcomes based on their underlying memory system (i.e., Training Time and Recall Accuracy).

Motor performance during Training (i.e., Training Time) was my main measure of a tool task primarily requiring procedural memory, and thus I predicted that learning would require performance-based feedback. As shown by Roy (2014), I hypothesized that practice would result in improved motor performance across both massed and spaced trials after a 3-week delay, whereas observation would not. Because observation would not facilitate motor learning, I also predicted that it could impact the effectiveness of spacing. Specifically, I hypothesized that a spacing effect may not be found with observation because it would not engage cognitive and neural processes (e.g., feedback-based learning) required for motor learning and retention.

In contrast, for Recall Accuracy, my primary measure of declarative memory, my hypotheses were less clear. On one hand, it was possible that there would be no performance differences between practice and observation, as Roy (2014) observed on immediate testing. However, I assessed Recall after a 3-week delay, so I thought it was possible that overall, practice learning may result in better performance than observation because it involves generating a response, which is similar to the testing effect (Racsmány, Szöllösi, & Bencze,

2018; Roediger III & Butler, 2011; Roediger III & Karpicke, 2006a). In terms of how learning type impacted spacing effects with Recall, I hypothesized that the spacing effect would be observed for both practice and observation, as both learning methods would be effective for acquiring declarative information (Roy, 2014).

Method

Participants

Thirty-two adults (17 females, 15 males) aged between 18 and 29 years ($M = 22.88$, $SD = 3.22$) participated in the study. They were recruited through advertising at York University in Toronto, Ontario, and the surrounding community, and received monetary compensation for their participation. Inclusion and exclusion criteria were the same as in Experiment 2. The York University Ethics Review Board approved the study, and participants provided written consent.

Materials

The same materials were used as in Experiment 2.

Design and procedure

Participants individually completed two sessions (S1, S2), separated by a 3-week delay (refer to Figure 1). As in Experiment 2, S1 consisted of the acquisition phase, and S2 assessed retention. Experiment 3 had one within-subjects factor, **Training schedule**, with two levels of massed vs. spaced, and one between-subjects factor, **type of learning**, with two levels of observation vs. practice. These two factors were orthogonally combined, and participants were randomly assigned to the following acquisition conditions: 16 participants completed massed observation and spaced observation, and another set of 16 participants completed massed practice and spaced practice. Further details about each condition are discussed in the following section.

As in Experiment 2, twelve tools were divided into two equal sets (Set A and B), and the thirteenth tool was required for the S1 Training schedule, and was not included in any data analyses or S2. Tools sets were also counterbalanced as previously described.

Session 1 (Acquisition)

Training Trials. Participants completed two trials for all 13 tools. For each tool, participants began by watching the instructional video (refer to Experiment 2 for full details). After the video, T1 and T2 were then completed using observation or practice, and under a massed or spaced schedule. During the practice learning condition, participants completed the Training trials in the traditional manner, whereby they fully demonstrated the task by physically interacting with the tool and its recipients, as described in Experiment 2 (also see Fernandes et al., 2017 for full details). For observational learning, participants viewed the instructional video again, but did not physically interact with the tool or the recipient(s) in front of them, thus limiting the degree of performance-based feedback. The Training schedule variable affected when T2 occurred in relation to T1, and massed and spaced Training were carried out in the way as in Experiment 2.

For the *massed practice* condition, participants watched the instructional video and then completed T1 and T2 consecutively under the practice learning method (see Figure 1). For *massed observation*, participants viewed the instructional video three times successively (i.e., initial video demonstration, followed by two additional viewings for T1 and T2). For *spaced practice*, after watching the instructional video and completing T1 under practice learning, participants completed two Training trials for another tool before completing T2, where they used the tool to practice the task again. For *spaced observation*, participants first watched the instructional video two times in a row (initial video demonstration, T1). After completing T1,

participants completed two Training trials for another tool before completing T2, where they once again viewed the instructional video without interacting with the tool.

Delay

After S1, there was a 3-week delay.

Session 2 (Retention)

S2 began with the Recall test, followed by the Use-to-command test. Participants then watched the instructional video and then completed one final Training trial (T3) where they performed the task.

Scoring and Statistical Analyses

The same scoring methods were used as in Experiment 2. I also employed a similar approach to my statistical analyses with the use of parametric statistics for all measures. As in Experiment 2, I conducted analyses of Training and Use-to-Command Times using both total time to errorless attempt and time of errorless attempt. As a similar pattern of results were found for both time measures, I only report time of errorless attempt below. I performed all pairwise comparisons using Bonferroni corrections, and raw, unadjusted, *p*-values are reported.

Results

Training Time

Training Time is displayed in Figure 2. I initially examined only the practice conditions to determine if a spacing effect was present during any of the three Training trials (as in Experiment 2). I then analyzed observation and practice in T3 to determine if Training with performance-based feedback (i.e., practice) resulted in better performance after a 3-week delay compared to observation. I also compared the first “practice” Training trial for each learning condition (T1 for practice learning, T3 for observational learning); I hypothesized that

performance would be similar, as observational learning in S1 would not engage procedural memory, or improve motor performance.

Practice conditions. For practice learning only, a 2-way within-subjects ANOVA examined Training Time across the three trials for massed and spaced schedules (see Figure 2). There was a significant main effect of trial, $F(2, 30) = 33.12$, $p < .001$, $\eta^2 = .69$, demonstrating that overall, participants became faster from T1 to T2 ($p < .001$) and from T2 to T3 ($p = .037$). Despite the interaction ($p = .070$) and main effect of schedule ($p = .079$) failing to reach statistical significance, I used follow-up paired t-tests to compare performance at each trial because of a priori predictions and findings from Experiment 2. There was not a significant difference between Training schedules in T1 or T2. However, tools that were practiced under a spaced schedule were significantly faster than massed practice after the 3-week delay in T3, $t(15) = 2.96$, $p = .01$, $d = .74$. Thus, as in Experiment 2, compared to massed practice, spaced practice resulted in better performance after a 3-week delay in S2, but not during acquisition in S1.

Practice vs. Observation. A 2-way mixed-design ANOVA using one within-subjects factor (Training schedule) and one between-subjects factor (learning type) examined Training Time in T3. There was a significant interaction, $F(1, 30) = 5.07$, $p = .032$, $\eta^2 = .14$. Follow-up simple effect analyses demonstrated that in T3, for observational learning, there was not a significant difference in completion time for tools trained with massed and spaced schedule. However, for practice learning, tools trained with spaced trials were significantly faster than those trained with massed trials, $F(1, 30) = 14.55$, $p = .001$, $\eta^2 = .33$. There was also a main effect of learning condition, $F(1, 30) = 5.07$, $p = .032$, $\eta^2 = .14$, such that overall, practice resulted in better Training performance than observation in T3.

A second 2-way mixed ANOVA, using the factors of learning condition and Training schedule, then compared performance for practice in T1 to observation in T3 (i.e., the first “practice” learning trial for each condition). None of the effects were significant, showing that there were no differences in Training performance across the four experimental conditions on the first trial where participants physically practiced the task. Thus, this result shows that despite having the opportunity to view the task, participants in the observe condition did not show any motor improvements when assessed in T3.

In summary, as in Experiment 2, for practice, the spacing effect was only observed during T3, a trial that assessed retention after three weeks, and not during acquisition in S1 (T1, T2). In contrast, observation did not improve performance, and no spacing effects were observed.

Training Number of Attempts

A 2-way within-subjects ANOVA examined the number of attempts made during Training for the practice learning conditions using schedule and trial as factors. None of the effects were significant, demonstrating that for practice, the number of attempts did not vary across T1, T2 or T3, or between massed and spaced schedules (grand $M = 1.54$, $SD = 0.35$). A 2-way mixed ANOVA then compared the number of attempts in T3 with learning condition and schedule as factors. None of the effects were significant, indicating that in T3, the number of attempts were comparable across all four conditions (grand $M = 1.47$, $SD = 0.34$).

Taken together, these findings showed that the number of attempts did not change across trials for practice learning, or differ between experimental conditions in T3.

Recall Accuracy

A 2-way mixed ANOVA with learning type and Training schedule as factors examined Recall Accuracy for functional and perceptual knowledge in S2 (see Figure 3). For both types of information, there was a significant main effect of schedule (functional: $F(1, 30) = 14.24$, $p = .001$, $\eta^2 = .32$; perceptual: $F(1, 30) = 5.39$, $p = .027$, $\eta^2 = .15$), where spaced schedules resulted in higher Recall Accuracy than massed schedules. There was also a main effect of learning condition, (functional: $F(1, 30) = 26.29$, $p < .001$, $\eta^2 = .47$; perceptual: $F(1, 30) = 54.38$, $p < .001$, $\eta^2 = .64$), with higher Recall Accuracy for practice than observation. With the absence of a significant interaction, these results indicated that the magnitude of the spacing effect did not differ between practice and observational learning, though practice resulted in higher Recall Accuracy overall.

Use-to-command Accuracy

A 2-way mixed ANOVA with learning condition and training schedule as factors examined Use-to-command Accuracy. There was a main effect of schedule, $F(1, 30) = 6.41$, $p = .017$, $\eta^2 = .18$, whereby spaced schedules had higher Use-to-command Accuracy than massed schedules (see Figure 4). There was also a main effect of learning type, $F(1, 30) = 12.16$, $p = .002$, $\eta^2 = .29$, such that practice resulted in higher accuracy than observation. The interaction was not significant, indicating that that both learning conditions showed a comparable spacing effect, though practice resulted in more accurate tool demonstrations than observational learning.

Use-to-command Time

Using learning condition and training schedule as factors, a 2-way mixed ANOVA revealed that overall, practice resulted in faster Use-to-command Time than observation, $F(1, 30) = 5.86$, $p = .022$, $\eta^2 = .16$ (see Figure 5). However, the interaction and main effect of schedule were not significant, indicating no spacing effects.

Experiment 3 Discussion

Experiment 3 concurrently examined two acquisition conditions (i.e., Training schedule and learning type) to determine their impact on the retention of different tool properties. In S1, half of the participants completed two training trials under massed and spaced practice, and the other half completed Training with massed and spaced observation. Retention of various tool-related tasks was then assessed after a 3-week delay. I was most interested in determining how training schedule and type of learning interacted because I hypothesized that declarative and motor-procedural memory had unique properties, and thus would be dissimilarly affected by the different acquisition conditions. Results showed that physical enactment providing feedback-based learning appeared to be required to obtain a spacing effect when performance primarily relied on motor-procedural memory, as observation was not effective for motor learning (i.e., Training Time). In contrast, for Recall Accuracy, which largely requires declarative memory, spacing effects were demonstrated with both observation and practice learning.

Motor Performance

Findings from Experiment 3 first revealed that physical practice was required for motor learning in tool use. Regardless of Training schedule, with practice, participants improved across Training trials (i.e., Training Time became faster from T1 to T2 to T3). In contrast, when motor retention was assessed in S2 for the observation conditions, performance in T3 was comparable to T1 for the practice conditions. Thus, in order to obtain improvements with motor performance, individuals needed to practice the task, as opposed to simply viewing it, which is consistent with results from Roy (2014).

Moving beyond the overall benefit of practice, I also wanted to determine whether physical practice, which provides performance-based feedback, was necessary for the spacing

effect in motor performance. As demonstrated in Experiment 2, results showed that when examining motor retention, compared to massed trials, spaced trials were beneficial when used with practice learning (i.e., spaced practice was faster than massed practice in T3). In contrast, as predicted, spacing effects were not demonstrated with observation (i.e., no Training Time differences between massed and spaced observation in T3). These findings are notable because they suggest that when it comes to motor-procedural processes, spacing effects are not observed if the learning method primarily engages declarative memory (i.e., observation).

Finally, when examining practice conditions only (i.e., massed vs. spaced practice in T1, T2, and T3), the findings replicated the results from Experiment 2. I found no differences between spaced and massed practice during the acquisition phase (i.e., T1 and T2). However, during retention in T3, spaced practice resulted in faster Training Time than massed practice.

Recall

Recall Accuracy served as my primary measure of declarative memory, and I assessed recall of functional-associative and perceptual tool knowledge. As demonstrated in past studies (Roy, 2014; Roy et al., 2015) and Experiment 2, overall, Recall Accuracy was higher for functional-associative than perceptual knowledge. More critically though, results showed that practice produced higher Recall performance than observation for both types of information, regardless of whether a massed or spaced schedule was used. These findings are inconsistent with results from Roy (2014), which did not find a difference between practice and observation on Recall accuracy. However, in their study, Recall was assessed immediately after training, not after 3-week delay. The differences in retention intervals may account for the discrepant findings, and also speak to possible mechanisms underlying these effects. Many verbal learning studies have demonstrated that restudying information can be better after shorter retention

intervals, and testing effects are more robust when assessed after longer delay periods. It has been proposed that testing produces a stronger memory trace because it reduces forgetting of recently learned material. Thus, after longer delays, the amount of forgetting is greater for studied than tested items, which then reveals the long-term benefits of testing (Racsmany et al., 2018; Roediger III & Karpicke, 2006a; Toppino & Cohen, 2009).

In terms of the impact of learning type on Training schedule, results indicated that the magnitude of the spacing effect was comparable for practice and observation. In other words, a spaced schedule resulted in higher Recall Accuracy of functional-associative and perceptual information, regardless of the type of learning method used. Therefore, unlike motor performance, spacing appeared to improve Recall Accuracy, regardless of whether information was acquired through practice or observation.

Skilled Tool Use

Skilled tool use was assessed during the Use-to-command test, and consisted of both Accuracy and Time scores. For Accuracy, results showed the same performance patterns as Recall, my other measure of declarative memory (Fernandes et al., 2017; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy et al., 2015). That is, overall practice resulted in higher Use-to-command Accuracy than observation, though the magnitude of the spacing effect was similar for both types of learning. For Time, results indicated that practice resulted in faster performance than observation. However, as in Experiment 2, no spacing effects were found.

General Discussion Experiments 2 and 3

The current study used complex tools to examine the role of memory in the spacing effect. Experiment 2 first demonstrated that spacing practice trials during acquisition enhanced retention of various tool properties that require different types of memory after three weeks. To

better understand how the underlying memory system may impact the spacing effect, Experiment 3 then examined how the type of learning (i.e., practice versus observation) interacted with spacing in the retention of tool properties after a 3-week delay. Results showed a critical distinction between properties that are primarily mediated by different memory systems. For Recall Accuracy (declarative measure), compared to massed trials, spaced trials enhanced performance regardless of the learning method that was used. In contrast for Training Time (motor-procedural measure), spacing was only effective when participants practiced the task, and not with observation. This pattern of results demonstrates an important limitation for the spacing effect; for tool actions in particular, performance-based feedback received through physical practice was necessary to obtain spacing effects with complex tools. Currently, many theoretical accounts for spacing and contextual interference effects exist, and these effects have been demonstrated with a broad range of stimuli (Brady, 2004; Cepeda et al., 2006; Maddox, 2016; Magill & Hall, 1990). However, to my knowledge, this is the first study to show that the effectiveness of spacing may depend critically on the memory system responsible for encoding the information.

Below I provide a more thorough discussion of the results from two experiments. I first discuss the role that memory systems may have within the spacing effect by closely examining findings across my primary measures of motor-procedural (Training Time) and declarative memory (Recall Accuracy), followed by my secondary measure (Use-to-command). Then I consider more general theoretical considerations.

Motor Performance

Feedback-based learning and the spacing effect.

Experiment 2 first showed spaced practice resulted in better motor retention than massed practice, and Experiment 3 demonstrated that feedback-based learning appeared to be required to obtain such effects (i.e., no spacing effects were obtained with observation) because participants did not show any motor improvements after only viewing the task. Together, these results suggest that for tool-related motor performance, in order for spacing to be effective, the employed learning method needs to engage motor-procedural memory.

The failure to obtain spacing effects with observational learning during Training did not occur because the measure was insensitive in assessing motor performance. Spacing effects were obtained when practice training trials were used, which shows the measure demonstrated motor learning when given the appropriate conditions. Furthermore, the null effects with motor improvements likely do not reflect a general ineffectiveness of observation to facilitate learning (e.g., the method was not engaging) because spacing improved retention on the Recall task (discussed below). Instead, findings provide further support that striatally-mediated procedural learning requires feedback, both in tasks that require a skilled motor response (Roy, 2014) and those that do not (Knowlton et al., 1996; Poldrack et al., 2001; Shohamy et al., 2004). Results are also consistent with past research demonstrating that with motor performance, action-based learning tends to be better than pure observation (Cordovani & Cordovani, 2016; Shea et al., 2000), and extends the findings of Roy (2014) by showing that the dissociation between observation and practice was not only obtained on an immediate test, but also after a 3-week delay. It is important to acknowledge though that some research has found that observational learning is equally effective as action-based learning, such as with implicitly-based problem-solving tasks (Osman, 2008; Osman et al., 2014). Thus, task characteristics and the specific cognitive processes and underlying neural regions should be carefully considered. For tool use in

particular, performance-based feedback seems to be crucial, which may be because it provides sensory and tactile feedback that enables the learner to adjust and optimize their motor responses (Roy, 2014).

Improvements from T2 to T3.

Both Experiments 2 and 3 showed that Training time became faster across trials, and particularly from the end of acquisition (T2) to the beginning of retention (T3) for massed and spaced practice conditions. In previous studies with healthy adults using massed practice only, findings have consistently shown that tool-related motor performance did not improve, but was stable, for the last training trial in S1 and the first training trial in S2, demonstrating procedural memory's robustness to forgetting effects (Fernandes et al., 2017; Roy & Park, 2010; Roy et al., 2015). The finding that performance became faster with spaced practice is consistent with past research demonstrating that spacing has enhanced performance after a sufficient delay (Brady, 1998; Lee & Magill, 1983; Shea & Zimny, 1983). However, it is puzzling why massed practice also resulted in improvements from T2 to T3. It is possible that the use of mixed trials (i.e., massed and spaced trials are interleaved during acquisition) as opposed to pure trials (i.e., massed trials are completed separately from spaced trials) contributed to this finding. For instance, it has been proposed that enhanced retention with spaced trials could be a consequence of greater inter-task comparisons for during acquisition (Shea & Morgan, 1979). It may be that because I used mixed trials within my design, participants made inter-task comparisons for all tools. That is, regardless of whether a tool was trained under a massed or spaced schedule, during T1 they may have compared task processes to the previously practiced tool, possibly contributing to improved performance from T2 to T3.

Recall

Experiment 2 initially demonstrated that compared to massed practice, spaced practice resulted in higher Recall Accuracy for both perceptual and functional-associative information. However, unlike motor performance, Experiment 3 showed that spacing effects were observed regardless of the learning method used (i.e., spaced observation and spaced practice resulted in higher accuracy than massed observation and massed practice, respectively). Overall though, practice produced higher performance than observation. The preserved spacing effect across both practice and observation may reflect that fact that both forms of learning resulted in some declarative learning, as Recall performance has been shown to largely require declarative memory mediated by the hippocampus (Roy & Park, 2010). Though practice seems to produce a superior memory trace overall, observation still allowed learners to acquire declarative knowledge. Thus, it appeared as though spacing can still improve memory, as long as the employed learning method engages the primary mediating memory system(s) for a specific ability. These findings also consistent with the notion that declarative memory tends to be more flexible than procedural memory; that is, declarative knowledge can often to applied in situations that differ from the acquisition context, whereas procedural memory can be more closely associated with acquisition conditions and may not transfer as easily to other contexts (Albouy et al., 2013; Reber, Knowlton, & Squire, 1996).

The benefit of practice over observation for Recall Accuracy may involve processes similar to those found in the testing effect. That is, during observation, participants were presented with the to-be-learned information during each training trial. However, in the practice condition, they had to produce a response by performing the task, which likely required retrieving some information from memory (e.g., the overall function of the tool, correct starting placement of recipient(s), task steps). Also, the finding that participants had higher recall

accuracy for information that was not directly “tested” during acquisition (i.e., perceptual information), also supports the idea that the testing benefits can emerge even if information is not intentionally encoded. For instance, it has been argued that during response generation, individuals can incidentally retrieve information. Though perhaps less effective than intentionally acquiring knowledge, incidental encoding may still result in testing effects (Karpicke & Zaromb, 2010).

My results are consistent with past research that have combined testing and spacing effects into a single experiment to examine how they interacted, such as with verbal information (Cull, 2000) and name-face stimulus pairs (Carpenter & DeLosh, 2005) in healthy adults, as well as naming in individuals with aphasia (Middleton, Schwartz, Rawson, Traut, & Verkuilen, 2016). Generally, these studies showed preserved spacing and testing effects, such that spaced trials enhanced memory more than massed trials, and test trials improved memory more than study trials. They also demonstrated that the effects of testing and spacing can combine to enhance memory beyond the individual effects of either factor alone, where the greatest retention occurred for tested items that were presented at spaced intervals.

Of note, as previously discussed, declarative memory includes both episodic and semantic information, which rely on different neural regions and have distinct properties (Binder & Desai, 2011; Kalénine & Buxbaum, 2016; Moscovitch et al., 2005; Tulving, 1985). My experiments were not designed in a way that allowed me to examine whether tool-related declarative memory was primarily episodic versus semantic. On one hand, it seems plausible that Recall performance reflects episodic memory, as participants had limited exposure to each tool. Models of memory transformation or consolidation (McClelland, McNaughton, & O'Reilly, 1995a; Winocur, Moscovitch, & Bontempi, 2010) argue that semantic information initially relies on the

hippocampus and is episodic in nature. However, through gist extraction or repetition, the information eventually becomes semantic and is independent from hippocampal processing. In contrast, the serial-parallel-independence (SPI) model (Tulving, 2002; Tulving & Markowitsch, 1998) proposes that semantic memory develops first, from which episodic memory critically depends on, and also argues that semantic memory can be acquired after single exposure. This model is supported by previous research that has demonstrated that individuals with developmental amnesia can acquire semantic, but not episodic, information (Gardiner, Brandt, Baddeley, Vargha-Khadem, & Mishkin, 2008; Vargha-Khadem et al., 1997). Based on the SPI model, it could then be argued that declarative knowledge of the tool task is semantic. However, it is also possible that some of the recall items rely on hippocampal processing (e.g., extrinsic features such as recalling the function and recipient of the tool) while others do not (e.g., intrinsic features such as the tool colour) (Blumenthal et al., 2017). Future research could aim to provide a more nuanced understanding of tool-related declarative memory.

Skilled Tool Use

Of secondary interest, I also assessed skilled tool use with my Use-to-command task. For Accuracy, which is heavily mediated by declarative memory (Roy, 2014; Roy & Park, 2010, 2016; Roy et al., 2015), Experiment 2 demonstrated a spacing effect. In Experiment 3, results were similar to Recall, such that spacing effects were observed for both types of learning, though overall practice resulted in higher Use-to-command Accuracy than observation.

Physically interacting with the tool and practicing the task may have helped encode more declarative aspects of the task (e.g., recipient placement, order of task-related steps) because it required the participant to generate a response during each training trial. It is also possible that because this task involved physically performing the motor action as well, practice was

beneficial because it also provided performance-based feedback and engaged procedural memory, potentially contributing to an individual's ability to use the tool. To accurately demonstrate a tool's use after a delay, not only do individuals need to retrieve task details from memory, but it also requires them to carry out the motor action itself, and practice may have enhanced both of these processes. Regardless of the specific mechanism, the spacing effect was found for both learning conditions, likely because both practice and observation were effective learning methods.

Findings from Use-to-command Time somewhat support these potential explanations. Overall, Experiment 3 showed that practice resulted in faster completion times than observation. These performance differences could be due to the lack of motor-procedural learning that occurred with observation, and further indicate that feedback is necessary to acquire tool-related motor actions. However, no spacing effects were found in either experiment. It is possible that spacing may not enhance the cognitive processes underlying the motor component of skilled tool use. This explanation seems unlikely though because spacing effects were found for motor retention during Training with the use of practice trials. Instead, there may be a limitation in the measure itself, as it is highly influenced by the Accuracy score (i.e., completion time only includes tools that were accurately demonstrated). Consequently, for each participant, different tools comprised the score, and there was great variability across tools' completion times, rendering comparisons across experimental conditions difficult.

Theoretical Implications

Taken together, results from these experiments demonstrated that for complex tools, the spacing effect can be largely impacted by the underlying memory system and the employed learning method. On one hand, spacing effects were observed regardless of the learning method

used for Recall performance, which is mainly mediated by declarative memory. This finding is consistent with the Desirable Difficulties Hypothesis (Bjork, 1994) from the verbal literature, which combines spacing and testing effects into a single theoretical account (though also see Cuddy & Jacoby, 1982). The theory proposes that retrieval difficulty and the strength of a memory trace are positively associated (i.e., as retrieval difficulty increases, the memory trace becomes stronger). Generally, any condition that makes initial retrieval more difficult, but then enhances long-term retention, can be viewed as a “desirable difficulty”. Thus, both spaced and test trials can separately constitute a “desirable difficulty” and improve performance, or they can combine for even further retention enhancements (Bjork, 1994; Roediger III & Karpicke, 2006a). However, based on this theory, it is unclear why I found no spacing effects with observational learning for motor performance.

In fact, many theories for the spacing and contextual inference effects exist, yet none fully account for my pattern of results. Generally, theoretical accounts share the overall principle that spacing enhances a memory trace because it requires greater cognitive processing during acquisition (e.g., more elaborative encoding or greater retrieval processes), but they do not carefully consider the role of the underlying memory system. My results showed that for spacing to be effective, the learning method must first engage the appropriate underlying memory system. With motor actions specifically, performance-based feedback may be required to obtain spacing effects.

In terms of specific memory mechanisms, findings suggest that spaced observation only enhanced declarative processing, whereas spaced practice enhanced both declarative and motor-procedural memory. For instance, I observed a spacing effect for recall of tool-related perceptual information, suggesting that participants remembered more tool-related visual features (e.g., tool

colour) with spaced trials, which reflect more declarative aspects of the task. Thus, it possible that for motor performance, spaced practice may be partially beneficial because it enhances encoding of task details (Pauwels et al., 2018; Shea & Morgan, 1979; Shea & Zimny, 1983). On the other hand, Experiment 3 also demonstrated that physical practice was important for motor performance and subsequent spacing effects, so the motor-procedural aspects of the task, such as action planning and initiation, might also be important. This notion of a dual process model for the spacing effect is consistent with recent findings from Pauwels et al. (2018). In their study, spaced practice resulted in greater attention to task-related visual features and visual processing, whereas massed practice was associated with greater movement automaticity and striatal activity. The authors proposed that because spacing causes learners to switch back and forth between different tasks, it may have resulted in increased attentiveness to visual information. However, in order to perform the motor correctly, this “declarative” information also needs to be integrated with somatosensory features, and combined with motor-procedural aspects of the task.

Limitations and Future Directions

There are limitations in the current study that could be addressed in future research. I specifically focused on assessing retention after a 3-week delay, as opposed to immediate test performance, because this stage of learning is likely more indicative of permanent learning, and delays and forgetting seem to be important factors in the spacing and testing effects (Kantak & Winstein, 2012; Roediger III & Karpicke, 2006a; Schmidt & Bjork, 1992). However, an examination of test performance immediately following training would allow for a more thorough understanding of how spacing and learning type may interact to influence performance (e.g., determine if there are short-term benefits that diminish over time, examine the rate of forgetting between immediate and delayed test).

Moreover, though I believe that performance-based feedback is a critical component of practice trials for motor-procedural skills, more precise characteristics of feedback-based learning that is required for tool-related motors are unclear. For example, in my study, participants received naturally occurring feedback mainly in the form of correcting motor output when an error was made (e.g., dropped a recipient object). This feedback differs from predetermined and prescheduled, trial-by-trial feedback that tends to be used in many feedback studies, such as with probabilistic classification learning. Future work could more closely assess components of feedback that are relevant to motor learning with tools in particular (e.g., the role of sensorimotor vs. visual information).

In addition, for tool-related actions in particular, my findings demonstrate the importance of using practice trials and receiving feedback to optimize performance, which could potentially extend to other procedurally-mediated abilities. A vast number of abilities rely on procedural memory, but some do not involve a skilled motor response. For instance, procedural memory can be required for tasks that require very minimal actions (e.g., implicit sequence learning) (Reber & Squire, 1998; Wilkinson et al., 2009). However, even if tasks do not have a skilled motor component, the act of making a response may still be beneficial. As discussed previously, with probabilistic classification learning (i.e., weather prediction task), learning involved greater striatal activity when participants made a response and received feedback, as opposed to when they just observed the correct answer (Poldrack et al., 2001). Thus, it is possible that my findings with striatally-mediated motor actions could extend to other tasks that also rely the striatum, though further research is needed to investigate the generalizability of these findings.

Conclusion

The current study examined the spacing effect using complex tools, and I was particularly interested in assessing how spacing interacted with the learning method employed (i.e., practice versus observation). Tools are multifaceted, and the use of such stimuli allowed me to investigate how spacing affected different memory systems within a single study. This novel integration was important because verbal and motor learning studies both have independently assessed the benefits of spacing, but the two literatures exist quite separately. By assessing spacing in both declaratively- and motor-procedurally-mediated abilities, I was able to investigate the role of underlying memory systems in the spacing effect.

Overall, I found an important distinction for the spacing effect in declarative and motor-procedural memory. Spacing was effective regardless of the learning method used for Recall performance. However, for motor performance, spacing effects were only observed with practice, and generally, observation did not result in improvements. Thus, in order to observe spacing effects, the employed learning method must first engage the primary underlying memory system. Furthermore, regarding specific memory enhancements, my findings also suggest that spaced practice may be particularly beneficial because it enhances both declarative and motor-procedural memory, and both of these processes may jointly contribute to various aspects of tool use.

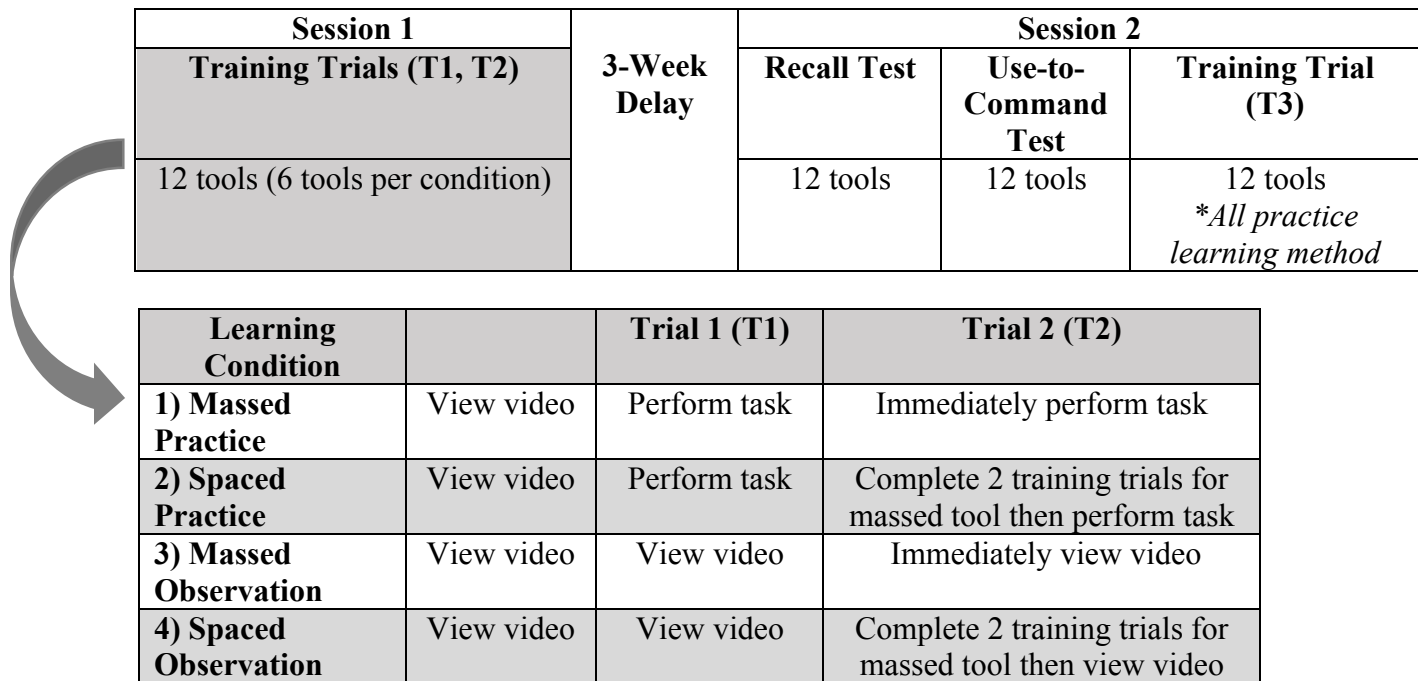


Figure 1. Design of Experiment 3

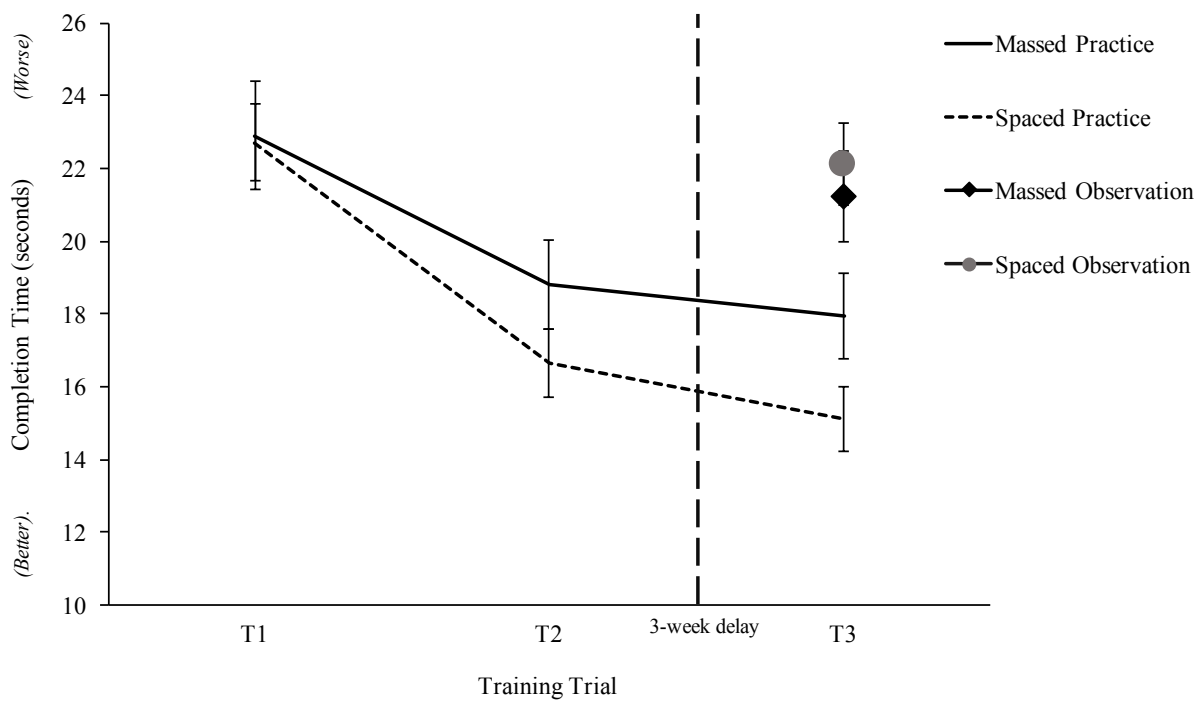


Figure 2. Mean completion time (+/- SE) for all acquisition conditions across Training trials.

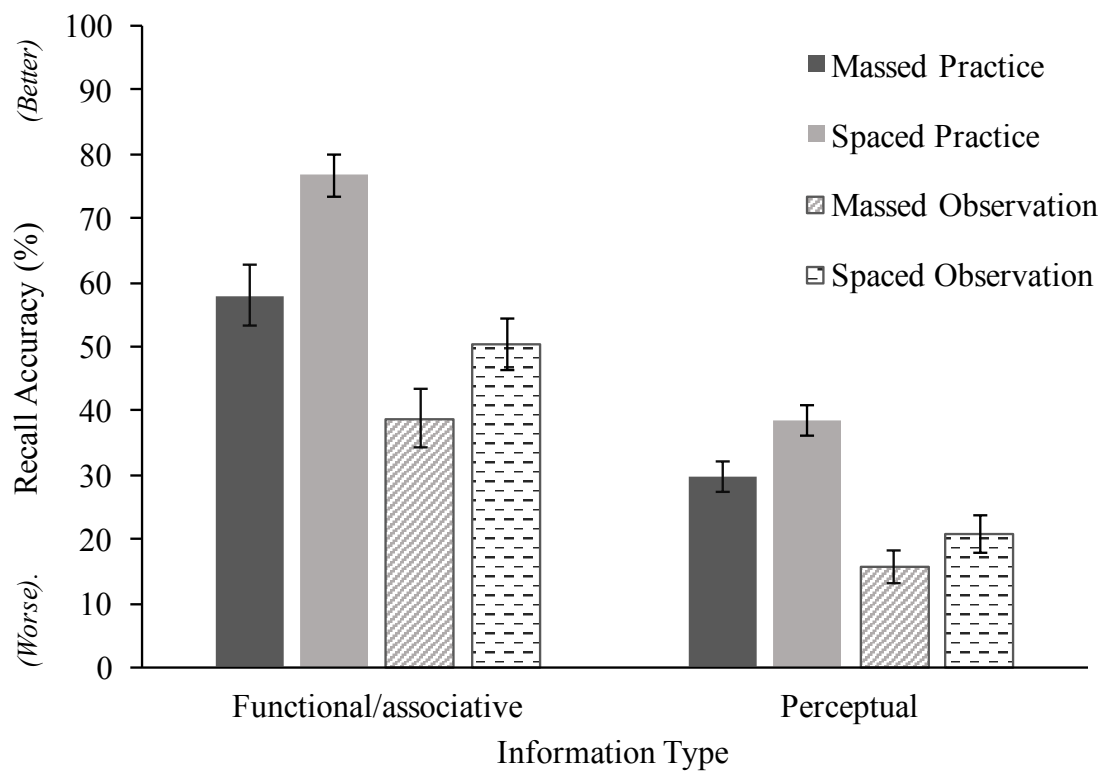


Figure 3. Percentage of correct responses (+/- SE) for Recall test items assessing functional/association and perceptual information.

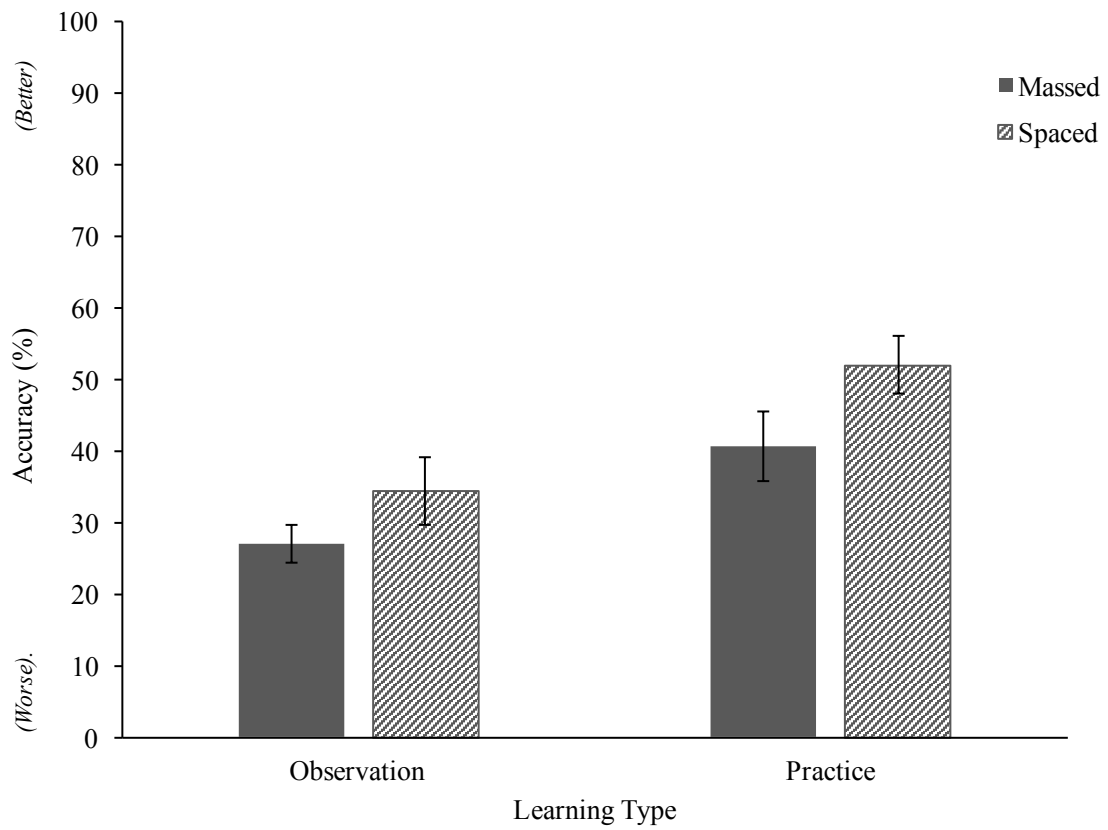


Figure 4. Percentage of correct demonstrations for Use-to-command (+/- SE) for massed and spaced schedules, and observation and practice learning.

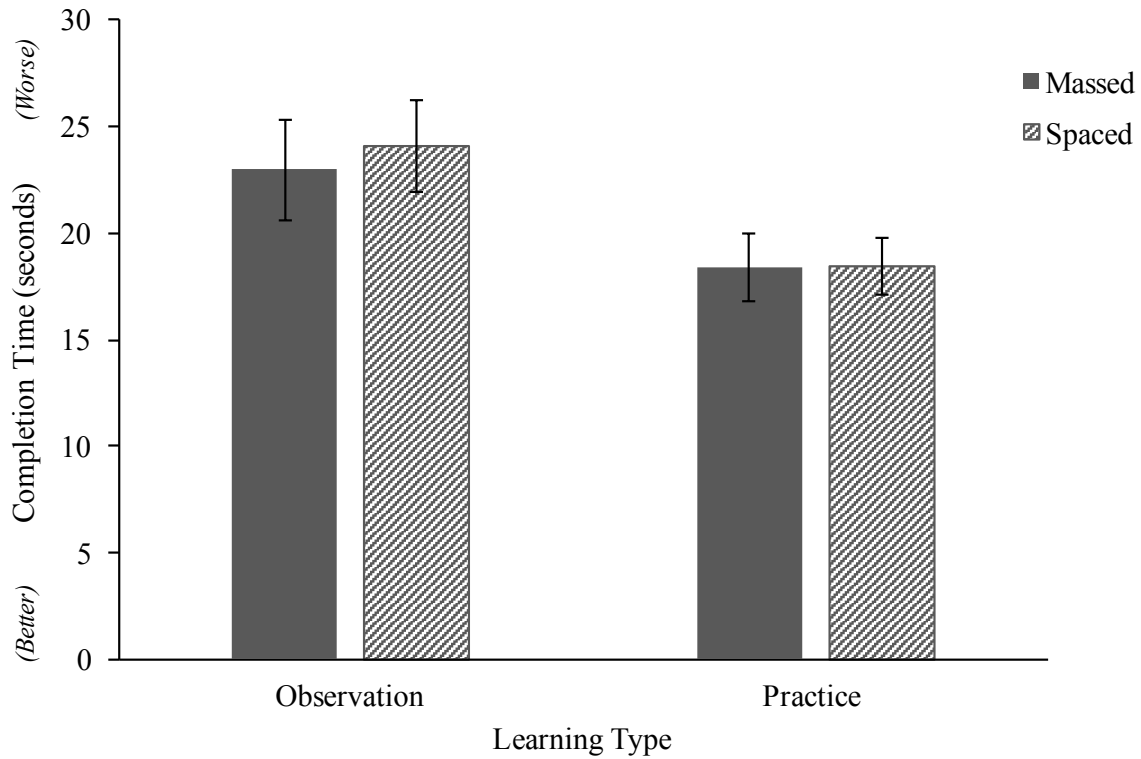


Figure 5. Mean completion time during Use-to-command (+/- SE) for massed and spaced schedules, and observe and practice learning.

Chapter 5: General Discussion

The primary goal of my dissertation was to examine how various acquisition and test conditions impacted how declarative and motor-procedural memory mediated performance on various tool properties. Previous research from my lab demonstrated that both types of memory may differentially support tool-related knowledge and abilities (Fernandes et al., 2017; Roy, 2014; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy et al., 2015), and my objective was to better understand how these systems may interact with each other. Using three behavioural experiments, I manipulated acquisition conditions that I hypothesized would impact underlying cognitive and neural mechanisms, ultimately affecting performance during acquisition and/or retention periods in healthy adults and individuals with PD. In Experiment 1, I investigated the effects of additional, massed practice on tool use in individuals with PD and healthy age-matched controls. Experiment 2 then assessed the impact of spaced training trials on different tool properties in healthy young adults, and Experiment 3 furthered investigated the spacing effect by examining how the distribution of training trials interacted with learning type (observe vs. perform). By examining performance patterns across populations, acquisition and test conditions, tool properties and learning stages, this research furthered theoretical knowledge about memory systems' involvement in tool use, as well as the flexible interactions between declarative and motor-procedural memory more generally.

Subsequently, I synthesize findings across experiments by discussing the various acquisition and test conditions that may impact how memory systems facilitate performance of various tool properties, and the resulting theoretical implications. I then highlight the importance differentiating between learning stages (i.e., acquisition versus retention) when assessing performance. From there, I discuss how my results apply to complex tools more generally by

proposing that memory may be a necessary cognitive process to successfully use some tools. In closing, I examine the practical and clinical implications stemming from my findings and provide areas of future research.

Memory Interactions in Tool Use

Results from my experiments revealed that tool use requires both declarative and motor-procedural memory. However, memory for certain properties may be more heavily mediated by one system than another, and various factors may further impact how these two types of memory facilitate performance. My results suggested that for healthy adults, tool-related motor learning and retention tends to be mediated by motor-procedural memory, though declarative memory may also support certain aspects. Motor learning theories have previously proposed interactions, such that early acquisition, which results in rapid and large gains, may be declaratively- and hippocampally-mediated, whereas later learning is associated more with procedural and striatal involvement (Albouy et al., 2013; Doyon et al., 2009; Doyon et al., 2018). My results from Experiment 1 supported this model through examination of performance patterns across PD participants and healthy controls. Healthy adults exhibited the expected pattern of findings with large initial improvements, retention across delays, and smaller improvements with practice as participants moved towards achieving automaticity. However, individuals with PD showed impaired retention after 1-week and 3-week delays, even though within-session acquisition was intact. This finding indicated that the striatum plays a critical role in motor retention. In contrast, relatively preserved within-session learning with PD participants could reflect the use of declarative memory (Carbon et al., 2010; Dagher, Owen, Boecker, & Brooks, 2001; Knowlton et al., 1996). Together, these results suggested that although declarative memory may support the acquisition of some aspects of tool-related motor learning, striatally-mediated motor-procedural

memory is ultimately needed to retain such improvements after a delay and maintain performance over long periods of time.

Effects of acquisition conditions.

As both memory systems likely contributed to tool-related motor learning, results from my three experiments also demonstrated that acquisition conditions might alter the relative contributions of declarative and motor-procedural memory, as the number of training trials, training schedule (i.e., massed vs. spaced) and learning method (i.e., practice vs. observation) all impacted critical aspects of performance. For instance, increasing the number of massed, Training trials in Experiment 1 improved motor learning within and across sessions; additional practice might have facilitated increased striatal processing in healthy adults, and compensatory declarative processing in individuals with PD. These possibilities are supported by past research demonstrating decreasing hippocampal activity, but increasing striatal activation with practice in healthy adults (Albouy et al., 2013; Albouy et al., 2008), and use of hippocampal compensation in PD on tasks that typically require the striatum (Gobel et al., 2013; Moody et al., 2004).

Findings from Experiments 2 and 3 also revealed that in addition to motor-procedural memory, declarative memory may contribute to motor performance with tools. In both experiments, Recall Accuracy was superior with spaced than massed training trials, which included both functional/associative and perceptual information. In particular, the finding of higher perceptual accuracy (i.e., superior knowledge about a tool's appearance) suggested that compared to massed practice, spaced practice might be beneficial because it enhanced the visual processing of task details during motor learning with complex tools (Pauwels et al., 2018; Shea & Morgan, 1979; Shea & Zimny, 1983). This interpretation of results supports the notion that for

tool-related motor actions, spaced trials may be beneficial, at least in part, because they enhanced declarative knowledge associated with a particular tool.

Despite this support for declarative memory involvement, Experiment 3 demonstrated that importance of engaging motor-procedural processes during tool-related motor acquisition. In this experiment, results showed that observational learning likely biased the use of declarative memory because participants did not physically interact with the tool and only viewed the task. However, in addition to engaging declarative memory, practice enabled procedural processing to occur as participants carried out the action associated with each tool. Most critically, participants only exhibited motor learning when they received performance-based feedback while practicing using the tool, and not with pure observation. In addition, spacing effects were only observed with practice. Taken together, these findings suggested that physically practicing that task and engaging motor-procedural memory was ultimately necessary for motor learning, which is consistent with past tool-related research (Fernandes et al., 2017; Roy, 2014; Roy & Park, 2010; Roy et al., 2015). Thus, for complex tools, enhancements of declarative memory may aid retention of declarative aspects of the tool, but this memory system alone cannot sufficiently support motor learning and retention.

Effects of test conditions.

Results not only indicated that acquisition conditions affected how multiple memory systems interacted to facilitate performance with tools, but the testing environment also influenced the extent to which an individual relied on declarative and/or motor-procedural memory. For example, some tests in my dissertation required recall of declarative aspects of the tool, whereas others required motor-procedural processes (i.e., Training). A more interesting and more important finding involves the comparison of Training and Use-to-command performance.

In both tasks, participants were required to carry out previously demonstrated actions associated with the tool within a time limit. However, a key difference was that during Training, participants watched an instructional video immediately prior to performing the task, whereas in the Use-to-Command test, participants demonstrated a tool's use after a delay. I hypothesized that performance on the latter task required greater use of declarative memory because the learner had to first recall how to use the tool correctly (i.e., Accuracy score). That is, because the test retrieval cue consisted only of the tool and recipient (in a neutral location), it likely required participants to retrieve other declarative knowledge associated with the task before being able to perform the tool-related action itself using motor-procedural memory (i.e., Completion Time score) (Roy & Park, 2010, 2016; Roy et al., 2015). This interpretation is consistent with findings from Roy and Park (2010) who investigated tool use in D.A., a patient with hippocampal amnesia. When D.A. demonstrated the task immediately after viewing an instructional video showing the tool's use, his performance was unimpaired relative to healthy controls (i.e., performance improved across Training trials and was retained after a 3-week delay). In contrast, D.A. was impaired in the Use-to-command test when there was a delay between viewing the video and his performance of the task.

In summary, my results showed that the novel complex tools used in my experiments have both declarative and motor-procedural components when participants practiced their use. Such findings may extend to tool use more generally; results from Weisberg, Van Turennout, and Martin (2007) suggested that familiar tools may also have contributions from both memory systems. More broadly, Stanley and Krakauer (2013) have argued against the idea that motor skills only involve procedural processes. Support for this position comes from findings showing that explicit knowledge may play an important role even in seemingly simple adaption (Taylor,

Krakauer, & Ivry, 2014) and motor sequence (Wong, Lindquist, Haith, & Krakauer, 2015) tasks used to investigate motor skill learning. Thus, it may be that a broad range of skilled actions require an interaction between declarative and procedural processes.

Theoretical implications.

Thus, overall, results from this dissertation provide cohesive evidence that tool use is facilitated by interacting relationships between declarative and motor-procedural memory, which depends critically on acquisition and test conditions. Such findings are consistent with past research proposing that the nature of the interaction between memory systems (e.g., cooperative, competitive or compensatory) can be modulated by modifying the context in which encoding and retrieval occurs (Foerde et al., 2006; Foerde, Race, et al., 2013; Mattfeld & Stark, 2015; Packard & Goodman, 2013; Stanley & Krakauer, 2013). Here, my manipulation of various key training factors, and examination of multiple tool properties demonstrated that declarative and motor-procedural memory both contribute to tool use, and their relationship may be flexible and may change under certain conditions. That is, these two systems might make unique contributions to performance. For instance, declarative knowledge can be rapidly acquired, yet it is more likely to be decline over time, whereas procedural memories tend to take longer to acquire, but are more robust to forgetting (Ellenbogen et al., 2006; Gabrieli et al., 1993; Squire, 2004). At times, they may compete with each other, such as with the use of compensatory interactions in PD motor performance (i.e., striatal dysfunction and decline in procedural processing resulted in increase in hippocampal and declarative processing). However, their differential properties and distinct functional contributions may also allow them to cooperate with each other, where both systems can be concurrently enhanced to improve performance.

Results from my experiments also suggest that tool-related motor performance was

heavily mediated by motor-procedural memory. However, it may also involve some declarative processing, which could be one of the memory processes that are enhanced with spacing, as suggested by findings from Experiments 2 and 3. Likewise, it is possible that while recall of tool attributes relies primarily on declarative memory, it may include procedural processes as well, and the relative contributions of these memory systems may differ depending on the acquisition and retrieval environment. For instance, recent research on the testing effect using verbal paired associates demonstrated that compared to test trials, study trials were associated with greater “automaticity” or proceduralization (Racsmany et al., 2018). Perhaps it is possible then for different acquisition conditions (e.g., training schedule and learning type) to work together in a complementary fashion to influence memory interactions. Spacing may have enhanced more of the declarative memory component, whereas practice learning improved procedural memory more, which together heightened both memory systems. The idea of cooperative interactions between these two memory systems has been observed in past studies, such that hippocampus and striatum both contributed to declarative memory encoding and retrieval (Sadeh et al., 2011; Scimeca & Badre, 2012). Moreover, as demonstrated by the Use-to-command test, it seems likely that successful performance of some tasks may inherently require use of both declarative and motor-procedural memories. Taken together, these possibilities support the notion that the interacting relationships among memory systems is complex and can be impacted by a multitude of factors.

Distinguishing Between Acquisition and Retention

Though my findings demonstrated substantial evidence for enhanced performance under particular acquisition conditions (e.g., additional massed practice in PD, spaced practice with healthy adults), results differed depending on when performance was assessed. Learning can be

broadly divided into acquisition and retention phases, though the exact operationalization of these terms varies from study to study. In my dissertation, I defined these phases as immediate performance that accompanies practice or follows immediately after practice (acquisition), and performance demonstrated after a delay of at least 24 hours (retention). Throughout my three experiments, I observed key performance differences between these two learning stages.

Experiments 2 and 3 both showed that spacing effects were only observed after a 3-week delay during motor retention, as there were no performance differences between massed and spaced practice during acquisition trials in S1. Furthermore, in Experiment 1, notable differences were observed in PD participants when examining within-session acquisition versus retention for motor performance. Compared to healthy controls, PD participants had impaired retention after 1-day and 3-week delays, yet they consistently made significant gains within each session.

Performance differences between these two stages could be due to a number of factors. On one hand, performance during acquisition may be temporary and impacted by a number of transitory factors (e.g., attention, motivation) (Kantak & Winstein, 2012; Rohrer & Taylor, 2007; Schmidt & Bjork, 1992; Soderstrom & Bjork, 2015). For example, in the acquisition phases of my experiments, it is possible that some of the memory for the skill was held short-term memory which partially mediated performance at that time. However, after the 3-week delay, performance reflected permanent changes to memory. Thus, it could be argued that compared to acquisition or immediate test performance, retention after a sufficient delay may be a more accurate measure of long-term memory.

In addition, the cognitive processes primarily mediating performance likely varies across learning stages. For instance, some contextual interference and spacing effect theories hypothesize that spacing may hinder acquisition, but benefit long-term retention. For example,

the action-plan reconstruction account (Lee & Magill, 1983) posits that compared to blocked trials, forgetting may occur with random trials because a learner practices intervening movements. That is, each time the motor is enacted, it must be retrieved and reconstructed from memory. Such within-session forgetting may impede initial acquisition, but aids delayed retention. This performance pattern has been typically found in various motor studies (Brady, 1998; Magill & Hall, 1990; Merbah & Meulemans, 2011; Shea & Morgan, 1979; Simon & Bjork, 2001). However, inconsistencies exist (Lee & Genovese, 1988; Leite et al., 2013; Lin et al., 2010; Spittle et al., 2012), which could be attributed to many methodological factors (e.g., task type, complexity, length of delay) (Brady, 1998; Donovan & Radosevich, 1999; Lee & Genovese, 1988).

Experiment 1 also contributes to the concept of differential cognitive processing, by suggesting that early and late motor learning might vary in the relative use of declarative and procedural memory. It is possible that early acquisition periods are mediated more by declarative memory and hippocampal processing, whereas after practice, retention reflects greater reliance on procedural memory and striatal processing (Albouy et al., 2013; Albouy et al., 2012). Moreover, different performance patterns between acquisition and retention could also be a consequence of faster forgetting rates for declarative than procedural memory (Ellenbogen et al., 2006; Gabrieli et al., 1993; Squire et al., 1993; Tulving, 1985). Because performance appears to be a product of declarative and motor-procedural memory, variations in forgetting rates could also result in performance differences between acquisition and retention.

As a number of factors could contribute to performance differences, it is important to clearly define, separately assess and compare performance at the various motor learning stages. Such distinctions are not always made, which could potentially limit interpretation of findings

(Kantak & Winstein, 2012; Schmidt & Bjork, 1992). For my three experiments, key differences were observed between acquisition and retention, which aided my discussion of potential cognitive and neural mediators.

The Role of Memory in Complex Tools

Although one of my main goals was to examine the interactions between memory systems, findings from my experiments also contributed to my understanding of tool use. Previous research has shown that tool use requires various cognitive abilities and neural processes (Gallivan, McLean, Valyear, & Culham, 2013; Goldenberg & Spatt, 2009; Lewis, 2006). For instance, research on apraxia has demonstrated that the left parietal lobe is important because it is likely responsible for the skillful manipulation of objects (Buxbaum & Saffran, 2002). Consistent with this notion, one theoretical account emphasizes the importance of retrieving stored information from memory (i.e., sensory-motor memories) during skilled tool use (Buxbaum, 2017), while others have argued that successful tool use can be achieved primarily through technical reasoning (Osiurak, 2014; Osiurak & Badets, 2016). This latter account denies the importance of any sort of memory in tool use, making it inconsistent with other theories (Buxbaum, 2017), past research from my lab (Fernandes et al., 2017; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy et al., 2015), and the current dissertation's findings. Results from the current three experiments provided substantial evidence that memory is required, for at least the complex tools used in my studies.

The main assumption of technical reasoning is that when using a tool, people do not rely on previously acquired knowledge (e.g., sensory-motor, declarative or motor-procedural memories). Instead, tool use mainly requires mechanical problem-solving abilities, where individuals apply “abstract” information about physical principles and functional parameters to

figure out how to properly use a tool (Osiurak, Reynaud, Navarro, & Lesourd, 2016). The lack of previously acquired knowledge is problematic because it suggests that tool-specific learning is non-existent (e.g., no savings with practice) (Buxbaum, 2017), and my three studies clearly demonstrate that acquisition conditions can affect subsequent performance, with some experimental manipulations leading to greater improvements than others. For example, Experiment 3 showed that for motor performance, observation was not a sufficient learning method, as participants needed to physically practice the task to exhibit learning. Based solely on technical reasoning, it is unclear why feedback-based learning would be required to learn tool-related actions. To my knowledge, Osiurak and Badets (2016) do not clearly specify boundaries in which technical reasoning is effective, so it is uncertain why observation would be an unsuccessful approach for mechanical problem solving (i.e., do people need to physically interact with a tool to apply technical reasoning skills?). Furthermore, Experiment 2 demonstrated that compared to massed practice, spaced practice resulted in superior Training and Recall performance, and I proposed that these benefits were due to enhanced motor-procedural and declarative memory traces. Again, it is unclear how spacing would improve technical reasoning, as this model argues that people apply general mechanical knowledge to specific tools as they encounter them. Lastly, in Experiment 1, individuals with PD exhibited a specific deficit with tool use, where they were mainly impaired with motor retention, which I hypothesized was due to striatal dysfunction. This finding, along with past research demonstrating similar impairments in PD (Fernandes et al., 2017; Roy et al., 2015) demonstrated the importance of striatal activation and motor-procedural memory involvement in tool-related actions.

It is important to note that I am not proposing that tool use relies solely on declarative and motor-procedural memory, but rather that memory systems play a critical role in at least

some complex tools, along with other cognitive abilities. It is possible that technical reasoning can be successfully applied to certain tools (Bril, Rein, Nonaka, Wenban-Smith, & Dietrich, 2010; Osiurak & Badets, 2016), though for many tools, the function, grasp and manner of manipulation are unclear from its appearance (Buxbaum, 2017; Roy & Park, 2018). Thus, under some circumstances technical reasoning may be useful, whereas other times individuals may need to rely heavily on previously acquired, tool-specific information which includes manipulation knowledge (Buxbaum, 2001, 2017; Buxbaum & Saffran, 2002), as well as declarative and motor-procedural memory (Fernandes et al., 2017; Roy, 2014; Roy & Park, 2018; Roy & Park, 2010, 2016; Roy et al., 2015).

Practical and Clinical Implications

Beyond these various theoretical considerations, the findings from my three experiments also have important practical implications. First, my experimental stimuli and measures were designed in such a way to increase ecological validity. For example, past studies have largely used computer-based tasks to investigate procedural memory (e.g., weather prediction task), or simple motor (Donovan & Radosovich, 1999; Lee & Genovese, 1988) or verbal learning skills (Janiszewski et al., 2003) to examine the spacing effect, which have notable advantages (e.g., facilitating administration of several learning trials within a relatively short period of time). In addition, many existing studies have examined a particular aspect of tool use in isolation (e.g. grasping, knowledge of tool attributes) (Creem & Proffitt, 2001; Silveri & Ciccarelli, 2009; Warrington, 1975). However, my goal was to investigate tool attributes in a more integrative approach; doing so not only allowed me to examine multiple memory systems within a single experiment, but could also be more applicable to real-world functioning.

My emphasis on retention, as opposed to acquisition, should also be noted. Many spacing

effect studies have examined performance after a short delay (e.g., immediate test occurring less than 24 hours after acquisition) (Cepeda et al., 2006; Katak & Winstein, 2012). However, in many practical situations, individuals often acquire new knowledge or skills, which is then followed by extended periods of nonuse (Arthur et al., 2010). Thus, to increase ecological validity, it is important to demonstrate that enhancements are long-lasting, even when a complex skill is not practiced for quite some time. In my experiments, the 3-week delay allowed me to demonstrate the robustness of experimental manipulations (i.e., acquisition conditions) with complex stimuli.

Regarding acquisition conditions themselves, Experiments 2 and 3 demonstrated that spaced practice is a powerful way to concurrently enhance both motor-procedural and declarative memory. Previous research has made similar recommendations, such as with use of spaced or random trials when learning some real-world motor actions (Farrow & Buszard, 2017; Hall, Domingues, & Cavazos, 1994; Memmert, 2006; Merbah & Meulemans, 2011). Similarly, spaced retrieval (i.e., combined spacing and testing effects) has been extensively examined in the verbal learning literature, where it has been successfully implemented in educational (Hopkins, Lyle, Hieb, & Ralston, 2016; Kang, 2016; Kapler, Weston, & Wiseheart, 2015), workplace (Kim, Wong-Kee-You, Wiseheart, & Rosenbaum, 2019), and clinical settings (Balota et al., 2006; Cermak, Verfaellie, Lanzoni, Mather, & Chase, 1996). My results from Experiments 2 and 3 suggest that the effectiveness of spaced practice also extends to tools, which require complex cognitive abilities. One possible limitation to implementing spaced practice is that it may be more time consuming and requires some planning and organization skills. However, the potential benefits are quite considerable and extend to many different tasks, so recommendations to use this type of training seem well-supported.

When making real-word recommendations, it is also imperative to consider the type of performance an individual ultimately wants to achieve. That is, suggested training conditions can vary depending on the type of information or skills being acquired, and the context in which they will later be used. For instance, although spaced practice appears to optimize retention performance for many tool properties, observation also resulted in learning that primarily required declarative memory (i.e., Recall and Use-to-command Accuracy). Though perhaps less effective than practice, my results showed that participants acquired declarative knowledge solely through observing the task. Such findings are consistent with transfer-appropriate processing, where performance can be enhanced when training and test conditions engage similar cognitive processes (Brady, 1998; Lee, 1988). With my tool task, both observational learning and the Recall test mainly required declarative processing, resulting in compatible training and test conditions. However, as motor performance largely requires motor-procedural memory, observation was not an adequate learning approach.

For clinical recommendations, results from Experiment 1 suggested that additional, massed practice benefitted motor performance in individuals with PD. Although PD participants still exhibited retention impairments relative to controls, more practice was associated with enhanced learning during the initial acquisition session, and greater overall improvements. Thus, with this patient population, it seems important to capitalize on preserved within-session learning; people with PD may still be able to build upon a particular motor action or skill, but require opportunities to practice within a session.

Future Directions

Findings across my experiments demonstrated that manipulating key conditions during acquisition can have substantial effects on retention performance, such as enhancements of

declarative and motor-procedural memory with spaced practice in healthy adults. Future research could further investigate spacing by examining how it impacts performance patterns in individuals with PD. Though additional, massed practice benefitted some aspects of motor performance in Experiment 1, it seems possible that spaced practice could further enhance motor learning in PD through biasing the use of relatively preserved declarative memory (Pauwels et al., 2018). On the other hand, others have argued that hippocampal compensation in PD may not be effective under circumstances (i.e., declarative memory cannot support some procedural memory functions) (Carbon et al., 2010), so it is currently unclear how spaced practice would affect tool use in PD. This follow-up study could help determine how to maximize rehabilitation approaches to aid motor deficits in PD, as well as better understand the cognitive mechanisms that may be supporting motor performance. Use of neuroimaging in future studies could further the understanding of neural mechanisms involved in tool use and complement the current behavioural findings.

Conclusion

The current dissertation enhanced the understanding of how memory systems may interact during tool use by examining the impact of acquisition and test conditions on various tool attributes. Findings across experiments provide strong, cohesive evidence that the nature of the training and test environment may affect how declarative and motor-procedural memory support various knowledge, actions and skills that are required for complex tools. Performance across various training conditions and populations suggest that certain tool properties may be primary mediated by a certain memory system, though multiple types of memory may ultimately contribute to performance. The employed learning method, and amount and distribution of training trials may affect how memory systems interact to facilitate performance, demonstrating

the flexible, dynamic and complex nature of memory.

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