Context-specificity in Implicit Sequence Learning

Context-specificity in Implicit Sequence Learning:
Evidence for Episodic Representations

By
Maria Cecilia D'Angelo, B.Sc. (hons.)

A Thesis Submitted to the School of Graduate Studies in Partial Fulfillment of the
Requirements for the Degree Doctor of Philosophy

McMaster University

DOCTOR OF PHILOSOPHY (2013) McMaster University (Psychology)

TITLE: Context-specificity in Implicit Sequence Learning: Evidence for Episodic

Representations

AUTHOR: Maria Cecilia D'Angelo, B.Sc. (hons.) (McMaster University)

SUPERVISOR: Professor Bruce Milliken

NUMBER OF PAGES: xviii, 223

Abstract

Cognitive psychologists have long been interested in the nature of the representations that underlie human behaviours. In the domain of human memory, two main accounts have been forwarded to explain how memory is represented. The multiple memory systems account posits that different phenomenological experiences of memory are the result of separate and distinct representations. In contrast, the processing account posits that there is one memory system, and that different phenomenological experiences of memory are the result of the processes engaged in when probing memory. The explanatory power of these two accounts has been evaluated in a number of domains, where it has been shown that a processing view can accommodate many of the key findings that previously led researchers to propose a separate systems framework. The goal of this thesis was to extend this work by assessing the nature of the representations that underlie implicit sequence learning. The empirical portions of this thesis provide preliminary evidence suggesting that contextual features are incorporated into implicit sequence learning. Overall, the results reported in the empirical chapters of this thesis are consistent with a processing account, as they indicate that the episodic representations that are involved in explicit remembering also support performance in implicit memory tasks.

Acknowledgements

This thesis is the product of a less than linear path, and is a reflection of the support I have been fortunate enough to receive both academically and personally over the last few years. I cannot thank everyone who has inspired, supported, and influenced me, but I will do my best to acknowledge those who have directly influenced me as I completed this thesis.

I have to begin by thanking my supervisor, Bruce Milliken. Bruce, you have been a wonderful mentor. Over the last few years your enthusiasm for research has motivated me and the thoughtfulness with which you conduct research has given me a standard I hope to achieve. Thank you for supporting me as I pursued different lines of research and for encouraging me to go not once, but twice to Granada. Throughout this process you have always been ready to help me achieve my goals (except, of course, when my goal was to beat you at darts!).

To my other two co-authors, Juan Lupiáñez, the optimist who was always looking into the future, and seeing the accepted versions of papers we had not even started to work on. Juan, your love of science truly is contagious and has served as a big motivation for me. To Luis Jiménez, who always made time for me, even with last minute deadlines. Your thoughtfulness when conducting research has also impacted me greatly.

To my committee members and former supervisors, Scott Watter and Karin Humphreys. Karin, thank you for giving me the freedom to pursue my interests, even if that meant switching labs. Your endless support and belief in me has allowed me to gain confidence in my academic abilities. Scott, I have always admired how much you seem to

know about different topics and your ability to link ideas across so many different areas. Thank you for always having your door open when I needed a chat.

I must also acknowledge a few people who made a great impact on me through early exposures to research. Meredith Young, thank you for giving me the opportunity to follow you around and learn about your research. You have been a wonderful mentor to me, and a truly amazing friend. Kevin Eva, thank you for supporting my pursuits as an undergraduate student and during my first year of graduate school. To Margo Wilson, one of the most curious people I have ever had the pleasure to know. And to Lee R. Brooks, I hope the introduction to this thesis conveys the appreciation I have for having had the opportunity to be *Brooksified* (see Eva & Allen, 2005).

Over the last five years I have switched labs and temporarily joined others, and in doing so I have been fortunate to make some wonderful friends. There is a special solidarity that comes from going through graduate school together, and I have learned a lot from my lab mates over the last five years. To Sandra, my former office mate and dear friend, thank you for your patience, advice, and your ability to read my mind. To my fellow Milliken lab members: Ellen, thank you for getting excited about research ideas with me, and for helping me feel at home in the lab. Adam (spadaraj), you always kept me on my toes with your jokes. Thank you for teaching me how to be cool. Chris, our discussions about stats may have at times turned to arguments, but thank you for always providing a good challenge, as well as a good laugh. Mitch, I have always enjoyed our long theoretical debates and our literary moments on Friday afternoons. Tammy, do not let them rope you into doing all of the organizing, but thank you for taking some of the work off my hands! To the members of the lab in Granada including: Maryem, Bea, Eli,

Elena, and María R, you made Granada feel like home. Maryem, thank you for the endless conversations, the suggested readings, and for the walks through Granada. Bea, thank you for the dinners and the conversations, and for organizing my life in Granada. Eli, thank you for your friendship, and for sharing your love of soccer and peanut butter with me. I hope to one-day repay the support you all have given me.

This thesis is an academic endeavour, but without my friends and family this all would have meant very little. To Melaina, Natalia, Cara, Kasia, Sophia, Lisa, Liz, Jesse, and Sandra. Although we may not always get crafting done, our craft nights are one of my favourite nights of the week. I am fortunate to have such a great network of friends. To Elise, Julia, and Maria Ines, you three have been able to keep me motivated even from long distances. Thank you for the emails, messages, and visits.

To Dave, no one else knows this journey better than do you. Thank you for always supporting me as I have pursued my interests, even if it meant being apart for months at a time. Your patience has calmed me and your confidence in me has allowed me to achieve my goals. I love you very much.

To my parents, Ricardo and Elizabeth, who taught me that curiosity is to be encouraged, and that knowledge is something meant to be shared. Thank you for teaching me the balance between work and life. Papi, thank you for your patience and for your sense of humour. Mami, you are the best role model a young woman could ask for, thank you for always believing in me. To my brother and sister, Ricardo and Mariana. Ricky, my joke master, and Nana, my personal IT and emotional support. I know that you two will achieve all of your goals, I am so proud to be your big sister! Los quiero mucho.

Table of Contents

Preface

This is a 'sandwich' thesis. The first two empirical chapters (Chapters 2 and 3) have been published in peer-reviewed journals. Chapter 4 is the final version of a manuscript that has been submitted for publication. I am the first author for each empirical chapter, and my supervisor and two collaborators are co-authors. The remainder of the preface is design to clarify my contributions to the manuscripts that make up the empirical chapters of this thesis.

The first empirical chapter is a reprint of D'Angelo, M.C., Jiménez, L., Milliken, B., & Lupiáñez, J. (2013). On the specificity of sequential congruency effects in implicit learning of motor and perceptual sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 39,* 69-84. My role in this manuscript included experimental design, data collection (running human participants), and data analysis. I was also the primary writer.

The second empirical chapter is a reprint of D'Angelo, M.C., Milliken, B., Jiménez, L., & Lupiáñez, J. (2013). Implementing flexibility in automaticity: Evidence from context-specific implicit sequence learning. *Consciousness and Cognition, 22*, 64-81. My role in this manuscript included experimental design and programming, data collection, and data analysis. I was also the primary writer.

The third empirical chapter is the following manuscript D'Angelo, M.C., Milliken, B., Jiménez, L., & Lupiáñez, J. (under review). Re-examining the Role of Context in Implicit Sequence Learning. *Consciousness and Cognition.* Manuscript ID: CONCOG 13-134. My role in this manuscript included

experimental design and programming, data collection, and data analysis. I was also the primary writer.

The reader should note that the empirical chapters are manuscripts that have each been intended to 'stand alone' as published work. Given this preparation of the empirical chapters, there is some redundancy within the theoretical introductions and discussions in the empirical chapters. The reader will also note that there is also some redundancy in the descriptions of the methodology used within the empirical chapters, as the same sequences were used across the three empirical chapters, and the same procedure was used in the second and third empirical chapters. Despite this overlap, the experiments included in each manuscript are unique and are intended to address distinct theoretical questions within the common theoretical issue of this thesis.

List of Figures

on the preceding trial. Top Right Panel: Mean RT for training and control motor sequence trials in Experiment 2 as function of the type of perceptual sequence trial presented on the preceding trial. Bottom Left Panel: Mean RT for training and control perceptual sequence trials in Experiment 2 as function of the type of motor sequence trial presented on the preceding trial. Bottom Right Panel: Mean RT for training and control perceptual sequence trials in Experiment 2 as function of the type of perceptual sequence trial presented on the preceding trial.

List of Tables

CHAPTER 1: Introduction

Since the cognitive revolution, a goal of research in cognitive psychology has been to understand the internal representations that underlie human behaviour. In particular, this question has been at the forefront of research within the domain of human memory. Research in this domain has led to two general views of how human memory is organized. In the multiple memory systems view, it has been suggested that there are multiple, separate memory systems that are each supported by different underlying representations, while in the processing view it has been argued that distinct manifestations of memory arise from different processes that act on one memory system supported by a common form of representation. The goal of this thesis is to contrast these two views in implicit memory tasks, where retrieval is not accompanied by awareness. More specifically, I will examine if it is necessary to assume that separate representations underlie implicit and explicit memory effects, or if the same representations that govern explicit remembering may also support implicit influences of previous experiences.

To provide the historical context for this problem, I will first briefly review the multiple memory systems framework, in which memory is divided up into separate systems with different underlying representations. In this review I will describe the episodic/semantic distinction as an example where the multiple memory systems framework has been contrasted with a processing account of memory. I will then describe the distinction made between implicit influences of previous experiences on performance (implicit memory) and the explicit recall of previously experienced events (explicit memory). Following this description, I will outline how research conducted in

category learning and artificial grammar learning, two subdomains within implicit memory, has provided evidence that the same episodic representations that are retrieved in tasks requiring explicit remembering are also retrieved when the influence of previous experiences is not accompanied by awareness. Finally, I will briefly review the literature on implicit sequence learning, the subdomain in which the empirical sections of the thesis have been situated, where I will also outline current views of the representations involved in this type of learning.

Multiple Memory Systems Versus the Processing View

There has been a long tradition in memory research to distinguish between different phenomenological experiences of memory. Even William James distinguished between *memory* and *habit* (1890). Empirically, distinct forms of memory have been separated into categories based on observable differences, such as differences in the types of information that can be retrieved, differences in mechanisms for forgetting, as well as differences in whether retrieval is accompanied by awareness (e.g., Squire, 2004; Tulving, 1985). This latter dividing criterion was initially cast as distinguishing between declarative and non-declarative memory systems. Retrieval from declarative memory was proposed to occur with awareness, while retrieval from non-declarative memory was proposed to occur without awareness (e.g., Cohen & Squire, 1980; Squire & Zola-Morgan, 1988).   By this view, our conscious recollections are the product of a declarative memory system, while influences of previous experiences that occur without our awareness are the product of one or more systems that produce non-declarative forms of memory.

The multiple memory systems view has further divided each of declarative and non-declarative memory systems into additional subsystems (e.g., Tulving, 1985). For example, within declarative memory, Tulving (1972, 1983, 1986) proposed a distinction between memory for particular events (episodic memory) and memory for facts (semantic memory). The distinction here was made between the amount of contextual information that could be retrieved, where episodic memory is characterized by detailed representations that include information about a particular time and place, and semantic memories are retrieved without details about when or where the information was acquired. Therefore, within this framework, episodic memory is represented as episodes containing contextual information, while semantic memory representations are abstractions of previous experiences.   This distinction has been supported by task dissociations in patients suffering from amnesia. Amnesia is typically characterized by a lesion to the medial temporal lobe that is associated with the inability to form new memories (anterograde amnesia), as well as with difficulties recalling memories just prior to when the lesion occurred (retrograde amnesia). One key finding that has been used in support of the episodic/semantic distinction is that although amnesic patients suffer a loss of episodic memory, their semantic memory typically remains intact in terms of their retrograde amnesia (e.g., Vargha-Khadem, Gadian, Watkins, Connelly, Van Paesschen, & Mishkin, 1997).

In contrast to this multiple memory systems view, others have proposed a processing view of memory in which there is one memory system that can be accessed by different processes to produce phenomenologically different experiences of memory (e.g.,

Baddeley, 1984; Craik & Jacoby, 1979; Hintzman, 1984; 1986; McKoon, Ratcliff, & Dell, 1986; Roediger, 1984; Whittlesea, Brooks, & Westcott, 1994). Within this framework, the differences experienced in episodic memory versus semantic memory are not a result of different underlying representations that are encoded in parallel, but rather, these phenomenological differences are due to the processes used to access memory from one common system during retrieval. For example, if all experiences are represented as episodes, then processes that selectively retrieve one particular episode would produce experiences of episodic memory, while processes that concurrently retrieve multiple, similar episodes would produce the experience of semantic memory.

In sum, the separate systems account posits that there are parallel memory systems that each independently store experiences. Retrieving one type of representation versus another will give rise to different phenomenological experiences of memory. Given that the multiple memory system view might be argued to offer a more complex representational account of behaviour than does a view based on one memory system, the question is whether the additional level of complexity is required. To address this question, it must first be demonstrated that a processing account is also able to account for the data explained by the multiple memory systems account.

Using a multiple trace model of memory (Minerva 2), Hintzman (1984, 1986; see also Humphreys, Bain, & Pike, 1989) showed that it is possible to model classic dissociations between episodic and semantic memory tasks using a single memory system. In Hintzman's model, all experiences are stored in memory as separate memory traces, or instances. A key assumption of the model is that any time an individual attends

to something, that experience or *episode* is stored as a memory trace. Importantly, when participants encounter the same stimulus twice, the original memory trace is not strengthened, but rather another, highly similar, memory trace is stored. When memory is probed, all traces that are similar to the probe will be retrieved and together produce an "echo". In this model Hintzman argued that dissociations between episodic and semantic memory arise from how memory is probed. When memory is probed using a very specific cue, only a very small number of specific traces will be retrieved, and so the resulting echo produced by the model will contain more specific details that are common to these traces. The specific details that accompany retrieval when only a select few traces are retrieved will produce the experience of context-rich episodic memory.

However, memory can also be probed such that a large number of similar traces are retrieved. When a probe is less specific, a wider array of traces can be retrieved, which may differ in contextual details. As these traces are summed together to form the *echo*, the specific details that distinguish these traces will be masked.   The echo produced by a less specific memory probe will lack episodic details, and thus produce the experience of semantic memory. Therefore, using Minerva 2, Hintzman was able to demonstrate that the same underlying memory traces can be retrieved in a way where contextual details are preserved and produce the experience of episodic memory, as well as in ways in which contextual details are lost so that the resulting experience is retrieval in the absence of episodic information, as in semantic memory. The key to whether the experience is of episodic or semantic memory retrieval is not in what representations are stored, but rather in how memory is probed. In these simulations Hintzman was able to

demonstrate that a single memory system model could account for differences in the

contextual details that accompany experiences of semantic versus episodic memory.

The Distinction Between Implicit and Explicit Memory

The goal of this thesis is to assess the separate systems and processing accounts of

memory when retrieval is not accompanied by awareness. As stated above, the

classification of memory based on awareness has been used to separate declarative and

non-declarative memory systems. The non-declarative and declarative memory systems

are also commonly referred to as implicit memory and explicit memory (e.g., Graf &

Schacter, 1985). The distinction between implicit memory and explicit memory has been

supported by task dissociations in healthy adults (e.g., Jacoby & Dallas, 1981; Tulving,

Schacter, & Stark, 1982). One example of a task dissociation used to support this

distinction examined the effect of deep versus shallow processing of study items on tests

of implicit and explicit memory (Jacoby & Dallas, 1981). During the study phase of their

experiment, Jacoby and Dallas had participants answer questions about words that were

presented. The questions could either require shallow processing (e.g., the question asked

whether a letter was present in the study word) or deep processing (e.g., the question

asked about the meaning of the study word). Following the study phase, some

participants completed a recognition test (an explicit test), in which they had to indicate if

a presented word was one they had studied (*old*) or was not a word they had studied

(*new*), while other participants completed a perceptual identification task (an implicit

test), in which they had to identify a briefly presented word. In support of the

implicit/explicit distinction, Jacoby and Dallas found that although performance on the

explicit test differed as a function of the level of processing participants had engaged in for that word during the study phase (with better memory for deep versus shallow processing), the levels of processing manipulation did not have an effect on the perceptual identification task.

Another example of a task dissociation used to support the distinction between implicit and explicit memory examined the effect of retention intervals on implicit and explicit memory (Tulving et al., 1982). In this experiment, participants studied a list of words during a study phase, after which their retention was measured using both an explicit and an implicit memory test. These tests were administered one-hour after the study phase, and then again 7-days later. For some items, participants were given a recognition test (an explicit test), while other items were tested using a word-fragment completion test (an implicit test), in which participants simply were asked to fill in a word-fragment so that it made a word. This test does not explicitly require that participants recall words that they have previously studied, but typically, performance is influenced by previously studied words, such that there is a greater probability that participants will complete the fragments with studied words than with other, unstudied words that would also fit the fragments. Critically, Tulving et al. found that while performance on the recognition test decreased in efficiency from the one-hour test to the test that occurred a week later, performance on the word-fragment test was fairly stable across the retention interval. This dissociation was taken as evidence for the implicit/explicit memory distinction, as the two types of memory show different effects of retention interval.

As in the semantic/episodic distinction, the implicit/explicit distinction has also been supported by the memory impairments observed in amnesic patients (e.g., Knowlton, Ramus, & Squire, 1992; Warrington & Weiskrantz, 1970). Specifically, Warrington and Weiskrantz found that although amnesic patients showed a deficit in performance on explicit memory tests, such as recall and recognition, their performance on implicit memory tests, such as identifying word fragments and stem completion was similar to that of healthy controls. This task dissociation, along with other similar dissociations observed in amnesic patients, led some researchers to propose that there are two parallel memory systems, which separately represent explicit and implicit memory (e.g., Knowlton et al., 1992), and that structures within the medial temporal lobe, including the hippocampus, are critical to explicit memory.

However, as with the episodic/semantic distinction, the dichotomy between implicit and explicit memory systems has been challenged by processing views in which the dissociations between implicit and explicit memory are explained by differences in the processes engaged in at the moment of test. Once again, these processing models posit a single memory system that can be accessed using different retrieval processes which are sometimes accompanied by awareness (e.g., Blaxton, 1989; Higham & Vokey, 1994; Kinder & Shanks, 2001; 2003; Neal & Hesketh, 1997; Whittlesea, 2002; Whittlesea & Dorken, 1993, 1997; Whittlesea & Price, 2000; Whittlesea & Wright, 1997). This processing view of memory has also been generally applied to behaviour in performance tasks where participants are unaware of the influence of previous experiences (e.g., Brooks, 1978; Logan, 1988, 1990; Hommel, 1998).

Implicit learning and memory has been studied extensively with two learning tasks, one that assesses categorization based on learning of complex artificial grammars, and another that assesses incidental learning of complex sequential structures. To illustrate how the multiple memory systems and the processing views have been applied to performance in these tasks, I will first describe the subdomain of artificial grammar learning and categorization, where I will describe how the separate systems and processing views have been applied to this subdomain. Following this description I will show how similar ideas have been applied to the subdomain of implicit sequence learning, where I will argue that the issue of episodic representations in implicit sequence learning has largely been ignored.

Categorization and Artificial Grammar Learning

The incidental learning of complex categories has been studied in the artificial grammar learning literature through the use of judgment of grammaticality tasks. In a common variant of this task, participants are incidentally taught finite state grammars, such as the grammar shown in Figure 1. Using grammars such as the one shown here, it is possible to create letter strings by moving through the various nodes in the grammar (e.g., "PTVPS"). Letter strings that follow the rules of the grammar are considered grammatical or legal. For example, Reber (1967) asked participants to memorize grammatical letter strings generated from this grammar. Following the study phase, Reber informed participants that there had been an underlying structure present across the items, and asked participants to categorize new items based on whether they followed the same underlying structure as the previously encountered/studied items. Reber found that

participants showed sensitivity to the grammar in a classification task, where they

classified grammatical items as consistent with the grammar to which they had been

exposed, and classified non-grammatical items as inconsistent with that grammar.
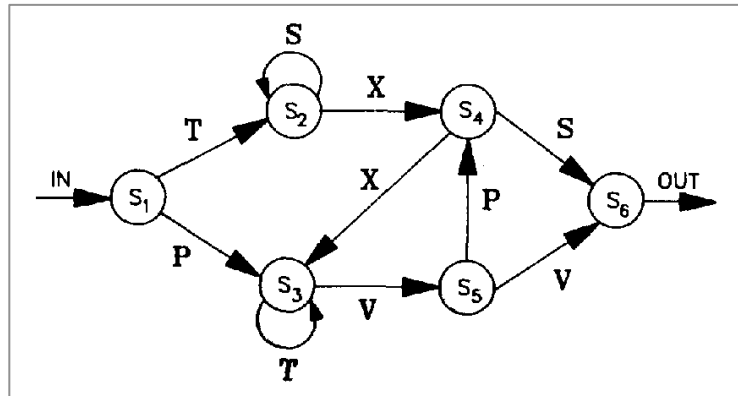
Figure 1. Example of a finite state grammar used to generate letter strings. Figure taken from Reber (1989), reprinted with permission.

In this task, Reber and others have pointed to two key results as evidence for the

view that participants perform the task using abstract representations of the artificial

grammar they are trained on (e.g., Reber, 1967, 1989). The first key finding for abstract

representations comes from performance when the letter-set used to generate the letter

strings is changed for the categorization phase, such that grammatical and non-

grammatical items are presented but with different letters. Despite the different letters

used in the test phase, participants continue to show sensitivity to the grammar, (e.g.,

Reber, 1967). The fact that participants were able to demonstrate sensitivity to the

underlying grammar, even when the letter sets differed between the study and test phases,

was interpreted as evidence that surface characteristics of the items were not guiding

performance, and that participants had represented an abstraction of the underlying grammar.

As in the distinctions described above, the second piece of evidence for the use of abstract representations in artificial grammar learning tasks has come from studies where performance on categorization and recognition memory tasks is evaluated in amnesic patients (e.g., Channon, Shanks, Johnstone, Vakili, Chin, & Sinclair, 2002; Knowlton & Squire, 1993, 1996; Knowlton, Ramus, & Squire, 1992). Within this task-dissociation, performance on categorization tasks has been argued to be the result of implicit memory that is formed across multiple experiences, while recognition relies on explicit, episodic memory for previous events (e.g., Knowlton & Squire, 1993). In one example showing this dissociation, Knowlton et al. (1992) had amnesic patients and healthy controls memorize letter strings derived from an artificial grammar. Following the study phase, both groups of participants completed a categorization task. In the second half of the experiment, the groups of memorized letter strings derived from a second artificial grammar, and were then tested on that grammar using a recognition memory test. In the recognition test, participants were shown the same grammatical letter strings they had just studied, as well as novel, non-grammatical letter strings. The results of this experiment demonstrated that although the performance of the amnesic patients was similar to that of the healthy controls on the categorization task, performance on the recognition memory task was significantly lower for amnesic patients relative to the healthy controls. This task dissociation has been interpreted as evidence that implicit learning relies on separate, abstract representations, which are spared in amnesic patients.

However, these two pieces of evidence may not necessitate the assumption that abstracted representations underlie performance in the artificial grammar learning task. For example Brooks and Vokey (1991) argued that the design used by Reber (1967) confounds similarity and grammaticality of the letter strings used in the categorization test, even when a novel set of letters is used. Namely, the grammatical letter strings presented in the categorization test were more similar to the letter strings that had been initially studied than were the non-grammatical letter strings, both in the same letter set and different letter set conditions. This confound is important because episodic processing accounts could predict that both literal similarity and relational similarity may be used to make grammaticality judgments in the absence of abstracted representations (e.g., Brooks & Vokey, 1991; Vokey and Brooks, 1992). In the changed letter set condition, literal similarity is unlikely to play a role in guiding judgments of grammaticality, but the relational similarity between a training item such as "TSSXS" and a test item "KMMLM", could guide judgments of grammaticality in the absence of abstract representations of the grammar.

To address this confound, Brooks and Vokey (1991) orthogonally manipulated the grammaticality and similarity of the letter strings used in the categorization phase to the items used in the study phase, both in a same letter set condition and a changed letter set condition. Similarity was manipulated such that test items were similar to those used at study when they contained the same types of transitions as were present in the study items. Test letter strings were dissimilar when they did not contain the same transitions that had been present in the study items. Importantly, similar and dissimilar letter strings

were also grammatical or non-grammatical with respect to the grammar that participants

had been exposed to at study. Critically, Brooks and Vokey showed that the same results

could be independently measured based on similarity and grammaticality when the two

were orthogonally manipulated, suggesting that abstracted grammars or pooled instances

could produce Reber's results (see also Perruchet, 1994, for another account based on

recognition of fragmentary representations, such as bigrams). Therefore, good

performance in classifying novel letter strings as grammatical/non-grammatical in the

changed letter set condition is consistent with both the view that abstracted

representations underlie performance, as well as the alternative single system view that

episodic representations underlie performance. Indeed, research examining the role of

similarity to previous instances in these and other categorization tasks has suggested that

episodic details influence behaviour, and that abstraction can be the product of the

processes engaged in during retrieval, or can arise based on task constraints that influence

how participants attend to the stimuli (e.g., Brooks, 1978; Whittlesea, 1987; Whittlesea &

Dorken, 1993; Whittlesea & Leboe, 2000; Whittlesea & Wright, 1997; for a review see

Neal & Hesketh, 1997).

In addition to this evidence, Jamieson and colleagues (Chubala & Jamieson, 2012;

Jamieson & Hauri, 2012; Jamieson & Mewhort, 2009a, 2010, 2011) have demonstrated

that it is possible to simulate many classic results from artificial grammar learning

experiments using Minerva 2 (Hintzman, 1986). In fact, Jamieson, Holmes, and Mewhort

(2010) were able to simulate the second piece of evidence in favour of separate

representations using Hintzman's multi-trace model. By manipulating the integrity of the

representations that are stored in memory, Jamieson et al. were able to simulate the

dissociation between categorization and recognition memory in amnesic patients as a

single memory deficit in a single store model of human memory. Based on their

simulations, Jamieson et al. argue that amnesic patients show a greater deficit in

recognition memory because there is a greater reliance on global similarity in this task, as

compared to the categorization task. Also consistent with a processing view are the

results of a meta-analysis that assessed categorization performance in amnesic patients,

which showed that amnesic patients also show a small impairment in categorization tasks

(Zaki, 2004).

In sum, a review of the literature on categorization and artificial grammar learning

suggests that the dissociation between implicit and explicit memory may be based on

evidence that can also be accommodated by a single system account.

Implicit Sequence Learning

Given the compelling evidence for episodic representations in other subdomains

within implicit memory, I now turn to implicit sequence learning, the subdomain in which

the empirical portion of this thesis is situated. Implicit sequence learning is another

domain in which researchers have argued for a distinction between implicit and explicit

memory, as participants are able to learn complex structures without awareness that

learning has taken place. The two pieces of evidence for this separate systems view arise

from the dissociation that healthy participants seem to show between implicit and explicit

knowledge of the sequences, as well as from the sparing of implicit learning in amnesic

patients. I will first describe the methodology used to measure implicit sequence

knowledge, after which I will briefly describe some task-dissociations that have been found in healthy participants and amnesic patients.   From there, I will describe some current accounts of how implicit sequence learning is represented, and show that the majority of accounts focus on separate, single-level accounts which ignore the notion that episodic representations may also underlie behaviour in this domain.

Measuring Implicit Sequence Learning

Implicit sequence learning is typically measured using the serial reaction time (SRT) task, in which participants must respond to a target on every trial. In the standard version of the SRT task, on every trial one target appears at one of four marked locations. Participants are instructed to respond to the location of the target, as quickly and accurately as possible using the key corresponding to the target's current location. Unbeknownst to participants, on a high proportion of trials the target's location is selected based on a relatively complex sequence. Despite this seeming lack of awareness, participants show evidence that they have incidentally learned the training sequence. The evidence that participants have learned the sequence is derived from the gradual improvement in performance that participants show across blocks when responding to the training sequence (e.g., Nissen & Bullemer, 1987). Sequence learning has also been evidenced by the cost, relative to performance for the training sequence, associated with responding to a target when its location is either randomly selected (e.g., Cohen, Ivry, & Keele, 1990) or is selected using a control sequence (e.g., Schvaneveldt & Gomez, 1998).

There is some variability in the literature in terms of what types of sequences participants are exposed to, as well as the method of presenting the sequences. In early

studies, the sequences used contained unique transitions, where knowledge of a target's location on an immediately preceding trial is sufficient to predict specifically where the target will appear next (e.g., Nissen & Bullemer, 1987). In contrast, more recent studies have used sequences with ambiguous transitions, where the location of a target cannot be uniquely predicted based on where the target had appeared on the immediately preceding trial. For example, Reed and Johnson (1994) developed second-order conditional sequences (SOCs) in which the target's location is ambiguous based on its location on the immediately preceding trial, but is uniquely predicted based on the target's location on the two most recent trials. Participants are more likely to become aware of sequential structures when they contain unique transitions (e.g., Nissen & Bullemer), and learning of sequences with unique transitions is often affected less by a concurrent secondary task than is learning of sequences containing ambiguous transitions (e.g., Cohen, Ivry, & Keele, 1990).

In addition to different transition structures, there are also differences in how sequences are employed in the SRT task. In early work, sequences were used deterministically, such that the sequences were used on every trial to select the location of the target (e.g., Nissen & Bullemer, 1987). When the sequence is used deterministically, learning is often evaluated by examining the cost in performance in a transfer block where the location of the target is randomly selected on every trial (e.g., Cohen et al., 1990). Sequences can also be used probabilistically, such that the location of the target is selected according to the sequence on a high proportion of trials, and noise is introduced by selecting the location of the target using a control sequence on a small proportion of

trials. Probabilistic training can occur in two main ways, which are depicted in Figure 2.

When using complete sequence substitutions, the location of the target is deterministically

selected based on the training sequence over a number of full iterations of the sequence,

but on some proportion of iterations, a control sequence is substituted in and used

deterministically to select the location of the target (e.g., Jiménez & Vázquez, 2005). In

contrast, in the trial by trial substitution method, control trials are introduced on a trial to

trial basis, such that on every trial there is a high probability that the location of the target

will be selected according to the training sequence, but there is also a small probability

that the location of the target will be selected according to a control sequence (e.g.,

Schvaneveldt & Gomez, 1998).
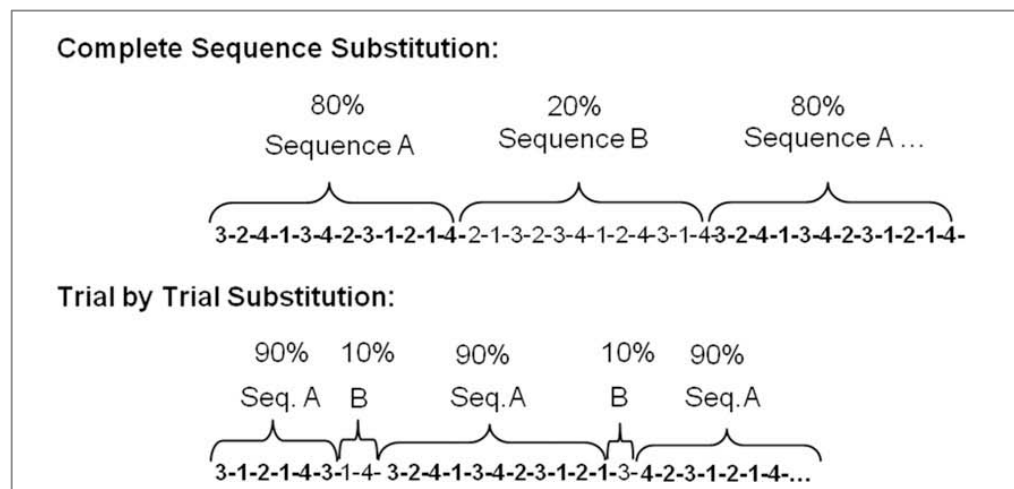
Figure 2. A depiction of the complete sequence substitution and the trial-by-trial
substitution methods. Figure taken from Jiménez et al. (2009), reprinted with permission.

The implicit nature of this learning has been assessed through task dissociations,

in which the expression of sequential knowledge on an implicit task (e.g., the SRT task) is

compared to the expression of that same knowledge on an explicit task (e.g., a cued-

generation task). When participants show the expression of learning only in the implicit task, the learning is considered implicit. The tasks used to measure explicit knowledge of sequences varies; in some experiments participants are asked to generate the location of a target based on a fragment of the sequence (e.g., Jiménez & Vázquez, 2005; Wilkinson & Shanks, 2004; Willingham, Nissen, & Bullemer, 1989), while in other studies participants are given a recognition task where they are asked whether a sequence of target locations was presented in the SRT task (e.g., Perruchet & Amorim, 1991). Another method of assessing awareness that has been applied in the implicit sequence learning literature makes use of the process dissociation procedure (e.g., Jacoby 1991), in which participants are asked to generate the sequences under two different conditions (e.g., Destrebecqz & Cleeremans, 2001; but see Fu, Dienes, & Fu, 2010). In the inclusion condition, participants are required to generate the regularities of the training sequence, in which case both implicit and explicit processes can jointly influence performance. In the exclusion condition, participants are told to avoid generating the regularities of the training sequence, in which case implicit and explicit processes are set in opposition to one another. If performance differs across these two conditions, it is assumed that participants were aware of the sequential regularities.

At this point, it should be noted that the use of such task dissociations to assess explicit knowledge of sequences has been the subject of a long debate in the implicit learning literature. On one side, there are some researchers who argue that it is possible to measure processes that occur in the absence of awareness (e.g., Destrebecqz & Cleeremans, 2001; Merikle & Reingold, 1991; Reingold & Merikle, 1988,), while on the

other side there are researchers who claim that measures of implicit awareness are always

contaminated by explicit knowledge (e.g., Green & Shanks, 1993; Norman, Price, Duff,

& Mentzoni, 2007; Perruchet & Amorim, 1991; Shanks & St. John, 1994). A detailed

description of these arguments is beyond the scope of this thesis, however, these

arguments stem from the process purity problem, which is present in most task

dissociations used to assess awareness. The process purity problem refers to the fact that

no current test can be shown to be selectively sensitive to explicit or implicit influences of

memory. However, the goal of this thesis is not to determine how to assess awareness in

implicit memory tasks, but rather to argue that the representations that are involved are

the same across implicit and explicit tasks. Therefore, the notion of implicit memory in

sequence learning that I refer to in this thesis is that of unintentional influences of

previous experience (see Dennett, 1993, and Neal & Hesketh, 1997 for similar

arguments), or in other words, memory retrieval that occurs automatically and

unintentionally.

    As with the other distinctions discussed above, the distinction between implicit

and explicit memory in sequence learning has also stemmed from evidence of task

dissociations in amnesic patients. Indeed, in the first study that reported implicit

sequence learning, Nissen and Bullemer (1987) found that Korsakoff's patients with

anterograde amnesia were able to show intact learning in the SRT task, despite having no

awareness of the sequences in a self-report task (see also Nissen, Willingham, &

Hartman, 1989; Reber & Squire, 1994; but see Curran, 1997). In contrast, healthy

controls were able to show learning in their SRT task, but as the sequences were

presented deterministically and contained unique transitions, the healthy controls reported

awareness of the sequences in a self-report task. This dissociation between amnesic

patients and healthy controls on implicit versus explicit tasks has been used by some

researchers as evidence for separate implicit and explicit memory systems (e.g., P.J.

Reber & Squire, 1994; Squire, 1992; see also Willingham, 1998 for a formal model of

separate systems in sequence learning).

Representing Implicit Sequence Learning

Within the sequence learning literature, accounts of the representations that

underlie different types of sequential knowledge have distinguished between explicit and

implicit learning (e.g., Hazeltine, Grafton, & Ivry, 1997; Sanchez, Gobel, & Reber, 2010;

Sanchez & Reber, 2013; Willingham & Goedert-Eschmann, 1999). However, in contrast

to the artificial grammar learning and categorization literatures, there has been little

evidence for abstract conceptual representations in implicit sequence learning (e.g.,

Gomez, 1997; Gomez & Schvaneveldt, 1994; Knowlton & Squire, 1996; Francis,

Schmidt, Carr, & Clegg, 2009). As opposed to positing abstract representations most

current accounts have carved implicit sequence learning further based on the levels of

representation that are thought to be involved (e.g., Keele, Ivry, Mayr, Hazeltine, &

Heuer, 2003). The single-level accounts that have been proposed have primarily focused

on the dichotomy between response-based and stimulus-based learning.

Response-based accounts of sequence learning have posited that sequence

learning arises through bindings between successive responses. In other words, these

accounts hypothesize that learning occurs through associations formed between the

response made on the immediately preceding trial and the response made on the current

trial. Response-based learning has been supported by patterns of activation in

neuroimaging studies of sequence learning, which have shown activation in motor areas

associated with sequence learning (e.g., Grafton, Hazeltine, & Ivry, 1998; Willingham &

Koroshetz, 1993). Further evidence is derived from studies showing that damage to or

deterioration of motor areas impairs implicit sequence learning, such as in patients with

Parkinson's disease (e.g., Siegert, Taylor, Weatherall, & Abernethy, 2006; for a review

see Doyon, 2008). Furthermore, the view that response-response bindings underlie

sequence learning is supported by studies that show an elimination of sequence learning

effects when participants are told to respond to the target using different effectors (e.g.,

Berner & Hoffmann, 2008; Verwey & Clegg, 2005). In another variant of this account,

Willingham and colleagues have argued that learning is based on bindings between

successive response-locations rather than the responses themselves (e.g., Deroost,

Zeeuws, & Soetens 2006; Willingham et al., 1990; Witt & Willingham, 2006).

In contrast to accounts of sequence learning that focus exclusively on response

level representations, others have argued that stimulus level representations are included

in sequence learning. The role of stimulus level representations in sequence learning is

supported by experiments that have shown that learning is stimulus-specific, and does not

transfer to novel stimuli (e.g., Abrahamse, Van der Lubbe, & Verwey, 2008, but see

Abrahamse, Van der Lubbe, & Verwey, 2009; Willingham 1999). In one account that

includes both stimulus and response level representations, Ziessler and colleagues have

argued that learning occurs through response-effect bindings between a response and the

stimulus that follows that response (e.g., Ziessler, 1998; Ziessler & Nattkemper, 2001).

For example, in Ziessler's (1998) study, participants were required to respond to the

identity of a target embedded amongst distractors. The identity of the target was selected

according to a sequence, allowing Ziessler to measure sequence learning effects. Ziessler

also associated the response made to a target with the target's relative location on the

subsequent trial. Importantly, Ziessler found that participants' performance suffered

when the association between the response and the subsequent location of the target was

disrupted, providing evidence for response-effect bindings in sequence learning.

Further evidence for response-effect learning has been provided by Hoffmann,

Sebald, and Stöcker (2001, see also Stöcker, Sebald, & Hoffmann, 2003). In their study,

Hoffmann et al. (2001) included tones as irrelevant response effects during sequence

learning. Later, when the mapping changed between the responses and their associated

tones, sequence learning was disrupted. The response-effect learning accounts are a step

toward integrated representations, as they are consistent with ideomotor approaches to

action control in which the actual production of a movement is influenced by the internal

anticipation of the sensory consequences of that action, as action and sensory perception

are represented together in memory (e.g., Hommel, 1996; Hommel, Müsseler,

Aschersleben, & Prinz, 2001; Kiesel & Hoffmann, 2004).

Despite the evidence for accounts of sequence learning that focus on response-

level representations, there are some results that are hard to reconcile with accounts based

on response-level representations. Results such as observational learning (e.g., Howard,

Mutter, & Howard, 1992; Song, Howard, & Howard, 2008), effector independent

learning (e.g., Cohen et al., 1990), and pure perceptual learning (e.g., Deroost & Soetens 2006a; Mayr, 1996; Remillard, 2003) together suggest that learning can be based entirely on stimulus-stimulus bindings in the absence of response-level representations. For example, Howard et al. (1992) reported that participants who had simply observed a sequence during a training phase performed as well in a transfer phase as did participants who had responded to the target throughout the training blocks.

In line with the stimulus-based learning account is the finding that learning is not always effector-specific (e.g., Cohen et al., 1990). For example, Cohen et al. trained participants on a sequence where they responded to the location of a target using three different fingers, one for each of the response buttons associated with the possible target locations. In a transfer phase, participants continued to respond to the location of the target using the three response buttons, but using the same finger for the three response buttons. Using this design, Cohen et al. found that learning transferred in the switch from using different fingers to using the same hand for all three locations, showing effector-independent learning.

Lastly, accounts of stimulus-stimulus bindings are supported by the occurrence of pure perceptual learning, where participants are able to learn a sequence related to a perceptual dimension that is uncorrelated with the sequence of responses made. For example, Mayr (1996) had participants complete a variant of the SRT task, where the target could appear at one of four marked locations, but participants responded to the identity of a target. In Mayr's study, the identity of the target on every trial was selected by one sequence and the location at which it could appear was selected by another,

uncorrelated sequence. Given that participants responded based on the identity of the target, the sequence used to select the identity of the target reflects learning based on response-level features, while the sequence used to select the location of the target reflects learning based on a perceptual dimension. Using this design, Mayr showed that participants can learn a sequence of locations independent of their learning of a sequence of responses (see also Deroost & Soetens 2006a; Mayr, 1996; Remillard, 2003).

In sum, across the literature, there has been evidence for many single-level accounts for the representations involved in sequence learning. Given the evidence supporting each of the different accounts, a question that arises is whether accounts that posit separate single-level representations are necessary to explain the data, or if a processing account assuming episodic representations will suffice. It is possible that the results described above could be captured by a single memory system, where attention can bias reliance on response and stimulus characteristics, leading to learning that can seem more or less tied to specific response-level and stimulus-level characteristics. Indeed, although this issue has largely been ignored in the sequence learning literature, there is some evidence that supports the view that episodic representations may underlie implicit sequence learning (e.g., Abrahamse & Verwey, 2008; Jiménez, Vaquero, & Lupiáñez, 2006; and see Jamieson & Mewhort, 2009b for the application of Minerva 2 to performance on the SRT).

Given the nature of the SRT task, one approach that can be used to examine whether episodic representations underlie sequence learning is to determine whether learning is context-specific. Evidence of context-specificity in implicit sequence learning

would suggest that contextual features are bound to the representations that underlie performance. Furthermore, the notion that episodic representations underlie sequence learning would be supported if the acquisition and expression of implicit sequence learning depends on context in the same way that context influences retrieval in explicit remembering tasks (e.g., Godden & Baddley, 1975; Morris, Bransford, & Franks, 1977; Tulving & Thomson, 1973).

Overview of the Empirical Chapters

In contrast to research conducted in other subdomains of implicit memory, research on implicit sequence learning has not yet focused on whether a processing view based on episodic representations can account for behaviour in this domain. Evidence for episodic representations in implicit sequence learning would offer support for the view that behaviour arises based on processes that act on one common memory system. To that end, in the empirical chapters of this thesis I will examine the role of contextual features on implicit sequence learning, by looking for evidence of context-specificity in sequence learning.   Specifically, in Chapter 2, I will examine the specificity of learning when participants concurrently learn a motor sequence and a perceptual sequence, by demonstrating that implicit sequence learning is modulated by the context provided by an immediately preceding trial. In Chapter 3, I will extend the finding of context-specificity in implicit sequence learning by examining how context can be used to distinguish learning of two complementary motor sequences. Lastly, in Chapter 4, I will examine further the conditions under which context-specific sequence learning can arise in learning different types of sequential structures. I will then argue that the results from the

present work suggest that implicit sequence learning can be context-specific, which in turn serves as evidence that episodic representations may underlie implicit sequence learning effects.

CHAPTER 2: On the Specificity of Sequential Congruency Effects in Implicit

Learning of Motor and Perceptual Sequences

D'Angelo, M.C., Jiménez, L., Milliken, B., & Lupiáñez, J. (2013).

Journal of Experimental Psychology: Learning, Memory and Cognition, 39, 69-84.

Copyright © 2013 by the American Psychological Association.

Reproduced with permission

Preface

Chapter 2 presents the results of three experiments in which the specificity of sequence learning effects was assessed when participants simultaneously learned a motor sequence and a perceptual sequence. In Experiments 2 and 3 the specificity of learning was examined by assessing the expression of learning as function of the information presented in the immediately preceding trial. The results of these experiments demonstrate that the expression of sequence learning is specific, such that learning is only expressed when the immediately preceding trial contains information consistent with the training sequence. Furthermore, the results of these experiments show that these modulations are learning- type specific, as the expression of motor sequence learning was only influenced by the motor sequence information contained in the preceding trial, while the expression of perceptual sequence learning was only influenced by the perceptual sequence information present in the immediately preceding trial. These results constitute a first demonstration of context-specificity in the simultaneous learning of two sequences.

The reader should note that this chapter is not framed in terms of the themes outlined in the introduction of this thesis, but is instead framed in terms of the conflict monitoring theory of trial-by-trial adaptations that are observed in response to conflict. This framing was chosen as the article followed up on previous work by Jiménez, Lupiáñez, and Vaquero (2009) and Beesley, Jones, and Shanks (2012). However, despite the difference in framing, the results from the experiments presented in this chapter also speak to the issue of context-specificity in implicit sequence learning.

Abstract

Individuals experience less interference from conflicting information following events that contain conflicting information. Recently, Jiménez, Lupiáñez, and Vaquero (2009) demonstrated that such adaptations to conflict occur even when the source of conflict arises from implicit knowledge of sequences. There is accumulating evidence that momentary changes in adaptations made in response to conflicting information are conflict-type specific (e.g. Funes, Lupiáñez, & Humphreys, 2010a), suggesting that there are multiple modes of control. The current study examined whether conflict-specific sequential congruency effects occur when the two sources of conflict are implicitly learned. Participants implicitly learned a motor sequence while simultaneously learning a perceptual sequence. In a first experiment, after learning the two orthogonal sequences, participants expressed knowledge of the two sequences independently of each other in a transfer phase. In Experiments 2 and 3, within each sequence, the presence of a single control trial disrupted the expression of this specific type of learning on the following trial. There was no evidence of cross-conflict modulations in the expression of sequence learning. The results suggest that the mechanisms involved in transient shifts in conflict-specific control, as reflected in sequential congruency effects, are also engaged when the source of conflict is implicit.

Introduction

Implicit memory is thought to be a very rigid form of expertise, where knowledge is applied exclusively in the context in which it was acquired (e.g. Abrahamse & Verwey, 2008). However, some recent work has demonstrated that the expression of implicit knowledge can be adapted flexibly, and that it can be sensitive to momentary violations of learned structures underlying previously acquired tendencies (Jiménez, Lupiáñez, & Vaquero, 2009). Whereas this prior research focused on the learning of motor sequences, the goal of this study is to assess whether this sensitivity in implicit learning extends to knowledge of a perceptual sequence, and additionally whether sensitivity to momentary violations of a learned structure is specific to the particular type of knowledge being expressed, perceptual or motor.

Implicit sequence learning

Skill acquisition has often been studied in the laboratory through the use of serial reaction time (SRT) tasks. In the standard version of this task, participants respond as quickly and accurately as possible to the location of a target stimulus on every trial. The target often appears in one of four possible locations, and participants respond by pressing a key that corresponds to the current location of the target. Unbeknownst to the participant, the location at which the target stimulus appears follows a relatively complex sequence. Sequence learning is evidenced by the gradual improvement in responding to trials generated by a training sequence (Nissen & Bullemer, 1987), as well as by a cost associated with responding to a trial in which the location is either randomly generated

(Cohen, Ivry, & Keele, 1990), or generated by a control sequence (Schvaneveldt & Gomez, 1998).

Sequence learning can occur with or without the intention to learn, although the learning observed appears to be qualitatively different when participants learn intentionally than when they learn incidentally (Jiménez, Vaquero, & Lupiáñez, 2006). One qualitative difference of note is that intentional learners but not incidental learners can express their acquired knowledge flexibly, by transferring their learning across changes in surface structure. Specifically, Jiménez et al. (2006, Experiment 2) trained intentional and incidental learners on a sequence during a training phase in which learners responded to the location of a single target. In a later transfer phase, both groups of learners responded to the same target that was now accompanied by distractors. Importantly, the location of the targets was still predicted by the training sequence, but was now accompanied by distractors. Jiménez et al. showed that intentional but not incidental learners transferred sequential knowledge from the training phase to the transfer phase. These results suggest that implicit memory is rigidly expressed in its acquisition context, and that the expression of implicit knowledge is not flexibly controlled.

However, a recent study reported by Jiménez et al. (2009) challenges this view, in that they found implicit learning to be sensitive to momentary violations of previously acquired knowledge of sequential structure. By analogy to the literature on conflict adaptation (Gratton, Coles, & Donchin, 1992), a target on one trial that is well predicted by the sequential structure of prior trial-to-trial transitions might be regarded as a

31

congruent trial. In contrast, a target on one trial that violates the sequential structure of prior trial-to-trial transitions can be regarded as an incongruent trial. Within this framework, Jiménez et al. (2009) demonstrated that sequential congruency effects can be measured in both intentional and incidental learning. Using a probabilistic trial-by-trial substitution method, Jiménez et al. (2009) had participants complete a standard SRT task in which, in the training blocks, the location of the target was predicted by a second-order conditional sequence on 90% of the trials. In two transfer blocks the probability that the target location was predicted by the training sequence was reduced to 20%. The results of the transfer blocks revealed that both intentional and incidental learners produced a sequence learning effect only on trials that were preceded by training (congruent) trials, and that the expression of learning was completely eliminated following control (incongruent) trials. These results demonstrate that the expression of implicit knowledge can be constrained by momentary violations of learned tendencies. One interpretation of these results is that the expression of implicit learning on a given trial depends on the adjustment of control triggered by the detection of conflict in the preceding trial, as proposed in Botvinick and colleagues' conflict monitoring hypothesis (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004).

Conflict adaptation effects

The conflict monitoring model proposes that the cognitive system engages control when it encounters competition between the correct responses for a given task and some relatively automatic, but ultimately incorrect, response tendencies (Botvinick et al. 2004). Interference tasks, such as the Eriksen flanker task (Eriksen & Eriksen, 1974), Stroop task

(Stroop, 1935), and Simon task (Simon, 1969) have been used extensively to study

cognitive control, as all three tasks require that participants override processing of an

irrelevant aspect of the stimulus in order to correctly respond based on the task relevant

aspect. For example, in the Eriksen flanker task, participants must indicate the direction

of a central target arrow while ignoring the direction of flanker arrows presented on either

side of the target. On compatible trials the direction of the flanker arrows is compatible

with the correct response to the central target arrow (e.g. $<<<<<$), while on

incompatible trials the direction of the flanker arrows is incompatible with the correct

response to the target arrow (e.g. $>><>>$). The difference in performance for

incompatible and compatible trials is referred to as the interference effect, and is a

measure of the time needed to overcome conflict or competition derived from task-

irrelevant information. Typically, participants take longer to respond and make more

errors on incompatible relative to compatible trials, although the size of the interference

effect is modulated by the proportion of compatible trials (e.g. Corballis & Gratton,

2003), as well as by the compatibility of the preceding trial (e.g. Gratton, Coles, &

Donchin, 1992).

   The influence of the preceding trial on the size of the interference effect is referred

to as a conflict adaptation effect, or a sequential congruency effect (Gratton et al., 1992).

With reference to the Eriksen flanker task, the interference effect is typically larger

following compatible trials than following incompatible trials; in fact, an interference

effect is often only present following compatible trials. The conflict monitoring model

proposes that sequential congruency effects reflect transient shifts in control that are

initiated by the dorsolateral prefrontal cortex (dLPFC) after the detection of conflicting or competing information by the anterior cingulate cortex (ACC) (e.g. Botvinick et al., 2001; De Pisapia & Braver, 2006). According to this framework, sequential congruency effects arise due to a reactive process that increases control when individuals encounter incompatible trials relative to compatible trials. These transient shifts in control reduce the processing of task-irrelevant information on the current trial, but also carry forward and continue to reduce task-irrelevant processing on the following trial. As a consequence, performance on both compatible and incompatible trials is affected less by irrelevant information following incompatible trials than following compatible trials, which in turn results in smaller interference effects following incompatible than following compatible trials.

The conflict-monitoring model forwarded by Botvinick and colleagues suggests that there is a single conflict monitoring mechanism that engages a general form of control when conflict is detected. An alternative account that has been gaining support suggests that there are multiple modes of control, which resolve conflict in a domain-specific manner (e.g. Egner, 2008). Evidence favoring this alternative account is derived from studies that have examined the specificity of sequential congruency effects. Here, the key issue concerns whether sequential congruency effects can occur across different conflict types. In particular, if the detection of conflict engages a general form of control, then experiencing conflict on a preceding trial will lead to reduced interference on a following trial regardless of whether the conflict type is the same or different from one trial to the next. Conversely, if the detection of a particular type of conflict engages a

specific mode of control based on the type of conflict detected, then reduced interference ought to occur on the following trial only if the same type of conflict is present in both trials. A caveat, here, is that the examination of cross-conflict sequential effects is only valid if the two types of conflict-tasks that are used reflect independent sources of conflict (Egner, 2008).

Using this approach, Funes, Lupiáñez and Humphreys (2010a; see also Egner, Delano, & Hirsch, 2007; Notebaert & Verguts, 2008, Condition 2; Wendt, Kluwe, & Peters, 2006) have demonstrated that sequential congruency effects are specific to the type of conflict occurring in a preceding trial, consistent with the idea that there are multiple modes of control (e.g. Egner, 2008). Funes et al. (2010a, Experiment 2) used a combined-conflict paradigm to measure spatial Stroop and Simon interference while maintaining the same stimuli and same task across the spatial Stroop conflict and Simon conflict conditions. Specifically, on every trial participants responded to the direction of an arrow that pointed either up or down. Responses were recorded using two response keys, one on the left side of the keyboard and one on the right side of the keyboard, that were arbitrarily associated with up and down responses. Critically, the arrow appeared in one of four locations; left, right, above, or below a central fixation point. Spatial Stroop interference was measured by comparing spatially congruent trials with spatially incongruent trials, where a congruent trial was one in which the direction in which the arrow pointed (e.g., up) matched its location in the display (e.g., top), and an incongruent trial was one in which the direction in which the arrow pointed (e.g., up) was opposite its location (e.g., bottom). Simon interference was independently measured on trials in

which the arrow appeared to the left or right of fixation by comparing congruent trials, in which the stimulus appeared on the same side of fixation as the correct response key, with incongruent trials, in which the stimulus appeared on the opposite side of fixation as the correct response key. Critically, sequential congruency effects were found only when the conflict type of the preceding trial matched that of the current trial (e.g., Simon trials followed by Simon trials, or Stroop trials followed by Stroop trials). In other words, Funes et al. found that sequential congruency effects were specific to conflict type, consistent with the idea that there are separate modes of control for different types of cognitive conflict.

The results from Funes et al. (2010a) strongly suggest that sequential congruency effects reflect a transient form of cognitive control that is conflict type specific, rather than a top-down form of cognitive control that generalizes across conflict type. The results are also inconsistent with a model of stimulus driven control, as Funes et al. observed conflict-specific sequential congruency effects despite using the same stimuli and task across two conflict contexts (Experiment 2), and generalization of sequential congruency effects across axes when the same conflict type was measured on two axes, even if different stimuli were used on each axis (Experiment 4). Overall, the results reported by Funes et al. support a model in which transient control is engaged based on specific conflict processing (e.g. De Pisapia & Braver, 2006).

The specificity of sequential congruency effects in sequence learning

The goal of the current study was to determine whether the conflict-specific sequential congruency effect reported by Funes et al. (2010a) occurs when the source of

conflict is implicitly learned. To that end, we examined the specificity of sequential congruency effects in participants who concurrently learned a motor sequence and a perceptual sequence. In Experiment 1, there were two distinct goals. First, we aimed to identify a procedure that could be used to measure two types of implicitly learned sources of congruency, one related to motor sequences and the other to perceptual sequences. Second, we aimed to confirm that these motor and perceptual sequence learning effects reflect two independent sources of learning, as suggested by Egner (2008) for independent sources of conflict. In Experiment 2, sequence learning effects were examined for both motor and perceptual sequence learning, and two additional goals were addressed. First, we aimed to replicate the sequential congruency effects in motor sequence learning reported by Jiménez et al. (2009), and to extend this finding to perceptual sequence learning. Second, the specificity of the sequential congruency effects in implicit sequence learning was assessed in two ways, by examining the influence of the preceding trial's motor sequence status on the expression of perceptual sequence learning on the current trial, as well as by examining the influence of the preceding trial's perceptual sequence status on the expression of motor sequence learning on the current trial. In Experiment 3, we replicated the results of Experiment 2 and examined whether sequential congruency effects are present when the proportion of trials consistent with a training sequence is decreased.

Experiment 1

As described above, the purpose of Experiment 1 was two-fold. First, we wanted to find a procedure in which concurrent motor and perceptual sequence learning could be

measured, given that perceptual sequence learning effects can be difficult to obtain (e.g. Deroost & Soetens, 2006a; Rüsseler, Münte, & Rösler, 2002). Second, we wanted to examine whether motor sequence learning and perceptual sequence learning effects interact with each other. To address these issues, participants completed an SRT task in which they were concurrently exposed to a motor sequence and a perceptual sequence.

Prior studies have demonstrated that participants do not show perceptual learning for sequences with higher order constraints (Deroost & Soetens, 2006a), and that perceptual learning is more likely to occur when the spatial dimension is attended (Deroost & Soetens, 2006a, 2006b; Mayr, 1996, Remillard, 2009). Given these particular constraints, participants were trained on sequences containing first-order conditional structures. Simpler sequential structures are probably more open to explicit learning effects if they are presented repeatedly without noise, over extended periods of training. However, Deroost and Soetens (2006a) have reported evidence of concurrent motor and perceptual sequence learning using a probabilistic design in which first-order conditional sequence structures are derived from noisy finite-state grammars. Specifically, Deroost and Soetens used a sequence structure in which two legal successors are arranged with similar likelihood after each possible first-order context, and in which the remaining non-sequence successors replace the legal ones over a relatively large proportion of trials (i.e. on 20% of the trials).

Using these sequences, participants in the present study completed an identification task in which they were asked to respond to a target item shown amongst three distractor items. The identity of the target item was predicted by one sequence (the

motor sequence, as this was the dimension related to the motor responses) while the location of the target item amongst the distractors was predicted by a second, complementary sequence (the perceptual sequence, as this was the dimension related to perceptual learning). Distractors were presented in the unoccupied locations to encourage participants to serially search for the target item, thus drawing attention towards the spatial dimension, and also increasing the utility of learning the perceptual sequence.[1]

Methods

Participants. Thirty-six undergraduate students (35 females; mean age = 22.2 years) enrolled at the University of Granada participated in the experiment in exchange for course credits. They had never participated in similar experiments before. All participants had normal or corrected to normal vision.

Apparatus and Stimuli. The sequence of stimuli was generated by a personal computer and presented on a 15 inch Samsung color monitor. The experimental program was designed on INQUISIT 3 software. Responses were entered through the keyboard. All participants were tested individually, and sat approximately 57 cm from the screen.

The stimuli consisted of four target shapes; a heart, spade, diamond, and club. Distractor shapes were always identical to one another and were the shape that resulted from all four target shapes overlaid on one another. All the shapes subtended 1.3 degrees of visual angle vertically and 1.5 degrees horizontally, except for the heart, which subtended 1.5 degrees both vertically and horizontally. All shapes were black in color.

---

[1] Indeed, in a pilot study, perceptual sequence learning was not observed when participants were asked to respond to the color of a single target that appeared in one of four locations.

Procedure. To minimize the effects of any spatial mapping between the location of the target and that of the required response, the stimuli were displayed along the vertical axis, whereas the response keys were aligned horizontally. Four square-shaped placeholders distributed over the vertical axis of the computer screen marked the locations at which the target stimulus could appear. A target shape was presented on each trial at one of the four locations marked by the placeholders, and on every trial distractor items occupied the remaining three locations. Participants were told to respond to the identity of the target item, where the target was defined as the oddball item, which was always a heart, spade, diamond, or club. Participants used their middle and index fingers from both hands to respond to keys mapped to each of the four target shapes (using the Z, X, N, and M, keys mapping on to the heart, spade, diamond, and club, respectively). Following incorrect responses an error tone lasting 500ms was presented through headphones, during which a fixation screen containing the four placeholders was presented. The next trial appeared immediately after correct responses (with a 0ms response-to-stimulus interval) and after the auditory feedback for incorrect responses.

Two sequences were used to assign the identity and location of target shape on every trial. These two sequences were derived from the artificial grammars used by Deroost and Soetens (2006a; Soetens, Melis, & Notebaert, 2004), and are shown in Figure 1. The grammars were modified so that in one grammar the two outer positions of the grammar (1 and 4) predicted each of the first two positions (1 and 2), and the two inner positions (2 and 3) predicted each of the final two positions (3 and 4). Conversely, in the second grammar the two outer positions predicted each of the final two positions,

and the inner two positions predicted each of the first two positions. From any position in the grammar, there is an equal probability of transitioning to either of two predicted positions, and repetitions do occur. For example, starting from position 1 in Grammar A shown in Figure 1 there is a 50% probability of transitioning to position 1, and a 50% probability of transitioning to position 2. Additionally, if starting from position 1 in Grammar A, this grammar does not have legal transitions from position 1 to positions 3 or 4. Trials in which the target's identity (or location) is predicted by transitions consistent with the training sequence are referred to as training trials, and trials in which the target's identity (or location) is not predicted by transitions consistent with the training sequence are referred to as control trials. Given the complementary nature of the two grammars, control trials for Grammar A are in fact transitions that are consistent with the sequence derived from Grammar B, and vice versa.
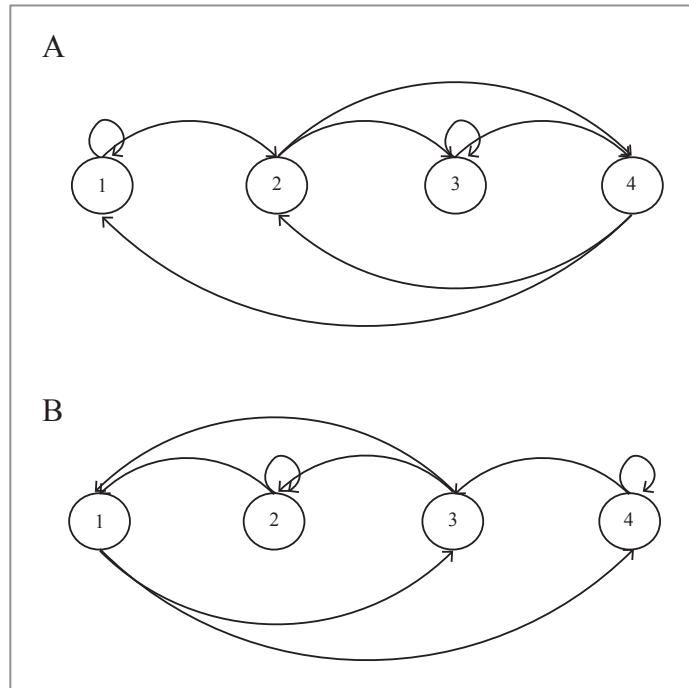
Figure 1. Depicts the grammars used to generate the sequences in Experiments 1 and 2. The assignment of grammar A and B as the motor and perceptual training sequences was counterbalanced between participants.

It is important to note that in a probabilistic design using trial-to-trial substitutions, such as what was used in the current studies, target identities and target locations are selected on a trial-to-trial basis. For example, if a block of trials contains 80% training trials, and if the target's identity or location on the current trial corresponds to position 1 in grammar A, then there is a 40% likelihood of transitioning to each of positions 1 and 2 and a 10% likelihood of transitioning to each of positions 3 and 4. Following control trials and incorrect responses, the identity or location of the target on the following trial was selected based on the identity or location that had been presented

on the previous trial (i.e. the control trial or the trial in which an incorrect response was made were used to select the identity or location of the target on the following trial).

For the motor sequence, which predicted the identity of the target item, and therefore the required response, the positions 1 through 4 corresponded in order to the heart, spade, diamond, and club. For the perceptual sequence, which predicted the location of the target item, the positions 1 through 4 corresponded to the vertical locations, in order, beginning with the top-most location (position 1) to the bottom-most location (position 4). The assignment of the two sequences to the identity and location dimensions was counterbalanced between participants.

Before beginning the experimental trials, participants first completed a practice block containing 30 trials. In this initial practice block, both the identity and location of the target stimulus were randomly determined on every trial. In the practice block, the images of the four target shapes were presented horizontally at the base of the screen on every trial, aligned with their respective response keys, to facilitate learning of the shape-key mappings. Participants responded to the stimuli appearing on the vertical axis.

Following the practice block, participants were trained over seven blocks of 100 trials. The identity and location of the target for the first trial in all blocks were selected randomly. In block 1, the identity and location of the target on all the following trials were randomly selected. In blocks 2-7, the identity and location of the target on all following trials were selected according to the training sequences, independently for the motor and perceptual sequences; the 2 sequences were uncorrelated. After the seven training blocks, participants completed four transfer blocks in which the probabilities

were shifted from 100% of trials selected according to the training sequences to only 80% of trials selected according to the training sequences. As in the previous blocks, trial selection according to the motor and perceptual sequences occurred independently of one another. After the transfer blocks, the training probabilities were restored to 100% over a final training block to re-establish the learned contingencies before measuring sequence knowledge directly using a series of generation tasks. Between all training and transfer blocks participants were given feedback on their mean reaction time (RT) and accuracy.

Participants completed two sets of cued generation tasks, one for each of the two sequences, to assess their ability to make direct predictions in response to a fragment of the sequence being tested. Trials in which a fragment of the sequence was presented are referred to as cue trials. Given that the sequences used in the current study are first-order sequences in which legal transitions according to the training grammars are dependent only on the identity or location of the preceding trial, only one fragment was presented on each cued generation trial. Participants completed a series of cued generation trials in response to the identity of the target stimulus to assess their awareness of the motor sequence, as well as a series of cued generation trials in response to the location of the target stimulus to assess their awareness of the perceptual sequence. The presentation order of the identity and location generation tasks was counterbalanced between subjects.

For the motor sequence cued generation task, the test began with a cue trial in which participants responded as in the standard SRT task (using the keys z, x, n, m), but in this case the target stimulus appeared alone within a square placeholder at the centre of the screen. Following their response to the cue trial, participants were presented with an

empty square placeholder in the centre of the screen and were asked to generate the most likely successor of the item they responded to in the previous display, again using the same responses used in the standard SRT task. Given the nature of the grammars used to generate the sequences, two training successors were equally likely for each cue trial. For example, in the case of a participant for whom Grammar A was assigned as the motor sequence, the presentation of a heart in a cue trial would have the heart or the spade as equally likely training successors, and the diamond or the club as equally likely control successors.

For the perceptual sequence cued generation task, the task began with a cue trial in which participants responded to the location of an empty square placeholder that appeared along the vertical axis in the middle of the screen, where the other three placeholders were each occupied by the distractor shape. For these trials, participants responded to the uppermost, upper middle, lower middle, and lowest locations along the vertical axis using respectively the '9', '6', '3', and '.' keys on the number pad. Participants were not given instructions about which fingers to use. Following their response to the cue trial, participants were presented with four empty square placeholders along the central vertical axis of the screen and were asked to generate the most likely successor of the location they responded to in the previous display, again using the same response keys ('9', '6', '3', '.'). For these trials, participants had to generate where the target stimulus was most likely to appear following the location indicated in the cue trial. Once again, given the nature of the sequences used, two target locations were equally likely for each cue trial. For example, in the case of a participant for whom Grammar B

was assigned as the perceptual sequence, the presentation of the empty placeholder in the uppermost location in the cue trial would have the lower middle or the lowest locations as equally likely successors, and the upper middle or the uppermost locations as equally unlikely successors. For both generation tasks, each of the four possible cues was presented four times, in random order, thus completing a full set of 16 generation trials for each of the motor sequence and perceptual sequence generation tasks.

Indirect measures of sequence learning for the motor and perceptual sequences were derived by analyzing differences in mean RTs in the transfer blocks for training and control trials, separately for each sequence type. Direct measures of sequence learning were derived from performance on the generation tasks, by assessing whether participants generated more often the training or control successors of all the relevant cues. To determine whether motor and perceptual sequence learning effects were independent, mean RTs over the transfer blocks were compared for training and control trials as a function of both motor sequence trial type and perceptual sequence trial type.

Results

SRT Performance. RTs for the first trial of each block and for trials in which an error was made (2.9% of the trials) were not included in the analyses. In addition, RTs that were more than three standard deviations from the mean for each block, defined separately for each participant (2.1%), were treated as outliers and eliminated from the analyses. Mean RTs were then computed for each of the training and control motor sequence trials, as well as for each of the training and control perceptual sequence trials, separately for each block for each participant. Motor sequence learning was analyzed

using an analysis of variance with Transfer Block (1-4) and Trial Type (training/control) as within subjects factors. Perceptual sequence learning was analyzed in the same manner. Here and in all subsequent experiments, for the effects and interactions involving Transfer Block, we report nominal degrees of freedom along with Greenhouse-Geisser ε and adjusted p-levels.

Mean RT as a function of motor sequence trial type and block is presented in the left panel of Figure 2. For the motor sequence learning, the analysis revealed a main effect of Trial Type, $F(1,25) = 41.97$, $\eta^2_p = .55$, $p < .001$. Reaction times were faster for training trials (912ms) than for control trials (961ms). Mean RT as a function of perceptual sequence trial type and block is presented in the right panel of Figure 2. For perceptual sequence learning, the analysis revealed a main effect of Trial Type, $F(1,35) = 14.16$, $\eta^2_p = .29$, $p = .001$. Reaction times were faster for training trials (916ms) than for control trials (946ms).
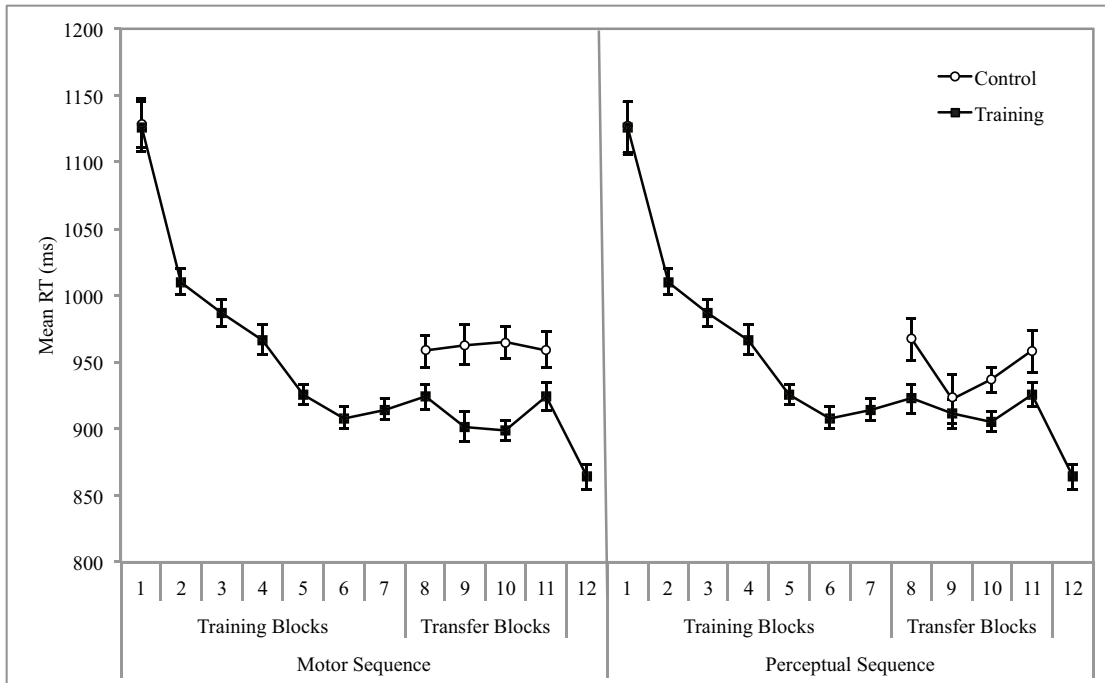
Figure 2. Mean RT as a function of training and control trials across training (blocks 1-7, and 12) and transfer (blocks 8-11) in Experiment 1, separately as a function of the motor and perceptual sequences. Error bars in this and all other figures represent the corrected standard error of the mean.

Independence of motor and perceptual learning. To assess the independence of the motor and perceptual sequence learning effects, mean RTs from the Transfer Blocks as a function of both motor sequence status and perceptual sequence status were submitted to an analysis of variance with Motor Sequence Trial Type (2) and Perceptual Sequence Trial Type (2) as within subjects factors. This analysis revealed main effects of both motor sequence trial type, $F(1,35) = 21.18$, $\eta^2_p = .38$, $p < .001$, and perceptual sequence trial type, $F(1,35) = 7.59$, $\eta^2_p = .18$, $p = .009$. Importantly, the interaction between motor and perceptual sequence trial types was not significant $F<1$. This additive pattern is consistent with the hypothesis that participants expressed the motor and

perceptual learning independently of one another. Mean RTs from the transfer blocks as

a function of motor sequence trial type and perceptual sequence trial type are presented in

Table 1.

Table 1. Mean reaction times (ms) and corrected standard errors as a function of motor
sequence trial type (training/control) and perceptual sequence trial type (training/control)
from the transfer blocks in Experiment 1 and training blocks in Experiments 2 & 3.

		Perceptual Sequence Trial Type	
	Motor Sequence Trial Type	Training	Control
Experiment 1	Training	906 (7)	934 (7)
	Control	956 (7)	990 (5)
Experiment 2	Training	900 (3)	919 (3)
	Control	924 (7)	943 (5)
Experiment 3	Training	889 (3)	903 (4)
	Control	930 (5)	943 (6)

Generation Task Performance. The implicit nature of the sequence learning

was derived from a comparison of sensitivity to the sequence in an indirect task (i.e.

performance on the SRT) to sensitivity to the sequence in a direct task (i.e. performance

on the generation tasks) (Reingold & Merikle, 1990). Performance on the generation

tasks was assessed by comparing the number of trials in which participants completed a

cue with a training successor to the number expected by chance. Chance performance is

derived from the idea that if sequence knowledge does not guide selection of successors

in the generation trials, then all four targets (or target locations) should be equally likely

to occur. As two of the targets (or target locations) are training successors for each cue, chance performance on the generation trials is the likelihood of selecting either of the two training successors by chance alone, which is .50.

To assess sensitivity in the direct task, mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the motor sequence generation tasks, participants did not generate more training successors (.53) from the cues than expected by chance, $t(35) = 1.01$, $p = .321$, $d = 0.17$ (control successors generated = .47). For the perceptual sequence generation tasks, participants did generate slightly more training successors (.55) from the cues than expected by chance, $t(35) = 2.35$, $p = .025$, $d = 0.39$ (control successors generated = .45).

Although the results did reveal some sensitivity to the probabilistic sequence in the perceptual sequence generation task, it is important to note that performance on generation tasks can be sensitive to both explicit and implicit forms of knowledge. As such, the modest effect observed in the perceptual sequence generation task does not necessarily undermine the view that implicit rather then explicit learning processes underlie the perceptual sequence learning effect observed in the indirect task. Nonetheless, this is an important issue to address. Indeed, we address this issue at length following discussion of the results of Experiments 2 and 3.

Discussion

The first goal in Experiment 1 was to confirm that our task was capable of measuring concurrent motor and perceptual sequence learning. To reiterate, previous work that has focused on measuring concurrent motor and perceptual sequence learning

has demonstrated that it can be difficult to find such effects reliably, and therefore it was

important to show that with our procedure we can measure concurrent learning of

uncorrelated motor and perceptual sequences. The second goal of Experiment 1 was to

evaluate whether learning effects in motor and perceptual sequence learning are

independent of one another. Participants completed an SRT task in which the identity

and the location of the target stimulus were independently determined by two different

sequences, derived from two complementary artificial grammars. The results of this

experiment indicate that participants were able to concurrently learn the motor and

perceptual sequences. In terms of our second goal, the results of this experiment indicate

that the motor sequence and perceptual sequence learning effects were independent of one

another. The additive pattern of motor and perceptual learning effects validates our

assumption that motor and perceptual learning effects are independent. Recall that a

caveat of examining cross-conflict sequential congruency effects is that the two sources

of conflict, or in this case sources of automatic response tendencies, are independent of

one another. Therefore the independence of the two types of learning allows us to

proceed and address the main question of this paper, which asks whether sequential

congruency effects (or modulations of learning effects as a function of the sequence status

of the preceding trial) can be observed in both motor and perceptual implicit learning, and

if the sequential congruency effects are conflict-type specific.

Experiment 2

The results of Experiment 1 indicate that we were able to measure concurrent

learning of a motor and a perceptual sequence. Now that we have a procedure with which

we can measure independent concurrent learning of uncorrelated motor and perceptual

sequences, we can proceed with the primary goal of this study, which is to examine

sequential congruency effects in both motor and perceptual sequence learning. Sequential

congruency effects involve the measurement of learning effects on one trial (performance

on training versus control trials, which can be considered analogous to congruency effects

in interference tasks) as a function of whether the target on the prior trial was a training

trial (which can be considered analogous to congruent trials in interference tasks) or a

control trial (which can be considered analogous to incongruent trials in interference

tasks) with the training sequence. To address this issue in Experiment 2, the design of

Experiment 1 was modified so that both motor and perceptual sequence learning effects

could be measured across all 12 experimental blocks. Specifically, across the 12

experimental blocks, the probability of transitions consistent with the training sequence

was .80, while the probability of transitions consistent with the control sequence was .20,

for each of the motor and perceptual sequences, independent of one another.

Methods

      Participants. Forty undergraduates (34 females; mean age = 20.3) enrolled at the

University of Granada or McMaster University participated in the experiment in

exchange for either course credit or $10. They had never participated in similar

experiments before. All participants had normal or corrected to normal vision.

      Apparatus and Stimuli. The apparatus and stimuli were identical to those used

in Experiment 1 with the exception that some of the participants tested at McMaster

University were tested in groups of two rather than individually, and for all McMaster

participants stimuli were presented on a 15inch Sony CRT monitor.

Procedure. The procedure was identical to that described in Experiment 1 with

the following exceptions. After the practice block of 30 trials, which was identical to that

described in Experiment 1, participants completed 12 blocks of 100 trials. The identity

and location of the target for trial 1 of each block were selected randomly. The identity

and location of the target on all subsequent trials in a block were selected according to the

training motor sequence for 80% of the trials, and according to the training perceptual

sequence for 80% of the trials.

Sequence learning was assessed as in Experiment 1 with the following exceptions.

Indirect measures of sequence learning for the motor and perceptual sequences were

derived from the mean RTs for training and control trials across all 12 blocks. The

independence of motor learning and perceptual learning effects was examined by

comparing mean RTs for training and control trials as a function of both motor sequence

trial type and perceptual sequence trial type across all 12 blocks.

Sequential congruency effects were assessed as a function of training period by

examining the effect of sequence learning (i.e. the difference between responding to

training and control trials) as a function of the preceding trial type (training vs. control).

Sequential congruency effects were first assessed separately for the motor sequence

learning and perceptual sequence learning to replicate the results of Jiménez et al. (2009)

and extend the finding to perceptual sequence learning. Following the analysis of within-

sequence sequential congruency effects, we examined the specificity of the sequential

congruency effects by assessing whether the effect of motor sequence learning was modulated by the perceptual sequence status of the preceding trial, as well as whether the effect of perceptual sequence learning was modulated by the motor sequence status of the preceding trial.

Results

      SRT Performance. RTs for the first trial of each block, and for trials in which an error was made (3.5% of the trials) were not included in the analyses. In addition, RTs that were more than three standard deviations from the mean of each condition defined by the factorial combination of block and trial type factors, separately for each participant (2.1%), were treated as outliers and eliminated from the analyses. Mean RTs were computed from the remaining observations for the training and control motor sequence trials, as well as for the training and control perceptual sequence trials, separately for each block for each participant. Motor sequence learning and perceptual sequence learning were each analyzed using an analysis of variance with Block (1-12) and Trial Type (training/control) as within subjects factors.

      Mean RT as a function of motor sequence trial type and block are presented in the left panel of Figure 3. The analysis revealed a main effect of block, $F(11,429) = 15.52$, $\eta^2_p = .29$, $p < .001$, $\varepsilon = .55$. Importantly, the analysis also confirmed a main effect of trial type, $F(1,39) = 35.56$, $\eta^2_p = .48$, $p < .001$. Responses were faster for training trials (904ms) than for control trials (929ms). The interaction between block and trial type was not significant, $F(11, 429) = 1.09$, $\eta^2_p = .03$, $p = .368$, $\varepsilon = .65$.
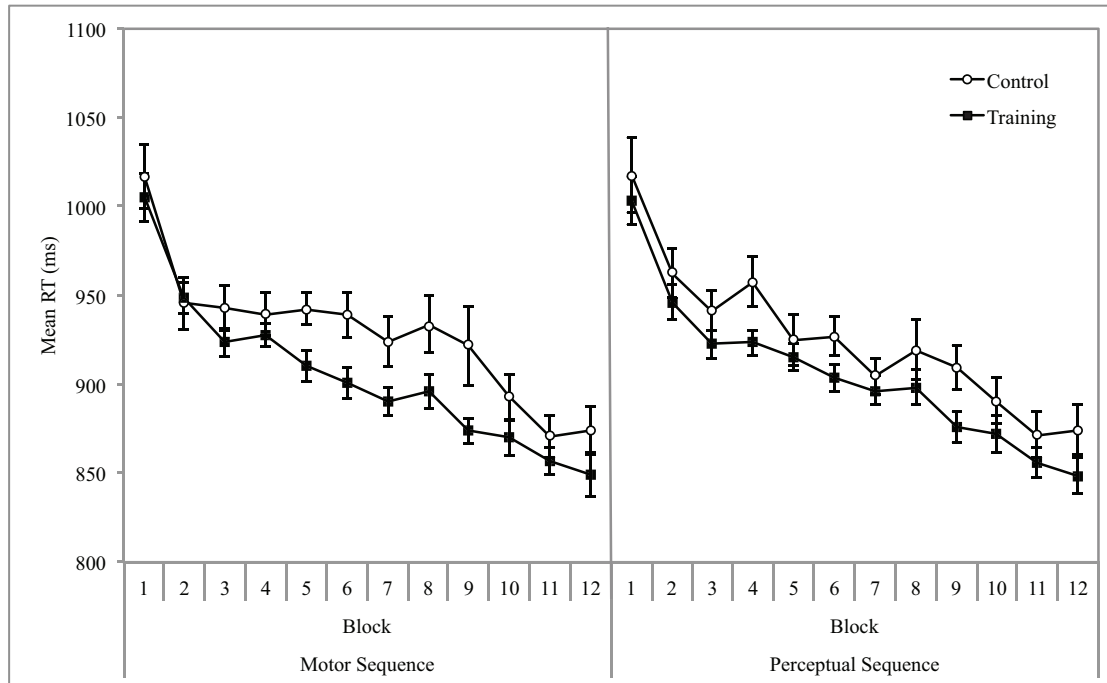
Figure 3. Mean RT as a function of training and control trials across 12 training blocks in Experiment 2, separately as a function of the motor and perceptual sequences.

Mean RT as a function of perceptual sequence trial type and block are presented in the right panel of Figure 3. The analysis revealed a main effect of block, $F(11,429) = 16.68$, $\eta^2_p = .30$, $p < .001$, $\varepsilon = .58$. Importantly, the analysis also revealed a main effect of trial type, $F(1,39) = 26.39$, $\eta^2_p = .40$, $p < .001$; responses were faster for training trials (905ms) than for control trials (925ms). The interaction between block and trial type was not significant, $F(11, 429) = .372$, $\eta^2_p = .01$, $p = .932$, $\varepsilon = .71$.

Independence of motor and perceptual learning. The independence of the motor sequence learning and perceptual sequence learning was assessed by analyzing mean RTs as a function of both motor sequence status and perceptual sequence status in an analysis of variance with Motor Sequence Trial Type (2) and Perceptual Sequence

Trial Type (2) as within subjects factors. This analysis revealed both main effects of motor sequence trial type, $F(1,39) = 31.09$, $\eta^2_p = .44$, $p < .001$, and perceptual sequence trial type, $F(1,39) = 25.05$, $\eta^2_p = .39$, $p < .001$, that are described in the previous analyses. Importantly, the interaction between motor and perceptual sequence trial types was not significant, $F<1$. This additive pattern indicates that participants learned and expressed knowledge of the motor and perceptual sequences independently of one another. Mean RTs as a function of motor sequence trial type and perceptual sequence trial type are presented in Table 1.

Sequential congruency. In line with common practice in the literature, for the analysis of sequential congruency effects post-error trials were excluded, as they are typically associated with increased RTs (Rabbitt, 1966). Sequential congruency effects were analyzed separately for the motor and perceptual sequence learning, by submitting RTs to two separate analyses of variance with Trial Type (training/control), and Preceding Trial Type (training/control) included as within subjects factors.

Mean RTs for each motor sequence trial type and preceding motor sequence trial type are presented in the top left panel of Figure 4. For motor sequence learning, the analysis revealed a main effect of trial type $F(1,39) = 25.58$, $\eta^2_p = .40$, $p < .001$. Importantly, the analysis revealed an interaction between trial type and preceding trial type, $F(1,39) = 5.31$, $\eta^2_p = .12$, $p = .027$. This interaction reflects a significant motor sequence learning effect (29ms) when the preceding trial followed the training sequence, $t(39) = 6.68$, $p < .001$, which was no longer significant when the preceding trial type was a control trial, $t(39) = 1.62$, $p = .114$ (mean motor sequence learning effect = 11ms).
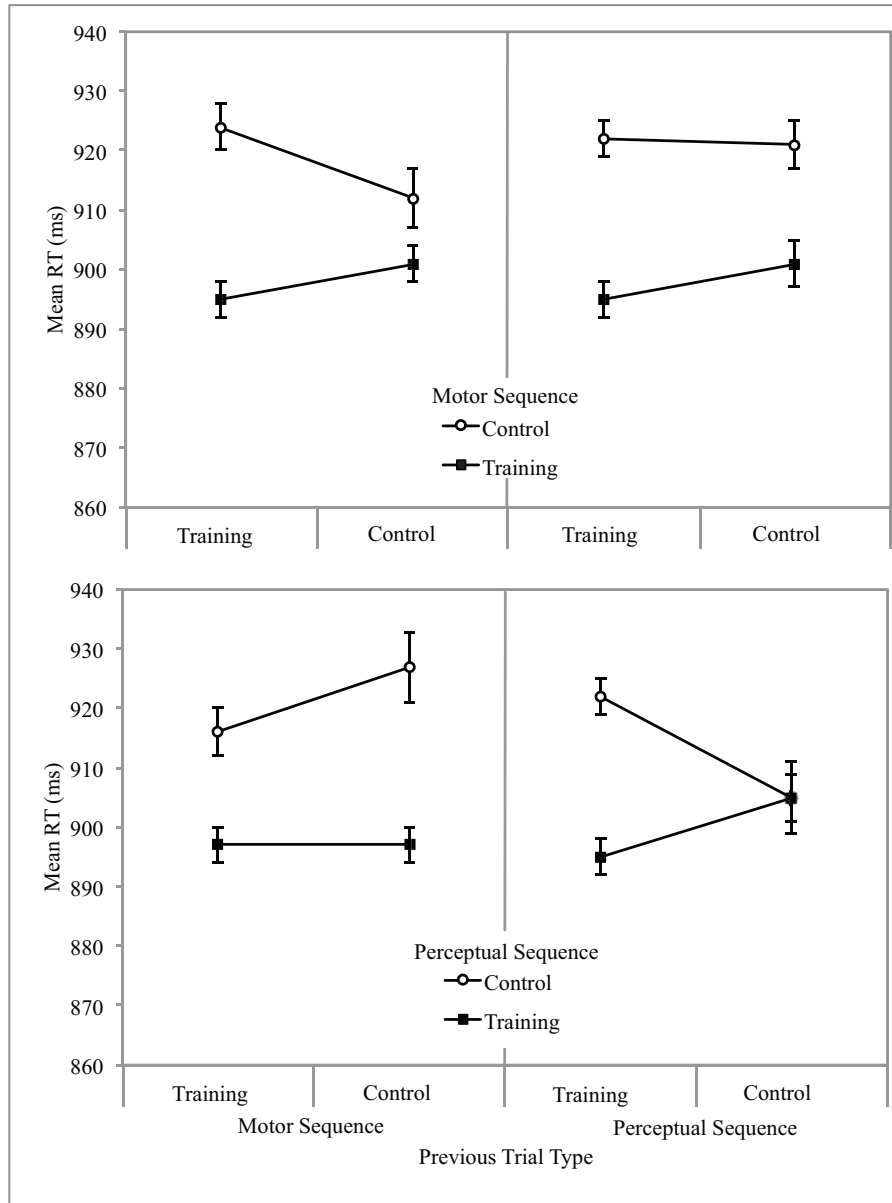
Figure 4. *Top Left Panel:* Mean RT for training and control motor sequence trials in Experiment 2 as function of the type of motor sequence trial presented on the preceding trial. *Top Right Panel:* Mean RT for training and control motor sequence trials in Experiment 2 as function of the type of perceptual sequence trial presented on the preceding trial. *Bottom Left Panel:* Mean RT for training and control perceptual sequence trials in Experiment 2 as function of the type of motor sequence trial presented on the preceding trial. *Bottom Right Panel:* Mean RT for training and control perceptual

sequence trials in Experiment 2 as function of the type of perceptual sequence trial presented on the preceding trial.

Mean RTs as a function of perceptual sequence trial type and preceding perceptual sequence trial type are presented in the bottom right panel of Figure 4. For perceptual sequence learning, the analysis revealed a main effect of trial type $F(1,39) = 8.72$, η^2_p = .18, p = .005. Importantly, the analysis revealed an interaction between trial type and preceding trial type, $F(1,39) = 8.07$, $\eta^2_p = .17$, $p = .007$.   This interaction reflects significant perceptual sequence learning effect (27ms) when the location of the target symbol on the preceding trial was predicted by the training sequence, $t(39) = 7.04$, p < .001, which disappeared completely when the preceding trial was a control trial, $t(39) =$ -.05, p = .959 (mean perceptual sequence learning effect = 0ms).

Specificity of sequential congruency effects. The specificity of the sequential congruency effects was examined using two complementary analyses. First, the effect of motor sequence trial type was examined as a function of the preceding trial's perceptual sequence status. Second, the effect of perceptual sequence trial type was examined as a function of the preceding trial's motor sequence status. If the sequential congruency effects reported above reflect the engagement of a general form of control, then sequential congruency effects should emerge in these two analyses. Conversely, if the sequential congruency effects reported above reflect a process-specific form of control, as suggested by previous work (Funes et al., 2010a; 2010b), then there should be no evidence of sequential congruency effects in the following analyses.

Mean RTs as a function of motor sequence trial type and preceding perceptual sequence trial type are presented in the top right panel of Figure 4. The analysis of motor sequence trial type as a function of the preceding trial's perceptual sequence status did not reveal an interaction between the two factors, $F(1,39) = 1.01$, $\eta^2_p = .03$, $p = .321$.

Mean RTs as a function of perceptual sequence trial type and preceding motor sequence trial type are presented in the bottom left panel of Figure 4. In the analysis of perceptual sequence trial type as a function of preceding trial's motor sequence status, the interaction between trial type and preceding trial type also failed to reach significance, $F(1,39) = 1.68$, $\eta^2_p = .04$, $p = .203$. As such, there was no evidence in either analysis that the sequential congruency effects for either motor learning or perceptual learning generalized to the other form of learning.

Generation Task Performance. Performance on the generation tasks was assessed by comparing the number of trials in which participants completed a cue with a training successor to the number expected by chance. Mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the motor sequence generation tasks, participants generated marginally more training successors (.54) from the cues than expected by chance, $t(39) = 1.89$, $p = .066$, $d = 0.30$ (control successors generated = .46). For the perceptual sequence generation tasks, participants generated more training successors (.55) from the cues than expected by chance, $t(39) = 3.16$, $p = .003$, $d = 0.50$ (control successors generated = .45). Once again, as for the perceptual sequence learning in Experiment 1, the pattern of results showed a modest ability to discriminate between training and control successors for both

the perceptual and motor sequence learning. We address this issue in detail following the results of Experiment 3.

Discussion

The goal of Experiment 2 was first to replicate and extend the finding of sequential congruency effects for motor sequence learning reported by Jiménez et al. (2009) to the concurrent learning of motor and perceptual sequences. The results of indirect and direct measures of learning in Experiment 2 indicate that participants were able to learn independently the motor and perceptual sequences with the design employed in Experiment 2. More important, the results of Experiment 2 replicate the sequential congruency effects in motor learning reported by Jiménez et al. and extend the finding to perceptual sequence learning. The second goal of Experiment 2 was to examine the specificity of sequential effects in sequence learning. The results of Experiment 2 indicate that the sequential congruency effects measured were specific to the type of conflict associated with each type of sequence learning, as the transition to a motor sequence control trial did not attenuate perceptual learning measured on the following trial, and transition to a perceptual sequence control trial did not attenuate the motor sequence learning measured on the following trial. This result is broadly consistent with previous work that has demonstrated conflict-type specificity of sequential congruency effects in interference tasks (e.g. Funes et al., 2010a). Experiment 3 was conducted to replicate these key effects with another group of participants.

Experiment 3

The goal of Experiment 3 was primarily to provide a replication of the sequential congruency effects and the specificity of these effects, as reported in Experiment 2. A secondary goal of Experiment 3 was to examine whether sequential congruency effects are observed when target identity and location are randomly selected. To that end, sequential congruency effects were also examined in a set of transfer blocks where the proportion of training trials and control trials were each set to .50.

Methods

Participants. Fifty-six undergraduates (38 females; mean age = 20) enrolled at McMaster University participated in the experiment in exchange for course credit. They had never participated in similar experiments before. All participants had normal or corrected to normal vision. Two participants did not complete the perceptual sequence generation task due to computer errors.

Apparatus and Stimuli. The apparatus and stimuli were identical to those used in Experiment 2 with the following exceptions. Participants were tested in groups of two or three, and stimuli were presented on a 15inch Sony CRT monitor. The experimental program was designed using Presentation® experimental software (v.10.3, www.neurobs.com).

Procedure. The procedure was identical to that described in Experiment 2 with the following exceptions. After the practice block of 30 trials, which was identical to that described in Experiment 2, participants completed 15 blocks of 100 trials, including 10 training blocks, 4 transfer blocks, and a final training block to re-establish the learned

contingencies before the generation tasks were presented. The identity and location of the target for trial 1 of each block were selected randomly. Participants were trained across 10 blocks in which the identity and location of the target on all subsequent trials were selected according to the training motor sequence for 80% of the trials, and according to the training perceptual sequence for 80% of the trials, independent of one another. Blocks 1-10 are referred to as training blocks.

Following the training blocks, participants completed four transfer blocks in which the identity and location of the target on all trials were selected according to the training motor sequence for 50% of the trials, and according to the training perceptual sequence for 50% of the trials, independent of one another. Given that the training sequences were derived from artificial grammars in which 2 training successors were equally likely to follow any one position within the grammar, training probabilities of 50% within a block of trials results in the random selection of identities/locations. Blocks 11-14 are referred to as transfer blocks. Lastly, the training probabilities were restored over a final training block (block 15), as a way to re-establish the learned contingencies before proceeding to the Generation Task.

Sequence learning was assessed as in Experiment 2 with the following exceptions. Indirect measures of sequence learning for the motor and perceptual sequences were each derived from the mean RTs for the respective training and control trials and were analyzed separately for the first 10 training blocks and for the 4 transfer blocks. The independence of motor learning and perceptual learning effects was examined by comparing mean RTs for training and control trials as a function of both motor sequence

trial type and perceptual sequence trial type across the 10 training blocks. Sequential

congruency effects were assessed as in Experiment 2 with the exception that all

sequential congruency effects were assessed separately for training and transfer blocks.

Results

      SRT Performance.   RTs for the first trial of each block, and for trials in which

an error was made (5.4% of the trials), were not included in the analyses. In addition,

RTs that were more than three standard deviations from the mean of each condition

defined by the factorial combination of block and trial type factors, separately for each

participant (2.3%), were treated as outliers and eliminated from the analyses. Mean RTs

were computed from the remaining observations for the training and control motor

sequences, as well as for the training and control perceptual sequences, separately for

each block for each participant. Motor sequence learning and perceptual sequence

learning were each analyzed using an analysis of variance with Training Block (1-10) and

Trial Type (training/control) as within-subject factors. To examine sequence learning

effects in the transfer blocks, motor sequence learning and perceptual sequence learning

were each analyzed using an analysis of variance with Transfer Block (11-14) and Trial

Type (training/control) as within-subject factors.

      Mean RT as a function of motor sequence trial type and block are presented in the

left panel of Figure 5. The analysis of motor sequence learning in the training blocks

revealed a main effect of block, $F(9,495) = 26.96$, $\eta^2_p = .33$, $p < .001$, $\varepsilon = .67$.

Importantly, the analysis also confirmed a main effect of trial type, $F(1,55) = 37.63$, η^2_p

$= .41$, $p < .001$. Responses were faster for training trials (913ms) than for control trials

(949ms). The interaction between block and trial type was not significant, $F(9, 495) =$ 1.10, $\eta^2_p = .02$, $p = .361$, $\varepsilon = .76$. The analysis of motor sequence learning in the transfer blocks revealed a main effect of trial type, $F(1,55) = 11.35$, $\eta^2_p = .17$, $p = .001$. Responses were faster for training trials (865ms) than for control trials (883ms), indicating that participants continued to express sequence knowledge when the identity of the target was no longer predicted by the motor training sequence.
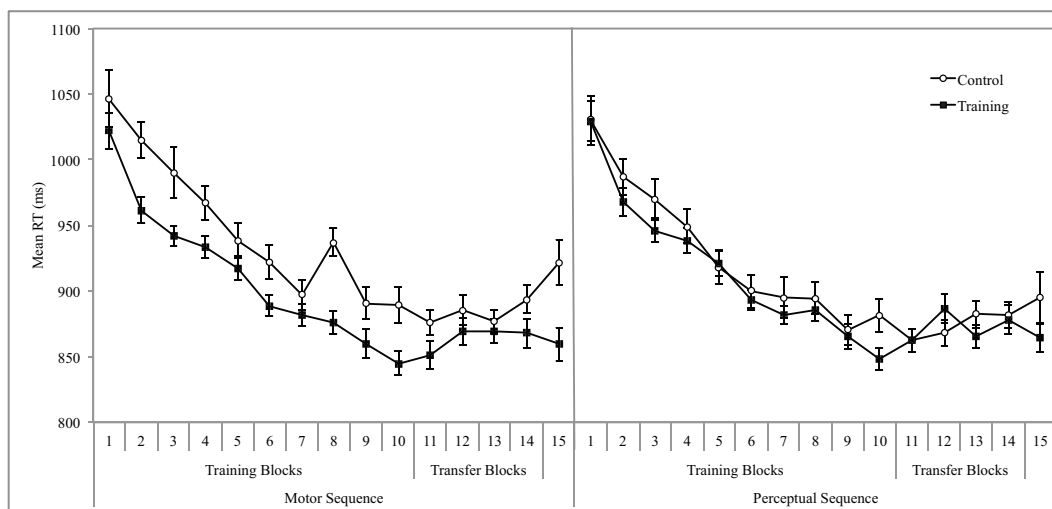
Figure 5. Mean RT as a function of training and control trials across training (blocks 1-10, and 15) and transfer (blocks 11-14) in Experiment 3, separately as a function of the motor and perceptual sequences.

Mean RT as a function of perceptual sequence trial type and block are presented in the right panel of Figure 5. The analysis of perceptual sequence learning in the training blocks revealed a main effect of block, $F(9,495) = 28.81$, $\eta^2_p = .34$, $p < .001$, $\varepsilon = .68$. Importantly, the analysis also confirmed a main effect of trial type, $F(1,55) = 7.77$, $\eta^2_p = .12$, $p = .007$. Responses were faster for training trials (918ms) than for control trials (929ms). The interaction between block and trial type was not significant, $F(9, 495) =$

0.57, $\eta^2_p = .01$, $p = .792$, $\varepsilon = .84$. The analysis of perceptual sequence learning in the

transfer blocks revealed no significant effects. In contrast to the analysis of motor

sequence learning, the main effect of perceptual sequence trial type was not significant

$F(1,55) = 0.011$, $\eta^2_p = .00$, $p = .917$.

  Independence of motor and perceptual learning. The independence of the

motor sequence learning and perceptual sequence learning was assessed by analyzing

mean RTs from the training blocks as a function of both motor sequence status and

perceptual sequence status in an analysis of variance with Motor Sequence Trial Type (2)

and Perceptual Sequence Trial Type (2) as within-subject factors. This analysis revealed

a main effect of motor sequence trial type, $F(1,55) = 51.55$, $\eta^2_p = .48$, $p < .001$. The main

effect of perceptual sequence trial type was also significant $F(1,55) = 6.56$, $\eta^2_p = .11$, p

$= .013$. Importantly, the interaction between motor sequence trial type and perceptual

sequence trial type was not significant, $F(1,55) = 0.001$, $\eta^2_p = .00$, $p = .972$. Once more,

this additive pattern indicates that participants learned and expressed knowledge of the

motor and perceptual sequences independently of one another. Mean RTs as a function

of motor sequence trial type and perceptual sequence trial type for the training blocks are

shown in Table 1.

Sequential congruency. Sequential congruency effects were analyzed in the same way

as in Experiment 2. Sequential congruency effects were analyzed separately for the

motor and perceptual sequence learning, by submitting RTs to two separate analyses of

variance with Trial Type (training/control) and Preceding Trial Type (training/control)

included as within subjects factors. Sequential congruency effects were analyzed

separately for performance on the training blocks and transfer blocks.

Mean RTs for motor sequence trial type and preceding motor sequence trial type,

for training blocks are presented in the top left panel of Figure 6. For the training blocks,

the analysis revealed a main effect of trial type $F(1,55) = 27.38$, $\eta^2_p = .33$, $p < .001$. More

importantly, the analysis revealed an interaction between trial type and preceding trial

type, $F(1,55) = 5.81$, $\eta^2_p = .096$, $p = .019$. This interaction reflects a significant motor

sequence learning effect (47ms) when the preceding trial followed the training sequence,

$t(55) = 6.85$, $p < .001$, which was not significant when the preceding trial type was a

control trial, $t(55) = 1.48$, $p = .092$ (mean motor sequence learning effect = 17ms).
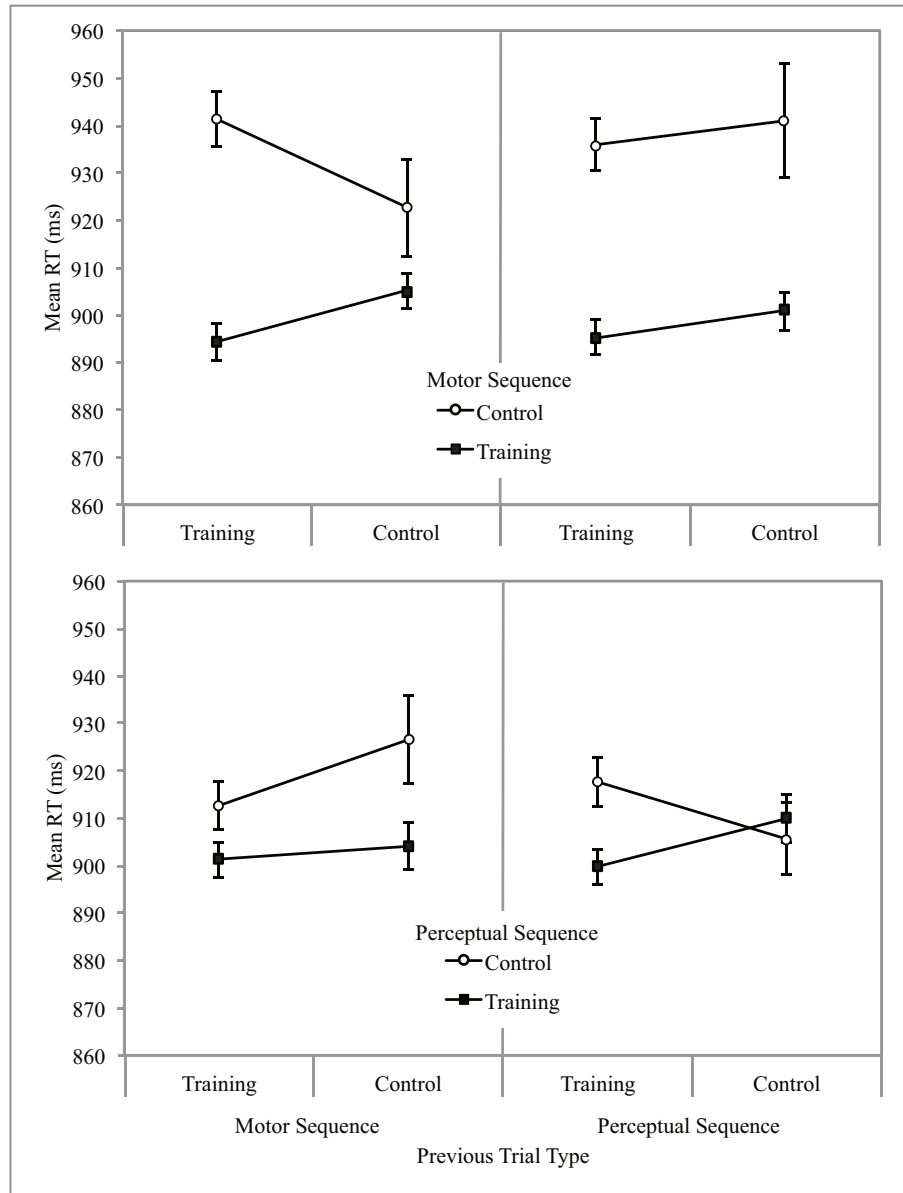
Figure 6. *Top Left Panel:* Mean RT for training and control motor sequence trials in Training Blocks (1-10) of Experiment 3 as function of the type of motor sequence trial presented on the preceding trial. *Top Right Panel:* Mean RT for training and control motor sequence trials in Training Blocks (1-10) of Experiment 3 as function of the type of perceptual sequence trial presented on the preceding trial. *Bottom Left Panel:* Mean RT for training and control perceptual sequence trials in Training Blocks (1-10) of Experiment 3 as function of the type of motor sequence trial presented on the preceding trial. *Bottom Right Panel:* Mean RT for training and control perceptual sequence trials in

Training Blocks (1-10) of Experiment 3 as function of the type of perceptual sequence trial presented on the preceding trial.

For the transfer blocks, the analysis revealed a main effect of trial type $F(1,55) =$ 14.50, $\eta^2_p = .21$, $p < .001$. The interaction between trial type and preceding trial type was not significant, $F(1,55) = 2.72$, $\eta^2_p = .05$, $p = .105$, although the pattern of results is consistent with the pattern observed in the training blocks. Planned comparisons indicate that there was a significant motor sequence learning effect (34ms) when the preceding trial followed the training sequence, $t(55) = 3.64$, $p = .001$, which was not significant when the preceding trial type was a control trial, $t(55) = 0.57$, $p = .571$ (mean motor sequence learning effect = 6ms).

Mean RTs for perceptual sequence trial type and preceding perceptual sequence trial type, for training blocks are presented in the bottom right panel of Figure 6. For the training blocks, the analysis revealed a significant interaction between trial type and preceding trial type, $F(1,55) = 4.44$, $\eta^2_p = .08$, $p = .040$. Planned comparisons indicate that there was a significant perceptual sequence learning effect (18ms) when the preceding trial followed the training sequence, $t(55) = 3.47$, $p = .001$, which was eliminated when the preceding trial type was a control trial, $t(55) = -0.456$, $p = .650$ (mean perceptual sequence learning effect = -4ms).

For the transfer blocks, the analysis revealed no significant main effects. The interaction between trial type and preceding trial type was not significant, $F(1,55) = 1.20$, $\eta^2_p = .02$, $p = .279$. Planned comparisons indicate that the perceptual sequence learning effect (-4ms) was not significant when the preceding trial followed the training sequence,

$t(55) = -0.543$, $p = .589$, nor when the preceding trial type was a control trial, $t(55) =$ 0.851, $p = .399$ (mean perceptual sequence learning effect = 5ms).

Specificity of sequential congruency effects. As in Experiment 2, the specificity of the sequential congruency effects was examined using two complementary analyses. First, the effect of motor sequence trial type was examined as a function of the preceding trial's perceptual sequence status. Second, the effect of perceptual sequence trial type was examined as a function of the preceding trial's motor sequence status. These crossed sequential congruency effects were analyzed separately for performance on the training blocks and transfer blocks.

Mean RTs as a function of motor sequence trial type and preceding perceptual sequence trial type are presented for training blocks in the top right panel of Figure 6. The analysis of motor sequence trial type as a function of the preceding trial's perceptual sequence status for the training blocks did not reveal an interaction between the two factors, $F(1,55) = 0.001$, $\eta^2_p = .00$, $p = .975$. For the analysis of the transfer blocks, the interaction between motor sequence trial type and preceding perceptual sequence trial type was also not significant, $F(1,55) = 0.00$, $\eta^2_p = .00$, $p = .991$.

Mean RTs as a function of perceptual sequence trial type and preceding motor sequence trial type are presented for training blocks in the bottom left panel of Figure 6. The analysis of perceptual sequence trial type as a function of the preceding trial's motor sequence status for the training blocks did not reveal an interaction between the two factors, $F(1,55) = 1.03$, $\eta^2_p = .02$, $p = .315$. For the analysis of the transfer blocks, the

interaction between motor sequence trial type and preceding perceptual sequence trial type was also not significant, $F(1,55) = 0.855$, $\eta^2_p = .02$, $p = .359$.

Generation Task Performance. Performance on the generation tasks was assessed by comparing the number of trials in which participants completed a cue with a training successor to the number expected by chance. Mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the motor sequence generation tasks, participants generated marginally more training successors (.53) from the cues than expected by chance, $t(55) = 1.91$, $p = .061$, $d = 0.26$ (control successors generated = .47). Two participants did not complete the perceptual sequence generation task due to a computer error, but the participants who did complete the task did not generate more training successors (.49) from the cues than expected by chance, $t(53) = -.286$, $p = .776$, $d = 0.04$ (control successors generated = .51).

Supplementary analyses to control for direct knowledge of the sequences.

Given the marginally significant effect in the motor sequence generation tasks in Experiments 2 and 3, and the significant effect in the perceptual sequence generation task in Experiment 2, the effects of motor sequence learning, perceptual sequence learning, and all sequential congruency effects were reanalyzed after removing, for each participant, those RTs that corresponded to the parts of the training sequence that had been correctly generated in response to the appropriate cues. In other words, RTs that were possibly associated with explicit knowledge were removed and the remaining RTs were analyzed. For example, if a participant was trained on Grammar A for the motor sequence and that participant generated the heart (corresponding to position 1 in the

grammar) more than once when he or she was prompted with the fragment containing a heart, then RTs corresponding to that particular training sequence transition were removed from the data for this particular learner. Using this method, approximately 44% of trials were excluded from Experiment 2 and 33% of trials were excluded from Experiment 3. Given that the structure of the training blocks in Experiments 2 and 3 were identical, and that this exclusion method eliminated a large number of trials, the remaining observations for Experiments 2 and 3 were combined for the following analyses. For Experiment 2, only data from the first 10 training blocks were included in the following analyses. For Experiment 3, the two participants who did not complete the perceptual generation task were not included in the analyses involving perceptual sequence learning or in the analyses of sequential congruency effects involving perceptual sequence learning.

The pattern of results was not substantially changed by these restrictions. The corresponding ANOVA for the effect of motor sequence learning in the training block over those trials which were not generated better than chance still showed a significant main effect of trial type, $F(1,95) = 10.39$, $\eta^2_p = .10$, $p = .002$. The corresponding ANOVA for the effect of perceptual sequence learning in the training block over those trials which were not generated better than chance still showed a significant main effect of trial type, $F(1,93) = 7.12$ $\eta^2_p = .07$, $p = .009$. Mean RTs for the analyses of sequential congruency effects on training trials that were not generated better than chance are depicted in Figure 7. For the motor sequential congruency effect, the analyses conducted on those training trials that had not been generated better than chance also showed a

significant interaction between trial type and preceding trial type, $F(1,95) = 15.91$, $\eta^2_p =$ .14, $p < .001$. For the perceptual sequential congruency effect, the analyses conducted on those training trials that had not been generated better than chance also showed a significant interaction between trial type and preceding trial type, $F(1,93) = 11.44$, $\eta^2_p =$ .11, $p = .001$. For the analyses examining the specificity of the sequential congruency effects, the analyses conducted on those training trials that had not been generated better than chance also revealed no significant interactions between motor sequence trial type and preceding perceptual sequence trial type, $F < 1$, or perceptual sequence trial type and preceding motor sequence trial type, $F(1,93) = 1.33$, $\eta^2_p = .01$, $p = .251$. Overall, these analyses reinforce the claim that both the effects of sequence learning and those of sequential congruency within the training blocks are non-conscious.
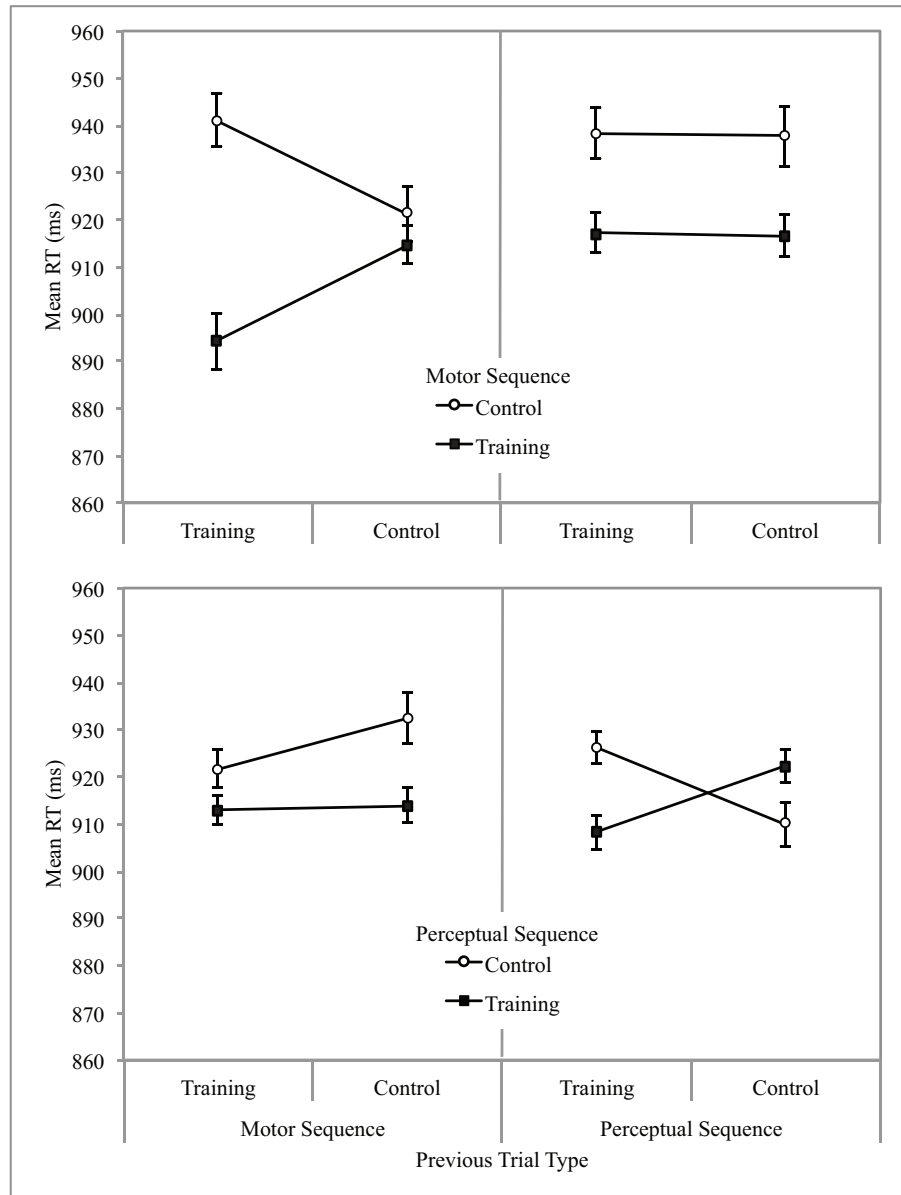
Figure 7. *Top Left Panel:* Mean RT for training and control motor sequence trials in Training Blocks (1-10) of Experiment 2 and 3 as function of the type of motor sequence trial presented on the preceding trial. *Top Right Panel:* Mean RT for training and control motor sequence trials in Training Blocks (1-10) of Experiment 3 as function of the type of perceptual sequence trial presented on the preceding trial. *Bottom Left Panel:* Mean RT for training and control perceptual sequence trials in Training Blocks (1-10) of Experiment 3 as function of the type of motor sequence trial presented on the preceding trial . *Bottom Right Panel:* Mean RT for training and control perceptual sequence trials in Training Blocks (1-10) of Experiment 3 as function of the type of perceptual sequence

trial presented on the preceding trial. In all panels, mean RTs for training trials include only trials that participants did not generate above chance in the generation tasks.

Discussion

The goal of Experiment 3 was first to replicate the results of Experiment 2, and second to examine whether sequential congruency effects are maintained when the identity and location of the target are randomly determined. To that end, four transfer blocks were included in which the target's identity and location were randomly selected. The results of indirect and direct measures of learning in Experiment 3 indicate that participants were able to learn independently the motor and perceptual sequences in the training blocks of the experiment. More important, the results of Experiment 3 replicate the sequential congruency effects in motor learning and in perceptual learning in the training blocks. Further, the results of Experiment 3 replicate the findings of Experiment 2, which indicate that the sequential congruency effects measured were specific to the conflict associated with control trials within each of motor and perceptual sequence learning, as the transition to a motor sequence control trial did not attenuate perceptual sequence learning measured on the following trial, and the transition to a perceptual sequence control trial did not attenuate the motor sequence learning measured on the following trial. Once again, these results are broadly consistent with previous work that has demonstrated conflict-type specificity of sequential congruency effects in interference tasks (e.g. Funes et al., 2010a).

The results also indicate that while sequential congruency effects within motor sequence learning and within perceptual sequence learning were observed in the training

blocks, the effects were no longer reliable in the transfer blocks. These results may indicate that there is a trade-off between conflict-specific transient control that produces sequential congruency effects, and proactive modes of control that are engaged in response to conflict predicted by the global context. In any case, the addition of the transfer blocks here was intended to be exploratory, and a more in-depth analysis of the trade-off between transient and proactive modes of control in sequence learning is left for future work.

Finally, and of primary importance, the results of the analyses of training trials that were not generated better than chance corroborate all of the previous analyses in suggesting that independent motor and perceptual sequence learning effects can be measured with our task, that sequential congruency effects for motor and perceptual sequence learning can also be measured, and that these sequential congruency effects are learning-type specific. Perceptual sequence learning effects are modulated by the perceptual sequence learning status, but not the motor sequence learning status, of the immediately preceding trial. Motor sequence learning effects are modulated by the motor sequence learning status, but not the perceptual sequence learning status, of the immediately preceding trial. The fact that these analyses were conducted using only transitions that were not generated by participants with higher than chance likelihood clearly suggests that the underlying learning processes are non-conscious.

General Discussion

The goal of the present study was to examine the specificity of sequential congruency effects measured using implicit learning methods. To address this issue, a

task was needed in which both motor sequence learning and perceptual sequence learning could be observed, and it was necessary to demonstrate that these two forms of learning could impact performance independently. The results of Experiment 1 satisfied both objectives, as participants concurrently learned a motor sequence and a perceptual sequence, and the motor sequence and perceptual sequence learning effects did not interact. The additive effects of motor sequence and perceptual sequence in turn validated the analysis of cross-conflict sequential congruency effects carried out in Experiments 2 and 3 (Egner, 2008). In Experiment 2, we replicated the sequential congruency effects for motor sequence learning reported by Jiménez et al. (2009), and extended the finding of sequential congruency effects to perceptual sequence learning. Of particular interest, in Experiment 2 we found no evidence that the sequential congruency effects generalized across the type of sequence learning; the perceptual sequence trial type of the preceding trial did not modulate the expression of motor sequence learning on the current trial, nor did the motor sequence trial type of the preceding trial modulate the expression of perceptual learning on the current trial. In Experiment 3 we replicated the sequential congruency effects in motor and perceptual sequence learning, while also replicating the specificity of the sequential congruency effects.

Sequential Congruency Effects in Sequence Learning

Before discussing the implications of the results from the current set of experiments, a discussion of an alternative interpretation of the sequential congruency effects reported by Jiménez et al. (2009) is warranted. As was discussed in the

introduction, Jiménez et al. (2009) interpreted their finding of sequential congruency effects in motor sequence learning as evidence for transient control processes that can inhibit or reduce the contribution of automatic response tendencies. In contrast to this interpretation, Beesley, Jones, and Shanks (2012) have recently proposed an associative learning account of sequential congruency effects in sequence learning.

The interpretation of sequential congruency effects in sequence learning described by Beesley et al. (2012) suggests that sequential congruency effects are not due to the engagement of control, but are in fact due to learning of higher-order associations between elements of a sequence. Using the Simple Recurrent Network model (SRN, Elman, 1990) Beesley et al. simulated the sequential congruency effects reported by Jiménez et al (2009), demonstrating that sequence learning sequential effects can arise, from a computational perspective, because following control trials there is a decreased amount of sequence information that can be used to make predictions on the current trial. It is noteworthy, of course, that the SRN model does not have a mechanism to facilitate or inhibit responses by 'top-down' control processes, and therefore the simulations of Beesley et al. demonstrate, in principle, that sequential congruency effects need not be attributed to cognitive control processes. The results of the simulations also showed that the SRN model makes specific predictions concerning the magnitude of the sequential congruency effects across training. In particular, the SRN model simulations predicted that the magnitude of the sequential congruency effects should increase across training. Beesley et al. confirmed these predictions in a reanalysis of data originally reported in Experiment 3 of Shanks, Wilkinson, and Channon (2003).

At this point, it is clear that Beesley et al. (2012) have demonstrated that an associative model, such as the SRN, can adequately account for sequential congruency effects found when participants learn second-order conditional sequences. The associative account put forward by Beesley et al. has the advantage of being more parsimonious than an alternative cognitive control account. However, the associative account and the cognitive control account of sequential congruency effects in the SRT task differ in terms of their predictions when a simpler sequence structure is used, as was the case in the current set of experiments. In the current set of experiments first-order sequences were used in which the relevant sequential information is exhausted by the identity or the location of the target in a single previous trial. Recall that in these first-order sequences only the immediately preceding trial provides sequential information, meaning that by themselves the trials that occurred prior to the immediately preceding trial do not provide any sequential information. In these conditions the SRN is unable to extract additional predictive information out of a larger context, and therefore the associative account predicts no difference between the effect of sequence learning observed after a control trial or after a training trial. In contrast, if sequential congruency effects are not produced by the system's sensitivity to higher-order conditionals, but instead are produced by a control adaptation produced in response to an 'unusual' trial, then sequential congruency effects could be found when a simpler sequence structure is used. Indeed, we simulated the results of Experiments 2 and 3 using the SRN and found that, in contrast to the sequential congruency effects observed in the data from the human

participants, the model was unable to predict a sequential congruency effect when first-order sequences were used. Details of the simulations are provided in the Appendix.

The results of the simulations of Experiments 2 and 3 using the SRN indicate that although both an associative account and a cognitive control account can predict sequential congruency effects when second-order conditional sequences are used, the SRN does not predict sequential congruency effects when simpler sequence structures are used. At this point, given the results of the SRN simulations, we propose that the sequential congruency effects observed in the current set of experiments are better accounted for by a cognitive control account.

Control in sequence learning

To this point in the article, the sequential congruency effects reported have been assumed to be analogous to the sequential congruency effects that are often reported in interference tasks, such as the flanker task. Overall, in both sequence learning and interference tasks sequential congruency effects reflect the reduction of either sequence learning or an interference effect following trials requiring increased cognitive control. For example, in the flanker task sequential congruency effects reflect a smaller interference effect following incongruent trials. In the flanker task, the reduced interference effects are the result of slower performance on congruent trials and faster performance on incongruent trials following an incongruent trial. In this context, the engagement of control on an incongruent trial may result in a decrease in processing of flanking items present in the following trial. Similarly, in the current experiments the sequential congruency effects reflect a reduced sequence learning effect following control

trials. In sequence learning, the reduced sequence learning effects are the result of slower performance on training trials and faster performance on control trials following control trials. In this context, the engagement of control on a control trial may result in a reduced reliance on any predictions that are derived from sequence knowledge, the result of which is a decreased sequence learning effect.

On the specificity of sequential congruency effects

The purpose of the current study was to examine whether sequential congruency effects in implicit sequence learning are conflict-type specific. The results of the sequential congruency effects reported in Experiments 2 and 3 demonstrate that although the expression of motor sequence learning was modulated by the motor sequence status of the preceding trial, motor sequence learning was not modulated by the perceptual sequence status of the preceding trial. Similarly, although the expression of perceptual sequence learning was modulated by the perceptual sequence status of the preceding trial, perceptual sequence learning was not modulated by the motor sequence status of the preceding trial. These results add to the accumulating evidence that sequential congruency effects are conflict-type specific, and constitute the first demonstration of this specificity in an implicit learning task.

Together, these results and those reported in other domains (e.g. Egner, Delano, & Hirsch, 2007; Funes et al., 2010a; Notebaert & Verguts, 2008, Condition 2; Wendt, et al., 2006) support models of cognitive control that separate mechanisms for sustained control from mechanisms of transient control (e.g. De Pisapia & Braver, 2006). The collective set of results also suggest that the mechanisms involved in transient shifts in control, as

reflected in sequential congruency effects, are engaged by and operate in response to specific types of conflict.

Appendix

Because the parametrical exploration conducted by Beesley et al. (2012) suggested that the best fit for the pattern of results reported in Jiménez et al. (2009) was obtained with a Simple Recurrent Network (SRN) with 150 hidden units and a learning rate of .3, we conducted a simulation of the sequence learning results obtained in Experiments 2 and 3, using those same parameters. Full details of the model are specified in Beesley et al[2]. We ran 100 independent simulations for each experiment (50 simulations using Sequence A and 50 simulations using Sequence B as the training structure) and we obtained the effects represented in the following Figure.
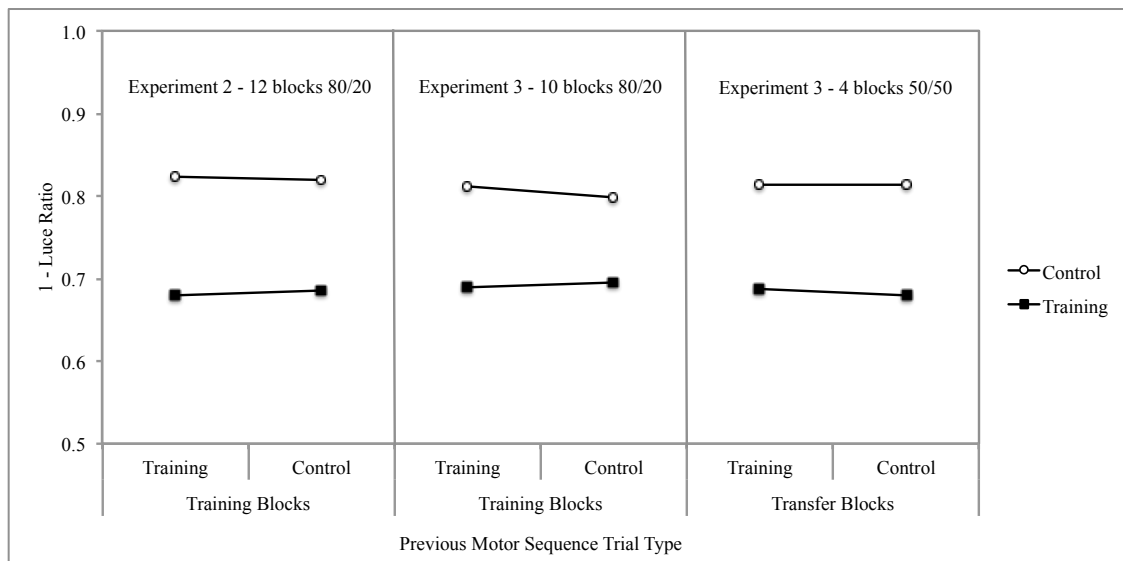
Figure A1. Performance of the SRN for the 12 training blocks in Experiment 2, the 10 training blocks in Experiment 3, and the 4 transfer blocks in Experiment 3.

---

[2] We are grateful to Tom Beesley, for granting access and helping us adapt his SRN simulation programs.

As it can be observed, the SRN learned about the training sequence in both cases, as attested by the difference between responding to training and control trials. The overall effect was maintained over the transfer blocks of Experiment 3, even with the removal of the predictable structure. However in none of these simulations was there any evidence of a sequential congruency effect comparable to what was observed in human participants. Overall these simulations show that when using first-order sequences where higher-order information does not provide any additional predictive information beyond what is provided in an immediately preceding trial the SRN model is unable to simulate sequential congruency effects comparable to what is observed in human participants.

CHAPTER 3: Implementing Flexibility in Automaticity:

Evidence from Context-specific Implicit Sequence Learning

D'Angelo, M.C., Milliken, B., Jiménez, L., & Lupiáñez, J. (2013).

Consciousness and Cognition, 22, 64-81

Preface

The experiments in the previous chapter demonstrated context-specificity in the expression of learning between two different modalities. Although this result is consistent with a processing account of memory, these results could also be accounted by models that posit separate, independent representations for motor and perceptual sequence learning. Therefore, Chapter 3 presents the results of three experiments in which the specificity of the expression of sequence learning was assessed when participants simultaneously learned two complementary motor sequences. The results from the three experiments show that context can guide the acquisition of learning two motor sequences, and the results from Experiment 3 show that the expression of learning can be context-specific if the two contexts are distinct from one another. These results constitute a first demonstration of context-specificity in the simultaneous learning of two motor sequences. The results from this chapter suggest that episodic representations underlie implicit sequence learning and provide compelling evidence in support of a processing account of memory.

Abstract

Attention is often dichotomized into controlled versus automatic processing, where controlled processing is slow, flexible, and intentional, and automatic processing is fast, inflexible, and unintentional. In contrast to this strict dichotomy, there is mounting evidence for context-specific processes that are engaged rapidly yet are also flexible. In the present study we extend this idea to the domain of implicit learning to examine whether flexibility in automatic processes can be implemented through the reliance on contextual features. Across three experiments we show that participants can learn implicitly two complementary sequences that are associated with distinct contexts, and that transfer of learning when the two contexts are randomly intermixed depends on the distinctiveness of the two contexts. Our results point to the role of context-specific processes in the acquisition and expression of implicit sequence knowledge, and also suggest that episodic details can be represented in sequence knowledge.

Introduction

From brushing our teeth to typing on a computer or reading, there are countless situations in which our behaviors are guided by seemingly automatic processes. In the domain of cognitive psychology, automatic processes are typically thought of as fast, effortless, and unintentional, but also somewhat rigid (Posner & Snyder, 1975; Shiffrin & Schneider, 1977). The notion that automatic processes are rigid stems from findings indicating that these processes can be activated and interfere with behavior when they are at odds with current goals (e.g., Stroop, 1935). A key issue for researchers is to understand how automaticity serves us so well in such a wide range of contexts in spite of its apparent rigidity. One potential answer to this question, which is the broad focus of the current paper, is that in fact automaticity gains its flexibility through sensitivity to contextual cues.

The specific focus of this paper is the role of contextual factors in the expression of automaticity in an implicit learning task. Implicit learning has often been defined as learning that occurs without intention or conscious effort, and in the absence of awareness of knowledge that has been acquired (Reber, 1993). As a consequence of this definition, implicit learning effects have largely been thought to reflect the engagement of automatic processes (Cleeremans & Jiménez, 1998; Frensch, 1998; Perruchet & Gallego, 1997). If the traditional view of automatic processes is correct, and if implicit learning effects indeed reflect the engagement of automatic processes, then the expression of implicit learning should be quite rigid. This conclusion is consistent with previous work showing patterns of rigid expression of sequence knowledge in incidental but not intentional

learners (e.g. Jiménez, Vaquero, & Lupiáñez, 2006), as well as with claims that there is

no control in implicit sequence learning (Abrahamse, Jiménez, Verwey, & Clegg, 2010;

Destrebecqz & Cleeremans, 2001; 2003). A primary aim of the present study was to

examine whether the presumed rigidity of automaticity can be overcome by reliance on

contextual cues in an implicit sequence learning task.

   In the laboratory, sequence learning is typically studied through the use of the

serial reaction time (SRT) task. In the standard version of this task, a target appears on

every trial at one of four marked locations. Participants respond to the location of the

target as quickly and accurately as possible by pressing a key corresponding to the

location of the target. Unbeknownst to participants, the location at which the target

stimulus appears is predicted by a relatively complex sequence. Sequence learning is

assessed by examining whether participants show a gradual improvement in responding

to trials generated by a training sequence (Nissen & Bullemer, 1987), as well as by

examining whether there is a cost to performance on trials in which the location of the

target is either randomly generated (Cohen, Ivry, & Keele, 1990), or is generated by a

control sequence (Schvaneveldt & Gomez, 1998).

Using Context to Implement Flexibility

   The goal of the current study was to determine whether contextual factors can be

used to control the acquisition and expression of implicit sequence learning, by training

participants on two complementary sequences that were each associated with distinct

contexts. Recently, Abrahamse and Verwey (2008) examined the role of contextual

factors in implicit sequence learning, and demonstrated the dependence of implicit

sequence learning on static contextual factors. More specifically, Abrahamse and

Verwey used a modified version of the SRT task to train participants on a second-order

conditional (SOC) sequence in a training context. In this experiment, context was defined

based on the shape of placeholders (triangle or rectangle), the background color (white or

grey), and the vertical location of the row of placeholders (top or bottom of screen). After

a series of training blocks, participants completed a transfer block in which the location of

the target continued to be selected based on the training sequence, but the context was

switched (e.g., participants were trained using triangles at the top of a white screen during

training, and completed a transfer block using rectangles at the bottom of a grey screen).

Importantly, performance was impaired in this transfer block, suggesting that sequence

knowledge was bound to the contextual factors present in the training blocks.

The context dependent sequence learning effect demonstrated by Abrahamse and

Verwey (2008) provides some initial evidence that task-irrelevant contextual factors can

be represented together with sequence knowledge. The goal of the current study was to

extend the study of context-dependent learning to the broader question of whether context

can control both the acquisition and expression of sequence knowledge. In Abrahamse

and Verwey's study participants were trained on only one sequence, and were only briefly

exposed to the secondary context, which was presented in isolation.   In addition,

participants were trained using a deterministic presentation of the training sequence,

meaning that learning was only measured by the gradual improvement in performance

across the training blocks, and by the impairment in performance in the transfer block, but

not by an online difference between training and control trials. Given our broader goal of

testing context-specificity in sequence learning, we developed a new procedure to assess whether context can indeed be used to implement flexibility in both the acquisition and expression of implicit sequence learning. Our new procedure allowed us to have an online measure of the acquisition of context-specific learning in a series of training blocks, and also allowed us to examine the specificity of the expression of learning in a series of transfer blocks where two contexts were randomly intermixed.

The Present Study

To examine whether reliance on contextual factors can lead to flexibility in the acquisition and expression of implicit sequence learning, we trained participants on two complementary sequences that were each associated with a distinct context. For the present set of experiments, we use the term context to refer to features that can aid participants in distinguishing between different sources of information, which are associated with different situations containing different statistical structures. In contrast to the procedure employed by Abrahamse and Verwey (2008), we used a probabilistic design using a trial-by-trial substitution method (Schvaneveldt & Gomez, 1998) to obtain an online measure of learning, which allows us to differentiate the acquisition from the expression of learning. Furthermore, and more important, we included transfer blocks in which the two contexts were randomly intermixed. These transfer blocks allowed us to examine whether sequence knowledge was indeed bound to the contextual features, as it was possible to assess whether the sequence learning effects would be expressed as a function of the reinstatement of training context in the transfer blocks.

In Experiment 1, there were two distinct goals. First, we aimed to identify a

procedure that could be used to measure learning of two complementary sequences as a function of context, by using target shape and response hand as contextual features. Second, we examined whether sequence knowledge was expressed when the two contexts were randomly intermixed. The results of Experiment 1 revealed significant context-specific sequence learning in the training blocks, but this learning effect was not evident in the transfer blocks in which the two contexts were randomly intermixed. In Experiment 2, we increased the distinctiveness of the two contexts by adding vertical location as an additional contextual feature. Here we replicated the context-specific implicit sequence learning effect reported in Experiment 1, and found a marginal learning effect in the transfer blocks. In Experiment 3, we increased the distinctiveness of the two contexts once again, by using target color rather than shape as a contextual feature. With the increased distinctiveness of the two contexts, we again replicated the context-specificity of learning in the training blocks, and found a significant learning effect in the transfer block. Considered together, the results offer strong support for the view that implicit sequence learning is mediated by context-specific learning processes.

Experiment 1

As stated above, the primary goal of Experiment 1 was to identify a procedure that could be used to measure context-specific sequence learning. To that end, participants were exposed to a training phase in which, on alternating blocks, two complementary sequences were each associated with a distinct context. Over these training blocks, trials followed the appropriate sequence in 80% of the trials, whereas the remaining 20% of the trials were illegal successors. The context associated with each of the two types of

training blocks was based on the target shape (triangle or square), as well as on the response hand (left or right). Over the transfer phase, participants completed four transfer blocks where the two contexts and sequences were randomly intermixed, so that 50% of the trials followed each of the two sequences, and where they had to respond using one hand or the other depending on the presented context. Lastly, awareness of the two sequences was assessed based on performance on two generation tasks, one for each of the two training contexts.

The training sequences were first-order sequences derived from noisy finite-state grammars. In these grammars, any given target location is associated with two legal successors that occur with equal likelihood. Participants were trained on the two sequences using a probabilistic design, such that on a relatively small proportion of trials ($p = .20$) illegal successors replaced the legal ones, providing us with an online measure of sequence learning for each context across the training blocks. The two sequences were complementary in the sense that each target location in the two grammars had complementary successors; the two legal successors for a given location in one grammar were illegal successors for that same location in the other grammar. Importantly, because the two sequences were complementary, if learning was not specific to the two contexts, there was no predictability regarding where the target would appear on any given trial, and therefore no learning should be observed.

A second goal of Experiment 1 was to examine whether sequence learning would be expressed when the two contexts are randomly intermixed. To that end, following the training blocks, participants completed a series of transfer blocks in which the two

contexts were randomly intermixed, and the probabilities of training trials within each context were reduced from .80 to .50. In the transfer blocks, sequence learning was examined as a function of whether or not the current trial context was reinstated from the immediately preceding trial.

Methods

Participants. Forty undergraduate students (20 females) enrolled at McMaster University participated in the experiment in exchange for course credit. Mean age of participants was 19 years. They had never participated in similar experiments before. All participants had normal or corrected to normal vision. Two participants did not complete the generation tasks due to computer errors.

Apparatus and Stimuli. The experiment was programmed using Presentation® experimental software (v.10.3, www.neurobs.com), which was also used to generate the sequence of stimuli. The stimuli were presented on a 15-inch Sony CRT color monitor. Responses were entered through the keyboard. Participants were tested in groups of two or three, and sat approximately 57 cm from the screen.

The target stimuli consisted of a black triangle or square. The triangle subtended 1.2º of visual angle vertically and 1.4º horizontally. The square subtended 1.3º of visual angle vertically and horizontally. The target shape could be either a triangle or a square, and could have either sharp or rounded corners.

Procedure. Participants completed a localization task in which the target was either a triangle or a square. On every trial a fixation cross was presented in the center of the screen along with four equally spaced dots in a horizontal line that marked the

locations where the target stimuli could appear. The dots were spaced apart by intervals

of 3º of visual angle, and were presented such that the fixation cross was halfway between

the two middle markers. On every trial a target shape appeared 1º of visual angle above

one of the four dots and participants were instructed to respond to the location of the

target as quickly and accurately as possible using either their left or right hand, depending

on the shape of the target. For example, for some participants responses to triangles were

made with the four fingers of their left hand and responses to squares were made with the

four fingers of their right hand. Participants responded by pressing the buttons 'z', 'x',

'c', and 'v' with their left hand, and the buttons 'n', 'm', '<', and '>' with their right

hand, for targets appearing, respectively, at the far left, middle left, middle right, and far

right locations. Response hands associated with the triangles and squares were

counterbalanced between subjects. Following incorrect responses an error tone lasting

500ms was presented through headphones. Participants were not required to correct these

incorrect responses. Rather, the fixation screen containing the four placeholders

remained on the screen during the auditory feedback, and the following trial began

immediately after the end of the feedback tone. Following correct responses, the next

trial appeared immediately after the response.

Sequences Derived From Complementary Grammars. Two sequences were

used to assign the location of the target on every trial; the location of triangles was

determined by one sequence, while the location of squares was determined by a second,

complementary sequence. These two sequences were derived from the artificial

grammars used by D'Angelo, Jiménez, Milliken, and Lupiáñez (in press), which were

modified versions of the grammars used by Deroost and Soetens (e.g. 2006; Soetens, Melis, & Notebaert, 2004), and are shown in Figure 1. In these grammars, the positions 1 through 4 corresponded to the locations, in order, beginning with the left-most location (position 1) to the right-most location (position 4). From any position in the grammar, there is an equal probability of transitioning to either of two predicted positions, and repetitions do occur. For example, starting from position 1 in Grammar A there is a 50% probability of transitioning to position 1, and a 50% probability of transitioning to position 2. Therefore, in Grammar A, there are no legal transitions from position 1 to positions 3 or 4. Trials in which the target's location is predicted by transitions consistent with the training sequence are referred to as training trials, and trials in which the target's location is not predicted by transitions consistent with the training sequence are referred to as control trials. Given the complementary nature of the two grammars, control trials for Grammar A are in fact transitions that are consistent with the sequence derived from Grammar B, and vice versa. Target locations were selected using a trial-to-trial substitution procedure (Schvaneveldt & Gomez, 1998). Using this procedure, if a block of trials contains 80% training trials, and if the target's location on the current trial corresponds to position 1 in grammar A, then there is a 40% likelihood of transitioning to each of positions 1 and 2, and a 10% likelihood of transitioning to each of positions 3 and 4.

Figure 1. The grammars used to generate the sequences in Experiments 1, 2, and 3. The assignment of grammar A and B for the two contexts (left hand/right hand) was counterbalanced between participants. Figure taken from D'Angelo, et al. (in press).

For the first trial in all blocks, the target's location was selected randomly. For all subsequent trials in the training blocks, the target location was selected based on the training sequence on 80% of trials and based on the control sequence on 20% of trials, using the sequence associated with the current context/target type. Following control trials, the location of the target on the subsequent trial was selected based on the location of the target on the control trial that had just been completed. Similarly, following an incorrect response, the location of the target on the subsequent trial was selected based on the actual target location for the trial that had just been completed. The assignment of the

two sequences to the triangle and square targets was counterbalanced between participants.

Before beginning the experimental trials, participants first completed two practice blocks each containing 30 trials. One block contained only triangles and the other block contained only squares, and within each block, responses were made with the assigned response hand. In these practice blocks, the location of the target was randomly determined on every trial. Following the practice blocks, participants were trained over ten blocks of 100 trials each in which the targets alternated from always triangles to always squares within a given block. The combination of response hand and target shape presented in the first block and on subsequent odd numbered blocks is collectively referred to as the primary context, and the combination associated with the even numbered blocks is collectively referred to as the secondary context. During the training phase, participants were trained on one sequence with the triangle targets and on a second, complementary sequence with the square targets. For example, one group of participants were trained on Sequence A with the triangles and their left hand on odd blocks and Sequence B with the squares and their right hand on even blocks.

After the training phase, participants completed a transfer phase consisting of four blocks of 100 trials each in which there was an equal likelihood that the target would be a triangle or a square on any given trial. Participants continued to respond to targets using the response hand associated with the target shape. Therefore, unlike in the training blocks where participants only responded with one hand within a block of trials, in the transfer blocks participants responded with both hands within a block of trials. In the

transfer blocks, the location of the target was selected based on the training sequence associated with the previous target on only 50% of trials, which, given the sequences used, is equivalent to the random selection of target locations on every trial. Following the transfer blocks, participants completed two additional training blocks, one with triangle targets and one with square targets, to re-establish the learned contingencies before measuring sequence knowledge directly using a series of generation tasks. Following each of the practice, training, and transfer blocks participants were given feedback on their mean reaction time (RT) and accuracy.

Secondary Counting Task. To reduce the likelihood that participants would become aware of the sequences, participants were instructed to engage in a secondary counting task in addition to the primary localization task in the training and transfer blocks. Participants were instructed to count the number of times the target shapes had rounded corners. At the end of each block of trials, participants typed in the number of round-corner targets they had counted, and were given feedback on their estimate before they began the next block of trials. The number of round-corner targets within each block varied from 40-60 targets.

Generation Tasks. Participants completed two sets of cued generation tasks, one for each of the two sequences, to assess their ability to make direct predictions in response to a fragment of the sequence being tested. Before beginning the generation tasks, participants were told that in these experiments participants sometimes feel as though the stimuli follow a certain order. Therefore, participants were explicitly

instructed to make their responses for this part of the experiment based on what they felt occurred in the previous part of the experiment, referring to the SRT task.

Trials in which a fragment of the sequence was presented are referred to as cue trials. Given that the sequences used in the current study are first-order sequences in which legal transitions according to the training grammars are dependent only on the location of the target on the preceding trial, only one fragment was presented on each cued generation trial. Participants completed a series of cued generation trials that assessed knowledge of the sequence that was associated with the primary context (e.g., the sequence that had been presented with triangles) and another series of cued generation trials that assessed knowledge of the sequence that was associated with the secondary context (e.g., the sequence that had been presented with squares). The presentation order of the two generation tasks was counterbalanced between subjects.

For each cued generation task, the test began with a cue trial in which participants responded as in the standard SRT task (using the appropriate keys based on target shape). Following their response to the cue trial, participants saw an empty fixation screen containing the fixation cross and the four marked locations, and were asked to generate the most likely location of a subsequent target that was the same shape as the target they had responded to in the previous display, again using the same responses used in the standard SRT task. Given the nature of the grammars used to generate the sequences, two training successors were equally likely for each cue trial. For example, in the case of a participant for whom Grammar A was assigned to triangle targets, the presentation of a triangle in position 1 on a cue trial would have positions 1 and 2 as equally likely training

locations, and positions 3 and 4 as equally likely control locations. For both generation tasks, each of the four possible cues was presented four times, in random order, thus completing a full set of 16 cue trials for each of the two generation tasks.

Results

Learning of the two sequences was assessed by separately analyzing differences in mean RTs and error rates for training and control trials as a function of training block and context. To determine whether participants expressed knowledge of the sequences in the transfer blocks, mean RTs and error rates from these blocks were separately compared for training and control trials as a function of whether the transition from the immediately preceding trial (trial *n-1*) to the current trial (trial *n*) reinstated the training context (e.g., if the targets in both trial *n* and trial *n-1* were triangles), or if the transition switched the context (e.g., if the target on trial *n-1* was a square and on trial *n* was a triangle). Awareness of the sequences was examined using performance on the generation tasks, by assessing whether participants generated more often the training or control successors of all the relevant cues.

RTs for the first trial of each block and for trials in which an error was made (4.4% of trials) were not included in the analyses. In addition, RTs that were more than three standard deviations from the mean for each block, defined separately for each participant (2.1% of trials), were treated as outliers and eliminated from the analyses.[3]

---

[3] Participants were generally accurate in counting the number of rounded-corner targets. On average, participants were off from the correct number of rounded-corner targets by ±4 per block across participants. The worst performance was for one participant who was off by ±9 targets on average per block.

Training Blocks. Mean RTs and error rates were computed for training and control sequence trials, separately for each block for each participant. Trial type was assigned based on the sequence associated with the context presented in that particular block. Context-specific sequence learning was analyzed using an analysis of variance with Training Block (1-10), Context (primary/secondary), and Trial Type (training/control) as within subject factors. All analyses were conducted separately on mean RTs and error rates. Here and in all subsequent experiments, for the effects and interactions involving Block, we report nominal degrees of freedom along with Greenhouse-Geisser ε and adjusted p-levels.

Mean RTs as a function of trial type, context, and block are presented in Figure 2. The analysis of mean RTs revealed a main effect of block, $F(4,156) = 21.74$, $\eta^2_p = .36$, $p < .001$, $\varepsilon = .508$. The analysis also revealed a main effect of context, $F(1,39) = 6.10$, $\eta^2_p = .14$, $p = .018$, as responses were faster in the secondary context (669ms) than in the primary context (686ms). More important, the analysis revealed a main effect of trial type, $F(1,39) = 23.47$, $\eta^2_p = .38$, $p < .001$. Responses were faster on training trials (669ms) than on control trials (686ms), reflecting a 18ms learning effect. The interaction between context and trial type was not significant, $F < 1$, indicating that the learning effects did not differ between contexts. The remaining interactions were not significant, all F's < 1.

Error rates as a function of block, context, and trial type are presented in Table 1. The analysis of error rates revealed only a main effect of context $F(1,39) = 4.15$, $\eta^2_p = .10$, $p = .048$. Participants made more errors in the primary context (3.1%) than the secondary context (2.5%). All other F's < 1.2, p's $> .33$.
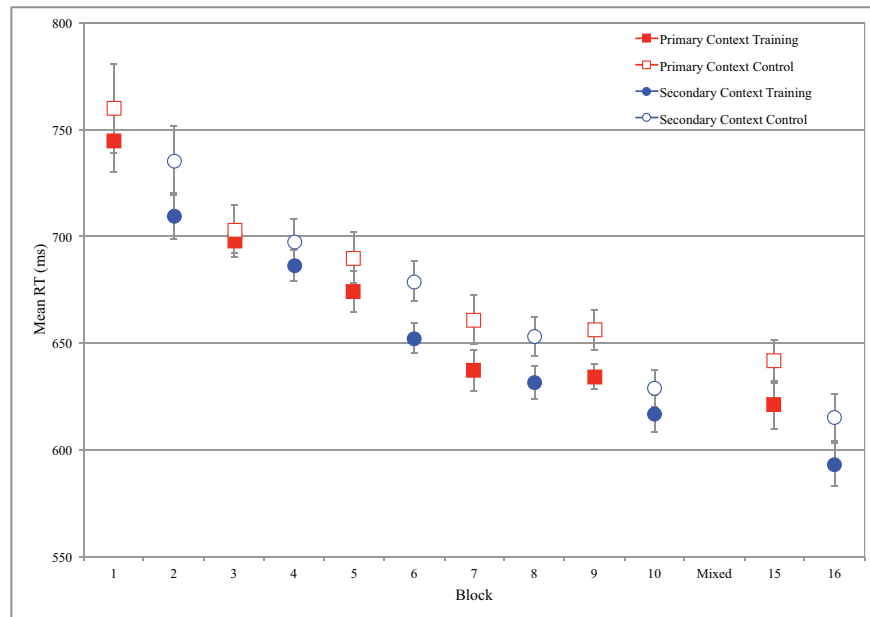
Figure 2. Mean RT(ms) for training and control trials (filled and unfilled shapes respectively) as a function of primary and secondary contexts (red squares and blue circles, respectively) across training blocks in Experiment 1. Error bars in this and all other figures represent standard errors of the mean that have been corrected to eliminate between-subject variability (Cousineau, 2005).

Table 1. Mean error rates and standard error of the means (%) as a function of Experiment, context, trial type, and block. Note that block number differed for primary and secondary contexts – odd numbered blocks are associated with the primary context and even numbered blocks are associated with the secondary context.

	Context	Trial Type	Block					
			1 / 2	3 / 4	5 / 6	7 / 8	9 / 10	15 / 16
1	Primary	Training	3.07	2.82	2.79	2.60	3.11	2.02
			(0.67)	(0.57)	(0.54)	(0.50)	(0.71)	(0.45)
		Control	2.93	3.54	3.25	3.04	3.36	1.77
			(1.19)	(1.12)	(0.75)	(0.77)	(1.11)	(0.69)
	Secondary	Training	2.02	2.78	2.46	2.22	2.70	2.28
			(0.38)	(0.60)	(0.46)	(0.51)	(0.49)	(0.55)
		Control	1.72	2.49	2.59	3.57	2.27	2.65
			(0.56)	(0.56)	(0.77)	(1.11)	(0.74)	(0.76)
2	Primary	Training	2.59	2.72	3.06	3.02	2.49	2.76
			(0.44)	(0.46)	(0.57)	(0.72)	(0.54)	(0.55)
		Control	2.50	2.51	3.42	1.90	4.15	4.79
			(0.61)	(0.52)	(0.82)	(0.54)	(0.77)	(1.14)
	Secondary	Training	2.28	2.55	2.43	2.81	3.11	2.58
			(0.38)	(0.40)	(0.55)	(0.64)	(0.79)	(0.48)
		Control	2.47	2.91	3.38	4.41	2.74	3.58
			(0.54)	(0.73)	(0.60)	(0.99)	(0.74)	(1.01)
3	Primary	Training	2.54	2.03	2.33	1.98	1.80	2.13
			(0.50)	(0.34)	(0.48)	(0.37)	(0.32)	(0.46)
		Control	3.12	2.30	2.12	2.40	2.07	2.87
			(0.79)	(0.59)	(0.65)	(0.63)	(0.72)	(0.77)
	Secondary	Training	2.69	1.93	1.90	2.08	2.16	2.22
			(0.55)	(0.36)	(0.32)	(0.35)	(0.42)	(0.49)
		Control	1.82	3.17	2.24	2.66	3.21	3.37
			(0.62)	(0.77)	(0.60)	(0.59)	(0.83)	(0.76)

Transfer Blocks. Mean RTs and error rates were computed for each of the training and control sequence trials as a function of whether the context was reinstated from trial $n-1$ to trial n (e.g., if the target was a triangle on two successive trials) or switched (e.g., if the target was a triangle on the current trial and a square on the preceding trial) across transfer blocks, separately for each participant. Trial type (training

vs. control) was assigned based on the sequence that had been associated with the context of trial *n-1* during the training blocks. For example, if trial *n-1* had a square target, then the sequence used during training blocks for square targets was used to define what constituted training and control targets for trial *n*. Note that although this assignment to trial type conditions is unambiguous for trials in which the context was reinstated, it is ambiguous for trials in which the context switched. This ambiguity stems from the fact that training trials for one sequence are control trials for the other sequence. As a result, when the context switches, a training trial with respect to the sequence associated with the trial *n-1* context is a control trial with respect the sequence associated with the trial *n* context. To illustrate this ambiguity, consider the example of a participant who was trained on Grammar A with triangles and Grammar B with squares. If during the transfer block a square was presented in the third position on trial *n-1*, and the next trial was a context-switch trial, according to Grammar B a triangle appearing in the first or second position on trial *n* would be considered a training trial. However, if trial type were assigned based on the sequence associated with the context on trial *n* (Grammar A), then a triangle appearing in the first or second position on trial *n* would instead be considered a control trial.

Given this ambiguity, a clear test of context-specific sequence learning in the transfer phase is offered only for context reinstated trials. Nonetheless, context-specific sequence learning was analyzed using an analysis of variance with Context Reinstatement (context reinstated/context switch) and Trial Type (training/control) as within subject factors. The analysis was conducted separately on mean RTs and error rates.

Mean RTs as a function of context reinstatement and trial type for the transfer blocks are presented in Figure 3. The analysis of mean RTs revealed a main effect of context, $F(1,39) = 129.00$, $\eta^2_p = .77$, $p < .001$, with faster responses when the context was reinstated (929ms) than when the context switched (1181ms). In other words, participants responded 250ms slower when they had to switch response hands from one trial to the next. The main effect of trial type was not significant, $F(1,39) = 0.97$, $\eta^2_p = .02$, $p = .330$, and the interaction between context and trial type was not significant, $F < 1$. Planned comparisons revealed a non-significant 12ms learning effect when the context was reinstated, (training trials = 923ms; control trials = 935ms), $t(39) = .969$, $p = .339$. When the context switched, there was also no significant effect of trial type, $t(39) = .225$, $p = .823$.
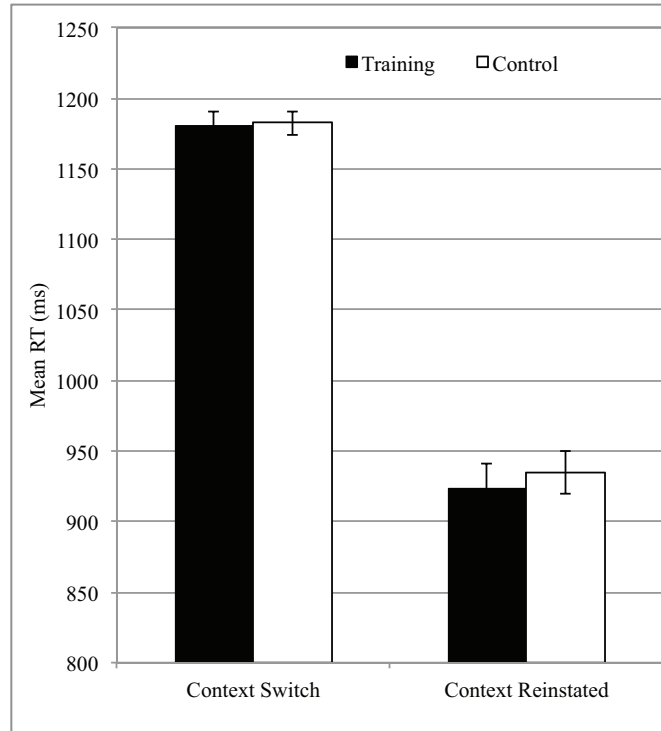
Figure 3. Mean RT for training and control trials as a function of trial *n-1* to trial *n* context reinstatement (context switched or context reinstated) in Experiment 1.

Error rates as a function of context reinstatement and trial type are presented in Table 2. The analysis of error rates revealed a main effect of context, $F(1,39) = 59.36$, $\eta^2_p = .60$, $p < .001$. Consistent with the RT data, participants made more errors when the context switched (13.2%) than when the context was reinstated (6.0%). The analysis also revealed a trend toward a significant interaction between context and trial type, $F(1,39) = 2.69$, $\eta^2_p = .06$, $p = .109$. Planned comparisons revealed that when the context was reinstated there were marginally more errors made on control trials (6.6%) than training trials (5.4%), $t(39)$ 2.01, $p = .052$. When the context switched there was no difference in the errors made on control trials (12.9%) and training trials (13.5%), $t(39) = 0.596$, $p = .555$.

Table 2. Mean error rates and standard error of the means (%) as a function of Experiment, context reinstatement, and trial type.

Experiment	Trial Type	Reinstated Context	Context Switch
1	Training	5.35 (0.67)	13.46 (1.33)
1	Control	6.62 (0.79)	12.90 (1.46)
2	Training	5.96 (0.86)	11.77 (1.36)
2	Control	6.68 (0.95)	9.94 (1.24)
3	Training	5.22 (0.69)	8.99 (1.06)
3	Control	5.17 (0.59)	7.53 (0.82)

Generation Task Performance. The implicit nature of the sequence learning was evaluated by assessing sensitivity to the sequences on the generation tasks, in particular by comparing the number of trials in which participants completed a cue with a training successor to the number expected by chance. Chance performance is derived from the idea that if sequence knowledge does not guide selection of successors in the generation trials, then all four target locations should be equally likely to occur. As two of the target locations are training successors for each cue, chance performance on the generation trials is the likelihood of selecting either of the two training successors by chance alone, which is .50.

Mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the generation task assessing the sequence presented in the primary context, participants did not generate more training successors (.51) from the cues than expected by chance, $t(37) = .461, p = .647, d = 0.07$

(control successors generated = .49). For the generation task assessing the sequence

presented in the secondary context, participants did not generate more training successors

(.50) from the cues than expected by chance, $t(37) = .338, p = .737, d = 0.05$ (control

successors generated = .50).

Discussion

      The purpose of Experiment 1 was to examine whether participants could learn two

complementary sequences that were associated with distinct contexts. Importantly,

through the use of a probabilistic training procedure, we were able to measure learning

effects throughout the training blocks. The results from the training blocks indicate that

participants learned two complementary sequences as a function of context, and that the

learning effects did not differ between the two contexts. The results from the generation

tasks indicate that participants were not able to express explicit knowledge of the

sequences, suggesting that the learning occurred incidentally and in the absence of

awareness. These results suggest that the current procedure can be used to measure

context-specific implicit sequence learning. To our knowledge, this constitutes the first

demonstration of such an effect.

      It is important to note, however, that the learning effects in the training blocks

could conceivably be explained by an alternative to context-specific learning.   It is

possible that participants did not learn the two sequences as a function of context, but

simply learned and relearned the two sequences. In particular, in the training blocks the

two contexts were temporally distinct, making it possible that participants learned and

then relearned the two sequences across the training blocks, but did not actually encode

an association between knowledge of each of the two sequences and the two distinct contexts. For example, participants may have learned Sequence A in the primary context, then learned Sequence B in the secondary context, then re-learned Sequence A when returning to the primary context, then re-learned Sequence B when returning to the secondary context, and so forth. To examine whether the sequence learning measured was due to learning and re-learning of the two different sequences rather than to context-specific learning, we can assess the learning effects in the transfer blocks. Recall that in the transfer blocks the two contexts were intermixed at random and there was no probabilistic structure for participants to re-learn. As such, any evidence of learning in the transfer blocks offers strong support for the context-specific learning hypothesis. Notably, the RTs from the context reinstated trials of the transfer blocks did not reveal a significant sequence learning effect.

Despite the failure to find a significant sequence learning effect in the RTs, the corresponding sequence learning effect in the error rates approached significance, suggesting that the expression of sequence knowledge in the transfer blocks might well occur with greater contextual support for learning. Note that in the transfer phase of Experiment 1, the identity of the target was the only perceptual signal that marked the distinction between the two contexts, and so any context-specific processing hinged on participants first identifying the target's shape. With this in mind, we reasoned that context-specific learning effects might occur in the transfer blocks if the contexts were cued earlier in processing, by a more distinctive contextual cue. In Experiment 2, we

tested this idea by adding vertical location of the target arrays as an additional contextual cue (e.g. Crump, Gong, & Milliken, 2006).

Experiment 2

The purpose of Experiment 2 was to examine whether adding separate vertical locations for the target arrays would allow us to measure context-specific expression of learning when the two contexts are randomly intermixed in the transfer blocks, a finding that would support our claim that sequence knowledge is bound to contextual features. To that end, Experiment 2 was identical to Experiment 1, with the targets appearing at one of four marked horizontal locations, but now there were two possible vertical positions for the marked locations, either above or below a central fixation cross. In this experiment, the vertical position of the marked locations was redundant with target shape and response hand in defining the context that was associated with a particular sequence. For example, for one group of participants, when the target appeared in one of the four locations above fixation the target was always a triangle and participants responded with the right hand, and when it appeared in one of the four locations below fixation the target was always a square, and participants responded with the left hand.

Methods

Participants. Forty undergraduate students (27 females) enrolled at McMaster University participated in the experiment in exchange for course credit. The participants had a mean age of 19 years. They had never participated in similar experiments before. All participants had normal or corrected to normal vision.

Apparatus and Stimuli. The apparatus and stimuli were identical to that used in Experiment 1.

Procedure. The procedure was identical to that of Experiment 1 with the following exceptions. On every trial a fixation cross was presented in the center of the screen along with two rows of four equally spaced marked locations in a horizontal line. One row of marked locations was presented 2º above, and the other was presented 3.5º below the fixation cross, so that targets were presented at the same distance from the fixation point. Participants were informed that on every trial a target would appear above one of the eight dots, and they were to respond to the position of the target as quickly and accurately as possible, using either their left hand or right hand, depending on the target shape. The location (above or below fixation) in which the target appeared was perfectly correlated with the target shape and responding hand. For example, one group of participants always saw triangles above fixation and squares below fixation. The shape assigned to each of the two vertical locations and response hands was counterbalanced between participants.

As in Experiment 1, the two contexts were intermixed in the transfer blocks. However, the association between target shape and vertical location always matched what participants had been trained on in the training blocks. For example, for the group of participants who always saw triangles in the locations above the fixation cross in the training phase, targets above the fixation cross in the transfer phase were always triangles, and targets presented below the fixation cross were always squares.

Generation Tasks. As in Experiment 1, participants completed two sets of cued generation tasks, one for each of the two sequences. The tasks were identical to those in Experiment 1 with the following modification. In the generation tasks, the vertical locations were still perfectly correlated with the target shapes.

Results

RTs for the first trial of each block and for trials in which an error was made (4.2% of trials) were not included in the analyses. In addition, RTs that were more than three standard deviations from the mean for each block, defined separately for each participant (2.1%), were treated as outliers and eliminated from the analyses.[4]

Training Blocks. Mean RTs and error rates were computed for the training and control sequence trials, separately for each block for each participant. As in Experiment 1, trial type was assigned based on the sequence that was associated with the context presented within each block. Context-specific sequence learning was analyzed using an analysis of variance with Training Block (1-10), Context (primary/secondary), and Trial Type (training/control) as within subject factors.

Mean RTs as a function of trial type, context, and block are presented in Figure 4. The analysis of mean RTs revealed a main effect of block, $F(4,156) = 28.48$, $\eta^2_p = .42$, $p < .001$, $\varepsilon = .630$. The analysis also revealed a marginally significant main effect of context, $F(1,39) = 3.34$, $\eta^2_p = .08$, $p = .075$, with faster responses in the secondary context (670ms) than in the primary context (680ms). More important, the analysis revealed a

---

[4] Participants were generally accurate in counting the number of rounded-corner targets. On average, participants were off from the correct number of rounded-corner targets by ±4 per block across participants. The worst performance was for one participant who was off by ±9 targets on average per block.

main effect of trial type, $F(1,39) = 8.59$, $\eta^2_p = .18$, $p = .006$. Responses were faster on

training trials (670ms) than on control trials (680ms), reflecting a 10ms learning effect.

The interaction between context and trial type was not significant, $F < 1$, indicating that

the learning effects did not differ between contexts. The remaining interactions were not

significant, all F's < 1.
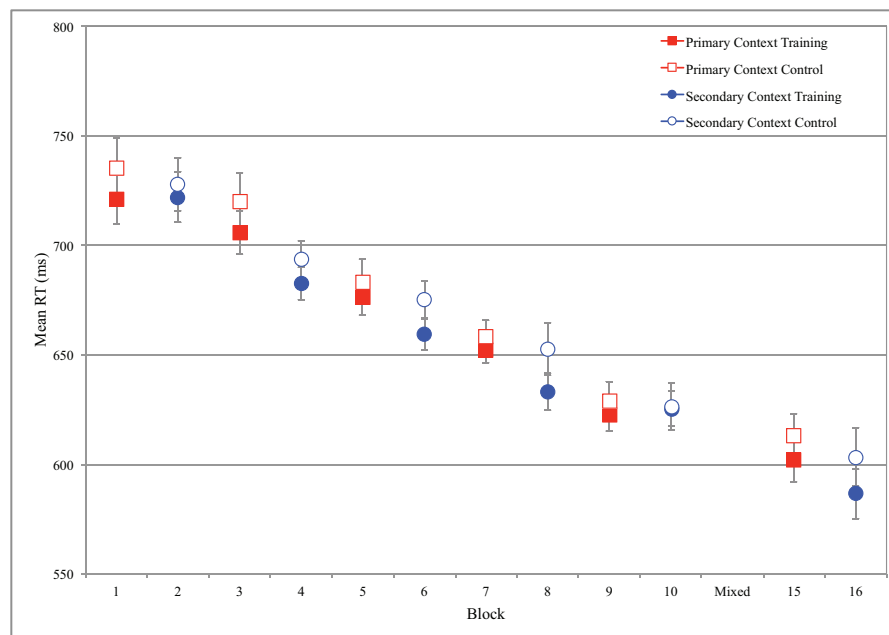
Figure 4. Mean RT(ms) for training and control trials (filled and unfilled shapes
respectively) as a function of primary and secondary contexts (red squares and blue
circles, respectively) across training blocks in Experiment 2.

Error rates as a function of trial type, context, and block are presented in Table 1.

The analysis of error rates revealed a three-way interaction between block, context, and

trial type, $F(4,156) = 3.34$, $\eta^2_p = .08$, $p = .017$, $\varepsilon = .854$. To examine the nature of this

interaction, the simple main effects of block and trial type were analyzed separately for

the primary and secondary contexts.

For the primary context, the analysis of error rates revealed a marginally significant interaction between block and trial type, $F(4,156) = 2.43$, $\eta^2_p = .06$, $p = .059$, $\varepsilon = .872$. To investigate the nature of this interaction, the simple main effect of trial type was analyzed separately for each block using paired-samples t-tests. For the first training blocks in this context (1, 3, 5, and 7), the t-tests did not reveal any significant differences between training and control trials (all t's < 1.5, p's $> .15$). For Block 9 the t-test revealed a significant difference between training and control trials ($t(39) = 2.25$, $p = .031$. Consistent with the general pattern in the RT data, participants made more errors on control trials (4.1%) than training trials (2.5%).

For the secondary context, the analysis of error rates revealed only a trend to a main effect of trial type, $F(1,39) = 2.89$, $\eta^2_p = .07$, $p = .097$. Consistent with the RT data, participants made more errors on control trials (3.2%) than on training trials (2.6%).

Transfer Blocks. Mean RTs and error rates were computed for the training and control sequence trials across transfer blocks, separately for each participant. Context-specific sequence learning was analyzed using an analysis of variance with Context Reinstatement (context reinstated/context switch) and Trial Type (training/control) as within subjects factors. The analysis was conducted separately for mean RTs and error rates.

Mean RTs as a function of context reinstatement and trial type for the transfer blocks are presented in Figure 5. The analysis of mean RTs revealed a main effect of context, $F(1,39) = 190.23$, $\eta^2_p = .83$, $p < .001$, with faster responses when the context was reinstated (801ms) than when the context switched (1035ms). The main effect of trial

type was not significant, $F<1$. The interaction between context and trial type was not significant, $F(1,39) = 1.66$ $\eta^2_p = .04$, $p = .20$. Planned comparisons nevertheless revealed that when the context was reinstated responses were marginally faster on training trials (793ms) than control trials (809ms) $t(39) = 1.64$, $p = .05$ (1-tailed), reflecting a 16ms learning effect. In contrast, when the context switched, there was no significant effect of trial type, $t(39) = .089$, $p = .929$.
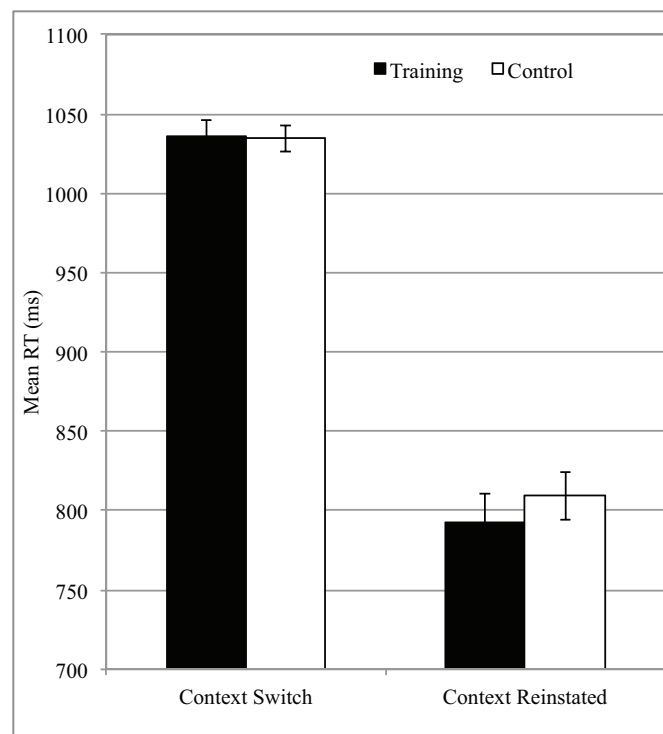
Figure 5. Mean RT for training and control trials as a function of trial *n-1* to trial *n* context reinstatement (context switched or context reinstated) in Experiment 2.

Error rates as a function of context reinstatement and trial type are presented in Table 2. The analysis of error rates revealed a main effect of context, $F(1,39) = 48.08$, $\eta^2_p = .55$, $p < .001$. Consistent with the RT data, participants made more errors when the context switched (10.9%) than when the context was reinstated (6.3%). The analysis also

revealed a significant interaction between context and trial type, $F(1,39) = 4.21$, $\eta^2_p = .10$, $p = .047$. Planned comparisons revealed that when the context was reinstated there was no difference in errors made for training (6.0%) and control trials (6.7%), $t(39) = 1.29$, $p = .204$. However, when the context switched participants tended to make more errors on training trials (11.8%) than control trials (9.9%), $t(39) = 1.76$, $p = .087$. The difference when context switched is difficult to interpret, as trial type was coded based on the sequence associated with the context on trial $n\text{-}1$, however the assignment would be reversed if trial type was coded based on the sequence associated with the context on the current trial (trial n), as the two sequences were complementary.

Generation Task Performance. To assess sensitivity in the generation task, mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the generation task assessing the sequence presented in the primary context, participants did not generate more training successors (.48) from the cues than expected by chance, $t(39) = .882$, $p = .383$, $d = 0.13$ (control successors generated = .52). For the generation task assessing the sequence presented in the secondary context, participants did not generate more training successors (.51) from the cues than expected by chance, $t(39) = .569$, $p = .573$, $d = 0.09$ (control successors generated = .49).

Discussion

The purpose of Experiment 2 was two-fold. First, we wanted to replicate the context-specific implicit sequence learning effect reported in the training blocks of Experiment 1. Second, we also examined whether context-specific learning could be

measured in the transfer blocks when vertical location was included as a contextual factor. The results from the training blocks in both RT and error rate measures indicate that participants were able to learn the two complementary sequences as a function of the two contexts. As in Experiment 1, the results from the generation tasks suggest that participants were not aware of the sequences, as they did not generate training successors more often than expected by chance. More important, the learning effect for reinstated context trials in the transfer block approached significance in the RTs. This effect provides preliminary evidence that participants are able to express context-specific sequence knowledge in the transfer blocks, which is inconsistent with the alternative explanation that participants simply learned and re-learned the sequences during training.

Experiment 3

In Experiment 3 we increased the distinctiveness of the two contexts once again, this time by increasing the distinctiveness of the targets themselves by introducing a difference between targets on the dimension of color rather than shape, with the goal of finding more robust context-specific learning effects when the two targets are randomly intermixed. Previous work investigating visual search has led some to argue that the processing of unique shapes and unique colors is pre-attentive and that both unique shape and color can each lead to pop-out in visual search (e.g. Treisman & Gelade, 1980). However, there is evidence to suggest that there is an asymmetry in the saliency of color pop-out compared to shape pop-out (Theeuwes, 1991). More specifically, Theeuwes found that a distractor presented in an odd color can interfere with pop-out of a unique target based on its shape, but a distractor presented with an odd shape does not interfere

with pop-out of a unique target based on its color. If oddness in color is more salient than oddness in shape, and if this saliency is critical to the rapid categorization of context that we presume underlies context-specific learning, then we may observe such an effect here with color targets whereas it was not easily observable with the shape targets in Experiments 1 and 2. To test this hypothesis, the target on each trial in Experiment 3 was always a circle, and participants used one hand to respond to the location of red circles, and the other hand to respond to the location of blue circles.

Methods

Participants. Forty undergraduate students (31 females) enrolled at McMaster University participated in the experiment in exchange for course credit. The participants had a mean age of 20 years. They had never participated in similar experiments before. All participants had normal or corrected to normal vision.

Apparatus and Stimuli. The apparatus and stimuli were identical to that used in Experiments 1 and 2 with the following exception. The stimuli were circles, which subtended 1.3º of visual angle vertically and horizontally. The target circles could be red or blue, and could be either bright or dim. The dim circles were set to be subjectively dimmer than the bright circles, as confirmed by lab members.

Procedure. The procedure was identical to that of Experiment 2 with the following exceptions. The target stimuli in Experiment 3 were red and blue circles. For the secondary counting task, participants counted the number of dim colored circles.

Results

RTs for the first trial of each block and for trials in which an error was made (3.3% of the trials) were not included in the analyses. In addition, RTs that were more than three standard deviations from the mean for each block, defined separately for each participant (2.1%), were treated as outliers and eliminated from the analyses.[5]

Training Blocks. Mean RTs and error rates were computed for the training and control sequence trials, separately for each block for each participant. As in Experiments 1 and 2, trial type was assigned based on the sequence that was associated with the context presented within each block. Context-specific sequence learning was analyzed using an analysis of variance with Training Block (1-10), Context (primary/secondary), and Trial Type (training/control) as within subject factors.

Mean RTs as a function of trial type, context, and block are presented in Figure 6. The analysis of mean RTs revealed a main effect of block, $F(4,156) = 15.81$, $\eta^2_p = .29$, $p < .001$, $\varepsilon = .484$. More important, the analysis revealed a main effect of trial type, $F(1,39) = 16.24$, $\eta^2_p = .29$, $p < .001$. Responses were faster on training trials (734ms) than on control trials (746ms), reflecting a 13ms learning effect. The interaction between context and trial type was not significant, $F < 1$, indicating that the learning effect did not differ between contexts. The main effect of context was not significant, $F(1,39) = 2.23$, $\eta^2_p = .05$, $p = .144$. All remaining interactions were not significant, all F's < 1.6.

---

[5] Participants were generally accurate in counting the number of dim targets. On average, participants were off from the correct number of dim targets by ±3 per block across participants. The worst performance was for one participant who was off by ±9 targets on average per block.
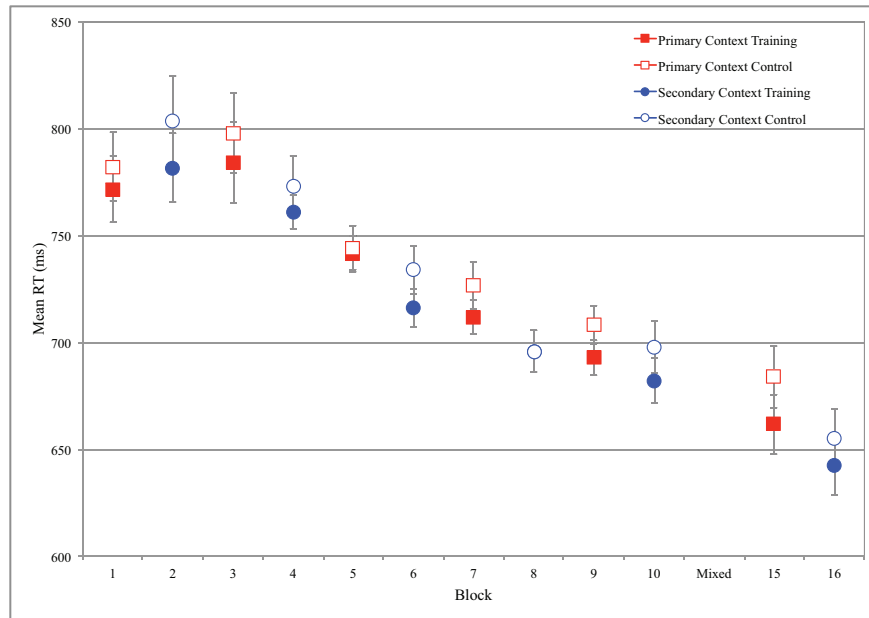
Figure 6. Mean RT(ms) for training and control trials (filled and unfilled shapes respectively) as a function of primary and secondary contexts (red squares and blue circles, respectively) across training blocks in Experiment 3.

Error rates as a function of trial type, context, and block are presented in Table 1. The analysis of error rates revealed only a marginal main effect of trial type, $F(1,39) = 2.87$, $\eta^2_p = .07$, $p = .098$. Consistent with the RT data, participants made more errors on control trials (2.5%) than on training trials (2.1%). No other effects approached significance (all F's < 1.1).

Transfer Blocks. Mean RTs and error rates were computed for the training and control sequence trials across transfer blocks, separately for each participant. Context-specific sequence learning was analyzed using an analysis of variance with Context Reinstatement (context reinstated/context switch) and Trial Type (training/control) as

within-subject factors. The analysis was conducted separately for mean RTs and error rates.

Mean RTs as a function of context reinstatement and trial type for the transfer blocks are presented in Figure 7. The analysis of mean RTs revealed a main effect of context, $F(1,39) = 212.43$, $\eta^2_p = .84$, $p < .001$ Responses were faster when the context was reinstated (875ms) than when the context switched (1121ms). The main effect of trial type was also significant, $F(1,39) = 6.03$, $\eta^2_p = .13$, $p = .019$, with faster responses on training trials (989ms) than control trials (1006ms). The interaction between context and trial type only approached significance, $F(1,39) = 1.92$, $\eta^2_p = .05$, $p = .17$. Nevertheless, planned comparisons revealed that when the context was reinstated responses were faster on training trials (861ms) than control trials (888ms), $t(39) = 3.12$, $p = .003$; reflecting a 27ms learning effect. In contrast, when the context switched, there was no significant effect of trial type, $t(39) = .696$, $p = .491$.
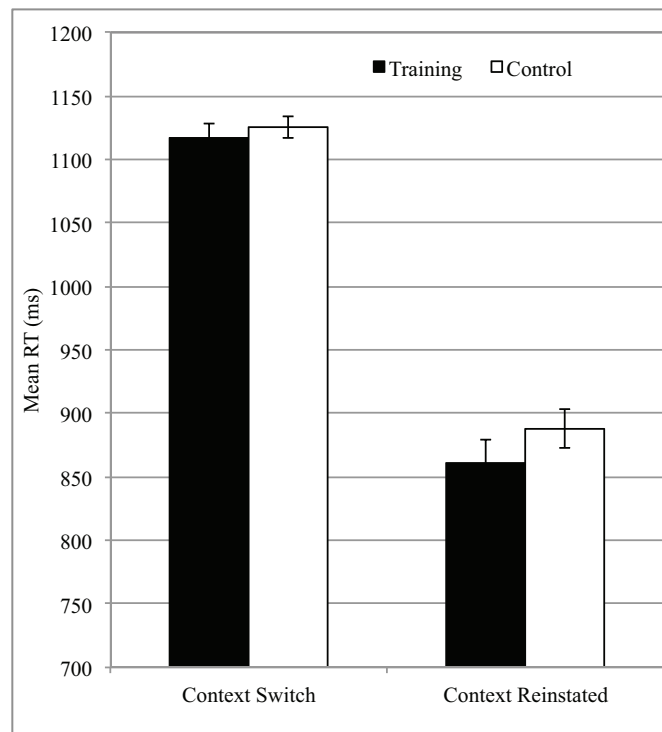
Figure 7. Mean RT for training and control trials as a function of trial *n-1* to trial *n* context reinstatement (context switched or context reinstated) in Experiment 3.

Error rates as a function of context reinstatement and trial type are presented in Table 2. The analysis of error rates revealed a main effect of context, $F(1,39) = 35.41$, $\eta^2_p = .48$, $p < .001$. Consistent with the RT data, participants made more errors when the context switched (8.3%) than when the context was reinstated (5.2%). The analysis also revealed a trend toward a main effect of trial type, $F(1,39) = 3.33$, $\eta^2_p = .08$, $p = .076$, and an interaction between context and trial type, $F(1,39) = 3.28$, $\eta^2_p = .08$, $p = .078$. Planned comparisons revealed that when the context was reinstated there was no difference in errors made for training (5.2%) and control trials (5.2%), $t(39) = 0.099$, $p = .922$. However, when the context switched participants made more errors on training trials (9.0%) than control trials (7.5%), $t(39) = 2.32$, $p = .026$. As discussed for the results of

Experiment 2, any differences for the context switch conditions are difficult to interpret, as trial type was coded based on the sequence associated with the context on trial *n-1*, and the assignment would be reversed if trial type was coded based on the sequence associated with the context on the current trial (trial *n*).

Given the significant learning effect for context-reinstated trials in the transfer blocks, we conducted an additional analysis to further investigate the nature of this learning effect. More specifically, we examined whether context-specific sequence learning could be measured across intervening trials that occurred in the alternative context. To that end, we assigned trial type based on the location of the target on the most proximate preceding trial that had occurred in the same context as the current trial. We included pairs of trials that had up to three intervening trials that occurred in the alternative context. For example, if the current trial was part of the primary context (red circle, left hand, above fixation), we classified that trial as training or control based on the position of the target in the most recent preceding trial that also occurred in the primary context. These two trials could be separated by up to three trials that all occurred in the secondary context (blue circle, right hand, below fixation). By classifying the current trial in this way, we examined whether the learning effects could still be observed with one, two, or three intervening trials, and whether the size of these learning effects differed from the learning effect observed when there were no intervening trials. Note that the RTs in the no intervening trials cells are the same as those reported in the context reinstatement cells described in the preceding analysis.

Mean RTs as a function of the number of intervening trials and trial type in the transfer blocks are presented in Figure 8. Context-specific learning across intervening trials was analyzed using an analysis of variance with Number of Intervening Trials (0/1/2/3) and Trial Type (training/control) as within subject factors. This analysis revealed a main effect of the number of intervening trials $F(3,117) = 59.05$, $\eta^2_p = .60$, $p < .001$; responses were faster when there were no intervening trials (875ms) than when there were one (1135ms), two (1109ms), or three (1101ms) intervening trials in the opposite context. More important, the analysis revealed a main effect of trial type $F(1,39) = 5.91$, $\eta^2_p = .13$, $p = .020$. Responses were faster on training trials (1040ms) than control trials (1070ms); reflecting a 30ms learning effect. Furthermore, the interaction between the number of intervening trials and trial type was not significant ($F < 1$), indicating that the size of the learning effect did not differ between the varying numbers of intervening items.   However, it is possible that the main effect of trial type in this analysis was driven by the learning effect present in the no intervening trials condition. With this in mind, context-specific learning across intervening trials was analyzed excluding the zero-intervening trials condition using an analysis of variance with Number of Intervening Trials (1/2/3) and Trial Type (training/control) as within subject factors. This analysis also revealed a main effect of trial type $F(1,39) = 3.90$, $\eta^2_p = .09$, $p = .028$ (1-tailed). Responses were faster on training trials (1100ms) than control trials (1130ms); again reflecting a 30ms learning effect. The main effect of number of intervening trials was not significant ($F < 1.5$), nor was the interaction with trial type ($F < 1$).
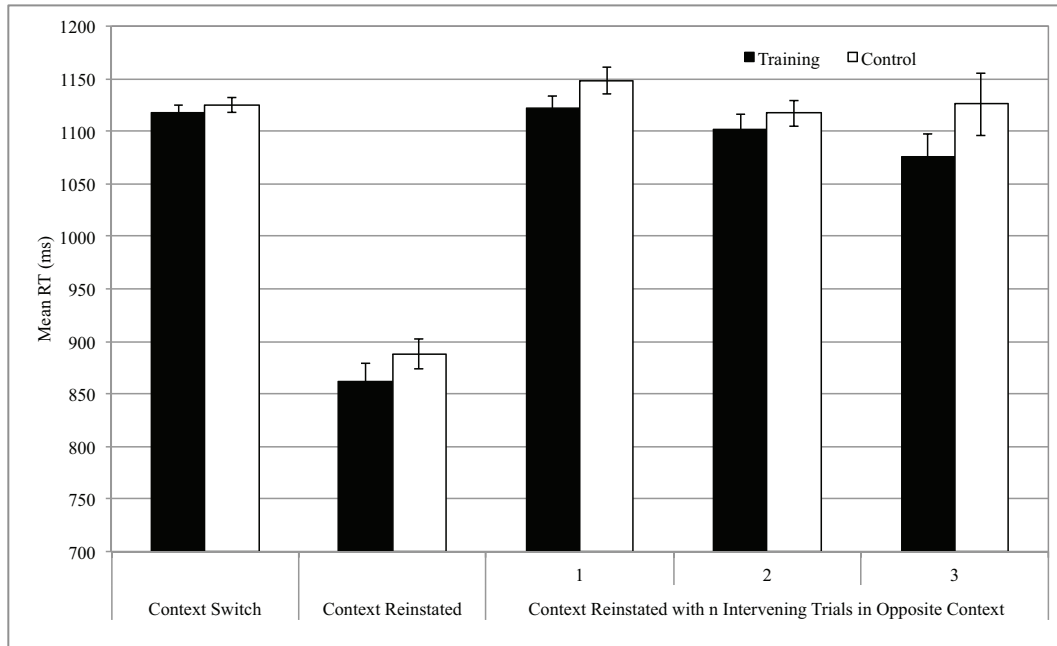
Figure 8. Mean RT for training and control trials as a function of the number of intervening trials presented in the opposite context in Experiment 3. Note that the RTs for the zero intervening trials condition are the same as those shown in the context reinstatement condition in Figure 7.

Generation Task Performance. To assess sensitivity in the generation task, mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the generation task assessing the sequence presented in the primary context, participants did not generate more training successors (.51) from the cues than expected by chance, $t(39) = .859, p = .396, d = 0.13$ (control successors generated = .49). For the generation task assessing the sequence presented in the secondary context, participants also did not generate more training successors (.51) from the cues than expected by chance, $t(39) = .470, p = .641, d = 0.07$ (control successors generated = .49).

Discussion

The purpose of Experiment 3 was to determine whether context-specific learning could be measured in the transfer blocks when the distinctiveness of the two contexts was increased by using target color, vertical location, and response hand as contextual features. The results from the training blocks and the generation tasks replicate the context-specific implicit sequence learning effects reported in Experiments 1 and 2. More important, the analysis of performance in the transfer blocks revealed that participants expressed context-specific sequence knowledge when the context was reinstated from the immediately preceding trial to the current trial. This learning effect strongly suggests that participants did not simply learn and re-learn the two sequences, but that participants learned the two sequences as a function of the associated training contexts. Furthermore, the results from the analysis of context-specific learning across intervening trials further suggests that contextual features can cue the expression of sequence knowledge associated with the current trial context.

General Discussion

The goal of the current paper was to examine whether flexibility in implicit sequence learning can be implemented through the reliance on contextual factors. To that end, we examined whether participants could acquire and express knowledge of two complementary sequences that were each associated with a set of distinct contextual features. More specifically, participants were trained on two sequences in two contexts on alternating blocks in a training phase. Following the training blocks, flexible expression of sequence knowledge was assessed in a transfer phase where the two

contexts were randomly intermixed. In these transfer blocks, learning effects were examined on trials in which the contextual features were reinstated from the immediately preceding trial. Across three experiments we manipulated the contextual features that were associated with the two sequences.

In Experiment 1, target shape (square/triangle) and response hand (left hand/right hand) were used as two contextual features that differed between contexts. The results of the training blocks in Experiment 1 indicate that participants were able to learn the two complementary sequences as a function of context, incidentally and without awareness of the sequence structures. The results of the transfer blocks in Experiment 1 did not reveal a significant learning effect for context-reinstated trials in the RT data. In Experiments 2 and 3, we examined whether increasing the distinctiveness of the two contexts from one another would allow us to measure flexible expression of sequence knowledge in the transfer blocks. In Experiment 2, the distinctiveness of the two contexts was increased by including vertical location (above/below fixation) as a third contextual feature (Crump et al., 2006), along with the features used in Experiment 1. The results of the training blocks in Experiment 2 replicated the context-specific implicit learning effects reported in Experiment 1. More important, the results of the transfer blocks in Experiment 2 showed a learning effect for context reinstated trials that approached significance, indicating that increasing the distinctiveness of the two contexts may well offer a path to demonstrating robust expression of sequence knowledge in the transfer blocks. Following that path a step further, in Experiment 3 we attempted to increase the distinctiveness of the target stimuli themselves, by using target color (red/blue) rather than target shape to

differentiate the two contexts (Theeuwes, 1991). The results of the training blocks in Experiment 3 replicated those of Experiments 1 and 2, in that participants showed context-specific implicit sequence learning. More important, the results of the transfer blocks in Experiment 3 revealed a significant learning effect on trials in which the context was reinstated from the preceding trial to the current trial, an effect that survived the inclusion of up to three intervening trials that occurred in the opposite context. In sum, across these three experiments there is compelling evidence that context-specific learning affords flexibility in implicit sequence learning, by adding contextual features to the implicitly bound representations. To our knowledge, this is the first demonstration that context can impart flexibility in implicit sequence learning, by offering the opportunity to learn and express learning of two sets of contingencies.

Context-specificity vs. Motor-specificity

Before discussing further the role of context in the present study, we turn to an alternative interpretation of the learning effects reported here. Given that participants learned two sequences with different hands, one interpretation of the present set of results is that the sequence learning effects were specific to particular motor contexts (i.e. response hand). In other words, it could be argued that participants simply learned one sequence of motor movements with their left hand and another sequence of motor movements with their right hand, in a similar way that pianists are able to learn to play a melody and accompanying chords with their right and left hands (Berner & Hoffmann, 2008; 2009). Therefore, it could be argued that this learning did not rely on bound contextual representations that included perceptual properties.

Although we agree that motor context likely plays a fundamental role in showing context-specific learning in the localization task used here, we argue that motor context is part of a bound representation of more general context features. In support of context-specificity, rather than simply motor-specificity, recall that the motor context was identical across Experiments 1-3, as participants always were trained on one sequence with their right hand and another with their left hand. If participants simply learned different sequences of motor movements, we should not expect any differences in the expression of sequence learning across these three experiments. However, the principled manner in which learning effects were revealed in the transfer blocks across Experiments 1-3, with a significant effect found only when measures were taken to maximize distinctiveness of the two contexts, suggests that contextual distinctiveness involves more than motor representations. Furthermore, the view that context-specific sequence learning relies on bound representations is consistent with other work examining the nature of the representations underlying implicit learning, which we elaborate upon below in Section 7.3.

Controlling Automaticity

Traditionally in cognitive psychology, automatic processes have been categorized as fast, precise, and unintentional, and as separate from more controlled and intentional processes (e.g. Posner & Snyder, 1975; Shiffrin & Schneider, 1977). As a consequence of this view, automatic processes are thought to be quite rigid, and indeed this conclusion is supported by a number of results demonstrating the rigidity of implicit sequence learning (e.g. Jiménez et al., 2006). In contrast to this traditional view, we propose that

although automatic processes are rigid, they can be flexibly expressed as a function of specific learned cues. In other words, flexibility in automaticity can be achieved through the incorporation of specific contextual features to sequence knowledge, whereby the presence of these features can later cue the expression of specific sequence knowledge. In this way, sequence knowledge is not obligatorily or rigidly expressed in all contexts, but rather is specifically expressed in the presence of contextual cues. The idea that the expression of implicit learning is not obligatory, and perhaps subject to a form of contextual control, is consistent with recent work that focuses on trial-to-trial modulations in the expression of sequence knowledge (D'Angelo et al., in press; Jiménez, Lupiáñez, & Vaquero, 2009). In particular, Jiménez et al. (2009) found that the expression of motor sequence learning in both intentional and incidental learners was eliminated following a single control trial. In interference tasks, such as the Eriksen flanker task (Eriksen & Eriksen, 1974) and the Stroop task (Stroop, 1935), trial-to-trial modulations, or sequential congruency effects, have been thought to reflect the online engagement of cognitive control in response to conflict (e.g. Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004; Gratton, Coles, & Donchin, 1992). Therefore, the finding of trial-to-trial modulations in implicit learning serves as compelling evidence against the view that automatic processes cannot be controlled. Furthermore, we have demonstrated that the reduction of sequence knowledge following the presence of a single control trial is sequence type specific (D'Angelo et al., in press). In this study, participants were concurrently trained on a motor sequence and an uncorrelated perceptual sequence. Importantly, the trial-to-trial modulations were sequence-type

specific, such that while motor sequence learning was eliminated following a motor sequence control trial, and perceptual sequence learning was eliminated following a perceptual sequence control trial, motor sequence learning was not modulated by the preceding trial's perceptual sequence status, nor was perceptual sequence learning modulated by the preceding trial's motor sequence status. We speculate that the specificity of these trial-to-trial modulations reflects a similar principle to that guiding performance in the current study, in the sense that both studies illustrate ways in which contextual information can bias or control the expression of automaticity. However, more research is required to elucidate whether the mechanisms underlying the flexibility seen in trial-to-trial modulations in implicit sequence learning are the same as those underlying the context-specific implicit sequence learning effects reported here.

The Nature of Representations Involved in Implicit Learning

On a final note, the context-specificity of implicit sequence learning demonstrated in this study speaks to a broader debate concerning the nature of the representations that support implicit learning. One view of the representational basis of implicit learning is that it occurs through the abstraction of the probabilistic structure inherent in the training items. By this view, the episodic details of the training items play no important role in the representations that support implicit learning effects (e.g., Reber, 1989). In contrast to this view, the context-specific sequence learning effects in the current study suggest that episodic context is an integral part of the knowledge structure that supports implicit sequence learning. A number of other studies in both the artificial grammar learning literature (e.g. Brooks & Vokey, 1991; Jamieson & Mewhort, 2009a; Whittlesea &

Dorken, 1993), and in the implicit sequence learning literature (e.g. Jamieson &

Mewhort, 2009b) are also supportive of this view. For example, Jamieson and Mewhort

(2009b) tested whether retrieval from a multitrace episodic memory can produce the

results from classic SRT studies. Using an adaptation of Hintzman's (1984) exemplar

model of memory, Minerva 2, Jamieson and Mewhort were indeed able to simulate the

results of Nissen and Bullemer (1987, Experiment 2), Stadler (1992, Experiment 1), and

Stadler and Neely (1997, Experiment 2). The results from these simulations, together

with the current results pointing to context-specificity in implicit sequence learning, offer

strong evidence for the role of episodic memory representations in implicit learning.

Given the evidence for the role of episodic memory representations in implicit

learning, it seems prudent to describe our views on how implicit learning (i.e.

automaticity) developed in the present set of experiments.   Based on the evidence

favoring episodic memory representations in implicit learning, we propose that the

learning effects reported here are another example of how automaticity develops as

instances from previous experiences are accumulated in memory (Logan, 1988).   More

specifically, similar to Jamieson and Mewhort (2009b), we propose that as participants

completed the task they encoded the response made on the preceding trial, the location of

the target on the current trial, the response made on the current trial, as well as the target

properties and other contextual information, and all this information was bound together

and represented an instance in memory. These instances accumulate as participants gain

experience with the task, and automaticity arises when behavior switches from being the

result of more controlled processing, in which an algorithm is used to generate a response,

to being the result of efficient retrieval of previous instances from memory (Logan, 1988). Within this framework, flexibility is the result of reliance on more specific cues, which are context features that are incorporated into the instances that represent previous experiences with each of the two learning contexts. The incorporation of these context features into instances can in turn lead to context-specific expression of knowledge when those contextual features are presented and are able to effectively cue the retrieval of appropriate instances.

Conclusions

In conclusion, the context-specificity in implicit sequence learning reported in the current study points to the role of context in implementing flexibility in the expression of automatic processes, and as evidence for episodic representations in implicit learning. More broadly, these results are consistent with other studies demonstrating the influence of context on performance when there is no explicit requirement to remember, such as in conjunction search (Chun & Jiang, 1998), pop-out search (Thomson, & Milliken, 2012), and task-switching (Allport & Wylie, 2000; Waszak, Hommel, & Allport, 2003). Collectively, the role of context-specific processing across these domains points to a broad principle, in which stimuli that are considered tools to measure perception and action also serve as memory cues of prior experiences that constrain how the past is integrated with the present.

CHAPTER 4: Re-examining the Role of Context in Implicit Sequence Learning

D'Angelo, M.C., Milliken, B., Jiménez, L., & Lupiáñez, J. (submitted).

Consciousness and Cognition, Manuscript ID: CONCOG-13-134

Preface

The experiments in the previous chapter demonstrated context-specificity in the expression of learning of two motor sequences. The goal of Chapter 4 was to examine further the role of context in implicit sequence learning. Therefore, Chapter 4 presents the results of three experiments in which the role of motor and perceptual contextual features were examined in learning of first-order conditional sequences. The results from these experiments were surprising, as participants were able to learn two motor sequences in the absence of distinct contextual information. In contrast to the results from Chapter 3, these results suggest that the learning effects found are due to learning and relearning of sequences rather than context specificity. In two additional experiments, the role of context was examined in learning of more complex sequential structures. The results from these latter experiments offer preliminary evidence that context-specific processes support the simultaneous learning of higher-order conditional sequences. Overall, the results from this chapter suggest that the role of context in learning of first-order conditional structures is more complicated that previously thought, but that episodic representations may underlie implicit sequence learning of higher order sequential structures.

Abstract

Implicit sequence learning typically develops gradually, is often expressed quite rigidly, and is heavily reliant on contextual features. Recently we reported results pointing to the role of context-specific processes in the acquisition and expression of implicit sequence knowledge (D'Angelo, Milliken, Jiménez, & Lupiáñez, 2013). Here we examined further the role of context in learning of first-order conditional sequences, and whether context also plays a role in learning second-order conditional structures. Across five experiments we show that the role of context in first-order conditional sequences may not be as clear as we had previously reported, while at the same time we find evidence for the role of context in learning second-order conditional sequences. Together the results suggest that temporal context may be sufficient to learn complementary first-order conditional sequences, but that additional contextual information is necessary to concurrently learn higher-order sequential structures.

Introduction

Sequential knowledge is important in our everyday lives. Drivers are able to coordinate a number of actions in sequence while attending to the roads, and often while also maintaining a conversation. The idea that sequential knowledge about one activity can be accessed while attention is directed to another activity is an important one in experimental psychology. In particular, it suggests that access to sequential knowledge can occur without intention, or automatically. Indeed, the implicit learning of sequences is now a well-studied laboratory phenomenon.

Implicit sequence learning is typically studied using the serial reaction time (SRT) task. In the most common variant of this task a single target appears on every trial at one of four marked locations. In this task, participants are instructed to respond to the location of the target on every trial by pressing a button corresponding to the target's current location. Unbeknownst to participants, the location of the target is predicted by a relatively complex sequence on the majority of the trials. Participants who are incidentally exposed to this structure are often unable to describe the underlying sequential structure. Despite this lack of awareness, participants show a gradual speeding of responses on trials where the target's location is predictable based on a training sequence (Nissen & Bullemer, 1987). Further evidence for sequence learning comes from the cost to participants' performance in responses made to a target when its location is either randomly selected (e.g. Cohen, Ivry, & Keele, 1990) or is generated by a control sequence (e.g. Schvaneveldt & Gomez, 1998).

A broad question in the implicit sequence learning literature that is beginning to receive attention is whether the representations that drive such effects are context-free or context-sensitive. Without systematic study of this issue, it seems that a reasonable argument can be made either way. Specifically, one might imagine that the representations supporting the learning of a predictable sequence of motor movements could be separate from the context-rich representations that we retrieve explicitly (e.g. P. J. Reber & Squire, 1994; Sanchez & P. J. Reber, 2013). Alternatively, one might view implicit sequence learning effects as being a product of the same representations that support explicit remembering, with differences in awareness attributed to processing differences associated with how those representations are accessed (e.g. Jamieson & Mewhort, 2009b). The broad aim of the research reported here was to examine whether implicit sequence learning is supported by context-dependent processes.

Context-Dependent Implicit Sequence Learning?

One of the first studies to point to the context-dependence of sequence learning was reported by Jiménez, Vaquero, and Lupiáñez (2006). They trained a group of intentional and a group of incidental learners on a second-order conditional sequence over a series of training blocks in which one target appeared alone on every trial. In a later transfer block, the target appeared amongst three distracting items, but its location was still selected based on the training sequence on 80% of the trials. The important result here is that although intentional learners continued to express sequence learning effects in the transfer block, the expression of sequence learning in incidental learners was completely eliminated in the transfer block. One explanation of this effect is that the

presence of distractors in the transfer block signals a change in context, which prevents the recruitment of previous learning episodes to support current performance, and thereby disrupts the expression of sequence learning.

More direct support for the notion that sequence learning is tied to context comes from work by Abrahamse and Verwey (2008). In a series of experiments, Abrahamse and Verwey trained participants on a sequence over a series of training blocks in one context. For example, participants would be trained on a sequence as they responded to the location of a target triangle that appeared along the top of the screen on a white background. Later, participants completed a transfer block in which the location of the target continued to be selected based on the trained sequence, but the context was shifted such that participants now responded to the location of a target rectangle that appeared along the bottom of the screen on a grey background. Participants showed learning in the training blocks, as evidenced by a gradual improvement in performance. However, performance suddenly slowed in the transfer block, when the context shifted, despite the fact that the target's location was still predicted by the training sequence. This decrement in performance when the context was changed constitutes evidence of the context-dependency of sequence learning.

In a recent study, we reported additional evidence that contextual features are bound to the representations that underlie sequential knowledge (D'Angelo et al., 2013). In a series of experiments, participants were trained on two complementary sequences that were associated with distinct contexts, and that were presented on alternating blocks during a training phase. For example, in one experiment participants were trained on a

sequence on odd numbered training blocks that required responses to red circles presented along the top of the screen with their left hand, while at the same time being trained on a complementary sequence on even numbered training blocks that required responses to blue circles presented at the bottom of the screen with their right hand. Across the three experiments, participants were able to learn the two sequences, despite the fact that the two sequences were complementary. We concluded that distinct contexts associated with the complementary sequences supported this learning process, with context defined broadly to include perceptual features and the effectors used to respond.

Present study

The purpose of the present study was to examine further the conditions under which context-specific sequence learning can arise. In particular, our prior study defined context broadly to include both perceptual and motor features, and it is not clear whether the association between one or the other of these sets of features was especially important to the results that we observed. To address this issue, we conducted three experiments that varied whether the complementary sequences were associated with both distinct motor and perceptual features, with distinct perceptual features only, or with neither distinct motor features nor distinct perceptual features. At the outset, we were particularly interested in whether the association between the two complementary sequences and different hands was critical to our effect, as prior studies have shown separate sequence learning effects for different response hands (e.g. Berner & Hoffmann, 2008; 2009). To preview our findings, the results of Experiments 1a-c were surprising, in that they suggested that neither distinct motor features nor distinct perceptual features

need be associated with two complementary first-order sequences for both sequences to be learned. In effect, the results from Experiments 1a-c suggest a surprisingly rapid form of sequence learning that does not depend on context. In Experiments 2a and 2b, we then asked whether learning of two more complex second-order conditional sequences (SOCs) might depend on the two sequences being associated with distinct contexts. Indeed, with these more complex sequences, we found preliminary evidence for such context-dependence.

Experiments 1a, 1b, and 1c: The role of distinct motor and perceptual features in context-specific implicit sequence learning.

The purpose of Experiments 1a-c was to assess further the relative contribution of distinct motor and perceptual features on concurrent learning of complementary sequences (D'Angelo et al. 2013). In Experiment 1a we conducted a replication of Experiment 3 from D'Angelo et al. (2013) to assess context-specific learning with distinct motor and perceptual features. In this experiment participants were trained on complementary first-order conditional sequences as a function of context. The two contexts differed in terms of perceptual features, namely target color (red or blue circle), and the vertical location of the possible target positions (top or bottom of the screen), as well as motor features, in which each context was associated with a separate response hand (left or right hand). Participants were trained on the two sequences on alternating blocks, while simultaneously performing a secondary counting task. Therefore, during the training blocks, participants shifted from responding with one hand to a particular target color and location within one block of trials to responding with the other hand in

the subsequent block to the other target color and location. Within these training blocks, the target's position was selected using the sequence associated with the current context on 80% of trials, while the target's position was selected by the complementary sequence on the remaining 20% of trials. In a later transfer block, the two contexts were randomly intermixed and the target's position was selected according to the training sequence within each context on only 50% of trials. The transfer blocks were included to further examine the processes underlying the learning effects present in the training blocks. Awareness of the two sequences was assessed using separate generation tasks for each of the two sequences, where the contextual features that had been associated with each sequence during the SRT task were maintained during the generation tasks.

In Experiment 1b we examined whether distinct motor contexts are necessary for concurrent learning of complementary sequences. To address this issue, we tested whether distinct perceptual features associated with the two sequences (in the absence of distinct motor contexts) would be sufficient to replicate the learning effects reported in our earlier work. As such, Experiment 1b was identical to Experiment 1a with the exception that participants responded to the location of targets using the same effectors in the two contexts.

Experiment 1c was conceived as a control experiment for Experiments 1a and 1b. As such, in Experiment 1c we removed the motor and perceptual features that were included in Experiments 1a and 1b. The training phase of Experiment 1c was identical to that of Experiment 1b, with the exception that the targets were always blue circles, and they appeared at one of four marked locations along an imaginary horizontal line across

the center of the screen. In addition, in Experiment 1c we included transfer blocks in which novel sequences were presented, in order to assess how rapidly learning of first-order conditional sequences can occur. Note that in Experiment 1c we were unable to assess sequence knowledge through performance on generation tasks, as there was no way to independently cue participants to generate knowledge of the primary versus secondary sequences.

Methods

　　Participants. Thirty-nine undergraduate students (20 females – mean age 19 years) enrolled at McMaster University participated in the experiment in exchange for course credit in Experiment 1a. Forty additional undergraduate students (32 females – mean age 18 years) participated in Experiment 1b in exchange for course credit, and another forty undergraduate students (29 females – mean age 19 years) participated in Experiment 1c.

　　The participants had never participated in similar experiments before. All participants had normal or corrected to normal vision. Two additional participants completed Experiment 1a but were excluded for the following reasons. One participant had an overall error rate that was three standard deviations greater than the average error rate of all participants in Experiment 1a and the other participant used the wrong response hand for a particular context throughout an entire block of trials. One additional participant completed Experiment 1b and one additional participant completed Experiment 1c, but both participants were excluded, as they did not complete the

secondary counting task. This and all other experiments reported here received ethics

approval from the McMaster University Ethics Board.

      Apparatus and stimuli. The experiments were programmed using Presentation®

experimental software (v.16.3, www.neurobs.com), which was also used to generate the

sequence of stimuli. The stimuli were presented on a 24-inch BenQ LED color monitor.

Responses were entered through the keyboard. Participants were tested in groups of two

or three, and sat approximately 57 cm from the screen.

      The target stimuli were circles with a diameter of 1.3º of visual angle. In

Experiments 1a and 1b the target circles could be red or blue, and could be either bright

or dim. The dim circles were set to be subjectively dimmer than the bright circles, as

confirmed by lab members. In Experiment 1c only blue circles were used, which could

be either bright or dim.

      Procedure. For the sake of clarity, we first describe the procedure of Experiment

1a, after which we note differences in Experiments 1b and 1c. As in Experiment 3 of

D'Angelo et al. (2013), participants completed a localization task in which the target was

either a blue or red circle. On every trial a fixation cross was presented in the center of the

screen along with two rows of four equally spaced marked locations in a horizontal line.

The locations were marked by dots, which were spaced apart by intervals of 3º of visual

angle. One row of marked locations was presented 2º above, and the other was presented

3.5º below the fixation cross, so that circles presented in the location below the fixation

cross appeared at the same distance from the fixation point as those in the same position

in the location above the fixation cross. On every trial one circle appeared 1º of visual

angle above one of the four dots and participants were instructed to respond to the

location of the circle as quickly and accurately as possible using either their left or right

hand, depending on the color of the circle. The location (above or below fixation) in

which the circle appeared was perfectly correlated with the color and responding hand.

For example, one group of participants always saw red circles above fixation and blue

circles below fixation, and for some participants responses to red circles were made with

the four fingers of their left hand and responses to blue circles were made with the four

fingers of their right hand. Participants responded by pressing the buttons 'Z', 'X', 'C',

and 'V' with their left hand, and the buttons 'N', 'M', '<', and '>' with their right hand,

for circles appearing, respectively, at the far left, middle left, middle right, and far right

locations. The color assigned to each of the two vertical locations was randomly selected

for each participant, while response hand was counterbalanced between participants.

Following incorrect responses an error tone lasting 500ms was presented through

headphones. Participants were not required to correct these incorrect responses. Rather,

the fixation screen containing the four placeholders remained on the screen during the

auditory feedback, and the following trial began immediately after the end of the

feedback tone. Following correct responses, the next trial appeared immediately after the

response.

        The procedure of Experiment 1b differed only in that participants responded to the

location of red and blue circles using the same effectors. Therefore, participants

responded by pressing the buttons 'C', 'V' 'N', and 'M', using the index and middle

fingers of each hand, for circles appearing, respectively, at the far left, middle left, middle right, and far right locations, both above and below the fixation cross.

The procedure of Experiment 1c was identical to that of Experiment 1b with the exception that in Experiment 1c the two sequences that participants were trained on were only differentiated by the block in which a particular sequence was presented. Therefore, on every trial, the target was a blue circle, which appeared at one of four marked locations equally spaced in a horizontal line, and presented such that the fixation cross was halfway between the two middle markers. Due to a programming error, performance on the counting task from the final block of trials was not recorded in this experiment.

Sequences Derived From Complementary Grammars. Once again for the sake of clarity, we describe the sequences as used in Experiment 1a, noting any differences in Experiments 1b and 1c where relevant. As in D'Angelo et al. (2013), two sequences were used to assign the location of the target on every trial; the location of red circles was determined by one sequence, while the location of blue circles was determined by a second, complementary sequence. These two sequences were derived from the artificial Grammars A and B used by D'Angelo et al. (2013), which were modified versions of the Grammars C and D used by Soetens, Melis, and Notebaert (2004). Note that all four grammars are shown in Figure 1, but only Grammars A and B were used in Experiment 1a, only Grammars C and D were used in Experiment 1b, and all four Grammars were used in Experiment 1c. In these grammars, the marked positions 1 through 4 correspond to the possible target locations, in order, beginning with the left-most location (position 1) to the right-most location (position 4). From any position in the grammar, there is an

equal probability of transitioning to either of two predicted positions, and repetitions do occur. For example, starting from position 1 in Grammar A there is a 50% probability of transitioning to position 1, and a 50% probability of transitioning to position 2. Therefore, in Grammar A, there are no legal transitions from position 1 to positions 3 or 4. Trials in which the target's location is predicted by transitions consistent with the training sequence are referred to as training trials, and trials in which the target's location is not predicted by transitions consistent with the training sequence are referred to as control trials. Given the complementary nature of the two grammars, control trials for Grammar A are in fact transitions that are consistent with the sequence derived from Grammar B, and vice versa. Target locations were selected using a trial-to-trial substitution procedure (Schvaneveldt & Gomez, 1998). Using this procedure, if a block of trials contains 80% training trials, and if the target's location on the current trial corresponds to position 1 in grammar A, then there is a 40% likelihood of transitioning to each of positions 1 and 2, and a 10% likelihood of transitioning to each of positions 3 and 4.

Figure 1. The grammars used to generate the sequences in Experiments 1a-c. Grammars A and B were used in Experiment 1a, and all four grammars were used in Experiments 1b and 1c. The assignment of grammars to the primary and secondary context (and novel sequences in Experiment 1c) was counterbalanced between participants.

On the first trial of every block, the target's location was selected randomly. On all subsequent trials in the training blocks, the location of the target was selected based on the training sequence on 80% of trials and based on the control sequence on 20% of trials, using the sequence associated with the current context/target type. Following control trials, the location of the target on the subsequent trial was selected based on the location of the target on the control trial that had just been completed. Similarly, following an incorrect response, the location of the target on the subsequent trial was selected based on the actual target location for the trial that had just been completed. The assignment of the two sequences to the red and blue circles was counterbalanced between participants in Experiments 1a and 1b.

The experimental design is as follows for Experiments 1a and 1b. Before beginning the experimental trials, participants first completed two practice blocks each

containing 30 trials. One block contained only red circles and the other block contained only blue circles, and in Experiment 1a, within each block, responses were made with the assigned response hand. In these practice blocks, the location of the target was randomly determined on every trial. As in D'Angelo et al. (2013), participants were then trained over ten blocks of 100 trials each in which the circle color alternated from always red to always blue within a given block. The combination of vertical location, target color, and response hand (in Experiment 1a), presented in the first block and on subsequent odd numbered blocks is collectively referred to as the primary context, and the combination associated with the even numbered blocks is collectively referred to as the secondary context. During the training phase, participants were trained on one sequence with the red circle targets and on a second, complementary sequence with the blue circle targets. For example, one group of participants in Experiment 1a was trained on Sequence A with the red circles and their left hand on odd blocks and Sequence B with the blue circles and their right hand on even blocks.

After the training phase, participants completed a transfer phase consisting of four blocks of 100 trials each in which there was an equal likelihood that the target circle would be red or blue on any given trial. In the transfer phase, the association between target color and vertical location always matched what participants had been trained on in the training blocks. For example, for the group of participants who always saw red circles in the locations above the fixation cross in the training phase, target circles above the fixation cross in the transfer phase were always red, and target circles presented below the fixation cross were always blue. In the transfer phase, participants in Experiment 1a

continued to respond to targets using the response hand associated with the target color. Therefore, unlike in the training blocks of Experiment 1a where participants only responded with one hand within a block of trials, in the transfer blocks of Experiment 1a participants responded with both hands within a block of trials. In the transfer blocks, the location of the target was selected based on the training sequence associated with the previous target on only 50% of trials, which, given the sequences used, is equivalent to the random selection of target locations on every trial.[6] Following the transfer blocks, participants completed two additional training blocks, one with red circle targets and one with blue circle targets, to re-establish the learned contingencies before measuring sequence knowledge directly using a series of generation tasks.

As mentioned above, in Experiment 1c all four grammars were used. For each participant, one pair of grammars was assigned as the training sequences, and the other pair of grammars was assigned as the novel sequences. For example, one group of participants were assigned Grammars A and B as the two training sequences (referred to as the primary and secondary sequences), and were exposed to Grammars C and D as the novel sequences (referred to as the first and second novel sequences). Assignment of the pairs of sequences as the primary and secondary training sequences, and as the two novel sequences was counterbalanced between participants.

In Experiment 1c, participants completed just one practice block. Following the practice block, participants were trained over 16 blocks of 100 trials each in which the

---

[6] Unfortunately we were unable to replicate our previous finding of the expression of learning in the transfer blocks in Experiments 1a and1b. The results of the transfer blocks are presented in the Appendix.

location of the target circle was selected based on the primary sequence in the odd-numbered blocks and was selected based on its complementary secondary sequence in the even-numbered blocks. Therefore, the sequence used to generate the location of the target on each trial alternated between blocks, with the exception of blocks 11 and 14, where two novel sequences were presented. In block 11, the first novel sequence was used to generate the location of the target, substituting the use of the primary sequence, and in block 14, the second novel sequence substituted the use of the secondary sequence to generate the location of the target. These two novel sequences were included as an alternative measure of how quickly participants learn the first-order conditional sequences.

Following each of the practice, training, and transfer blocks participants in all three experiments were given feedback on their mean reaction time (RT) and accuracy.

Secondary counting task. To reduce the likelihood that participants would become aware of the sequences, participants were instructed to engage in a secondary counting task in addition to the primary localization task in the training and transfer blocks. Participants were instructed to count the number of times the colour of the target circle was dim. At the end of each block of trials, participants typed in the number of dim targets they had counted, and were given feedback on their estimate before they began the next block of trials. The number of dim targets within each block varied from 40-60 targets.

Generation task. Following the experimental blocks, participants in Experiments 1a and 1b completed two sets of cued generation tasks, one for each of the two sequences

they had been trained on. The generation tasks were included to assess participants'

abilities to make direct predictions of where a target stimulus would appear in response to

fragments of the sequences they had been trained on. Participants were told that in these

experiments individuals sometimes feel as though the stimuli follow a certain order, and

were explicitly told that in this part of the experiment (the generation task) they should

make their responses based on what they felt occurred in the previous part of the

experiment (the SRT task).

Participants completed a block of cued generation trials that assessed knowledge

of the sequence that was associated with the primary context (e.g., the sequence that had

been presented with red circles) and another series of cued generation trials that assessed

knowledge of the sequence that was associated with the secondary context (e.g., the

sequence that had been presented with blue circles). The presentation order of the two

generation tasks was counterbalanced between subjects. Each generation task consisted

of 16 pairs of trials. The first trial in each pair was a cue trial, in which a fragment of the

sequence was presented. Given that the sequences used in the current study are first-

order sequences in which legal transitions according to the training grammars are

dependent only on the location of the target on the preceding trial, only one fragment was

presented on each cued generation trial.

Participants responded to the cue trial in the same way that they responded to

targets in the standard SRT task (using the appropriate keys based on target color/vertical

location in Experiment 1a). Following their response to the cue trial, participants saw an

empty fixation screen containing the fixation cross and the eight marked locations, and

were asked to generate the most likely location of a subsequent target that was the same

color as the target they had responded to in the previous display, again using the same

responses used in the standard SRT task. Given the nature of the grammars used to

generate the sequences, two training successors were equally likely for each cue trial. For

example, in the case of a participant for whom Grammar A was assigned to red targets,

the presentation of a red circle in position 1 on a cue trial would have positions 1 and 2 as

equally likely training locations, and positions 3 and 4 as equally likely control locations.

For both generation tasks, each of the four possible cues (starting positions) was

presented four times, in random order, thus completing a full set of 16 cue trials for each

of the two generation tasks.

   No generation task was included in Experiment 1c. Given that in Experiment 1c

we eliminated all contextual features that could distinguish the two sequences, with the

exception of the temporal block context, there was no real way to cue participants to

generate items based on one sequence or another. Given our inability to cue a particular

sequence, participants could have produced a null result on the generation task regardless

of whether they were aware or unaware of the sequences.[7]

---

[7] Despite the lack of a generation task, we are confident that any learning in this experiment would arise
unintentionally, and that participants would not be explicitly aware of the sequence structure, given that we
have not found evidence of awareness across all of our previous experiments with this particular design.
More specifically, there are factors present in our design that have been shown to minimize intentional
learning, such as training participants on probabilistic sequences using a trial-by-trial substitution method
(e.g. Cleeremans & Jiménez, 1998), using a secondary counting task (but see Shanks, Rowland, & Ranger,
2005), and by using a 0ms RSI (e.g. Destrebecqz & Cleeremans, 2001, but see Shanks, Wilkinson, &
Channon, 2003).

Results

As in D'Angelo et al. (2013), there were three different ways in which learning was assessed. First, we assessed learning of the two sequences in Experiments 1a-c by analyzing differences between mean RTs for training and control trials as a function of training block and context. Second, in Experiment 1c, rather than measuring transfer in a pair of transfer blocks, we examined how quickly learning occurs by comparing mean RTs for training and control trials in two novel sequence blocks, with learning effects for the primary and secondary sequences. Third, awareness of the sequences was examined in Experiments 1a and 1b using performance on the generation tasks, by assessing whether participants generated more often the training or control successors of all the relevant cues. All statistical tests were evaluated using an alpha value of .05.

RTs for the first trial of each block and for trials in which an error was made (3.1% of trials in Experiment 1a; 2.4% in Experiment 1b; 3.3% in Experiment 1c) were not included in the analyses. In addition, RTs that were more than three standard deviations from the mean for each block, defined separately for each participant (1.7% of trials in Experiment 1a; 1.7% in Experiment 1b; 2.4% in Experiment 1c), were treated as outliers and eliminated from the analyses.[8] All analyses of Experiment 1c were first analyzed including the sequence assignment as a between-subjects factor. There were no

---

[8] Participants were generally accurate in counting the number of dim targets. On average, participants were off from the correct number of dim targets by ±3 per block across participants in Experiment 1a; ±4 in Experiment 1b; and ±4 in Experiment 1c. The worst performance was for one participant who was off by ±8 targets on average per block in Experiment 1a; ±17 in Experiment 1b; and ±9 in Experiment 1c.

significant interactions with the sequence assignment (all F's < 1.2, p's > .280), therefore the analyses of Experiment 1c described below collapsed across this factor.

Training Blocks. Mean RTs were computed for training and control sequence trials, separately for each block for each participant in Experiments 1a-c. Trial type was assigned based on the sequence associated with the context presented in that particular block. Context-specific sequence learning was separately analyzed for each experiment using an analysis of variance with Training Block (1-10), Context (primary/secondary), and Trial Type (training/control) as within subject factors. Here and in all subsequent experiments, for the effects and interactions involving Block, we report nominal degrees of freedom along with Greenhouse-Geisser ε and adjusted p-levels.

Experiment 1a. Mean RTs as a function of trial type, context, and block are presented in the top panel of Figure 2. The analysis of mean RTs revealed a main effect of block, $F(4,152) = 10.90$, $\eta^2_p = .22$, $p < .001$, $\varepsilon = .89$. The analysis also revealed a main effect of trial type, $F(1,38) = 36.71$, $\eta^2_p = .49$, $p < .001$. Responses were faster on training trials (660ms) than on control trials (679ms), reflecting a 19ms learning effect. However, the main effect of trial type was qualified by the three-way interaction with block and context, $F(4,152) = 2.78$, $\eta^2_p = .07$, $p = .038$, $\varepsilon = .84$.
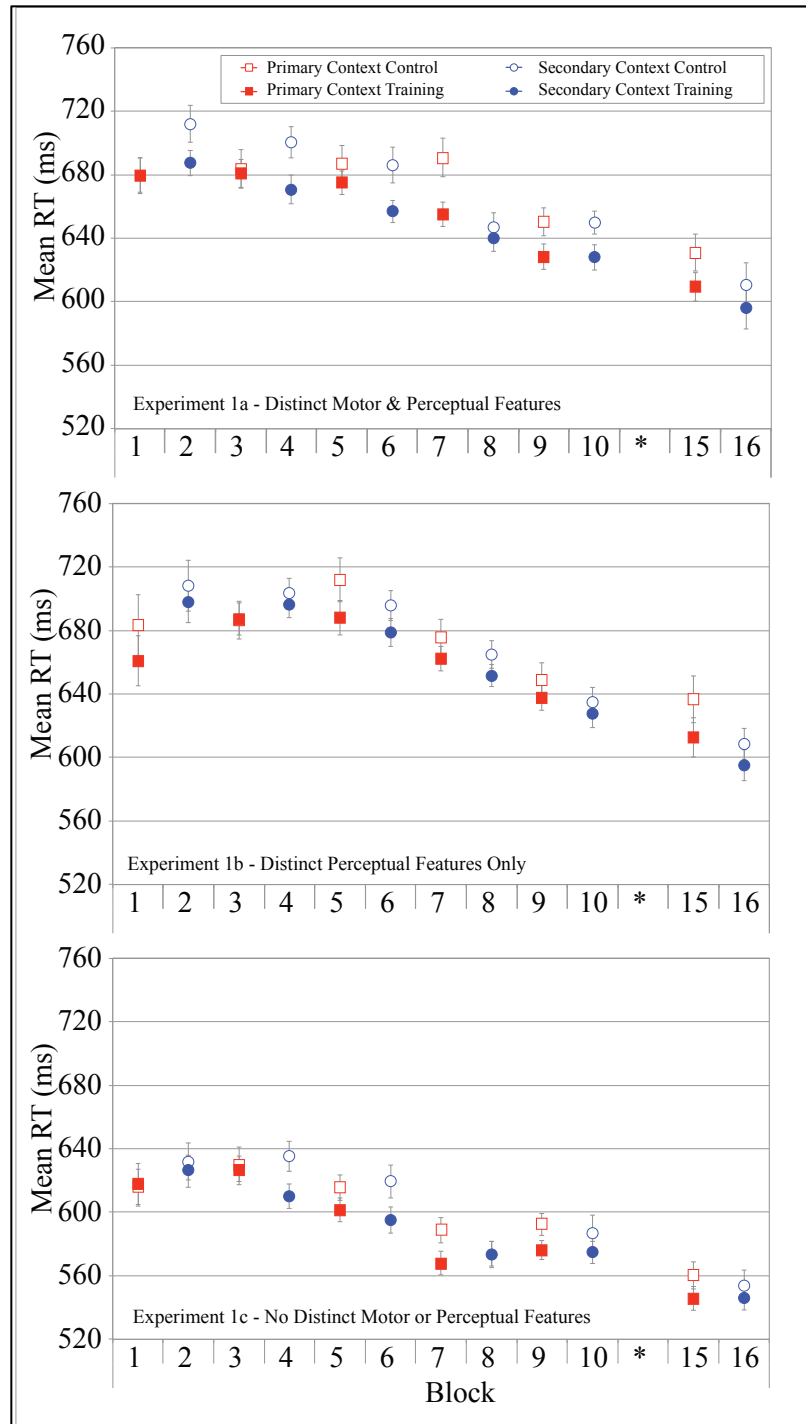
Figure 2. Mean RT(ms) for training and control trials (filled and unfilled shapes, respectively) as a function of primary and secondary contexts (red squares and blue circles, respectively) across training blocks in Experiment 1a (top), Experiment 1b (middle), and Experiment 1c (bottom). The * symbol represents the location of the

transfer blocks within the training block sequence. Error bars in this and all other figures represent standard errors of the mean that have been corrected to eliminate between-subject variability (Cousineau, 2005).

To investigate the nature of the interaction between trial type, block, and context, the simple main effects of trial type and block were analyzed separately for each context. For the primary context, the analysis revealed a main effect of block, $F(4,152) = 3.91$, η^2_p = .09, p = .005, ε = .96. The analysis also revealed a main effect of trial type, $F(1,38)$ = 17.03, η^2_p = .31, $p < .001$. Responses were faster on training trials (664ms) than on control trials (678ms), reflecting a 14ms learning effect. The interaction between block and trial type was not significant, $F(4,152) = 1.83$, η^2_p = .05, p = .137, ε = .86.

For the secondary context, the analysis revealed a main effect of block, $F(4,152)$ = 9.58, η^2_p = .20, $p < .001$, ε = .83. The analysis also revealed a main effect of trial type, $F(1,38) = 28.90$, η^2_p = .43, $p < .001$. Responses were faster on training trials (656ms) than on control trials (679ms), reflecting a 23ms learning effect. The interaction between block and trial type was again not significant, $F(4,152) = 1.53$, η^2_p = .04, p = .200, ε = .93. Thus, the general pattern of results for the primary and secondary contexts was similar, and the three-way interaction must owe to a subtle difference in the speed with which learning occurred across blocks for the two contexts (see Figure 2).

Experiment 1b. Mean RTs as a function of trial type, context, and block are presented in the middle panel of Figure 2. The analysis of mean RTs revealed a main effect of block, $F(4,156) = 6.60$, η^2_p = .14, p = .001, ε = .57. Importantly, the analysis revealed a main effect of trial type, $F(1,39) = 32.21$, η^2_p = .45, $p < .001$. Responses were faster on training trials (669ms) than on control trials (681ms), reflecting a 12ms learning

effect. The interaction between context and trial type was not significant, $F < 1$, indicating that the learning effects did not differ between contexts. The interaction between block and context was significant $F(4,156) = 2.79$, $\eta^2_p = .07$, $p = .037$, $\varepsilon = .84$. The remaining interactions were not significant, all F's < 1.4.

Experiment 1c. Mean RTs as a function of trial type, temporal context, and block are presented in the bottom panel of Figure 2. The analysis of mean RTs revealed a main effect of block, $F(4,156) = 11.92$, $\eta^2_p = .23$, $p < .001$, $\varepsilon = .80$. Importantly, the analysis revealed a main effect of trial type, $F(1,39) = 20.98$, $\eta^2_p = .35$, $p < .001$. Responses were faster on training trials (612ms) than on control trials (624ms), reflecting a 12ms learning effect. The interaction between the temporal context and trial type was not significant, $F < 1$, indicating that the learning effects did not differ between the temporal context associated with each sequence. The interaction between temporal context, block, and trial type was not significant, $F(4,156) = 2.33$, $\eta^2_p = .06$, $p = .070$, $\varepsilon = .84$. The remaining main effects and interactions were not significant, all F's < 1.5, p's > .20.

Novel Sequence Blocks (Experiment 1c). As another test of how quickly relearning can occur in the present study, we examined whether participants could learn untrained sequences that were each only presented in a single block of trials, and compared that learning with their relearning of the training sequences later in training. To compare the learning effects for the two novel (untrained) sequences with learning effects for the primary and secondary sequences in Experiment 1c, mean RTs were computed for the training and control sequence trials across two blocks for each of the primary sequences (Blocks 9 and 13), the secondary sequences (Blocks 10 and 12) and

the novel sequences (Blocks 11 and 14), separately for each participant. The two blocks

selected for each of the primary and secondary sequences were chosen such that one

block of each occurred before the presentation of the first novel sequence, and one block

of each occurred after the presentation of the first novel sequence block and prior to the

second novel sequence block. Learning was analyzed using an analysis of variance with

Sequence Type (primary/secondary/novel), Block (1/2) and Trial Type (training/control)

as within-subject factors.
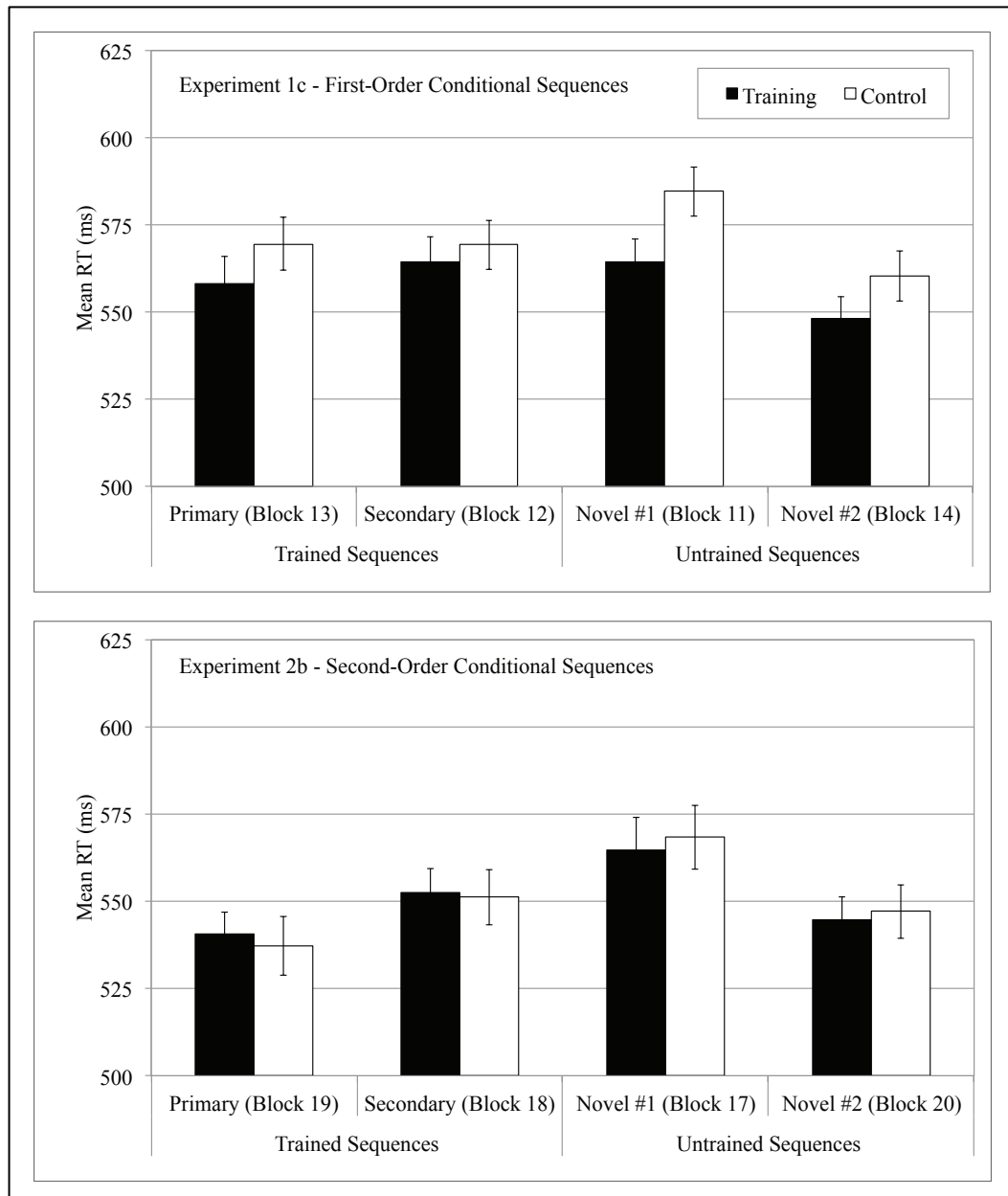
Figure 3. Mean RT for training and control trials as a function of sequence type for trained and untrained sequence blocks in Experiment 1c (top), and Experiment 2b (bottom). Note that training blocks 9 and 10 of Experiment 1c and training blocks 15 and 16 of Experiment 2b were also included in the analyses reported for each experiment.

Mean RTs as a function of trained and untrained sequences in the transfer blocks of Experiment 1c are shown in the top panel of Figure 3. The analysis of mean RTs revealed a main effect of block, $F(1,39) = 9.83$, $\eta^2_p = .20$, $p = .003$. The analysis also revealed a main effect of trial type, $F(1,39) = 19.04$, $\eta^2_p = .33$, $p < .001$. Responses were faster on training trials (578ms) than on control trials (592ms), reflecting a 14ms learning effect. Somewhat surprisingly, the interaction between the sequence type and trial type was not significant, $F < 1$, indicating that the learning effects did not differ between the blocks associated with each of the three sequences, including learning effects for the novel sequences. Furthermore, a planned comparison of the learning effects in the two novel sequence blocks with block and trial type as within-subject factors revealed a main effect of trial type, $F(1,39) = 8.85$, $\eta^2_p = .18$, $p = .005$. Responses were faster on training trials (570ms) than on control trials (587ms), reflecting a 17ms learning effect in the two novel sequence blocks. The interaction between block and trial type was not significant, $F < 1.1$, $p > .31$.

Generation Task Performance. Participants' awareness of the sequences they had been trained on was evaluated by assessing their sensitivity to the sequences on the generation tasks. Participants' sensitivity to the sequences was assessed by comparing the number of trials in which participants completed a cue with a training successor to the number expected by chance. We derived chance performance based on the assumption that if sequence knowledge does not guide behavior here, all four target locations would be chosen with equal likelihood. As two of the target locations are training successors for

each cue, chance performance on the generation trials is the likelihood of selecting either of the two training successors by chance alone, which is .50.

Experiment 1a. Mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the generation task assessing the sequence presented in the primary context, participants did not generate more training successors (.51) from the cues than expected by chance, $t(38) = .63$, $p = .534$, $d = 0.10$ (control successors generated = .49). For the generation task assessing the sequence presented in the secondary context, participants did not generate more training successors (.52) from the cues than expected by chance, $t(38) = 1.16$, $p = .253$, $d = 0.19$ (control successors generated = .48).

Experiment 1b. Mean proportions of training successors generated were submitted to a one-sample t-test to compare performance to chance (.50). For the generation task assessing the sequence presented in the primary context, participants did not generate more training successors (.48) from the cues than expected by chance, $t(39) = 1.17$, $p = .250$, $d = 0.19$ (control successors generated = .52). For the generation task assessing the sequence presented in the secondary context, participants did not generate more training successors (.51) from the cues than expected by chance, $t(39) = .29$, $p = .776$, $d = 0.05$ (control successors generated = .49).

Discussion

In Experiments 1a-c, we replicated our earlier finding that participants are able to learn two complementary sequences on alternating blocks. Somewhat surprisingly, the results from Experiment 1c demonstrate that distinct motor and perceptual features were

not necessary for this learning to occur. Therefore, although we had concluded that

distinct perceptual and/or motor contexts allowed concurrent learning of complementary

first-order sequences to occur (D'Angelo et al., 2013), the present data offer no support

for this view. In the present study, participants concurrently learned complementary

sequences under conditions in which only the temporal block structure of the experiment

served to distinguish the two sequences. In this case, rather than arguing that distinct

contextual features support concurrent learning of two complementary sequences, the

more parsimonious conclusion is that concurrent learning of complementary first-order

sequences is supported by remarkably fast learning of sequences within the time frame of

a single block of 100 or so trials.

The results of the generation tasks in Experiments 1a and 1b suggest that

participants were not able to explicitly generate the sequential information that they were

able to express knowledge of in their performance on the SRT task. Although we did not

measure generation performance in Experiment 1c, we used the same general design, and

so it is unlikely that participants in this latter experiment became aware of the sequences.

As such, it seems relatively safe to conclude that the remarkably rapid learning of

complementary first-order sequences observed here occurred unintentionally, and was not

accompanied by awareness of the sequences.

Furthermore, the finding that participants in Experiment 1c were also able to learn

two novel sequences with limited exposure to these sequences points to a rapid learning

account of the present results. The idea that participants adapt so rapidly to changes in

the probabilistic structure is quite surprising, given previous work showing rigid

expression of sequential knowledge in the face of changed probabilistic structures (e.g. Jiménez et al., 2006 – Experiments 3 & 4; Jiménez et al., 2009). For example, after training participants on one sequence over a series of training blocks, Jiménez et al. (2006, Experiment 3) reduced the percentage of training trials from 100% to 12.5% in a series of transfer blocks. Although intentional learners were able to adapt to the shift in the probability of encountering training trials, incidental learners did not show any adaptation, continuing to express learning effects in the transfer blocks. This insensitivity to the change in the probabilistic structure is a stark contrast to the rapid adaptation that we report here.

There is one notable difference between previous studies that have shown rigid expression of sequence learning, and the present studies that show rapid adaptation to changes in sequence probabilities. In particular, previous studies have used second-order conditional sequences (SOCs), whereas our studies have used first-order conditional sequences[9]. Recall that we chose to use first-order sequences specifically because participants typically learn these sequences faster than SOCs. However, they appear to be learning these sequences so fast that there is no opportunity to demonstrate the disambiguating role of context in the concurrent learning of two sequences. To pursue the idea that context can play this disambiguating role in the concurrent learning of two sequences, we reasoned that sequences must be used for which the learning occurs more

---

[9] A second notable difference between the present study and Jiménez et al. (2006, Experiment 3) is that the low probability of training trials in the transfer blocks in Jiménez et al.'s study constituted a full sequence, as they used a complete sequence substitution method, rather than a trial-by-trial substitution method used in the present study.

slowly than for the first-order sequences used to this point. As such, Experiments 2a and 2b assessed context-specific learning using SOCs.

Experiments 2a & 2b: The role of distinct motor and perceptual features in concurrent implicit learning of second-order conditional sequences

The goal of Experiments 2a and 2b was to examine the role that contextual information plays in learning more complex sequential structures, such as in learning SOCs. In second-order conditional sequences, the position of a target on trial n-1 does not exclusively predict where the target will appear on the subsequent trial, but knowing where the target appeared on trials n-1 and n-2 does exclusively predict the target's position on trial n. Given the ambiguous structure of the trial n-1 to n transitions in SOCs, participants typically show a more gradual development of learning when trained on these sequences. Therefore, if learning SOCs takes longer to unfold, then there may be greater utility in incorporating contextual features that prevent interference and help separate out conflicting information across the blocks. This hypothesis was tested by examining whether participants would show implicit learning of two complementary SOCs only when the sequences are signaled by distinct visual and motor features (Experiment 2a), or if participants would also show learning of two complementary SOCs in the absence of distinct motor and perceptual features (Experiment 2b). The use of SOCs in Experiments 2a and 2b also allowed us to contrast these results with other results in the literature, which have reported context-dependent learning when using SOCs (Abrahamse & Verwey, 2008; Jiménez et al., 2006 - Experiments 1 & 2).

In Experiment 2a we examined whether context-specific implicit sequence learning of complementary SOCs is possible when motor and perceptual information is present to differentiate the two sets of learning episodes. To that end, Experiment 2a was a replication of Experiment 1a using SOCs. However, as sequence learning with SOCs typically takes longer to develop, in Experiment 2a we increased the number of training blocks from 10 to 16, and increased the number of trials per block to 120 trials. In the transfer blocks of Experiment 2a, the two contexts alternated predictably every five trials, to ensure that there would be sufficient observations for each of the training and control trials for the context reinstated condition, in which trials n-2 to n appeared in the same context.

To assess whether context-specific sequence learning effects could be measured for higher order sequential structures in the absence of distinct motor and perceptual features, Experiment 2b was a replication of Experiment 1c using two complementary SOCs (Reed & Johnson, 1994). Once again, in this experiment we the increased number of training blocks and the number of trials per block as in Experiment 2a. As in Experiment 1c, the targets were always blue circles that appeared at one of four positions along the center of the screen, and following the 16 training blocks, toward the end of the experimental session, participants were exposed to two novel complementary sequences.

Methods

Participants. Forty undergraduate students (34 females – mean age 19 years) enrolled at McMaster University participated in Experiment 2a, and another 40 undergraduate students (24 females – mean age 19 years) participated in Experiment 2b

in exchange for course credit. They had never participated in similar experiments before. All participants had normal or corrected to normal vision. One additional participant completed Experiment 2a, but was excluded as this participant had an overall error rate that was three standard deviations greater than the average error rate of all participants. Due to a programming error the generation task was incorrectly administered for four of the participants in Experiment 2a.

Apparatus and stimuli. The apparatus and stimuli in Experiment 2a were identical to those in Experiment 1a, and the apparatus and stimuli in Experiment 2b were identical to those in Experiment 1c.

Procedure. The procedure of Experiment 2a was identical to that of Experiment 1a, and the procedure of Experiment 2b was identical to that of Experiment 1c.

Complementary second-order conditional sequences. In Experiments 2a and 2b, participants were trained on two complementary second-order conditional sequences (Reed & Johnson, 1994). By numbering the positions on the screen 1-4 from left to right, sequence A can be defined as 121432413423, and its complement, sequence B can be defined as 323412431421. Two additional complementary sequences were employed as the first and second novel sequences in Experiment 2b (131243214234 and 434213241231). These two sequences were selected to mirror the selection of novel sequences in Experiment 1c. For these two complementary novel sequences, approximately half (5/12) of the legal transitions within each novel sequence are shared with each of the two training SOCs.

As in the previous experiments, target locations in Experiments 2a and 2b were selected using a trial-to-trial substitution procedure (Schvaneveldt & Gomez, 1998). Using this procedure in the training blocks where participants were trained on sequence A with 80% training trials, if the target's location on the previous trial was position 1, and on the current trial the target is located at position 2, there is a 80% likelihood that the target will appear in position 1, and a 20% likelihood that the target will appear in position 4 on the next trial.

Participants in Experiment 2a were trained only on the two original complementary SOCs used by Reed and Johnson (1994). Participants were alternatingly trained on these two sequences, as a function of context across 16 training blocks, after which there was a transfer phase. In the transfer phase, participants completed four blocks of 120 trials each. In Experiment 2a, the context alternated every 5 trials during the transfer phase. We chose to alternate context in this manner to ensure that we would have sufficient observations of training and control trials in the context-reinstated condition. As in Experiments 1a and 1b, in the transfer blocks, the location of the target was selected based on the training sequence associated with the previous target on only 50% of trials.[10] Following the transfer blocks, participants in Experiment 2a completed two additional training blocks, one with red circle targets and one with blue circle targets, to re-establish the learned contingencies before measuring sequence knowledge using a series of generation tasks.

---

[10] As with Experiments 1a and 1b, we were unable to find evidence of the expression of learning in the transfer blocks. The results from the transfer blocks are shown in the Appendix.

The experimental design of Experiment 2b was identical to that of Experiment 1c with the following exceptions. After completing the two practice blocks, participants were trained over 22 blocks of 120 trials each. Over these blocks, the target's location was selected based on the primary sequence on odd-numbered blocks and based on the secondary sequence on even-numbered blocks, with the exception of blocks 17 and 20, in which participants were exposed to the first and second novel sequences.

Generation task. The generation tasks administered to participants in Experiment 2a were identical to those used in Experiments 1a and 1b with the following exceptions. Each generation task consisted of 24 sets of three trials. The first two trials in each triplet were the cue trials, which together formed a fragment of the sequence. Given that the sequences used in the current study are second-order sequences in which legal transitions according to the training grammars are dependent on the location of the target on the two preceding trials, two trials were used to present the fragment on each cued generation trial. Following their response to the cue trial, participants saw an empty fixation screen containing the fixation cross and the eight marked locations, and were asked to generate the most likely location of a subsequent target that was the same color as the target they had responded to in the previous two displays. For both generation tasks, each of the 12 possible cue pairs (starting positions) were presented twice, in random order, thus completing a full set of 24 cue trial pairs for each of the two generation tasks.

As in Experiment 1c, no generation task was administered to the participants in Experiment 2b, as there was no way to separately cue generation of the two training sequences.

Results

RTs for the first trial of each block and for trials in which an error was made (2.7% of trials in Experiment 2a; 3.0% in Experiment 2b) were not included in the analyses. In addition, RTs that were more than three standard deviations from the mean for each block, defined separately for each participant (1.8% in Experiment 2a; 1.9% in Experiment 2b), were treated as outliers and eliminated from the analyses.[11]

Training Blocks. Mean RTs were computed for training and control sequence trials, separately for each block for each participant in each of Experiments 2a and 2b. Context-specific sequence learning was analyzed separately for each experiment using an analysis of variance with Training Block (1-16), Context (primary/secondary), and Trial Type (training/control) as within subject factors.

Experiment 2a. Mean RTs as a function of trial type, context, and block are presented in the top panel of Figure 4. The analysis of mean RTs revealed a main effect of block, $F(7,273) = 16.12$, $\eta^2_p = .29$, $p < .001$, $\varepsilon = .56$. The analysis also revealed a main effect of context, $F(1,39) = 9.71$, $\eta^2_p = .20$, $p = .003$. More important, the analysis revealed a significant main effect of trial type, $F(1,39) = 12.25$, $\eta^2_p = .24$, $p = .001$. Responses were faster on training trials (583ms) than on control trials (589ms), reflecting a 6ms learning effect. The interaction between block and trial type, which is often

---

[11] Participants were generally accurate in counting the number of rounded-corner targets. On average, participants were off from the correct number of rounded-corner targets by ±3 per block across participants in Experiment 2a, and ±4 in Experiment 2b. The worst performance was for one participant who was off by ±12 targets on average per block in Experiment 2a, and ±12 in Experiment 2b.

reported in studies using SOCs, was not significant, $F(7,273) = 1.62$, $\eta^2_p = .04$, $p = .140$, ε = .88.
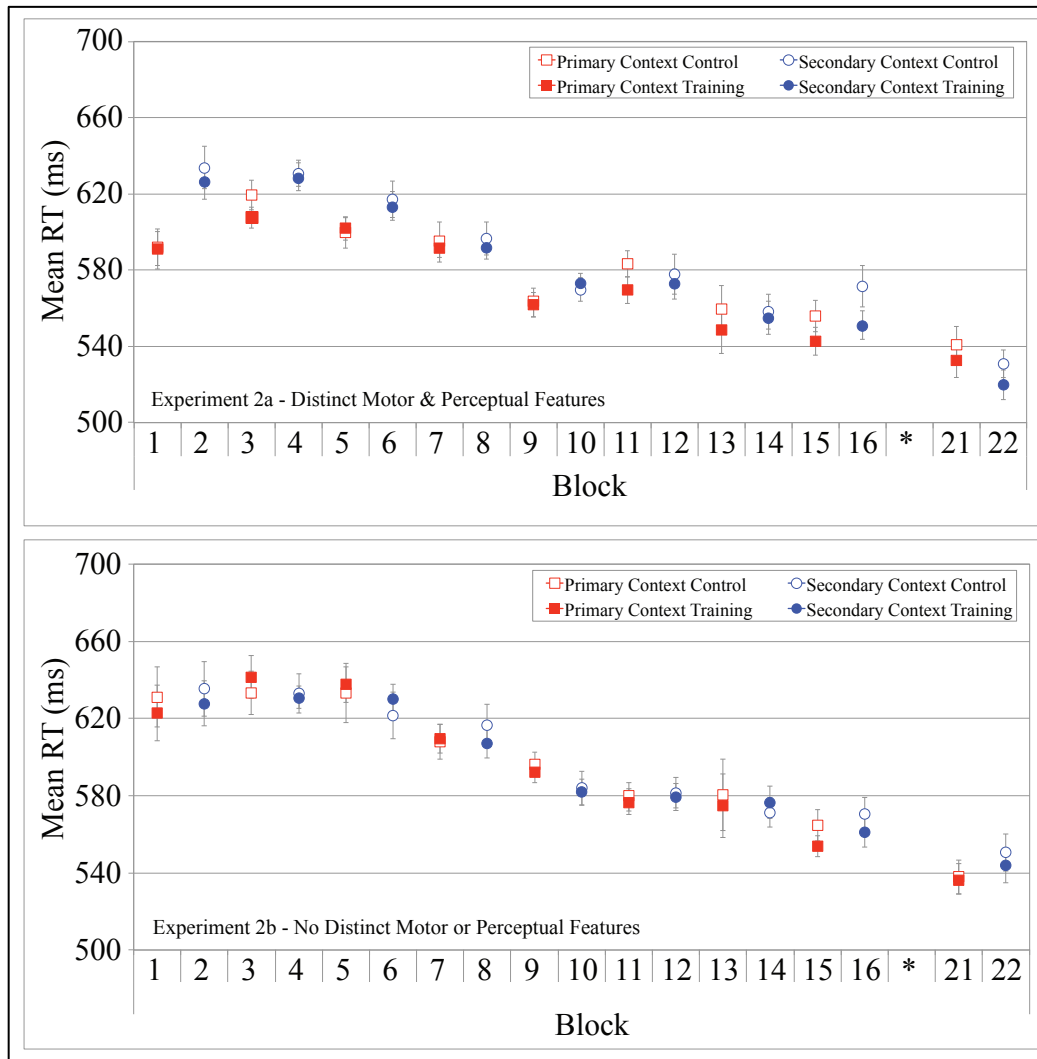
Figure 4. Mean RT(ms) for training and control trials (filled and unfilled shapes, respectively) as a function of primary and secondary contexts (red squares and blue circles, respectively) across training blocks in Experiment 2a (top) and in Experiment 2b (bottom). The * symbol represents the location of the transfer blocks within the training block sequence.

Experiment 2b. Mean RTs as a function of trial type, context, and block are

presented in the bottom panel of Figure 4. The analysis of mean RTs revealed a main

effect of block, $F(7,273) = 11.65$, $\eta^2_p = .23$, $p < .001$, $\varepsilon = .54$. More important, and in contrast to the results of Experiments 1c and 2a, the analysis did not reveal a main effect of trial type, $F(1,39) = 0.48$, $\eta^2_p = .01$, $p = .494$. Responses were not significantly faster on training trials (600ms) than on control trials (601ms). The remaining main effect and interactions were not significant, all F's < 1, p's > .519.

Novel sequence blocks (Experiment 2b). As in Experiment 1c, the learning effects in the two novel sequence blocks were compared with learning effects for the primary and secondary sequences. Mean RTs were computed for the training and control sequence trials across two blocks for each of the primary sequences (Blocks 15 and 19), the secondary sequences (Blocks 16 and 18) and the novel sequences (Blocks 17 and 20), separately for each participant. Learning was analyzed using an analysis of variance with Sequence Type (primary/secondary/novel), Block (1/2) and Trial Type (training/control) as within subjects factors.

Mean RTs as a function of trained and untrained sequences in the transfer blocks of Experiment 2b are shown in the bottom panel of Figure 3. The analysis of mean RTs revealed only a main effect of block, $F(1,39) = 7.35$, $\eta^2_p = .16$, $p = .010$. Importantly, the main effect of trial type was not significant, $F(1,39) = 2.67$, $\eta^2_p = .06$, $p = .110$, nor were the interactions with trial type (all F's < 1), which is consistent with the results from the analysis of RT from the training blocks. In contrast to the results for Experiment 1c, the planned comparison of the learning effects in the two novel sequence blocks of Experiment 2b did not reveal a main effect of trial type, $F(1,39) = 0.44$, $\eta^2_p = .01$, $p = .510$.

Generation Task Performance (Experiment 2a).   As in Experiments 1a and 1b, participants' sensitivity to the sequences was assessed by comparing the number of trials in which participants completed a cue with a training successor to the number expected by chance in Experiment 2a. With the SOC sequences, if sequence knowledge does not guide selection of successors in the generation trials, then all but the current target position should be equally likely to occur (33%), as repeats do not occur within the SOC sequences. To compare participants' generation performance to chance, we calculated for each participant a chance value, after excluding trials in which a participant selected the same target position that was presented in trial n-1. For example, if a participant responded with a repeated position on two of the 24 generation trials, then chance performance for this participant would be 24 – 2 repeats × .33, which is 7.26. Therefore, the total number of correct responses on the generation task for this participant would be compared to the number expected by chance, which is 7.26. Participants repeated positions fairly infrequently; the average number of repeats for the generation tasks was 0.75 and 1.17, when assessing knowledge of the sequence presented in the primary context and the sequence presented in the secondary context, respectively.

The number of training successors generated and the number expected by chance for each participant were submitted to a paired-sample t-test. For the generation task assessing the sequence presented in the primary context, participants did not generate more training successors (8.4) from the cues than expected by chance, after controlling for repeats (7.7), $t(35) = 0.93$, $p = .358$, $d = 0.16$. For the generation task assessing the sequence presented in the secondary context, participants did not generate more training

successors (8.1) from the cues than expected by chance (7.5), $t(35) = 0.84$, $p = .409$, $d = 0.14$.

Discussion

The purpose of Experiments 2a and 2b was to examine whether distinct motor and perceptual features are necessary to concurrently learn complementary higher-order sequential structures. The goal was to extend the results of our earlier experiments, where we had used first-order conditional sequences, to learning of sequences that arises more gradually. Typically, SOC sequence learning takes longer to develop, and so it seemed unlikely that participants would be able to rapidly learn and relearn the two sequences within each block of 120 trials. The results from the data presented here are consistent with this assumption. Whereas there was evidence of learning across the training blocks of Experiment 2a, there was no evidence of learning across the training blocks in Experiment 2b, nor was there evidence of learning of the novel sequences in Experiment 2b.

General Discussion

Recently, we provided the first evidence for concurrent learning of complementary first-order sequences (D'Angelo et al., 2013). Our view at the time was that the association between the complementary sequences and distinct contexts across training experiences was critical to this learning effect. The goal of the present study was to examine further the role of distinct motor and perceptual contextual information in guiding the acquisition and expression of sequential knowledge when participants are trained on complementary sequences. In Experiments 1a-c, we contrasted learning of

complementary first-order conditional sequences when participants were trained on two sequences as a function of both distinct motor and perceptual features (Experiment 1a), as a function of only distinct perceptual features (Experiment 1b), as well as in the absence of distinct motor and perceptual features (Experiment 1c). In Experiment 1a we replicated our earlier finding of concurrent learning of two complementary sequences in the training blocks. Similarly, in Experiment 1b we replicated the learning effects in the training blocks when participants responded to both sequences using the same effectors. Perhaps most surprisingly, in Experiment 1c we replicated the learning effects in the training blocks, despite the fact that sequences were associated with neither distinct motor nor distinct perceptual contexts. The most parsimonious account of results of Experiments 1a-c is that participants may not have concurrently learned the two sequences, but rather they may have rapidly learned and relearned the two sequences in successive blocks across the training phase. The learning/relearning account is also supported by the learning effects shown for the two novel sequences, which were the same in magnitude as the learning effects for the two well-practiced training sequences.

The results from Experiment 1c were unexpected given previous research in which incidental learning has been largely insensitive to changes in the probabilistic structure of target transitions (e.g. Jiménez et al., 2006 – Experiments 3 and 4). We hypothesized that the discrepancy between the results of Experiments 1a-c, which demonstrate rapid adaptation to shifts in probabilistic structure among incidental learners, and previous work that has shown little sensitivity to shifts in probabilistic structure, owes to differences in the sequences used. In work showing low levels of sensitivity to

changes in underlying probabilistic structures, participants were trained on higher-order conditional structures, such as SOCs. According to this general view, learning of first-order conditional sequential structures depends on rapid learning of local transitions, as observed in Experiments 1a-c.   In contrast, learning of second-order conditional sequential structures requires learning of sequential structure that includes ambiguity in local transitions. Learning of these higher-order conditional structures normally takes longer, and the higher tolerance to ambiguity in local sequence structure implies slower adaptation to changes in the frequency of learned transitions.

In Experiments 2a and 2b we tested our hypothesis and examined context-specific implicit sequence learning of higher-order conditional structures. We examined performance both when distinct motor and perceptual features are present to distinguish the two sequences (Experiment 2a), as well as in the absence of distinct motor and perceptual features (Experiment 2b).   In Experiment 2a we observed significant learning effects in the RT data in the training blocks, while in Experiment 2b we found no evidence of learning of the two sequences. These results suggest that, in contrast to the results of Experiment 1c, participants were not able to rapidly learn and relearn the SOCs.

Failing to replicate learning in the transfer blocks

Before we discuss the implications of the present set of findings on the nature of the representations that underlie implicit sequence learning, we to turn to a discussion of our failure to find learning effects in the transfer blocks of Experiments 1a, 1b, and 2a, which are described in the Appendix. Across the three experiments reported here where transfer blocks were included (Experiments 1a, 1b, and 2a), we were unable to find any

evidence for the expression of learning that we had previously reported (D'Angelo et al., 2013, Experiment 3). Recall that the expression of learning during a transfer phase is useful for drawing inferences about context-specific learning. Specifically, as the training probabilities were reduced and the contexts were intermixed at random in the transfer phase, relearning the sequences during the transfer phase is not possible. In our earlier work, we pointed to the expression of learning during the transfer phase as evidence for context-specific learning over the alternative, learning/relearning account of performance in the training blocks.

At this point it is not clear what to make of having found a transfer effect once before, but not having found it here. One possibility is that context-specific learning was absent both in our earlier study and in the current study, and all learning effects observed in both studies reflect rapid adaptation to probabilistic structures present in the design. This possibility is unsatisfying, given that the transfer effect in our earlier work was observed in a condition where rapid adaptation would have led to a null effect, as in the present studies.

Another possibility is that there may have been context-specific learning in both our prior work and in the current study, but the transfer effect may be a difficult effect to measure. With this possibility in mind, future work should aim at finding parameters and experimental designs that encourage participants to incorporate contextual features and to rely on context to guide performance. For example, the spatial context could be made more salient by separating the two contexts with a horizontal line, and by shifting the placeholders used in the two contexts so that they do not line up with one another.

Similarly, the perceptual contexts could be made more distinct by using a conjunction of distinct visual and auditory features to differentiate targets in the two contexts. Another issue to consider is that by randomly intermixing the two contexts in the transfer blocks, the overall 'experiment context' participants experienced was very different during transfer blocks and during training blocks. This unpredictability in terms of which context would appear may have cued processes that operated in opposition to the automatic cueing of sequence knowledge by context (e.g., perhaps control processes are cued in response to the unpredictability, which interfere with the automatic retrieval of previous experiences from memory). Therefore, in order to measure the expression of learning in a transfer phase, a different experimental design may be needed, in which unpredictability does not operate in opposition to context-specific retrieval of learning. In any case, more research is needed to understand the inconsistencies we have experienced in replicating this transfer effect.

Context and the representations that underlie implicit learning

We return now to the role that contextual features play in implicit learning, and how the incorporation of context provides insight into the representations that may underlie implicit learning. If context influences implicit learning, episodic details must somehow be incorporated into the representations that lead to the expression of implicit learning. Such a result would challenge accounts in which non-episodic representations underlie implicit learning effects (e.g. A.S. Reber, 1967; 1989, Cleeremans & McClelland, 1991; Gomez, 1997; Gomez & Schvaneveldt, 1994; Knowlton & Squire, 1996; for a review of such models in sequence learning see Abrahamse, Jiménez,

176

Verwey, & Clegg, 2010), as well as accounts which suggest that implicit learning arises through an implicit memory system that operates in parallel to, but independently from, an explicit memory system (e.g., Reber & Squire, 1994; Sanchez, & Reber, 2013). Context-specific sequence learning effects support the view that the episodic representations that are retrieved in explicit remembering may also be the representations that underlie implicit learning effects (e.g. Brooks & Vokey, 1991; Jamieson & Mewhort, 2005; Jamieson & Mewhort, 2009a; Jamieson & Mewhort, 2009b; Neal & Hesketh, 1997;Whittlesea & Dorken, 1993, 1997; Whittlesea & Wright, 1997).

The results from the present study add to our understanding of the role of context in implicit sequence learning.   In particular, the results of Experiments 1a-c are at odds with the argument we forwarded in our earlier study (D'Angelo et al., 2013), in that distinct contextual features were not necessary to produce concurrent implicit learning of complementary first-order conditional sequences in the present study. These results give us little reason to argue that contextual features were incorporated into the representations that supported implicit learning of first-order conditional sequences in the present study. A more difficult issue to assess is whether, for some reason, contextual features may have been incorporated into the learning of first-order sequences in our prior study but not the current study. Indeed, there were some subtle differences between the methods, which only in retrospect could have made a difference. For example, the proportional size of the stimuli in relation to the monitor used to present the stimuli differed across experiments, and may have encouraged participants in the present study to treat the two visual contexts as one. Whether subtle factors such as this one can account for the difference results

across our studies remains an important issue for further research, and will ultimately determine whether and when context plays a role in the implicit learning of first-order conditional sequences (D'Angelo et al., 2013).

In contrast to the mixed results using first-order conditional sequences, the results from Experiments 2a and 2b suggest that distinct contextual features play a role in the ability to concurrently learn two complementary sequences, when learning higher order sequential structures. The key difference between learning of first-order versus second-order conditional structures may be in how quickly learning occurs, and in how much interference arises from earlier learning in the absence of distinct contextual features. Given that learning of first-order conditional sequences arises very quickly, the additional binding of contextual features into learning may not be necessary to produce learning of these sequences. In contrast, given that learning of second-order conditional structures emerges more slowly over time, when completing the present task with SOCs, participants must link learning across intervening blocks of trials in which the opposite sequence is presented. Participants may only be able to link learning episodes across intervening blocks of trials in the presence of additional contextual support, in order to avoid interference from the complementary sequence in the immediately preceding block of trials. In summary, the results of Experiments 2a and 2b suggest that contextual features can be incorporated into the representations that underlie concurrent implicit learning of complementary SOC sequences.

Conclusion

Overall, the results of the present study demonstrate that remarkably rapid incidental learning may underlie the concurrent learning of complementary first-order sequences, while a slower and context-sensitive process underlies the concurrent learning of complementary SOC sequences. More work is required to clarify the conditions under which context is incorporated into the representations underlying sequential knowledge, and in particular on how to demonstrate the context-sensitive transfer of learned sequential structure.

Appendix

To determine whether participants in Experiments 1a, 1b, and 2a expressed knowledge of the sequences in the transfer blocks, mean RTs from these blocks were compared for training and control trials. We examined performance as a function of whether the trial was a context repeat or context switch trial. In Experiments 1a and 1b, context repeat trials where those in which the transition from the immediately preceding trial (trial *n-1*) to the current trial (trial *n*) reinstated the training context (e.g., if the targets in both trial n and trial n-1 were red circles). In contrast, context switch trials were those in which the transition from the immediately preceding trial (trial *n-1*) to the current trial (trial *n*) switched the training context (e.g., if the target in trial *n* was a red circle and the target on trial *n-1* was a blue circle). In Experiment 2a context reinstatement was assessed based on the overlap in context between the current trial and the two preceding trials.

Transfer Blocks (Experiments 1a and 1b)

Mean RTs were computed for each of the training and control sequence trials in the transfer blocks of Experiments 1a and 1b, as a function of whether the context was reinstated from trial *n-1* to trial *n* (e.g., if the target was a red circle on two successive trials) or switched (e.g., if the target was a red circle on the current trial and a blue circle on the preceding trial) across transfer blocks, separately for each participant. Trial type (training vs. control) was assigned based on the sequence that had been associated with the context of trial *n-1* during the training blocks. For example, if trial *n-1* had a blue circle target, then the sequence used during training blocks for blue circles was used to

define what constituted training and control targets for trial *n*. Note that although this assignment to trial type conditions is unambiguous for trials in which the context was reinstated, it is ambiguous for trials in which the context switched. This ambiguity stems from the fact that training trials for one sequence are control trials for the other sequence. As a result, when the context switches, a training trial with respect to the sequence associated with the trial *n-1* context is a control trial with respect to the sequence associated with the trial *n* context. To illustrate this ambiguity, consider the example of a participant who was trained on Grammar A with red circles and Grammar B with blue circles. If during the transfer block a blue circle was presented in the third position on trial *n-1*, and the next trial was a context-switch trial, according to Grammar B a red circle appearing in the first or second position on trial *n* would be considered a training trial. However, if trial type were assigned based on the sequence associated with the context on trial *n* (Grammar A), then a red circle appearing in the first or second position on trial *n* would instead be considered a control trial.

Given this ambiguity, a clear test of context-specific sequence learning in the transfer phase is offered only for context-reinstated trials. Nonetheless, context-specific sequence learning was separately analyzed in Experiments 1a and 1b using an analysis of variance with Context Reinstatement (context reinstated/context switch) and Trial Type (training/control) as within subject factors.

Experiment 1a. Mean RTs as a function of context reinstatement and trial type for the transfer blocks are presented in the left panel of Figure A1. The analysis of mean RTs revealed a main effect of context, $F(1,38) = 180.37$, $\eta^2_p = .83$, $p < .001$, with faster

responses when the context was reinstated (802ms) than when the context switched

(1048ms). In other words, participants responded 246ms slower when they had to switch

response hands from one trial to the next. The main effect of trial type was not

significant, $F(1,38) = 1.84$, $\eta^2_p = .05$, $p = .183$, and the interaction between context and

trial type was not significant, $F(1,38) = 1.35$, $\eta^2_p = .03$, $p = .253$. Planned comparisons

revealed no significant learning effect when the context was reinstated, (training trials =

803ms; control trials = 801ms), $t(38) = 0.17$, $p = .864$. When the context switched, there

was also no significant effect of trial type (training trials = 1058ms; control trials =

1039ms), $t(38) = 1.49$, $p = .144$.

    Experiment 1b. Mean RTs as a function of context reinstatement and trial type

for the transfer blocks are presented in the right panel of Figure A1. The analysis of mean

RTs revealed a main effect of context, $F(1,39) = 83.93$, $\eta^2_p = .68$, $p < .001$, with faster

responses when the context was reinstated (708ms) than when the context switched

(769ms). The main effect of trial type was not significant, $F<1$. The interaction between

context and trial type was significant, $F(1,39) = 5.18$, $\eta^2_p = .12$, $p = .028$. Planned

comparisons revealed that when the context was reinstated there was not a significant

learning effect (713ms on training trials versus 702ms on control trials), $t(39) = 1.76$ $p =$

.087. The effect of trial type also was not significant when the context switched, $t(39) =$

1.27, $p = .212$.

Figure A1. Mean RT for training and control trials as a function of trial *n-1* to trial *n* context reinstatement (context switched or context reinstated) in Experiment 1a (left panel) and Experiment 1b (right panel).

Transfer Blocks (Experiment 2a).

Mean RTs were computed for the training and control sequence trials across transfer blocks, separately for each participant. Context-specific sequence learning was analyzed using an analysis of variance with Context Reinstatement (context reinstated/context switch) and Trial Type (training/control) as within subjects factors. Given that in Experiment 2a participants were trained on second-order conditional sequences, context reinstatement was assessed based on the current trial and the two preceding trials. Therefore, only trials in which the two immediately preceding trials matched the current trial's context were considered to be context reinstated trials. Using this criterion, of the five trial chunks in which the context was maintained, the first two

trials of the chunk were considered context-switch trials and the last three trials of the chunk were considered context-reinstated trials.

Mean RTs as a function of context reinstatement and trial type for the transfer blocks are presented in Figure A2. The analysis of mean RTs revealed a main effect of context, $F(1,39) = 292.78$, $\eta^2_p = .88$, $p < .001$, with faster responses when the context was reinstated (617ms) than when the context switched (760ms). The main effect of trial type was also significant, $F(1,39) = 5.60$, $\eta^2_p = .13$, $p = .023$. Responses were faster on training trials (683ms) than on control trials (694ms), reflecting a 11ms learning effect. The interaction between context and trial type was not significant, $F(1,39) = 1.89$, $\eta^2_p = .05$, $p = .178$. Planned comparisons revealed that when the context was reinstated responses were not significantly different on training trials (615ms) as compared to control trials (618ms), $t(39) = 0.57$, $p = .570$. However, the effect of trial type was significant when the context switched, $t(39) = 2.10$, $p = .042$. When the context switched, responses were faster on training trials (750ms) than on control trials (769ms), reflecting a 19ms learning effect. An inspection of the data as a function of the individual trials within each 5-trial chunk showed that this learning effect was driven by performance on the second trials in each chunk, in which the context for trial n repeats from n-1, but differs from n-2. Given that there was no evidence of learning being expressed where we would explicitly predict that there should be an effect (i.e., in the context-repetition trials), we view this significant effect for the context switch trials to be a spurious finding, and overall we interpret these data as a failure to demonstrate a transfer effect.
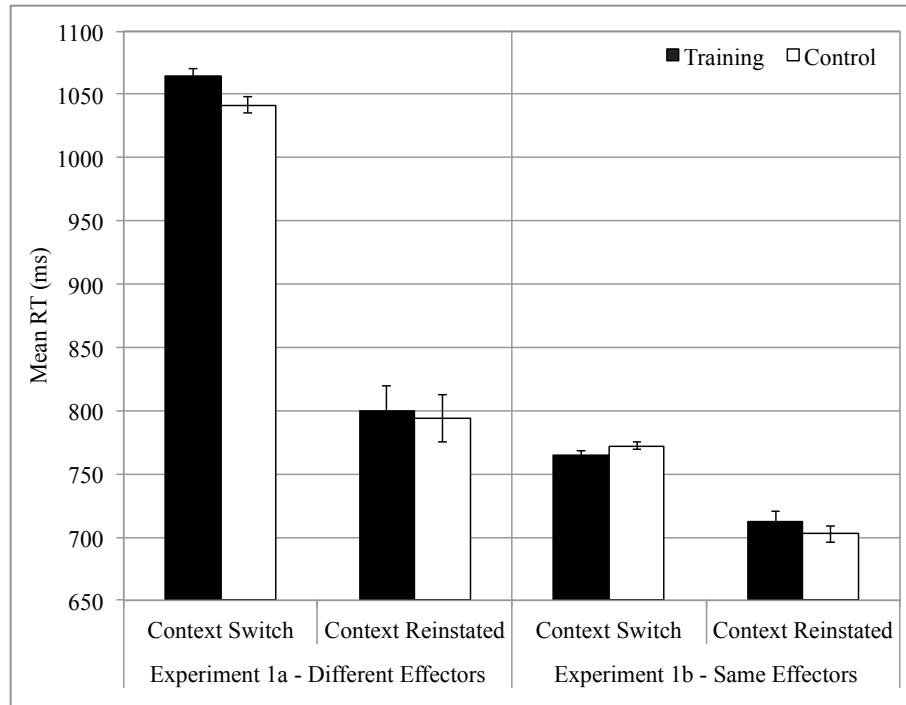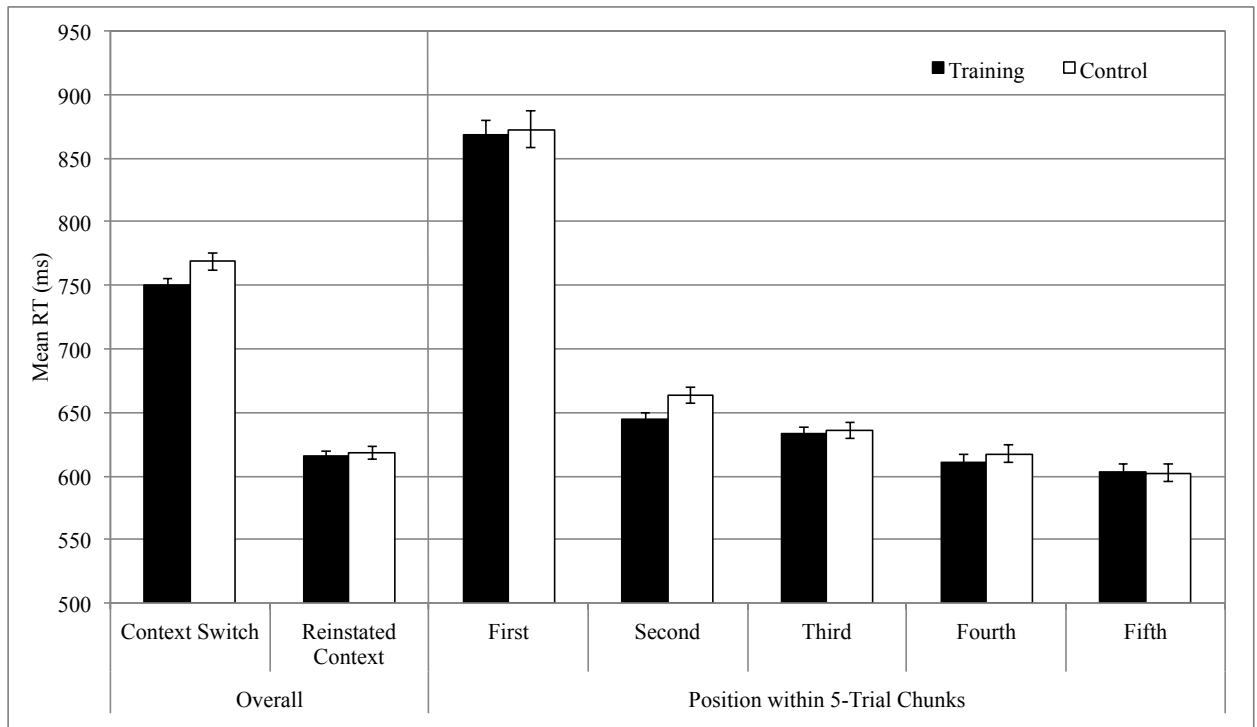
Figure A2. Mean RT for training and control trials as a function of trial *n-1* to trial *n* context reinstatement (context switched or context reinstated), as well as a function of the trial position within the 5-trial chunks appearing in the same context in Experiment 2a.

CHAPTER 5 – General Discussion

Given the substantial phenomenological differences that accompany remembering with and without awareness, it should not be surprising that the distinction between explicit and implicit influences of memory has been an important focus of study over the past several decades (Squire, 2004; Tulving, 1985). Indeed, implicit memory effects have often been attributed to representations that are formed separately but in parallel to representations that underlie explicit memory effects (e.g., Knowlton, Ramus, & Squire, 1992). However, it has also been demonstrated that a processing framework can accommodate many of the key findings that pushed researchers down the path toward a separate systems framework (e.g. Blaxton, 1989; Hintzman, 1986; Neal & Hesketh, 1997). Within a processing framework, different forms of memory are the result of differences in the processes that act on one common memory store, with diverse phenomenological experiences of memory arising from an equally diverse set of constraints on how memory is probed.

Despite previous work showing the applicability of processing accounts to the distinction between implicit and explicit memory (e.g. Brooks & Vokey, 1991, Jamieson & Mewhort, 2009a, Whittlesea & Wright, 1997), its applicability has yet to be thoroughly tested in the domain of implicit sequence learning. Given the paucity of research in implicit sequence learning, the broad goal of this thesis was to examine the applicability of a processing account to performance in this domain. To that end, in the empirical chapters of this thesis I examined whether the representations that underlie implicit sequence learning are episodic in nature, specifically by looking for evidence of context-

specificity in sequence learning. This approach was inspired by previous work that has examined context influences on performance across a wide range of tasks in which there is no explicit requirement to remember. To name just a few of those tasks, context-specific influences on performance have been documented in visual search (e.g. Chun & Jiang, 1998; Thomson & Milliken, 2012), perceptual identification (e.g. Jacoby, Baker, & Brooks, 1989), and conflict adaptation (e.g. Spapé & Hommel, 2008).

As a first examination of context-specificity in sequence learning, I assessed the specificity of implicit sequence learning when participants concurrently learned a motor sequence and a perceptual sequence in Chapter 2. In this chapter, I demonstrated that implicit sequence learning is modulated by the context provided by an immediately preceding trial (Experiments 2 and 3). In these experiments, learning was only expressed when the information present in the immediately preceding trial was consistent with the training sequence. Furthermore, I demonstrated that this modulation of learning is specific to the type of learning disrupted on a preceding trial, such that the expression of motor learning was only modulated by the status of the motor information present in the immediately preceding trial, and the expression of perceptual learning was only modulated by the perceptual information present in the immediately preceding trial. The specificity of these effects suggests that implicit learning is not automatically expressed, and that the expression of learning depends on the specific context provided by the immediately preceding trial.

Overall, although the specificity of learning that I report in Chapter 2 is consistent with a processing account that posits episodic representations, the results are also

consistent with other accounts of sequence learning. For example, it could be argued that the motor sequence was represented using response-level bindings (e.g., Deroost, Zeeuws, & Soetens, 2006), while the perceptual sequence was represented via stimulus-level bindings (e.g. Mayr, 1996). As different levels of representation could be involved in learning the perceptual and motor sequences, the specificity that I report could also be predicted by an account based on separate single-level representations. To rule out this alternative explanation, evidence of context-specificity is needed when participants learn two sequences that have overlapping levels of representation.

To address this alternative explanation, I looked for evidence of context-specificity when participants concurrently learned two motor sequences in Chapters 3 and 4. Before describing the results of these two chapters in detail, the reader should note that in Chapter 4 we were unable to replicate a transfer effect reported in Experiment 3 of Chapter 3. Yet in Chapter 3, this transfer effect was interpreted as a key piece of evidence for context-specificity in implicit sequence learning. Given the failure to replicate this transfer effect, any claim regarding context-specificity of implicit sequence learning based on this transfer effect in Chapter 3 must be made with caution. At present, it is unclear whether the transfer effect observed in Chapter 3 is a real one that supports context-specificity in implicit sequence learning, or if it is a Type I error. This is an issue that can only be settled with additional research. As such, although I have interpreted this effect in Chapter 3 and here in the General Discussion as if it is indeed a real one that has implications for our understanding of the role of context in implicit sequence learning, I

am also stating clearly here that the empirical evidence on this issue is currently not strong, and the interpretations offered here must be considered preliminary.

That said, the results of Chapter 3 do suggest that contextual features can guide the expression of implicit sequential knowledge. The results of Experiments 1-3 of Chapter 3 demonstrate that when participants are exposed to two complementary first-order sequences associated with distinct contexts, both sequences can be learned concurrently. The transfer effect in Experiment 3 of this study, in which a learning effect was expressed when context was reinstated in the transfer blocks, is a preliminary result suggesting that learning of sequential knowledge was bound to context, and that this context could be used to cue the appropriate sequential knowledge even when the two contexts were intermixed at random. However, as noted above, this conclusion must be considered preliminary, as we had difficulties replicating this transfer effect in Chapter 4. An important goal of future research should be to determine under which conditions contextual information can automatically guide the expression of sequential knowledge, as it seems to do in Experiment 3 of Chapter 3.

In Chapter 4, I further examined the role of motor and perceptual features in the context-specific learning effects that I report in Chapter 3. The results of Experiment 1c of Chapter 4 were surprising in that I found that participants learned two complementary sequences in the absence of distinctive contextual features. These results suggest that the learning effects measured in Experiments 1a and 1b could be due to rapid learning and relearning of the statistical regularities. To assess further the limits of this rapid learning and relearning process, I also examined the role of context when participants learn more

complex sequential structures (Experiments 2a and 2b of Chapter 4). When using second-order conditional sequences, I found that, unlike learning of first-order conditional structures, distinctive contextual features appear to be necessary for concurrent learning, as participants did not show evidence of learning in the absence of distinct contextual features. Therefore, despite the inconsistencies in the results presented in Chapter 3 and in Experiments 1a-c of Chapter 4, the results of Experiments 2a and 2b of Chapter 4 do point to a role for context in learning of higher-order sequential structures. The inconsistency in finding context-specificity with first-order sequences in Chapters 3 and 4 may be due to differences in the relative saliency of the contextual features between experiments, as well as the amount of attention that participants paid to the contextual features. This potential explanation is consistent with work demonstrating that context dependent memory effects in explicit memory tasks depend on the relative saliency and use of environmental contextual features (e.g. Smith & Vela, 2001). A clear avenue for future work is to test this explanation.

Therefore, the results of the empirical chapters of this thesis demonstrate that implicit sequence learning can be context-specific, and constitute a step forward in understanding whether contextual features are represented in implicit sequence learning. A key factor here is that although the role of context was not perfectly consistent across the experiments, the fact that it was possible to find context-specificity in implicit sequence learning suggests that the underlying representations may be episodic in nature. Indeed, any evidence for the incorporation of context into sequence knowledge is inconsistent with accounts based on single-levels of representations.

I will now turn to a discussion of how these results fit in with a processing account of memory based on episodic representations, as well as the implications these results have for the single-level accounts of implicit sequence learning described in the Introduction. In this section I will also discuss a dual-system model of implicit sequence learning, and I will describe how the results from the empirical chapters of this thesis fit in with this model. The last section of this General Discussion will be dedicated to a review of the neural substrates that have been implicated in implicit sequence learning.

Implications for Theoretical Models of Implicit Sequence Learning

To assess the results presented in the empirical chapters of this thesis, I will provide a brief overview of how these results fit in with existing models of implicit sequence learning. In the Introduction of this thesis, as well as in the empirical chapters themselves, I made reference to Minerva 2, a multi-trace model of memory that assumes a single memory store (Hintzman, 1986). I will now briefly describe how Jamieson and Mewhort (2009b) have adapted Minerva 2 to show how a single-store processing model of memory can account for the results from classic SRT experiments. Following this description, I will discuss how the present results fit in with this processing account. From there I will discuss the present data in terms of the single-level accounts I described in the Introduction.

Jamieson and Mewhort (2009b) examined whether implicit sequence learning effects could be simulated by a single, multi-trace model of memory using Minerva 2 (Hintzman, 1986). In their adaptation of Minerva 2, every trial in a serial reaction time task is stored as a separate memory trace, containing information pertaining to the current

location of the target stimulus, along with the response made to this stimulus. Importantly, each memory trace also contains information regarding the response that was made on the immediately preceding trial. As participants gain experience with a training sequence, the response made on the immediately preceding trial, along with the current location of the target serve as a retrieval cue for the response required to the current location of the target. This occurs because through exposure to the training sequence, more and more memory traces containing the transitions between successive target locations and the responses required are stored in memory. Therefore, according to their model, responses are speeded on trials where a target appears in a location consistent with a training sequence because the model is able to quickly obtain information about the required response through retrieval of instances stored in memory.

Using this adaptation of Minerva 2, Jamieson and Mewhort (2009b) were able to simulate a number of classic results from the implicit sequence learning literature with high fidelity. Not only were Jamieson and Mewhort able to simulate differences in performance when a target's location was selected randomly versus when it was selected based on a deterministic sequence presentation (Nissen & Bullemer, 1987), but they were also able to simulate more complex designs. In particular, Jamieson and Mewhort were able to simulate differences in performance across varying levels of sequence complexity, including first-order, second-order, and third-order deterministic sequences (e.g. Stadler, 1992, Experiment 1), as well as several types of probabilistic sequence (e.g. Jamieson & Mewhort, 2009b).

The context-specific learning effects reported in the empirical portions of this thesis fit nicely with this model, as the stimulus information that is represented in each memory trace can contain contextual information such as the vertical location of the target, as well as its colour or shape, while the response information can contain information about which specific effector was used to make a response. Therefore, the results presented in the empirical chapters of this thesis are consistent with Jamieson and Mewhort's implementation of Minerva 2.

As was described in the introduction of this thesis, a number of single-level accounts of sequence learning have been also been proposed in the literature. In these single-level accounts learning can occur through response-level bindings (e.g. Berner & Hoffmann, 2008), stimulus-level bindings (e.g. Mayr, 1996), or through response to stimulus bindings (e.g. Ziessler, 1998). One important difference between these single-level accounts and a processing account such as Jamieson and Mewhort's (2009b) model is that the single-level accounts posit separate representations for implicit learning as a function of different modalities. Therefore, single-level accounts are unable to explain effects in which multiple pieces of information are bound together to represent knowledge of sequential regularities.

In Chapters 3 and 4 of the present thesis, participants learned two complementary sequences that were associated with distinct contexts, a finding that is difficult for single-level accounts to accommodate. Furthermore, the results reported in Chapter 2 suggest that the processes involved in expressing motor and perceptual learning are fairly similar,

and so although the results could be accounted for by independent representations, they appear more consistent with an account that posits a single form of representation.

At this point, I should note that although the results reported in the empirical chapters of this thesis are somewhat inconsistent with single-level accounts, due to the apparent binding of information across different levels of representation, the results may be consistent with the dual-system model proposed by Keele, Ivry, Mayr, Hazeltine, and Heuer (2003). In their dual-system model, Keele and colleagues propose that learning within particular modalities (or levels of representation) occurs in a unidimensional system, while learning between modalities occurs in a multidimensional system. According to this dual-system model, the unidimensional system implicitly and unconditionally associates stimuli within a given modality, or level of representation. In contrast, Keele et al. argue that in the multidimensional system learning can occur implicitly but explicit knowledge can arise. In this multidimensional system, learning is dependent on attention, and can occur between different dimensions or modalities.

Within this dual-system framework, it would appear that context can only be incorporated into learning through the multidimensional system, in which information between different dimensions or modalities can be bound together. This dual-system model can perhaps be reconciled with a processing approach, if one assumes that the unidimensional systems lead to the sub-representations of each integrated memory trace, and that the integrated memory traces are the product of binding that occurs in the multidimensional system. For example, the representations of stimulus characteristics or response information present in each memory trace in Jamieson and Mewhort's model

(2009b) may be analogous to the associations formed in different unidimensional systems in Keele et al.'s (2003) model, while binding of these unidimensional representations into a memory traces is analogous to the binding across modalities that is described in the multidimensional system. However this explanation may not be consistent with the interpretation of the unidimensional system offered in Keele et al.'s model. In their dual-system model sequence learning can arise either from the multidimensional system, or in the unidimensional system through associations formed within a modality. In this latter proposal, where sequence learning can occur through associations within a modality, Keele et al. do not specify how temporal information is represented. Therefore, interpretations of the role of the unidimensional system in sequence learning are currently limited, as Keele et al. have not fully specified how learning in the unidimensional system occurs. An important avenue for future research would be to examine the specific predictions made by the dual-system model, and to examine where its predictions differ from the predictions made by a processing account based on episodic representations.

Neural substrates underlying Implicit/Explicit memory

The empirical portions of this thesis have focused on behavioural methods to examine the nature of the representations that underlie implicit sequence learning. However, models of implicit memory have also been evaluated based on the neural substrates that correlate with performance on implicit and explicit memory tasks. The notion that implicit and explicit memory systems are distinct and separable has been supported by research conducted with two main groups of patient populations, amnesic patients that have suffered damage or deterioration to their hippocampus, and patients that

have damage or deterioration to the basal ganglia (e.g. Squire, 2009). In general, both the

hippocampus and the basal ganglia have been shown to be involved in learning, with the

distinction that while hippocampal learning occurs quickly through the binding of

information from multiple streams of information (e.g. Atallah, Frank, & O'Reilly, 2004;

O'Reilly & Rudy, 2001), learning via the basal ganglia occurs more slowly, through

connections with frontal areas (e.g. Atallah et al., 2004; O'Reilly & Norman, 2002).

In this review I will first discuss research that has pointed to the hippocampus as a

structure critical to explicit but not implicit learning and memory, as well as some recent

findings that challenge this interpretation. I will then turn to a discussion of research that

has pointed to the basal ganglia as a structure critical to implicit memory. Finally, I will

discuss other neural substrates that have been implicated in implicit sequence learning,

and outline a model that could account for the numerous brain regions that support

implicit sequence learning.

As described in the introduction, early research with amnesic patients led

researchers to the conclusion that the hippocampus is crucial to the development of

explicit learning (e.g. Knowlton, Ramus, & Squire, 1992). Indeed, the dichotomy

between implicit and explicit memory has been supported by data suggesting that amnesic

patients have a selective impairment in explicit memory tasks (e.g. Knowlton et al., 1992;

Warrington & Weiskrantz, 1970). Within the domain of implicit sequence learning,

initial studies with Korsakoff's patients suffering from amnesia showed that although

these patients were able to demonstrate learning behaviourally in the serial reaction time

task, they lacked explicit awareness of the sequential structure (e.g. Nissen & Bullemer,

1987; Nissen, Willingham, & Hartman, 1989; Reber & Squire, 1994).   This dissociation between performance on implicit and explicit tasks was interpreted as evidence for the role of the hippocampus in explicit episodic memory, but not in implicit memory.

However, subsequent work suggests that this dissociation may not be that clear cut. For example, Curran (1997) measured learning effects with both first-order and second-order conditional sequences in controls and amnesiacs. As reported by other researchers (Reber & Squire, 1994), both groups demonstrated learning effects for both sequence types. Yet, at the same time, amnesic patients showed less evidence than controls of having learned higher-order associations. Consistent with Curran's results, Vandenberghe, Schmidt, Fery, and Cleeremans (2006) reported a study in which amnesic patients produced intact learning when trained on simple deterministic sequences, but did not produce a learning effect when trained on probabilistic sequences.

In general, these latter results are consistent with findings from other domains in which amnesic patients have produced deficits in performance on implicit tasks (e.g. Chun & Phelps, 1999). Results such as these have led researchers to conclude that the hippocampus and surrounding medial temporal lobe structures play an important role in quickly forming conjunctive associations, where information from multiple streams of processing are combined to form unified representations (e.g. Barense, Gaffan, & Graham, 2007; Ryan, Althoff, Whitlow, & Cohen, 2000; for a review, see O'Reilly & Rudy, 2001).

Whereas the hippocampus has been regarded as critical to explicit memory formation, research with patients with Parkinson's disease has suggested that the basal

ganglia is critical to implicit learning (e.g. Squire, 2009). Parkinson's disease is the result of cell death in the substantia nigra region of the basal ganglia. Patients with Parkinson's disease typically show difficulties in implicit sequence learning tasks both when trained on deterministic sequences (e.g. Jackson, Jackson, Harrison, Henderson, & Kennard, 1995; Vandenbossche, Deroost, Soetens, Coomans, Spildooren, Vercruysse et al., 2013; Vandenbossche, Deroost, Soetens, & Kerckhofs, 2009), and probabilistic sequences (e.g. Wilkinson & Jahanshahi, 2007; Wilkinson, Khan, & Jahanshahi, 2009). Although these results are compelling, the role of the basal ganglia in implicit learning requires additional study, as other researchers have found that implicit sequence learning is not always completely disrupted in patients with Parkinson's disease (e.g. Seidler, Tuite, & Ashe, 2007) or in patients with lesions to the basal ganglia (e.g. Shin, Aparicio, & Ivry, 2005).

In addition to the hippocampus and the basal ganglia, other brain regions have been implicated in implicit sequence learning in studies using repetitive transcranial magnetic stimulation (rTMS). Transcranial magnetic stimulation is a non-invasive procedure in which neurons in particular brain regions can be depolarized or hyperpolarized using electromagnetic induction. In rTMS, temporary *virtual* lesions can be induced by repeatedly stimulating a particular brain region, such that the neurons in a targeted region temporarily become unresponsive. Studies using rTMS procedures have pointed to the role of a number of other brain regions in implicit sequence learning, such as the dorsolateral prefrontal cortex (e.g. Robertson, Tormos, Maeda, & Pascual-Leone, 2011; but see Wilkinson, Teo, Obeso, Rothwell, & Jahanshahi, 2010), primary motor areas (e.g. Wilkinson et al., 2010), the cerebellum (e.g. Torriero, Oliveri, Koch,

Caltagirone, & Petrosini, 2004), as well as Broca's area (e.g. Clerget, Poncin, Fadiga, & Olivier, 2011).

Overall, the implication of a vast array of brain regions in sequence learning suggests that rather than there being a specific locus for implicit sequence learning, networks of different brain regions seem to be critical for the acquisition and expression of sequential knowledge. For example, it may be the case that the conjunction of information from distinct sources occurs in the hippocampus and surrounding structures (e.g. Barense et al., 2007; Ryan et al., 2000), which may bind patterns of activity representing response information from the motor cortex, and patterns of activity representing stimulus information from the parietal cortex. Furthermore, the hippocampus and other surrounding structures may also play a critical role in incorporating temporal context, where the order of stimulus events is also represented (e.g. Fortin, Agster, & Eichenbaum, 2002; Howard, Fotedar, Datey, & Hasselmo, 2005). In contrast, the basal ganglia may serve to co-ordinate the selection of what action to perform (e.g. Stocco, Lebiere, & Anderson, 2010), while the cerebellum may co-ordinate and control the sequence of specific motor movements (e.g. Doya, 2000). In this roughly sketched out model, the binding that the hippocampus performs between different neural regions is analogous to forming episodic representations that can later be retrieved to produce implicit sequence learning effects. Of course, this model is speculative, and more work is needed to connect theoretical models to the neural substrates that have been found to underlie behaviour in sequence learning tasks.

Conclusion

In summary, the goal of this thesis was to test whether the episodic representations that are thought to underlie explicit remembering also underlie performance in implicit learning tasks. The particular approach chosen in this thesis was to examine whether contextual information is encoded and retrieved when learning occurs unintentionally and in the absence of awareness. To that end, in the empirical chapters of this thesis I assessed whether implicit sequence learning effects are context-specific. The three empirical chapters provide preliminary results suggesting that contextual information can be incorporated into the representations that underlie implicit sequence learning effects. At this point, research examining the neural substrates that are involved in implicit sequence learning is inconsistent with a strict systems account of implicit sequence learning that posits separate neural substrates for implicit and explicit learning. However, more research is needed to confirm whether the brain regions associated with implicit sequence learning are consistent with a more processing oriented account. In any case, the results presented in this thesis provide support for the notion that implicit sequence learning effects may be supported by the same representations and neural substrates that support explicit remembering.

References

Abrahamse, E. L., Jiménez, L., Verwey, W. B., & Clegg, B. A. (2010). Representing serial action and perception. *Psychonomic Bulletin & Review, 17*, 603-623.

Abrahamse, E. L., Van der Lubbe, R. H. J., & Verwey, W. B. (2008). Asymmetrical learning between a tactile and visual serial RT task. *Quarterly Journal of Experimental Psychology, 61,* 210-217.

Abrahamse, E. L., Van der Lubbe, R. H. J., & Verwey, W. B. (2009). Sensory information in perceptual–motor sequence learning: Visual and/or tactile stimuli. *Experimental Brain Research, 197,* 175-183.

Abrahamse, E. L., & Verwey, W. B. (2008). Context dependent learning in the serial RT task. *Psychological Research, 72,* 397-404.

Allport, A., & Wylie, G. (2000). 'Task switching', stimulus-response bindings, and negative priming. In S. Monsell & J. S. Driver (Eds.), *Attention and performance XVIII: Control of cognitive processes* (pp. 35-70). Cambridge, MA: MIT Press.

Atallah, H. E., Frank, M. J., & O'Reilly, R. C. (2004). Hippocampus, cortex, and basal ganglia: Insights from computational models of complementary learning systems. *Neurobiology of Learning and Memory*, *82*, 253-267.

Baddeley, A. (1984). Neuropsychological evidence and the semantic/episodic distinction. *Behavioral and Brain Sciences, 7,* 238-239.

Barense, M. D., Gaffan, D., & Graham, K. S. (2007). The human medial temporal lobe processes online representations of complex objects. *Neuropsychologica, 45,* 2963-2974.

Beesley, T., Jones, F. W., & Shanks, D. R. (2012). Out of control: An associative account of congruency effects in sequence learning. *Consciousness and Cognition, 21,* 413-421.

Berner, M. P., & Hoffmann, J. (2008). Effector-related sequence learning in a bimanual-bisequential serial reaction time task. *Psychological Research, 72,* 138-154.

Berner, M. P., & Hoffmann, J. (2009). Integrated and independent learning of hand-related constituent sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 35,* 890-904.

Blaxton, T. A. (1989). Investigating dissociations among memory measures: Support for a transfer-appropriate processing framework. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15,* 657–688.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review, 108,* 624-652.

Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences, 8,* 539-546.

Brooks, L. R. (1978). Nonanalytic concept formation and memory for instances. In E. Rosch & B. Lloyd (Eds.), *Cognition and categorization* (pp. 169-211). Hillsdale. NJ: Erlbaum.

Brooks, L. R., & Vokey, J. R. (1991). Abstract analogies and abstracted grammars: Comments on Reber (1989) and Mathews et al. (1989). *Journal of Experimental Psychology: General, 120,* 316-323.

Channon, S., Shanks, D., Johnstone, T., Vakili, K., Chin, J., & Sinclair, E. (2002). Is implicit learning spared in amnesia?: Rule abstraction and item familiarity in artificial grammar learning. *Neuropsychologica, 40,* 2185-2197.

Chubala, C. M., & Jamieson, R. K. (2012). Recoding and representation in artificial grammar learning. *Behavior Research Methods*

Chun, M. M., & Jiang, Y. (1998). Contextual-cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology, 36,* 28-71.

Chun, M. M., & Phelps, E. A. (1999). Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nature Neuroscience, 2,* 844-847.

Cleeremans, A., & Jiménez, L. (1998). Implicit sequence learning: The truth is in the details. In M. A. Stadler & P. A. Frensch (Eds.), *Handbook of implicit learning* (pp. 323-364). Thousand Oaks, CA: Sage.

Cleeremans, A., & McClelland, J. L. (1991). Learning the structure of event sequences. *Journal of Experimental Psychology: General, 120,* 235-253.

Clerget, E., Poncin, W., Fadiga, L., & Olivier, E. (2011). Role of Broca's Area in implicit motor skill learning: Evidence from continuous Theta-burst magnetic stimulation. *Journal of Cognitive Neuroscience, 24,* 80-92.

Cohen, A., Ivry, R. I., & Keele, S. W. (1990). Attention and structure in sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16,* 17-30.

Cohen, N. J., & Squire, L. R. (1980). Preserved learning and retention of pattern analyzing skill in amnesia: Dissociation of knowing how and knowing that. *Science, 210,* 207–209.

Corballis, P. M., & Gratton, G. (2003). Independent control of processing strategies for different locations in the visual field. *Biological Psychology, 64,* 191-209.

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology, 1,* 42-45.

Craik, F. I. M., & Jacoby, L. L. (1979). Elaboration and distinctiveness in episodic memory. In L. G. Nilsson (Ed.), *Perspectives on memory research* (pp. 145-166). Hillsdale, NJ: Erlbaum.

Crump, M. J. C., Gong, Z., & Milliken, B. (2006). The context-specific proportion congruent Stroop effect: Location as a contextual cue. *Psychonomic Bulletin & Review, 13,* 316-321.

Curran, T. (1997). Higher-order associative learning in amnesia: Evidence from the serial reaction time task. *Journal of Cognitive Neuroscience*, *9*, 522-533.

D'Angelo, M. C., Jiménez, L., Milliken, B., & Lupiáñez, J. (2013). On the specificity of sequential congruency effects in implicit learning of motor and perceptual sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 39,* 69-84. doi: 10.1037/a0028474

D'Angelo, M.C., Milliken, B., Jiménez, L., & Lupiáñez, J. (2013). Implementing

Flexibility in Automaticity: Evidence from Context-specific Implicit Sequence

Learning. *Consciousness and Cognition, 22,* 64-81.

Dennett, D. C. (1993). *Consciousness explained.* Harmondsworth, U.K : Penguin

De Pisapia, N., & Braver, T. S. (2006). A model of dual control mechanisms through

anterior cingulate and prefrontal cortex interactions. *Neurocomputing, 69,* 1322-

1326.

Deroost, N., & Soetens, E. (2006a). Perceptual or motor learning in SRT tasks with

complex sequence structures. *Psychological Research, 70,* 88-102.

Deroost, N., & Soetens, E. (2006b). Spatial processing and perceptual sequence learning

in SRT tasks. *Experimental Psychology, 53,* 16-30.

Deroost, N., & Soetens, E. (2006c). The role of response selection in sequence learning.

The Quarterly Journal of Experimental Psychology, 59, 449-456.

Deroost, N., Zeeuws, I., & Soetens, E. (2006). Effector-dependent and response location

learning of probabilistic sequences in serial reaction time tasks. *Experimental

Brain Research, 171,* 469-480.

Destrebecqz, A., & Cleeremans, A. (2001). Can sequence learning be implicit? New

evidence with the process dissociation procedure. *Psychonomic Bulletin &

Review, 8,* 343-350.

Destrebecqz, A., & Cleeremans, A. (2003). Temporal effects in sequence learning. In L.

Jiménez (Ed.), *Attention and implicit learning* (pp. 181-213). Amsterdam: John

Benjamins.

Doya, K. (2000). Complementary roles of basal ganglia and cerebellum in learning and motor control. *Current Opinion in Neurobiology, 10*, 732-739.

Doyon, J. **(**2008). Motor sequence learning and movement disorders. *Current Opinion in Neurology, 21,* 478-483.

Egner, T. (2008). Multiple conflict-driven control mechanisms in the human brain. *Trends in Cognitive Sciences, 12*, 374-380.

Egner, T., Delano, M., & Hirsch, J. (2007). Separate conflict-specific cognitive control mechanisms in the human brain. *Neuroimage, 35,* 940-948.

Elman, J.L. (1990). Finding structure in time. *Cognitive Science, 14,* 179-211.

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics, 16,* 143-149.

Fortin, N. J., Agster, K. L., & Eichenbaum, H. B. (2002). Critical role of the hippocampus in memory for sequences of events. *Nature Neuroscience*, *5*, 458-462.

Francis, A. P., Schmidt, G. L., Carr, T. H., & Clegg, B. A. (2009). Incidental learning of abstract rules for non-dominant word orders. *Psychological Research, 73,* 60-74.

Frensch, P. A. (1998). Same concept, multiple meanings: On how to define the concept of implicit learning. In M. A. Stadler & P. A. Frensch (Eds.), *Handbook of implicit learning* (pp. 47-104). Thousand Oaks, CA: Sage.

Fu, Q., Dienes, Z., & Fu, X. (2010). The distinction between intuition and guessing in the SRT task generation: A reply to Norman and Price. *Consciousness & Cognition, 19,* 478-480.

Funes, M. J., Lupiáñez, J., & Humphreys, G. (2010a). Analyzing the generality of conflict

adaptation effects. *Journal of Experimental Psychology: Human Perception and*

Performance, 36, 147-161.

Funes, M. J., Lupiáñez, J., & Humphreys, G. (2010b). Sustained vs. transient cognitive

control: Evidence of a behavioral dissociation. *Cognition, 114,* 338-347.

Godden, D., & Baddeley, A. D. (1975). Context-dependent memory in two natural

environments: On land and under water. *British Journal of Psychology, 66*, 325-

331.

Gomez, R. L. (1997). Transfer and complexity in artificial grammar learning. *Cognitive*

Psychology, 33, 154-207.

Gomez, R. L., & Schvaneveldt, R. W. (1994). What is learned from artificial grammars?

Transfer tests of simple association. *Journal of Experimental Psychology:*

Learning, Memory, and Cognition, 20, 396-410.

Graf, P., & Schacter, D. L. (1985). Implicit and explicit memory for new associations in

normal and amnesic subjects. Journal of Experimental Psychology: Learning,

Memory and Cognition, 13, 45–53.

Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1998). Abstract and effector-specific

representations of motor sequences identified with PET. *Journal of Neuroscience,*

18, 9420-9428.

Gratton, G., Coles, M. G. H., & Donchin, E. (1992). Optimizing the use of information:

Strategic control of activation of responses. *Journal of Experimental Psychology:*

General, 121, 480-506.

Green, R. E. A., & Shanks, D. R. (1993). On the existence of independent explicit and

implicit learning systems: An examination of some evidence. *Memory &*

Cognition, 21, 304-317.

Hazeltine, E., Grafton, S. T., & Ivry, R. (1997). Attention and stimulus characteristics

determine the locus of motor sequence encoding: A PET study. *Brain, 120,* 123-

140.

Highman, P., & Vokey, J. R. (1994). Recourse to stored exemplars is not necessarily

explicit: A comment on Knowlton, Ramus, & Squire (1992). *Psychological*

Science, 5, 59-60.

Hintzman, D. L. (1984). MINERVA-2: A simulation model of human memory. *Behavior*

Research Methods, Instruments & Computers, 16, 96–101.

Hintzman, D. L. (1986). "Schema abstraction" in a multiple trace memory model.

Psychological Review, 93, 411-428.

Hoffmann, J., Sebald, A., & Stöcker, C. (2001). Irrelevant response effects improve serial

learning in serial reaction time tasks. *Journal of Experimental Psychology:*

*Learning, Memory, & Cognition***,** *27,* 470- 482.

Hommel, B. (1996). The cognitive representation of action: Automatic integration of

perceived action effects. *Psychological Research, 59,* 176–186.

Hommel, B. (1998). Event files: Evidence for automatic integration of stimulus-response

episodes. *Visual Cognition, 5,* 183–216.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding: A framework for perception and action planning. *Behavorial & Brain Sciences, 24,* 849-937.

Howard, M. W., Fotedar, M. S., Datey, A. V., & Hasselmo, M. E. (2005). The temporal context model in spatial navigation and relational learning: Toward a common explanation of medial temporal lobe function across domains. *Psychological Review, 112,* 75-116.

Howard, J. H., Jr., Mutter, S. A., & Howard, D. V. (1992). Serial pattern learning by event observation. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 18,* 1029-1039.

Humphreys, M. S., Bain, J. D., & Pike, R. (1989). Different ways to cue a coherent memory system: A theory for episodic, semantic, and procedural tasks. *Psychological Review, 96,* 208-233.

Jackson, G. M., Jackson, S. R., Harrison, J., Henderson, L., & Kennard, C. (1995). Serial reaction time learning and Parkinson's disease: Evidence for a procedural learning deficit. *Neuropsychologia*, *33*, 577-593.

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory & Language, 30,* 513-541.

Jacoby, L. L., Baker, J. G., & Brooks, L. R. (1989). Episodic effects on picture identification: Implications for theories of conceptual learning and theories of memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 15,* 275-281.

Jacoby, L. L., & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General, 110,* 306-340.

James, W. (1890). *Principles of psychology.* New York: Holt.

Jamieson, R. K., & Hauri, B. (2012). An exemplar model of performance in the artificial grammar task: Holographic representation. *Canadian Journal of Experimental Psychology, 66,* 98-105.

Jamieson, R. K., Holmes, S., & Mewhort, D. J. K. (2010). Global similarity predicts dissociation of classification and recognition: Evidence questioning the implicit/explicit learning distinction in amnesia. *Journal of Experimental Psychology: Learning, Memory and Cognition, 36,* 1529-1535.

Jamieson, R. K., & Mewhort, D. J. K. (2005). The influence of grammatical, local, and organizational redundancy on implicit learning: an analysis using information theory. *Journal of experimental psychology. Learning, memory, and cognition*, *31*(1), 9–23.

Jamieson, R. K., & Mewhort, D. J. K. (2009a). Applying an exemplar model to the artificial grammar task: Inferring grammaticality from similarity. *The Quarterly Journal of Experimental Psychology, 62,* 550-575.

Jamieson, R. K., & Mewhort, D. J. K. (2009b). Applying an exemplar model to the serial reaction-time task: Anticipating from experience. *The Quarterly Journal of Experimental Psychology, 62,* 1757-1783.

Jamieson, R. K., & Mewhort, D. J. K. (2010). Applying an exemplar model to the artificial-grammar task: String-completion and performance for individual items. *Quarterly Journal of Experimental Psychology, 63,* 1014-1039.

Jamieson, R. K., & Mewhort, D. J. K. (2011). Grammaticality is inferred from global similarity: A reply to Kinder (2010). *Quarterly Journal of Experimental Psychology, 64,* 209-216.

Jiménez, L., Lupiáñez, J., & Vaquero, J. M. M. (2009). Sequential congruency effects in implicit sequence learning. *Consciousness and Cognition, 18,* 690-700.

Jiménez, L., Vaquero, J. M. M., & Lupiáñez, J. (2006). Qualitative differences between implicit and explicit sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 32*, 475-490.

Jiménez, L., & Vázquez, G. A. (2005). Sequence learning under dual task conditions: Alternatives to a resource-based account. *Psychological Research, 69,* 352-368.

Keele, S. W., Ivry, R., Mayr, U., Hazeltine, E., & Heuer, H. (2003). The cognitive and neural architecture of sequence representation. *Psychological Review, 110,* 316-339.

Kiesel, A., & Hoffmann, J. (2004). Variable action effects: response control by context-specific effect anticipations. *Psychological Research, 68,* 155–162.

Kinder, A., & Shanks, D. R. (2001). Amnesia and the declarative/nondeclarative distinction: A recurrent network model of classification, recognition, and repetition priming. *Journal of Cognitive Neuroscience, 13,* 648–669.

Kinder, A., & Shanks, D. R. (2003). Neuropsychological Dissociations Between Priming and Recognition**:** A Single-System Connectionist Account. *Psychological Review, 110,* 728-744.

Knowlton, B. J., Ramus, S. J., & Squire, L. R. (1992). Intact artificial grammar learning in amnesia: Dissociation of category-level knowledge and explicit memory for specific instances. *Psychological Science, 3,* 172–179.

Knowlton, B. J., & Squire, L. R. (1993). The learning of categories: Parallel memory systems for item memory and category-level knowledge. *Science, 262,* 1747–1749.

Knowlton, B. J., & Squire, L. R. (1996). Artificial grammar learning depends on implicit acquisition of both abstract and exemplar-specific information*. Journal of Experimental Psychology: Learning, Memory, and Cognition, 22,* 169-181.

Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review, 95,* 492-527.

Logan, G.D. (1990). Repetition priming and automaticity: Common underlying mechanisms? *Cognitive Psychology, 22*, 1-35.

Mayr (1996). Spatial attention and implicit sequence learning: Evidence for independent learning of spatial and non-spatial sequences.

McKoon, G., Ratcliff, R., & Dell, G. S. (1986). A critical evaluation of the episodic-semantic distinction. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 12,* 295-306.

Merikle, P. M., & Reingold, E. M. (1991). Comparing direct (explicit) and indirect (implicit) measures to study unconscious memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 17,* 224-233.

Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning & Verbal Behavior, 16,* 519-533.

Neal, A., & Hesketh, B. (1997). Episodic knowledge and implicit learning. *Psychonomic Bulletin & Review, 4,* 24–37.

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology, 19,* 1-32.

Nissen, M. J., Willingham, D., & Hartman, M. (1989). Explicit and implicit remembering: When is learning preserved in amnesia? *Neuropsychologia, 27,* 341-352.

Norman, E., Price, M. C., Duff, S. C., & Mentzoni, R. A. (2007). Gradations of awareness in a modified sequence learning task. *Consciousness & Cognition, 16,* 809-837.

Notebaert, W., & Verguts, T. (2008). Cognitive control acts locally. *Cognition, 106,* 1071-1080.

O'Reilly, R. C., & Norman, K. A. (2002). Hippocampal and neocortical contributions to memory: Advances in the complementary learning systems framework. *Trends in Cognitive Sciences*, *6*, 505-510.

O'Reilly, R. C., & Rudy, J. W. (2001). Conjunctive representations in learning and

    memory: Principles of cortical and hippocampal function. *Psychological Review*,

    108, 311-345.

Perruchet, P., & Gallego, J. (1997). A subjective unit formation account of implicit

    learning. In D. Berry (Ed.), *How implicit is implicit learning?* (pp. 124-161).

    Oxford, United Kingdom: Oxford University Press.

Perruchet, P. (1994). Defining the knowledge units of a synthetic language: Comment on

    Vokey and Brooks (1992). *Journal of Experimental Psychology: Learning,*

    Memory, & Cognition, 20, 223-228.

Perruchet, P., & Amorim, M. (1992). Conscious knowledge and changes in performance

    in sequence learning: Evidence against dissociation. *Journal of Experimental*

    Psychology: Learning, Memory, & Cognition, 18, 785-800.

Posner, M. I., & Snyder, C. R. R. (1975). Attention and cognitive control. In R. L. Solso

    (Ed.), *Information processing and cognition: The Loyola symposium* (pp. 55-85).

    Hillsdale, NJ: Erlbaum.

Rabbitt, P. M. A. (1966). Errors and error correction in choice reaction tasks. *Journal of*

    Experimental Psychology, 71, 264-272.

Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of verbal learning*

    and verbal behavior, *6*, 855–863.

Reber, A. S. (1989). Implicit learning and tacit knowledge. *Journal of Experimental*

    Psychology: General, 118, 219-235.

Reber, A. S. (1993). *Implicit learning and tacit knowledge.* London: Oxford University Press.

Reber, P. J., & Squire, L. (1994). Parallel Brain Systems for Learning with and without Awareness. *Learning & Memory*, *1*, 217–229.

Reed, J., & Johnson, P. (1994). Assessing implicit learning with indirect tests: Determining what is learned about sequence structure. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 20,* 585-594.

Reingold, E., & Merikle, P. (1988). Using direct and indirect measures to study perception without awareness. *Attention, Perception, & Psychophysics*, *44*(6), 563–575.

Reingold, E. A., & Merikle, P. M. (1990). On the inter-relatedness of theory and measurement in the study of unconscious processes. *Mind & Language, 5,* 9-28.

Remillard, G. (2009). Pure perceptual-based sequence learning: A role for visuospatial attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 35,* 528-541.

Robertson, E. M., Tormos, J. M., Maeda, F., & Pascual-Leone, A. (2001). The role of the dorsolateral prefrontal cortex during sequence learning is specific for spatial information. *Cerebral Cortex, 11,* 628-635.

Roediger, H. L., III (1984). Does current evidence from dissociation experiments favor the episodic/semantic distinction? *Behavioral and Brain Sciences, 7,* 252-254.

Rüsseler, J., Münte, T. F., & Rösler, F. (2002). Influence of stimulus distance in implicit learning of spatial and nonspatial event sequences. *Perceptual and Motor Skills, 95,* 973-987.

Ryan, J. D., Althoff, R. R., Whitlow, S., & Cohen, N. J. (2000). Amnesia is a deficit in relational memory. *Psychological Science*, *11*, 454-461.

Sanchez, D. J., Gobel, E. W., & Reber, P. J. (2010). Performing the unexplainable: implicit task performance reveals individually reliable sequence learning without explicit knowledge. *Psychonomic bulletin & review*, *17*(6), 790–796.

Sanchez, D. J., & Reber, P. J. (2013). Explicit pre-training instruction does not improve implicit perceptual-motor sequence learning. *Cognition*, *126*, 341–351.

Schvaneveldt, R. W., & Gomez, R. (1998). Attention and probabilistic sequence learning. *Psychological Research, 61,* 175-190.

Seidler, R. D., Tuite, P., & Ashe, J. (2007). Selective impairments in implicit learning in Parkinson's disease. *Brain Research, 1137,* 104-110.

Shanks, D. R., Rowland, L. A., & Ranger, M. S. (2005). Attentional load and implicit sequence learning. *Psychological Research, 69,* 369-382.

Shanks, D. R., & St. John, M. F. (1994). Characteristics of dissociable human learning systems. *Behavioral & Brain Sciences, 17,* 367-447.

Shanks, D. R., Wilkinson, L., & Channon, S. (2003). Relationship between priming and recognition in deterministic and probabilistic sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29,* 248-261.

Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychological Review, 84,* 1-66.

Shin, J. C., Aparicio, P., & Ivry, R. B. (2005). Multidimensional sequence learning in patients with focal basal ganglia lesions, *Brain and Cognition, 58.* 75-83.

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

Simon, J. R. (1969). Reactions toward the source of stimulation. *Journal of Experimental Psychology, 81,* 174-176.

Soetens, E., Melis, A., & Notebaert, W. (2004). Sequence learning and sequential effects. *Psychological Research, 69,* 124-137.

Song, S., Howard, J. H., Jr., & Howard, D. V. (2008). Perceptual sequence learning in a serial reaction time task. *Experimental Brain Research, 189,* 145-158.

Spapé, M. M., & Hommel, B. (2008). He said, she said: Episodic retrieval induces conflict adaptation in an auditory Stroop task. *Psychonomic Bulletin & Review, 15,* 1117-1121.

Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory, 82,* 171-177

Squire, L. R. (2009). Memory and brain systems: 1969-2009. *Journal of Neuroscience, 29,* 12711-12716.

Squire, L. R., & Zola-Morgan, S. (1988). Memory: brain systems and behavior. *Trends in Neurosciences, 11,* 170–175.

Stadler, M. A. (1992). Statistical structure and implicit serial learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 18,* 318–327.

Stadler, M. A., & Neely, C. B. (1997). Effects of sequence length and structure on implicit serial learning. *Psychological Research/Psychologische Forschung, 60,* 14–23.

Stöcker, C., Sebald, A., & Hoffmann, J. (2003). The influence of response–effect compatibility in a serial reaction time task. *Quarterly Journal of Experimental Psychology, 56A,* 586-703.

Stocco, A., Lebiere, C., & Anderson, J. R. (2010). Conditional routing of information to the cortex: A model of the basal ganglia's role in cognitive coordination. Psychological Review, 117, 541–574.

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology, 28,* 643-662.

Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception & Psychophysics, 50,* 184-193.

Thomson, D. R., & Milliken, B. (2012). Contextual distinctiveness produces long-lasting priming of pop-out. *Journal of Experimental Psychology: Human Perception and Performance.* doi: 10.1037/a0028069

Torriero, S., Oliveri, M., Koch, G., Caltagirone, C., & Petrosini, L. (2004). Interference of
left and right cerebellar rTMSwith procedural learning. *Journal of Cognitive
Neuroscience*, *16*, 1605-1611.

Treisman, A. M., & Gelade, G. (1980). A feature integration theory of attention.
Cognitive Psychology, 12, 97-136.

Tulving, E. (1972). Episodic and semantic memory. In E. Tulving and W. Donaldson
(Eds.), *Organization of memory* (pp. 381-403). New York: Academic Press.

Tulving, E. (1983). *Elements of episodic memory.* Cambridge: Oxford University Press.

Tulving, E. (1985). How many memory systems are there? *American Psychologist, 40,*
385–398.

Tulving, E. (1986). What kind of a hypothesis is the distinction between episodic and
semantic memory? *Journal of Experimental Psychology: Learning, Memory, &
Cognition, 12,* 307-311.

Tulving, E., Schacter, D. L., & Stark, H. A. (1982). Priming effects in word-fragment
completion are independent of recognition memory. *Journal of Experimental
Psychology: Learning, Memory, & Cognition, 4,* 335-342.

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in
episodic memory. *Psychological Review, 80,* 352-373.

Vandenberghe, M., Schmidt, N., Fery, P., & Cleeremans, A. (2006). Can amnesic patients
learn without awareness? New evidence comparing deterministic and probabilistic
sequence learning. *Neuropsychologia, 44,* 1629-1641.

Vandenbossche, J., Deroost, N., Soetens, E., Coomans, D., Spildooren, S., Vercruysse, Nieuwboer, A., & Kerckhofs, E. (2013). Impaired Implicit Sequence Learning in Parkinson's Disease Patients With Freezing of Gait, *Neuropsychology, 27,* 28-36.

Vandenbossche, J., Deroost, N., Soetens, E., & Kerckhofs, E. (2009). Does implicit learning in non-demented Parkinson's disease depend on the level of cognitive functioning? *Brain and Cognition*, *69*, 194-199.

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science, 277,* 376-380.

Verwey, W. B., & Clegg, B. A. (2005). Effector dependent sequence learning in the serial RT task. *Psychological Research, 69,* 242-251.

Vokey, J. R., & Brooks, L. R. (1992). The salience of item knowledge in learning artificial grammars. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 18,* 328-344.

Warrington, E. K., & Weiskrantz, L. (1970). The amnesic syndrome: Consolidation or retrieval? *Nature, 228,* 628–630.

Waszak, F., Hommel, B., & Allport, A. (2003). Task-switching and long-term priming: Role of episodic stimulus-task bindings in task-shift costs. *Cognitive Psychology, 46,* 361-413.

Wendt, M., Kluwe, R. H., & Peters, A. (2006). Sequential modulation of interference evoked by processing task-irrelevant stimulus features. *Journal of Experimental Psychology: Human Perception and Performance, 32,* 644-667.

Wilkinson, L., & Jahanshahi, M. (2007). The striatum and probabilistic implicit sequence learning. *Brain Research, 1137,* 117-130.

Wilkinson, L., Khan, Z., & Jahanshahi, M. (2009). The role of the basal ganglia and its cortical connections in sequence learning: Evidence from implicit and explicit sequence learning in Parkinson's disease. *Neuropsychologia, 47,* 2564-2573.

Wilkinson, L., & Shanks, D. R. (2004). Intentional control and implicit sequence learning. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 30,* 354-369.

Wilkinson, L., Teo, J. T., Obeso, I., Rothwell, J. C., & Jahanshahi, M. (2010). The contribution of primary motor cortex is essential for probabilistic implicit sequence learning: Evidence from theta burst magnetic stimulation. *Journal of Cognitive Neuroscience, 22,* 427-436.

Willingham, D. B. (1998). A neuropsychological theory of motor skill learning. *Psychological Review, 105,* 558-584.

Willingham, D. B. (1999). Implicit motor sequence learning is not purely perceptual. *Memory & Cognition, 27,* 561-572.

Willingham, D. B., & Goedert-Eschmann, K. (1999). The relation between implicit and explicit learning: Evidence for parallel development. *Psychological Science, 10,* 531-534.

Willingham, D. B., & Koroshetz, W. J. (1993). Evidence for dissociable motor skills in Huntington's disease patients. *Psychobiology, 21,* 173-182.

Willingham, D. B., Nissen, M. J., & Bullemer, P. (1989). On the development of procedural knowledge. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 15,* 1047-1060.

Whittlesea, B. W. A. (1987). Preservation of specific experiences in the representation of general knowledge. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 13,* 3-17.

Whittlesea, B. W. A. (2002). Two Routes to Remembering (and Another to Remembering Not). *Journal of Experimental Psychology: General, 131,* 325-348.

Whittlesea, B. W. A., Brooks, L. R., & Westcott, C. (1994). After the learning is over: Factors controlling the selective application of general and particular knowledge. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 20,* 259-274.

Whittlesea, B. W. A., & Dorken, M. D. (1993). Incidentally, things in general are particularly determined: An episodic-processing account of implicit learning. *Journal of Experimental Psychology: General, 122*, 227-248.

Whittlesea, B., & Dorken, M. (1997). Implicit learning: Indirect, not unconscious. *Psychonomic Bulletin & Review*, *4*(1), 63–67.

Whittlesea, B. W. A., & Leboe, J. P. (2000). The heuristic basis of remembering and classification: Fluency, generation, and resemblance. *Journal of Experimental Psychology: General, 129,* 84–106.

Whittlesea, B. W., & Price, J. R. (2001). Implicit/explicit memory versus

   analytic/nonanalytic processing: Rethinking the mere exposure effect. *Memory &*

   Cognition, 29, 234–246.

Whittlesea, B. W. A., & Wright, R. (1997). Implicit (and explicit) learning: Acting

   adaptively without knowing the consequences. *Journal of Experimental*

   Psychology: Learning, Memory, and Cognition, *23*, 181–200.

Witt, J. K., & Willingham, D. T. (2006). Evidence for separate representations for action

   and location in implicit motor sequencing. *Psychonomic Bulletin & Review, 13,*

   902-907.

Zaki, S. R. (2004). Is categorization performance really intact in amnesia? A meta-

   analysis. *Psychonomic Bulletin & Review, 11,* 1048-1054.

Ziessler, M. (1998). Response–effect learning as a major component of implicit serial

   learning. *Journal of Experimental Psychology: Learning, Memory, & Cognition,*

   24, 962-978.

Ziessler, M., & Nattkemper, D. (2001). Learning of event sequences is based on

   response–effect learning: Further evidence from a serial reaction task. *Journal of*

   Experimental Psychology: Learning, Memory, & Cognition, 27, 595-613.