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Theoretical and Review Articles

Representing serial action and perception

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This article presents a review on the representational base of sequence learning in the serial reaction time task. The first part of the article addresses the major questions and challenges that underlie the debate on implicit and explicit learning. In the second part, the informational content that underlies sequence representations is reviewed. The latter issue has produced a rich and equivocal literature. A taxonomy illustrates that substantial support exists for associations between successive stimulus features, between successive response features, and between successive response-to-stimulus compounds. We suggest that sequence learning is not predetermined with respect to one particular type of information but, rather, develops according to an overall principle of activation contingent on task characteristics. Moreover, substantiating such an integrative approach is proposed by a synthesis with the dual-system model (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003).

The ability to sequence incoming information and ongoing action—and its development over practice—lies at the very heart of skilled performance. From playing sheet music on the piano to driving a car in a hectic city, the underlying skills inherently involve putting together the correct sequences of information and actions. The importance of sequence learning has long been recognized by the scientific community (e.g., Lashley, 1951) and has been addressed in a wide range of experimental tasks that include the likes of the Hebb digits task (e.g., Hebb, 1961), the discrete sequence production task (e.g., Verwey, 2003), and the serial reaction time (SRT) task (e.g., Nissen & Bullemer, 1987). Arguably, the latter has become the most popular task for studying sequence learning, with the number of SRT studies increasing substantially over the last few decades (for reviews, see Clegg, DiGirolamo, & Keele, 1998; Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; Rhodes, Bullock, Verwey, Averbeck, & Page, 2004; Robertson, 2007; Seger, 1994). For example, performing a search at Google Scholar (www.scholar.google.com) on the phrase "serial reaction time task" produced 43 hits for the period from 1987 to 1990, 604 hits for the period from 1991 to 2000, and 2,230 hits for the period from 2001 to 2010. A similar search at Scopus (www.scopus.com) produced values of 9, 91, and 322, respectively.

In its basic appearance (see Nissen & Bullemer, 1987), the SRT task is a continuous four-choice reaction time (RT) task in which participants respond to the location of the stimulus. Typically, a fixed response-to-stimulus interval (RSI) separates successive events. Unbeknownst to the participants, stimulus presentation is sequential; that is, individual events either follow a certain rule or are presented as a fixed-length string of events that is repeated continuously. Decreases in RTs and/or error percentages with practice provide evidence that learning has occurred. To differentiate sequence learning from general practice effects, it is a common practice now to insert a block consisting of either randomly ordered stimuli or a new sequence of stimuli toward the end of the practice phase. The cost in RT and/or accuracy of this random block, relative to the surrounding sequence blocks, serves as an index for sequence learning. Often, participants are apparently unable to (fully) express their sequence knowledge in other ways (e.g., recognition and free recall tests) than through the performance measures, and learning is

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characterized as implicit (e.g., Cleeremans, Destrebecqz, & Boyer, 1998; Seger, 1994; but see Shanks, 2005).

It should be noted, however, that these general characteristics are not always maintained. The SRT task has been modified on various occasions in order to test specific hypotheses, with changes in stimulus modality (e.g., visual, auditory, tactile), stimulus type (e.g., spatial, color, number), response modality (e.g., manual, verbal), stimulus–response (S–R) mapping (e.g., compatible vs. incompatible; one-to-one vs. two-to-one mapping), RSI, and nature of the regularity (e.g., deterministic vs. probabilistic).

The SRT task has provided the foundation for a highly productive area of research featuring behavioral, imaging (e.g., Curran, 1998; Hazeltine & Ivry, 2003), patient (e.g., Dominey, 2003; Doyon, 2008), animal (e.g., Christie & Dalrymple-Alford, 2004; Nixon & Passingham, 2000), developmental (e.g., Meulemans, Van der Linden, & Perruchet, 1998; Wilson, Maruff, & Lum, 2003), and computational (e.g., Cleeremans, 1993; Cleeremans & Dienes, 2008) approaches. With its relatively fast acquisition and objective index of sequence-specific performance gains, it offers an easy laboratory tool in the study of sequential skill. Moreover, the paradigm mimics important properties of real-life learning situations, since both our actions and many of the naturally occurring events that surround us entail some inherent structure.

At the same time, the broad scope of sequencing can make investigation and interpretation in the SRT task more complicated than its relatively simple design might suggest. A full evaluation of human sequence-learning phenomena touches upon a wide range of aspects of cognitive functioning, such as perception, attention, consciousness, motor control, memory, language, learning, and so forth. This complexity is also apparent in the sensitivity of the paradigm to even relatively minor parametric manipulations, sometimes making straightforward comparisons between studies difficult. For instance, variations in the stimulus-to-response mapping (e.g., Deroost & Soetens, 2006b) or the RSI (e.g., Destrebecqz & Cleeremans, 2001) have been shown to influence sequence learning.

In line with various other implicit-learning paradigms, such as artificial grammar learning (e.g., Redington & Chater, 2002), category learning (e.g., Ashby & Casale, 2003), and dynamic system control (e.g., Cleeremans et al., 1998), the central topic of SRT research has been the nature of sequence learning: What exactly is being learned, and how is this knowledge represented in the brain (Clegg et al., 1998; Goschke, 1998; Hazeltine, 2002; Stadler & Roediger, 1998)? Many studies related to this umbrella topic can be mapped onto two, relatively orthogonal issues. First, the SRT task is often employed as a tool for exploring implicit learning and for contrasting it with explicit learning—hence, for exploring the role of sequence awareness. This inherently raises the difficult question of how to define and operationalize implicit learning (e.g., Frensch & Rünger, 2003). Second, an ongoing debate concerns the precise informational content underlying the sequence representation that forms during training. Mainly, the latter issue has focused on implicit sequence learning (since the SRT task is primarily known as a task for exploring implicit learning) and, more specifically, on the dichotomy of (purely) stimulus-based versus (purely) response-based learning, although various alternatives have been proposed.

Below, we review recent progress on the nature of sequence learning. We will first present an overview on the various themes that have dominated the debate on awareness in sequence learning. Then, in the second part of the article, we will address the informational content that underlies sequence representations. This issue has recently provided a large pool of empirical findings and theoretical accounts, and we believe that an updated taxonomy is in place.

CONSCIOUS AWARENESS IN SEQUENCE LEARNING

Ever since Nissen and Bullemer (1987) published the foundation article on the SRT task, sequence awareness has been one of the major foci of SRT research (for a review, see Shanks, 2005). Within this scope, a number of more specific issues can be identified (see Table 1), although substantial interrelationships may exist between them.

Defining Implicit Learning

First, there has been extensive debate about the very definition of implicit learning. Dozens of attempts across the literature have sought to get to the heart of the concept, but it has proved immensely difficult to come up with an adequate qualification of implicit learning—certainly, one that matches the simplicity with which one can describe explicit learning: learning through hypothesis testing.[1] Nevertheless, many definitions of implicit sequence learning show overlap on at least two major criteria: (1) an incidental mode of learning and (2) an end product of learning that is relatively inaccessible to conscious awareness and/

Table 1
Major Questions Around Which the Debate on Implicit and Explicit Learning Has Centered

How should implicit sequence learning be defined?
How can implicit sequence learning be demonstrated?
How does explicit sequence knowledge arise?
Is there a single knowledge base underlying both implicit and explicit sequence learning?
Which learning precedes the other, implicit or explicit sequence learning?
What are the characteristics of implicit and explicit sequence learning effects?

or conscious control (e.g., Seger, 1994).[2] The former is tightly related to the set of instructions for participants in the SRT task and, therefore, relatively easy to control. Specifically, it may be argued that learning is incidental as long as participants have not been instructed to learn and, thus, are not made aware of the regularity to be learned. Ultimately, however, the criterion of an incidental mode of learning may only serve the purpose of protecting the "implicit" status of the end product of learning. The latter criterion, then, seems to be more significant, but it is also more problematic, since it holds a strong methodological challenge that can be referred to as the *process purity* problem (Curran, 2001).

Process Purity Problem

A second issue concerns the debate on whether the types of evidence being produced within the SRT field offer incontrovertible proof of implicit learning (e.g., Shanks, 2005; Shanks & St. John, 1994)—without questioning the existence of implicit learning as such. In order to make any conclusive claims about implicit learning and its characteristics, it is required to separate out influences from explicitly learned information and, therefore, to observe a dissociation between performances on an implicit and an explicit test. However, no current test can be shown to be sensitive solely to explicit or solely to implicit knowledge, which is referred to as the *process purity problem* (e.g., Curran, 2001; Frensch, 1998; Shanks & St. John, 1994). Indeed, one can argue that virtually all tasks within the field of cognitive psychology are maintained by both implicit and explicit processes (e.g., Jacoby, 1991; Stefaniak, Willems, Adam, & Meulemans, 2008; Sun, Slusarz, & Terry, 2005). In addition, it is hard to exclude the possibility that potential dissociations between implicit and explicit tasks are attributable to differences in task difficulty (Stefaniak et al., 2008).

Destrebecqz and Cleeremans (2001) attempted to separate out the respective contributions of both types of processing in an SRT task by applying Jacoby's (1991) process dissociation procedure (PDP) to sequence learning. Briefly, this approach consists of assessing sequence reproduction performance after training in two free-generation conditions: (1) an inclusion condition in which participants are required to reproduce the regularities of the training sequence, thereby allowing implicit and explicit knowledge to jointly facilitate performance, and (2) an exclusion condition in which participants are required to avoid reproducing the regularities of the training sequence, thereby rendering implicit and explicit effects to act in opposition. A difference in performance between these two free-generation conditions is taken as indicative of explicit knowledge. Moreover, the authors hypothesized that the development of explicit knowledge is specifically sensitive to the length of the RSI: The more time participants have, the more explicit knowledge they will require. Accordingly, Destrebecqz and Cleeremans observed a performance difference between the inclusion and exclusion tasks for participants trained on an SRT task with a relatively large RSI of 250 msec, whereas such a performance difference was absent for participants trained with rapid trial succession (i.e., absent RSI). Even though the PDP method arguably provides a more sophisticated approach to the awareness issue than do alternative methods (e.g., forced and free recall questionnaires), its value has not been completely beyond question (e.g., Fu, Dienes, & Fu, 2010; Fu, Fu, & Dienes, 2008; Norman, Price, & Duff, 2006; Wilkinson & Shanks, 2004).

Another approach is to circumvent the issue of awareness as much as possible by using complex, probabilistic sequences (e.g., Jiménez, Vaquero, & Lupiáñez, 2006; Schvaneveldt & Gomez, 1998). Supposedly, a major hallmark of implicit learning is that complex knowledge can be acquired unconsciously, whereas explicit learning should be inversely related to the complexity of the material to be learned (e.g., Jiménez & Vázquez, 2005). Therefore, increasing the complexity of the sequence to be learned should provide a relatively large proportion of implicit learning, since it limits the development of explicit learning.

Knowledge Base(s)

From the perspective that both implicit and explicit knowledge can be involved in guiding human behavior, a third empirical question concerns the underlying knowledge base(s). Specifically, one may ask whether implicit and explicit knowledge are extreme ends of a single knowledge base (i.e., the single-system view), or whether they proceed from separate knowledge bases (i.e., the multiple-systems view). This issue is far from resolved, and several perspectives have been successfully defended in this regard. In line with the single-system view, Cleeremans and Jiménez (2002) proposed a graded perspective on consciousness. From this perspective, findings that dissociate conscious and unconscious effects on behavior do not necessarily imply the existence of distinct knowledge bases that subserve implicit and explicit learning. Rather, it is suggested that representations are accessible for conscious awareness as much as they are of "sufficiently high-quality in terms of strength, stability in time, and distinctiveness" (p. 29), implying that the same representations (i.e., knowledge bases) are available and at play for implicit and explicit processing.

Conversely, in line with the multiple-system view, Willingham (1998) presented a learning theory (i.e., control-based learning theory; COBALT) in which an accurate but attention-demanding ventral cortical system underlies explicit learning, whereas a fast-working but slow(er)-developing dorsal cortical system is responsible for implicit learning processes in parallel. According to COBALT, an agent can switch between the two modes, weighing the accuracy and attentional demands of the situation. Overall, this implies different knowledge bases underlying implicit and explicit learning. A model that is strongly related to COBALT—although more specifically tuned to sequence learning—was developed by Keele et al. (2003) and will here be referred to as the *dual-system* model. The dual-system model more or less comprises the same two systems as COBALT, but with various extensions and modifications (e.g., multidimensional learning, the role of selective attention; see below for a detailed description), one of which is of particular importance here: Although this model is also an obvious exemplar of the multiple-system view, it could enable the incorporation of the major argument of the single-system view—namely, that implicit and explicit learning can be grounded within a single system. Specifically, Keele et al. (2003) proposed a dorsal system that is exclusively devoted to implicit learning and a ventral system that supports implicit learning from which explicit knowledge might or might not emerge. The latter matches a view in which implicit and explicit knowledge arise from a single knowledge base. The dual-system model of Keele et al. (2003), then, seems to integrate traditionally opposing views on this issue. In fact, in the second part of the present article, a similar integrative role for the dual-system model will be defended with regard to the informational contents underlying sequence learning.

From a multiple-system view, a fundamental question concerns the possible interaction between these multiple systems. Some authors (e.g., P. J. Reber & Squire, 1994; Squire, 1992) advocated the view that implicit and explicit learning proceed independently from each other and do not interact, even though they have a joint influence on behavior. The COBALT theory, in turn, assumes a unidirectional control, in that the explicit system can overrule the implicit system but not vice versa. An even more fundamental interaction between implicit and explicit systems was introduced through the unexpected-event hypothesis (Frensch et al., 2003; Rünger & Frensch, 2008), which is focused on the procedure behind the development of explicit knowledge. In brief, it posits the following stepwise procedure: (1) Implicit learning precedes explicit learning; (2) implicit knowledge impacts behavior and creates an experience of deviation from the expected task performance (e.g., being unusually fast but still correct while responding); (3) this unexpected event triggers the conscious system to search for a cause and, consequently; (4) leads to the discovery of verbalizable regularity. However, the presumption that implicit learning always precedes explicit learning is not without debate or controversy. Indeed, various traditional models of skill acquisition may be referred to as *top-down*, in the sense that learning is assumed to evolve from generic, verbal, declarative (i.e., explicit) knowledge that may eventually turn into procedural (i.e., implicit) skill (i.e., automaticity) with practice (Ackerman, 1988; Anderson, 1983, 1993; Logan, 1985). Hence, a fifth major issue concerns the question about which learning develops first (and under which conditions), explicit or implicit learning?

Characteristics of Implicit and Explicit Knowledge

We here loosely define explicit learning as a process of deliberate hypothesis testing and implicit learning as a byproduct of task execution that remains outside the scope of conscious control. A sixth challenge addresses the search for further features that distinguish implicit from explicit learning effects: How do they behave? Initially, the relative resistance to change of both types of learning effects was debated by referring to transfer of knowledge across domains (i.e., domain specificity) or to the extent to which they could survive neurological and psychological pathology (e.g., Dienes & Berry, 1997; A. S. Reber, 1993; Willingham, 1997). The outcome of this debate is not totally clear, but some would defend the view that implicit learning is robust to neurological and psychological pathology, whereas explicit learning effects are less sensitive to changes in task features (e.g., A. S. Reber, 1993).

The view that implicit and explicit learning effects behave differently in the face of various changes was reinforced, and put into a framework, by the work of Jiménez et al. (2006). The authors showed that implicit learning effects can easily survive a change in the regular structure (i.e., a decrease in sequence validity, such as switching from a fully predictive to a less predictive situation), but not a change in the surface structure of the task (i.e., combining the SRT task with a visual search task), whereas explicit learning effects behaved in the opposite way. Referring to the graded view on consciousness, then, they reasoned that the relatively weak implicit-learning effects are strongly dependent on the reinstatement of the overall practice conditions (see also Abrahamse & Verwey, 2008), whereas explicit-learning effects can often survive procedural changes but are highly sensitive to (changes in) strategic processes.

Another difference between implicit and explicit learning—and this brings us already within the realm of the next section of the present article—relates to the informational content of the respective representations. Willingham and colleagues (i.e., Knee, Thomason, Ashe, & Willingham, 2007; Willingham, 1999; Willingham, Wells, Farrell, & Stemwedel, 2000) explored this issue in a set of studies and proposed that implicit sequence learning in the SRT task is mainly tied to response locations (e.g., Willingham et al., 2000), whereas explicit learning arises from regularity across successive stimulus locations. This issue will obviously be extensively elaborated on in the second part of the article. For now, it suffices to note that this (probably overly simplistic) account would indicate that two distinct issues in relation to the nature of sequence learning—the issue of sequence awareness and the issue on the informational content of sequence representations—may not be completely orthogonal. However, whereas the precise informational content of explicit sequence learning has not been extensively explored, a rich literature has emerged for implicit sequence learning in this respect. In the next section, we will review this literature and provide a taxonomy of the various forms of sequence learning that have been proposed.

THE INFORMATIONAL CONTENT OF SEQUENCE REPRESENTATIONS

Here, we will address the precise informational content that underlies sequence learning in the SRT task. This issue has recently produced a rich literature of equivocal and even contradictory findings that warrants a status update. We will provide here a taxonomy (see Table 2), as well as some suggestions for future progress in unraveling the precise mechanisms that are involved.

Table 2
Overview of Studies That Provide Support for (V) or Evidence Against (X) the Different Forms of Sequence Learning That Are Discussed in the Literature (i.e., Perceptual Learning, Response Effect Learning, Response Selection Learning, Response-Based Learning, and Abstract Conceptual Learning)

	Level of Learning					Experimental Detail					
Reference	Perceptual	Response Effect	Response Selection	Response Based	Abstract Conceptual	Input Modality	Response Modality	Imperative Stimulus Feature	Regular Stimulus Feature	Regular Response	S–R Mapping
Abrahamse (2010, chap. 7)	–	–	X	–	–	vis	man	S	S	Y	com ⋁ inc
Abrahamse, Van der Lubbe, & Verwey (2008)	V		–	V	–	tac ⋁ vis	man	S	S	Y	com
Abrahamse & Verwey (2008)	V		–	–	–	vis	man	S	S	Y	com
Berger et al. (2005)	V	–	–	V	–	vis	man	S	S	N	com
Bischoff-Grethe, Goedert, Willingham, & Grafton (2004)	X	–	–	V	–	vis	man	S	S	Y	inc
Clegg (2005)	V		–	–	–	vis	man	S	S	Y	arb ⋁ com
Cock & Meier (2007)	V	–	–	–	X	vis	man	NS	NS (task)	N	arb
Dennis, Howard, & Howard (2006)	V	–	–	–	–	aud ⋀ vis	man	NS	NS	N	com
Deroost & Soetens (2006a)	V	–	–	V	–	vis	man	NS	S ⋀⋁ NS	Y ⋁⋀ N	arb
Deroost & Soetens (2006b)	V	–	–	–	–	vis	man	S	S	Y	com ⋁ inc
Deroost & Soetens (2006c)	–	–	V	–	–	vis	man	NS	S	N	arb
Dominey, Lelekov, Ventre-Dominey, & Jeannerod (1998)	–	–	–	–	X	vis	man	S	S	Y	com
Gheysen, Gevers, De Schutter, Van Waelvelde, & Fias (2009)	V	–	–	V	–	vis	man	NS	NS ⋁ none	Y ⋁ N	arb
Goschke & Bolte (2007)	–	–	–	–	V	vis	ver	NS	NS	N	com
Gotler, Meiran, & Tzelgov (2003)	–	–	–	–	V	vis	man	S	NS	N	com
Hazeltine (2002)	–	V	–	–	–	vis	man	NS	NS	Y	arb
Heuer, Schmidtke, & Kleinsorge (2001)	V	–	–	–	X	vis	man	NS	NS (task)	N	arb
Hoffmann & Koch (1997)	–	–	–	V	–	vis	man	S ⋁ NS	S ⋁ NS	Y	com ⋁ arb
Hoffmann, Martin, & Schilling (2003)	–	–	–	V	–	vis	man	NS	S	Y	arb
Hoffmann, Sebald, & Stöcker (2001)	–	V	–	–	–	vis	man	S	S	Y	com
Howard, Mutter, & Howard (1992)	V	–	–	–	–	vis	–	S	S	N	–
Kinder, Rolfs, & Kliegl (2008)	–	–	X	–	–	vis	oculo	S	S	Y	com
Koch (2001)	–	–	–	–	V	vis	man	NS	NS (task)	N	arb
Koch (2007)	–	–	V	V	–	vis	man	S	S	Y	com ⋁ inc
Koch & Hoffmann (2000)	V	–	–	V	–	vis	man ⋁ ver	S ⋁ NS	S ⋁ NS	Y	com ⋁ arb
Mayr (1996)	V	–	–	V	–	vis	man	S ⋁ NS	S ⋁ NS	Y	com ⋁ arb
Nattkemper & Prinz (1997)	X	–	–	V	–	vis	man	S	S	Y	com
Price & Shin (2009)	V	–	–	–	–	vis	man	NS	NS	N	arb
Remillard (2003)	V	–	–	–	–	vis	man	NS	S	N	arb
Remillard (2009)	V	–	–	–	–	vis	man	NS	S	N	arb
Rüsseler & Rösler (2000)	X	–	–	V	–	vis	man	S	S	Y	com
Schwarb & Schumacher (2009)	–	–	V	–	–	vis	man	S	S	Y	com ⋁ inc
Schwarb & Schumacher (2010)	–	–	V	–	–	vis	man	S	S	Y	com ⋁ inc
Song, Howard, & Howard (2008)	V	–	–	–	–	vis	–	S	S	N	–
Stadler (1989)	V	–	–	–	–	vis	man	S	S	Y	com
Stöcker, Sebald, & Hoffman (2003)	–	V	–	–	–	vis	man	S ⋁ NS	S ⋁ NS	Y	com ⋁ arb
Vakil, Kahan, Huberman, & Osimani (2000)	V	–	–	V	–	vis	man	S	S	N	com
Verwey & Clegg (2005)	–	–	–	V	–	vis	man	S	S	Y	com
Willingham (1999)	–	–	–	V	–	vis	man	S	S	Y ⋁ N	com ⋁ inc
Willingham, Wells, Farrell, & Stemwedel (2000)	X	–	–	V	–	vis	man	S	S	Y	com
Ziessler (1994)	–	V	–	V	–	vis	man	NS	S	N	arb
Ziessler (1998)	–	V	–	–	–	vis	man	NS	S	N	arb
Ziessler & Nattkemper (2001)	–	V	–	–	–	vis	man	NS	NS	Y	arb

Note—tac, tactile; vis, visual; aud, auditory; man, manual; ver, verbal; oculo, oculomotor; S, spatial; NS, nonspatial; Y, yes; N, no; com, spatially compatible; inc, spatially incompatible; arb, arbitrary; ⋀, and; ⋁, or; ⋀⋁, and/or.

Across the literature, different types of knowledge have been suggested to underlie the learning of sequences of events (see Table 2). To satisfactorily cope with all the disparate findings that are associated with these so-called single-level accounts, we believe that a comprehensive framework of sequence learning must involve a multilevel configuration. However, few attempts exist in the literature to substantiate such an integrative framework. Rather, it remains all too common to embrace the simple dichotomy of stimulus- versus response-based sequence learning, with individual findings being interpreted as supporting one while arguing against the other.

One major exception to this practice of testing single-mechanism accounts is the dual-system model proposed by Keele et al. (2003), which was already briefly mentioned above. In this second part of the article, this model will be discussed in more detail, since we believe that it can offer an integrative description of sequence learning. The dual-system model includes two parallel association systems: a set of unidimensional modules, each of which operates on a single dimension, and a multidimensional module operating both within and across dimensions. However, the model as currently instantiated does not always readily lend itself to testable predictions, because of its abstract nature, unfortunately leaving its current role in the field often restricted to an explanatory model. For example, within this dual-system model, the central concept of a dimension is not operationally defined, and no subsequent studies have attempted to tackle the role of dimensions in sequence learning. Here, we outline one way in which progress can be made, through providing a more tangible link of this model to the forms of sequence learning more frequently discussed in the SRT literature.

Below, we will first present a comprehensive review of the different types of learning that have been proposed to develop in the SRT task. This will clearly show that strong empirical support exists for various types. Building from an integrative approach, then, a synthesis is proposed between these multiple single-level mechanisms and the more overarching but somewhat abstract model depicted by Keele et al. (2003). This has mutual benefits. On the one hand, it allows the integration of multiple types of learning proposed in the literature within a framework that was developed from a set of major SRT studies. On the other hand, it could allow the dual-system model to explicitly relate to a rich literature, creating new and testable predictions on the way. However, we would like to note that positing a multilevel account of sequence learning obviously does not ultimately require the inclusion of the backbone provided by the dual-system model; the gist is the notion that various associations underlying sequence learning need to be considered within a single framework.

Reasoning from a multilevel approach to sequence learning, the important question for future research would no longer concern the nature of sequence learning as such but, rather, the precise determinants of the nature of sequence learning given a particular task and task context. Therefore, after having outlined the multiple single-level accounts and their synthesis into a multilevel approach, we will briefly discuss the potential relevance of the concept of task set for sequence learning and will describe some findings from the literature that provide preliminary support for this notion.

Multiple Single-Level Accounts

Two decades of investigation on the question about which associations underlie sequence learning has produced relatively strong support for three such associations: response location, perceptual, and response effect learning. Table 2 provides an overview of the relevant literature. Please note that for each study, we restricted ourselves to the main interpretations as described by the authors themselves. Occasionally, these authors acknowledged that their results could not distinguish between perceptual and response effect learning; in these cases, we placed the V-sign in between cells. In order to provide a comprehensive overview, we also included information about the input modality, the response modality, the type of features to respond to (i.e., imperative stimulus feature), the type(s) of features that contained the regularity (i.e., regular stimulus feature),[3] the type of stimulus-to-response-mapping (i.e., S–R mapping), and the question about whether response regularity was present. Table 2 shows that most studies employed visual stimuli and manual (i.e., keypress) responses, which may be seen as limiting the overall conclusions that can be drawn from the SRT research for perceptual–motor learning in general.

Notably, the three types of associations that emerge from Table 2 as firmly supported in the literature can be traced back to the formation of associations within and between stages of information processing (e.g., Sanders, 1990, 1998). We have depicted these types of associations more clearly in Figure 1 and will now discuss them in more detail. We will also briefly discuss the less documented alternatives (i.e., abstract conceptual learning and learning at the response selection stage).

Response-based learning. Response-based learning refers to the formation of associations between successive response features (see Figure 1B) and is thus, by definition, independent of the level of stimulus features. One initially perplexing pair of findings in sequence learning was the observed absence of effector-specific sequence learning in the SRT task (e.g., Cohen, Ivry, & Keele, 1990; Keele, Jennings, Jones, Caulton, & Cohen, 1995), whereas imaging and patient studies clearly indicate the involvement of motor areas in the brain (e.g., Grafton, Hazeltine, & Ivry, 1995, 1998; Willingham & Koroshetz, 1993). Willingham et al. (2000) offered a resolution to this apparent paradox by stressing the role of response locations. In their study, it was observed (1) that participants showed no reliable transfer when the stimulus sequence was maintained but response locations were changed, and (2) that participants showed transfer from a crossed-hand training phase to a normal hand test phase only when the sequence of response locations was maintained and showed no transfer when the sequence of finger movements was maintained. Willingham and colleagues proposed an account based on response location learning: Participants primarily learn

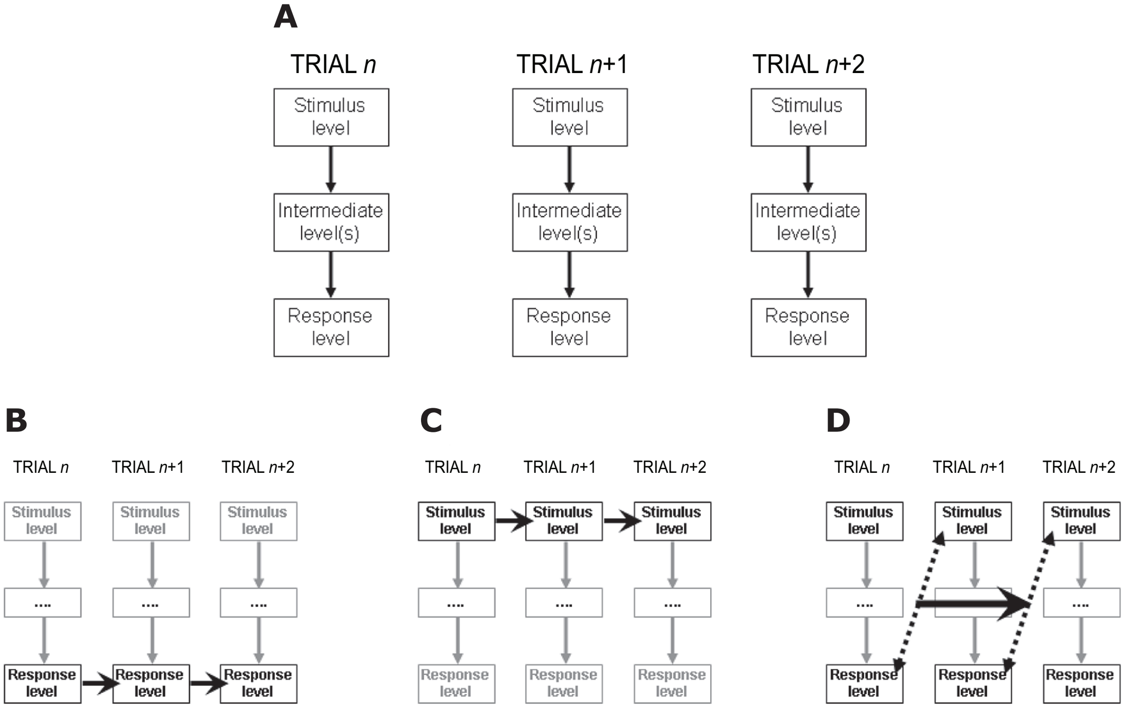

Figure 1. Information processing and sequence learning in the serial reaction time (RT) task. During early training, or in blocks with (pseudo)randomly structured trials, performance involves the same basic information-processing stages as a typical (four-)choice RT task (A). Processing at the stimulus level (e.g., encoding, identification), processing at intermediate levels (e.g., response selection), and processing at the response level (e.g., programming, execution). With training, associations may develop across trials (B) between successive response features, (C) between successive stimulus features (i.e., perceptual learning), or (D) between successive response-to-stimulus compounds (i.e., response effect learning).

a sequence of response locations, independently of the specific effectors used to act on these locations. This response location account was further supported by various subsequent studies (e.g., Deroost & Soetens, 2006a; Witt & Willingham, 2006).

The conclusion that sequence learning is not effector specific does not fit well with the notion that in many real-life tasks that involve sequential action, such as writing and typing, performance is typically affected by employing different effectors or effector groups (e.g., Gentner, Larochelle, & Grudin, 1988; Hicks, 1974; Jordan, 1995). Moreover, effector-specific sequence-learning effects have been found in studies with monkeys (e.g., Rand et al., 2000). Verwey and Clegg (2005) noted that these types of situations featuring effector-specific learning involve greater amounts of practice than is typical for the SRT task. In line with another study employing the discrete sequence production task (Verwey & Wright, 2004), Verwey and Clegg were able to detect an effector-specific component of sequence learning in the SRT task after extended practice, in addition to the typical effector-independent learning (see also Berner & Hoffmann, 2008; Deroost, Zeeuws, & Soetens, 2006). This finding suggests that at least two possible types of response-based representation can occur concurrently within the SRT task (see also Richard, Clegg, & Seger, 2009, for evidence of a potential third type of representation, direction of movement). However, there remain some unresolved questions about effector-specific learning with extended practice. For instance, it may indicate that, with extensive practice, the triggering of particular finger movements becomes increasingly automatic. Alternatively, the same result could also be accounted for by assuming that, over training, a body-based egocentric representation is progressively replaced by a hand-specific spatial reference frame (see Verwey, Abrahamse, & Jiménez, 2009).

Overall, response-based learning—and more specifically, response location learning—is arguably the dominant model of implicit sequence learning in the typical SRT task. It is supported by a wealth of behavioral findings (e.g., Deroost & Soetens, 2006a; Nattkemper & Prinz, 1997; Willingham, 1999) and fits well the frequently observed involvement of motor areas in the brain in SRT learning (e.g., Bischoff-Grethe, Goedert, Willingham, & Grafton, 2004; Grafton, Hazeltine, & Ivry, 1995, 1998, 2002). In addition, this account is congruent with the typically observed impaired sequence learning in clinical populations characterized by motor deficits (for a review, see Doyon, 2008). For instance, a meta-analysis by Siegert, Taylor, Weatherall, and Abernethy (2006) suggested that patients with Parkinson's disease are significantly impaired on implicit sequence learning.

However, although response-based sequence learning is well documented, on its own, it cannot easily incorporate various other findings in the SRT literature that have been mounting over the last decade.

Stimulus-dependent learning. Stimulus-dependent sequence learning may refer to any associations underlying sequence learning that involve stimulus features. On the one hand, this pertains to associations between successive stimulus features (either within or between single features, such as color, shape, and location), typically referred to as *perceptual learning* (see Figure 1C). On the other hand, associations may be formed between current response features and subsequent stimulus features (remember that in the typical SRT task, fixed and relatively small RSIs are employed, enabling each new stimulus to be interpreted as a direct effect of the preceding response), coined *response effect learning* (e.g., Ziessler & Nattkemper, 2001; see Figure 1D). Both these forms of sequence learning have received support in the literature, although specific experimental designs have sometimes made it impossible to disentangle their contributions (e.g., Abrahamse, Van der Lubbe, & Verwey, 2008; Clegg, 2005; Jiménez et al., 2006). Specifically, both perceptual and response effect learning predict low or absent transfer when the stimulus material is changed.

Abrahamse et al. (2008) showed that sequence learning does not always transfer well between different sets of stimuli (but see Abrahamse, Van der Lubbe, & Verwey, 2009; Willingham, 1999). Specifically, they observed only partial transfer from visual stimuli on a screen to tactile stimuli presented directly to the fingers for a response. Since response sequences were always identical, across both training and transfer phases and across stimulus conditions, these results suggest at least some role for stimulus modality. Along the same lines, Jiménez et al. (2006) observed no transfer when participants were first trained in a typical SRT setting and then tested in an adapted version with distractors appearing at the nontarget positions. Again, the response (location) sequence was maintained during testing. Finally, Clegg (2005) mapped two stimulus locations on each of two response keys. Response latencies increased when stimulus locations deviated from the learned sequence over a test phase, even when the response features remained the same (i.e., the stimulus did not appear at the expected location but, rather, at the alternative location that was mapped onto the same response). These results indicate that features of the stimuli are implicated in sequence learning, but cannot distinguish among perceptual learning of a sequence of stimuli, the learning of a sequence of S–R mappings, and the acquisition of sequence knowledge based on response effect contingencies.

Perceptual learning. Some definitions of perceptual learning confine it to (relatively long-lasting) changes to an organism's perceptual system (e.g., Goldstone, 1998). However, in the context of sequencing, perceptual learning refers to the possibility that stimulus features (such as location and shape) become bound into a higher level sequence representation, thereby facilitating responding to that series of stimuli when they reappear.

Empirical support for the involvement of stimulus locations in sequence learning that is independent of response-related processes stems mainly from studies in which (1) no overt responding was required[4] (i.e., observational learning) or (2) stimulus location followed a sequential structure independent of the response sequence. With regard to the former, Howard, Mutter, and Howard (1992) reported similar performance in a transfer phase from participants who had been responding throughout the experiment and those who had previously only observed the sequence. Willingham (1999) suggested that sequence learning through observation involved explicit, rather than implicit, learning. He observed no performance improvements on structured versus random trials after eliminating all data from participants who showed a relatively high awareness of the sequence (see also Kelly & Burton, 2001). However, Song, Howard, and Howard (2008) also found sequence learning with observation alone in an alternating SRT task, which has been claimed to produce little sequence awareness (Howard, Howard, Dennis, Yankovich, & Vaidya, 2004). Hence, it seems as if implicit sequence learning can develop from merely observing sequential order.

Various other studies have employed a fixed sequence of stimulus locations, whereas responses followed an independent, sometimes (pseudo)random, sequence (e.g., Deroost & Soetens, 2006a; Mayr, 1996; Remillard, 2003). This can be achieved by presenting a task-relevant stimulus feature (e.g., shape or color) across multiple potential stimulus locations. For instance, Remillard (2003; see also Deroost & Soetens, 2006c) employed a design in which six different stimuli, consisting of the letter pairs "xo" and "ox," were simultaneously presented at six fixed locations on the screen. An underline marked the location of one of the letter pairs, and participants were instructed to respond as quickly as possible to the identity of the marked letter pair. Although the identities of those target letter pairs and, therefore, the response series were unstructured, the stimulus location changed according to an independent probabilistic sequence. The sequence of stimulus locations was reliably learned, even though there the response-related information was unstructured.

Similar findings have been reported by Mayr (1996) and Deroost and Soetens (2006a). The task-irrelevant stimulus locations were sequentially structured over trials, whereas responses were made to a different, independent sequence of colors of the stimuli. Again, sequence learning based on stimulus locations was observed. Interestingly, Deroost and Soetens (2006a) showed that learning of the sequence of stimulus locations was strongest in (or even restricted to) the situation in which participants practiced a concurrent sequence of responses. When the response series was unstructured, little or no stimulus location learning seemed to develop.

In addition to the implicit learning of a sequence of stimulus locations, Gheysen, Gevers, De Schutter, Van Waelvelde, and Fias (2009) provided evidence for the implicit learning of a sequence of colors. They employed a serial color-matching task in which participants were required to match the colors of three centrally presented small squares with the color of a large target square and to select a response on the basis of a certain matching rule.

They observed clear implicit learning when regularity was imposed solely on the order of colors of successive target squares.

Support for the ability to implicitly extract regularity from input, such as with learning a fixed sequence of stimuli, also stems from paradigms other than the SRT task. For instance, Saffran, Johnson, Aslin, and Newport (1999) exposed participants to continuous sequences of nonlinguistic auditory stimuli whose elements were organized into "tone words" on the basis of statistical information. Adults could reliably extract this regularity. More important, the same was true even for 8-month-old infants, who most likely were not engaged in explicit learning. Likewise, the visual statistical learning (VSL) paradigm, in which participants are presented with a long series of visual stimuli, has shown implicit learning of statistical relationships among these stimuli (e.g., Turk-Browne, Isola, Scholl, & Treat, 2008). Given some of the surface similarities between the tasks, it is not implausible that the system underlying VSL is working also during SRT training, at least under some conditions. Finally, Olson and Chun (2001) showed that spatial attention can be guided to a target location on the basis of learned, sequentially structured event durations, event identities, and spatial–temporal event sequences, even when participants are unaware of the regularity (see also Clohessy, Posner, & Rothbart, 2001; but see Smyth & Shanks, 2008).

Response effect learning. A second proposed stimulus-dependent form of sequence learning is so-called *response effect learning*—that is, sequence learning based on associations between compounds of responses and subsequent stimuli. In an ingenious study, Ziessler and Nattkemper (2001; see also Ziessler, 1998) employed a flexible stimulus-to-response mapping that allowed them to vary the stimulus sequence while the response sequence was maintained. Predictable response-to-stimulus relationships improved serial learning, and the authors went as far as to state that "R–S learning is . . . the major learning mechanism working under serial learning conditions" (p. 612).

Further support for R–S learning was provided by a study of Hoffmann, Sebald, and Stöcker (2001). They mapped different tones as task-irrelevant response effects to the response keys and observed improved sequence learning as long as each tone was consistently and uniquely mapped onto a response (Experiment 1; see also Stöcker, Sebald, & Hoffmann, 2003). Moreover, for participants who had adapted to a contingent key–tone mapping during training, performance was significantly impaired when the mapping between response keys and tones was changed in a transfer block (Experiment 2). Stöcker et al. extended these findings by showing that the benefit from tones as task-irrelevant and contingent response effects occurs only when the tones are mapped ascending to response keys from left to right—thus, in a highly compatible manner.

These findings illustrate that response–effect associations benefit sequence learning. However, it remains uncertain whether this kind of component could play the major role attributed to it by some of its proponents. For instance, it is unclear how this type of representation could account for findings like those reported by Willingham (1999, Experiment 3; see also Abrahamse, 2010, chap. 7),[5] in which reliable transfer was observed when the stimulus patterns change while the response sequence is maintained, thus breaking the R–S coupling. In addition, one may wonder how response effect learning relates to sequence awareness. Response effect learning fits well with the ideomotor approach to action control, which points to the important role played by the mental anticipation of the sensory effects of a movement in the actual production of that movement (e.g., Hommel, Müsseler, Aschersleben, & Prinz, 2001). Even though the ideomotor approach does not specify whether this anticipation is necessarily a conscious process, it seems as if this mental anticipation comes close to implying some sort of conscious intention (e.g., Herwig & Waszak, 2009). It may be wondered, then, whether response effect learning could be taken as a mechanism underlying truly implicit knowledge. Below, we will propose that response effect learning occurs within the multidimensional module as depicted by Keele et al. (2003), which is the module supporting explicit learning.

Other forms of representation. Although most of the existing evidence of sequence learning can be classified along the dichotomy between stimulus- and response-dependent learning, this does not cover the whole range of possibilities. At least two more alternatives are discussed in the literature. Extensive support for these alternatives is currently absent (see Table 2), but that may be partly due to the relative complexity of exploring these accounts (especially at a behavioral level).

Response selection stage. One of the less discussed possibilities concerns learning at intermediate stages of information processing, such as the response selection stage: Can implicit sequence learning be represented by S–R rules? Initially, this idea was put forward by Willingham, Nissen, and Bullemer (1989), and some further support for it has been reported (even though Willingham and colleagues themselves abandoned the idea when it did not match with later findings; e.g., Willingham, 1999; Willingham et al., 2000). First, Schwarb and Schumacher (2009) found that spatial sequence learning relies on many of the same brain areas as spatial response selection. According to their interpretation, this would be in line with theories that localize sequence learning at the level of response selection processing. Second, sequence learning has been found to be better for spatially incompatible than for spatially compatible S–R mappings (Deroost & Soetens, 2006b; Koch, 2007). From the notion that incompatible mappings force more demanding response selection processes, this would fit with a response selection account.

However, although these results indicate a link between response selection and sequence learning, they do not provide direct support for the idea that implicit sequence learning is actually based on linking successive instances of S–R associations. For example, evidence that points directly to a role of response selection processes in implicit learning, such as a disruption of sequence learning when response outcomes (Hazeltine, 2002) or the S–R mappings (Schwarb & Schumacher, 2010) are changed, do not rule out response effect learning as the basis for performance. In addition, equally strong support has been reported against a response selection account of sequence learning.

Hoffmann and Koch (1997) demonstrated that manipulations of (nonspatial) S–R compatibility have no impact on sequence learning, and Kinder, Rolfs, and Kliegl (2008) showed that sequence learning occurs even under very high S–R compatible conditions (i.e., needing little response selection processing). Finally, results from Abrahamse (2010, chap. 7) suggest that it is perhaps explicit, but not implicit, sequence learning that benefits from incompatible S–R mappings. Accordingly, the advantage for the incompatible S–R mappings, as reported in Deroost and Soetens (2006b) and Koch (2007, Experiment 1), was not found in this study when a probabilistic sequence was employed, thereby hindering the development of explicit learning. Notably, Koch (2007) already speculated about the possibility that explicit learning modulated the effect of spatial S–R mappings, but he claimed that the sample sizes in his Experiment 1 "were probably too small to give meaningful results when the groups were post hoc classified into explicit and implicit learners" (p. 265).

Abstract conceptual learning. In some implicit-learning paradigms (e.g., abstract grammar learning; AGL) that seem related to the SRT task, abstract conceptual knowledge has been claimed to develop with training (e.g., Gomez, 1997; Gomez & Schvaneveldt, 1994; Knowlton & Squire, 1996; see also Francis, Schmidt, Carr, & Clegg, 2009). Abstract conceptual knowledge refers to knowledge that is independent of any surface information, such as stimulus or response features, but, rather, is related to some generally applicable rule. Although some abstract knowledge has been shown to generalize between different surfaces in AGL procedures, questions remain about whether learning and transfer of an underlying abstract structure is dependent on explicit memory retrieval (Gomez, 1997).

On the basis of the findings with AGL tasks, Dominey, Lelekov, Ventre-Dominey, and Jeannerod (1998) explored abstract sequence learning in the SRT task. They trained participants on a sequence with both predictable surface (i.e., the stimulus order) and abstract structure, half of them being kept naive as to the abstract structure (i.e., the implicit-learning group), and half of them receiving explicit information about the rule determining the abstract structure, as well as the instruction to use the rule (i.e., the explicit-learning group). Both groups showed sequence learning, but only the participants from the explicit group were able to transfer their knowledge to an isomorphic sequence (i.e., a different surface structure with the same underlying abstract rule). Two additional experiments in that study further supported this finding, and, overall, this study thus strongly indicates that abstract learning is conditional upon explicit processing and is not related to implicit learning.

A different conclusion, however, could be derived from a study by Goschke and Bolte (2007) in which a serial naming task was introduced. In this task, participants had to respond to pictures of objects simply by naming them. Whereas the individual objects were presented in a random order (thus implying a random order of the naming responses as well), the underlying semantic categories to which the objects belonged were structured. Participants learned this abstract sequence of categories, even in cases in which they showed no or little explicit knowledge of the structure on subsequent reproduction and recognition tests. This type of finding certainly raises the possibility that abstract learning may occur, but one may wonder to what extent the findings of Goschke and Bolte are generalizable to a standard SRT task.

Finally, a number of studies have investigated whether incidental sequence learning extends to sequences of tasks (and thus task sets). In these studies, participants were required to execute different choice tasks on a set of target stimuli, with the relevant task set for each trial indicated either by an instructional cue (e.g., Heuer, Schmidtke, & Kleinsorge, 2001; Koch, 2001) or by employing unique sets of stimuli for each task (e.g., Cock & Meier, 2007). It was observed that participants benefit from regularity in the order of task presentation, but the underlying mechanism is not yet commonly agreed upon. One possibility would be that people learn a conceptually driven order of task sets, such that, with practice, the next task set is preactivated on the basis of the previous trial(s) (e.g., Gotler, Meiran, & Tzelgov, 2003; Koch, 2001). Other authors, however, have attributed performance gains in a task sequence setting to mere perceptual learning on the basis of either the instructional cues (Heuer et al., 2001) or target stimulus percepts (Cock & Meier, 2007). Indeed, Cock and Meier observed no sequence learning in a condition that involved no instructional cues and in which regularity was available solely in the task order (and thus absent in the stimulus and response orders). So, we are inclined to conclude that the standard SRT task currently has witnessed no or little definite support for abstract conceptual learning.

To summarize the literature on the multiple single-level accounts, ample empirical support (see Table 2) exists for different types of associations underlying sequence learning in the SRT task—most notably, associations between successive stimulus features (perceptual learning), successive response features (response-based learning), and successive response-to-stimulus couplings (response effect learning). In contrast, the results are very sparse and somewhat contradictory concerning the involvement of either sequences of response-mapping decisions or abstract conceptual regularities (see also Table 2).

A Multilevel Approach

The idea of a distributed network of sequence-learning mechanisms is not new in the SRT literature. Most commonly, it has referred to different mechanisms for explicit and implicit sequence learning (e.g., Hazeltine, Grafton, & Ivry, 1997; Willingham & Goedert-Eschmann, 1999). Over the last decade, however, it has also been suggested occasionally that implicit sequence learning itself involves a distributed network of systems, although the precise qualification of the proposed levels varies considerably (e.g., Abrahamse et al., 2008; Bapi, Doya, & Harner, 2000; Clegg et al., 1998; Deroost & Soetens, 2006a, 2006c; Keele et al., 2003; Seger; 1997; Witt & Willingham, 2006). This suggestion matches the observation that various distinct brain areas are associated with implicit sequence learning and/or performance (for a review, see Hazeltine & Ivry, 2003; and see Schendan, Searl, Melrose, & Stern, 2003, for support of hippocampal involvement in addition).

Indeed, from examining the myriad of studies on the nature of sequence learning above, it seems apparent that a single-level account encompassing all observations from the sequence-learning literature has become increasingly unattainable. Although it is common and productive in cognitive science to take an oppositional view around a dichotomy of options (see Newell, 1973) with regard to the different forms of learning identified in the literature (and reviewed above), we propose here to integrate these forms into a multilevel account, rather than seeking to dismiss some. It is noteworthy that various models on related paradigms have paralleled such a move toward a multilevel configuration in order to capture the diverse, sometimes paradoxical findings, such as with category learning (Ashby & Casale, 2003), repetition priming (Race, Shanker, & Wagner, 2009), and discrete sequence learning (Verwey, 2003).

In depicting the nature of sequence learning in the SRT task, then, we need a framework that captures, beyond an explicit-learning component, the multilevel configuration of implicit learning. Various models across related paradigms, and varying substantially in their scope, seem to relate more or less to the issue (e.g., Ashby & Casale, 2003; Keele et al., 2003; Race et al., 2009; Verwey, 2003; Willingham, 1998). Two models that do so explicitly for sequence learning are the parallel processor model proposed by Verwey, and the dual-system model developed by Keele et al. (2003). The dual-system model has already been briefly discussed and will be further elaborated on below. Briefly, it assumes a multidimensional module that is sensitive to regularities both within and across different types of information (i.e., dimensions), and a set of unidimensional modules that are each specifically tuned to one particular type of information. In turn, the parallel processor model (Verwey, 2003) has been developed to model data obtained with relatively short and discrete keying sequences and comprises a general-purpose processor that works in different modes while using different inputs and several specialized single-purpose processors. Hence, on close inspection, these models share a main structure, with one system serving as an overarching processor, accompanied by a set of independent modules that are information specific. The correspondence between these models can be seen as converging evidence for the feasibility of such a processing architecture in sequence learning.

We will build upon the model depicted by Keele et al. (2003) in attempting to integrate the various forms of sequence learning present in the literature. This model was firmly grounded in the existing SRT literature, and it was developed to be plausible from a neurophysiological perspective. Regardless of this choice of framework, however, the core idea is that qualitatively different sequence representations can develop. We focus on the three forms that have received the most convincing support to date: perceptual (location) learning, response effect learning, and response location learning (see Table 2). As was stated above, these three forms can all be said to develop from associations within or between stages of information processing (e.g., Sanders, 1990, 1998; see Figure 1). Potential contributions to sequence learning at the level of response selection and at the level of abstract processing are not directly addressed.

The dual-system model. Keele et al. (2003) proposed a multidimensional and a unidimensional association system to be the representational base of complex sequential skills (see Table 3). The unidimensional system is composed of a set of modules that are each capable of associating within a single dimension, whereas the multidimensional system enables associations both within and across dimensions. Apart from this difference in associative abilities, the two systems differ in attentional requirements and the potential development of awareness. Learning within the unidimensional system is automatic, entirely implicit, and independent of attentional effort (i.e., unselective) because of its encapsulation. Sequence learning thus occurs for regularity present within any single dimension, even in the presence of uncorrelated (task-relevant) information within other dimensions. In contrast, the multidimensional system needs to be protected against these uncorrelated, noisy streams of information in order to do its job. This is achieved by making learning dependent on selective attention, so that the multidimensional system would associate only within and across attended dimensions. This

Table 3
Overview of the Main Characteristics of the Uni- and Multidimensional Systems of the Dual-System Model Proposed by Keele et al. (2003)

Unidimensional System	Multidimensional System
Dorsal stream (PC, SMA, MC)	Ventral stream (OC, MTC, ITC, IFC, DLPFC, PMC)
Uninterpreted stimuli	Categorized stimuli
Implicit	Implicit–explicit (the natural source of awareness)
Set of modules	Single module
Within dimensions and modalities (encapsulation)	Between dimensions or modalities
Unconditional access	Access to the system only for attended signals
Egocentric coding of locations	Allocentric coding of locations

Note—PC, parietal cortex; SMA, supplementary motor area; MC, motor cortex; OC, occipital cortex; MTC, medial temporal cortex; ITC, inferior temporal cortex; IFC, inferior frontal cortex; DLPFC, dorsolateral prefrontal cortex; PMC, premotor cortex.

makes this system the natural origin of explicit sequence knowledge: Learning that starts accruing implicitly in that system could end up becoming explicit when attentional processing gets focused on the structured relations.

These two systems combine into a powerful sequence-learning device. However, we believe that the model has not evolved to its full potential since its publication. From the more than 100 citations that the Keele et al. (2003) article received up to the writing of this article, it becomes clear that its role is limited mostly to providing either a post hoc framework from which to interpret particular observations or even merely a general background overview. Obviously, some studies have provided support for or against certain claims that were made by Keele et al. (2003). For instance, confirmation of involvement of the hippocampal system in implicit sequence learning (e.g., Ergorul & Eichenbaum, 2006; Schendan et al., 2003) strengthens the dual-system model's account of a possible congruency between the hippocampal structures of the brain and the hypothesized multidimensional system (both are said to underlie cross-dimensional associations). In contrast, studies by Liu, Lungu, Waechter, Willingham, and Ashe (2007) and Witt, Ashe, and Willingham (2008) provided evidence against the model's prediction that coding of locations in the ventral system should take place in an allocentric space (see also Willingham, 1998). Below, we will attempt to account for such a discrepancy in terms of task set.

Despite these individual counterexamples, the point remains that the dual-system model has rarely been the subject of investigation itself; the possible predictions that come from it have not been put to the test. Perhaps one reason for this is related to the lack of detailed specification of the workings of the model's main features. For instance, regarding the relation between attentional processes and sequence learning, a clear strength of Keele et al.'s (2003) dual-system model was in shifting the emphasis away from resource-based (i.e., processing limitation) accounts to selective attention (see also Jiménez & Méndez, 1999; Jiménez & Vázquez, 2005), even though the two may be inextricably linked to each other (e.g., Lavie, 1995; Lavie & Tsal, 1994). However, in claiming that only the multidimensional system is dependent on selective attention, the model seems to let the workings of the unidimensional system somewhat underspecified, implying the rather bold assumption that learning in this system will not be restricted in any way and, hence, that it will unselectively associate all predictive information contained within a single dimension. Below, we will discuss two studies that seem to contradict such a strong claim.

Another, more central problem that surely has deterred progress in exploring this model has to do with the rather abstract description of the concept of a dimension, which lies at the core of the distinction between unidimensional and multidimensional modules. As was stated above, this creates a gap between the various forms of sequence learning empirically explored in the literature and the specific predictions of the model. However, given that Keele et al. (2003) actually provided some clear hints concerning the interpretation of their concept of a dimension, the gap may not be theoretical in nature but, rather, may arise just because the relationship between the framework and the various forms of sequence learning that have been studied to date has not yet been made explicit. In the next sections of this article, we will offer a way to bridge this gap and will discuss further implications.

Synthesis. A possible strength of the Keele et al. (2003) dual-system model for sequence learning is that it provides a framework for integrating the multiple forms of sequence learning, for which strong empirical support exists across the literature, by mapping these onto its two systems. However, due to the abstract nature of the model, this mapping has not yet been clearly identified. Here, we propose that this mapping can be made explicit by defining dimensions mainly in terms of stimulus and response features: A dimension in the dual-system model is here regarded as equivalent to a specific type of feature, either at the stimulus level (e.g., shape) or at the response level (e.g., response location).[6]

On a trial-by-trial basis, performing the SRT task initially involves the same three basic information-processing stages as a typical (four-)choice RT task: stimulus encoding, response selection, and response execution (e.g., Donders, 1969; Sanders, 1990, 1998; Sternberg, 1969). However, due to the sequential regularity presented across trials in the SRT task, something extra happens over practice that enables participants to speed up performance through associative learning: A sequence representation is formed on the basis of the fixed order of events. The benefit taken from this memory representation becomes clear if, after some amount of practice, the sequential structure is removed from the task and RTs and error percentages increase. As we have seen above, the sequence representation may be based on various specific features or combinations of features available across processing stages (see Figure 1).

The two systems of the Keele et al. (2003) model may thus be interpreted as *associative learning systems that associate between (mainly the most) active feature representations from ongoing S–R processing stages, thereby enabling the facilitation of future action*. In doing so, the model more or less automatically generates the three main forms of sequence learning discussed above (i.e., S–S, R–R, and R–S associations), thereby providing an integrative perspective on these. Obviously, the focus of each of the unidimensional modules is restricted to a single feature type, whereas the multidimensional system can (temporarily) associate various feature types with the aid of some central maintenance system.

It has to be noted that this interpretation of the two systems is not so far removed from that hinted at by Keele et al. (2003) themselves: "In the SRT task, the term dimension has generally been used interchangeably with modality, and we maintain this convention. However, stimulus attributes within a modality can also constitute relevant dimensions for sequence learning. . . . Moreover, distinctions within the motor system (e.g., hands vs. feet) may also constitute dimensions" (p. 317). Indeed, by refining the definition of the concept of a dimension as referring to a type of feature from ongoing S–R processing stages, rather than to overall modalities (e.g., visual, auditory, etc.), the model becomes more directly relatable to a large literature on the nature of sequence learning. Making explicit the coupling between the concept of a dimension, on the one hand, and the various stimulus and response features claimed to be involved in sequence learning, on the other hand, enhances the dual-system model as a predictive model for future research and inspires new ways of thinking about sequence learning in general.

The multidimensional system. By defining the concept of a dimension as referring to a type of stimulus or response feature, the multidimensional system is allotted the capability of associating between (1) successive instances of one particular type of stimulus or response feature (e.g., shape-to-shape or location-to-location associations), (2) successive instances of either different types of stimulus features or different types of response features (e.g., associations between shape and location, such as in Jiménez & Méndez, 1999), (3) successive instances across types of stimulus and response features (e.g., response effect learning), and (4) successive instances of rich feature compounds such as whole objects. Whereas the former of these alternatives is shared with the unidimensional system (see below), the latter three are exclusively assigned to the multidimensional system, since they imply associating across different types of features.

As has already been noted by Keele et al. (2003), Jiménez and Méndez (1999) provided evidence in support of the notion that associating between stimulus features of a different kind is restricted to the attention-dependent multidimensional system. Specifically, they observed, for all participants, sequence learning on a primary task—responding to the locations of stimuli. However, at the same time, a sequential contingency was built between the shape of each stimulus and the next stimulus location (thus, across stimulus features). This contingency was learned only when participants needed to pay attention to the shape feature through a secondary counting task; hence, learning the sequential associations between different features of a series of stimuli was conditional upon attentional selection. This can nicely be interpreted from a perspective that relates the concept of a dimension to specific features within stimulus or response modalities, rather than to overall modalities.

Even though, to our best knowledge, it has never been directly explored, the reconceptualization of the dual-system model suggested here has similar implications for response effect learning. Response effect learning refers to the formation of sequence representations that are built from cross-dimensional compounds of features from a response and a subsequent stimulus. Such learning would be restricted to the multidimensional system, implying that these sequence representations would be accessible for conscious processing and conditional upon attentional processing. Some indirect support for the close relationship between awareness and response effect learning is provided by the observations (1) that studies supporting response effect learning typically report relatively high overall awareness scores (e.g., Ziessler & Nattkemper, 2001) and (2) that groups of participants that benefit from response effect learning consistently demonstrate higher levels of awareness than do those that could not (e.g., Hoffmann et al., 2001; Stöcker et al., 2003), although not always significantly so (the latter may be partly due to a lack of sensitive and process-pure awareness tests; see Destrebecqz & Cleeremans, 2001; Shanks & St. John, 1994).

Zirngibl and Koch (2002) reported further results congruent with a relationship between response effect sequence learning and awareness. They found that sequence learning in an SRT task was facilitated for verbal responses, as compared with manual ones. The authors suggested that this difference in sequence learning could be traced back to differences in the distinctiveness and salience of the naturally occurring response feedback (i.e., response effects). Importantly, this difference in sequence learning was not found in those participants who showed a significant behavioral learning effect but no explicit knowledge. This indicates that implicit learning could not be substantially boosted by the more salient response effects that are arguably provided by verbal responding.

Finally, support for the notion that response effect learning does not arise in the absence of attentional processing stems from a study by Deroost, Zeischka, and Soetens (2008). They had participants respond to the location of a red circle while, on each trial, a task-irrelevant blue circle was simultaneously presented at a different location. Independently of each other, the locations of both the relevant and the irrelevant circles were structured by a fixed sequential order. In line with earlier findings (Cock, Berry, & Buchner, 2002), participants acquired sequence knowledge even about the irrelevant sequence of blue circles, as witnessed by a so-called negative-priming effect: Performance was impaired (relative to performance on randomly structured trials) when the sequence of the task-irrelevant circle was imposed on the target circle in a test phase. Interestingly, however, the amount of negative priming obtained under these conditions was equivalent regardless of whether or not the two sequences were synchronized (i.e., running in phase because of equal sequence length). This implies that the overall configuration formed by the red and the blue circles was not bound with the previous response to form a response effect association, arguably because such response effect associations entail different dimensions (i.e., feature types) and, thus, involve only information that is selectively attended (i.e., the target circle).

Overall, there is at least indirect evidence consistent with the notion that response effect learning is restricted to the multidimensional system and, thus, tightly coupled to attentional processing and conscious accessibility. In terms of mapping the multidimensional system onto the ventral processing pathway (Keele et al., 2003), it could be predicted that disruption (e.g., by using transcranial magnetic stimulation) of ventral (and not dorsal) stream processing would impair response effect learning. This type of prediction arises only from an integration of the more abstract dual-system model with the types of representation discussed within the empirical work in the sequence-learning field. Although the veracity of this particular prediction remains one for future research, the general point remains that such testable predictions become more readily available from connecting the dual-system model with the specific processes implicated in sequence learning.

The unidimensional system. In the dual-system model of Keele et al. (2003), the encapsulated modules are proposed to take up automatically on those regularities occurring within a single dimension. From the notion that dimensions, as typified by Keele et al. (2003), can be translated into specific types of stimulus or response features, associations in these modules would arise between successive tokens of a given type of stimulus or response feature. It has been suggested that color (and sometimes also shape) information might often be outweighed by spatial information in the dorsal processing stream (e.g., Glover, 2004; Milner & Goodale, 2008; Ungerleider & Mishkin, 1982). So, it is possible that the dorsal, unidimensional system for sequence learning could be predominantly focused on associating between spatial feature types, such as location (cf. Koch & Hoffmann, 2000).

Keele et al. (2003) regarded the functioning of the unidimensional system as fully automatic and unselective, with associations forming regardless of attention. However, true automaticity has been hard to find within human information processing. For instance, even the Stroop interference effect, viewed for a long time as the gold standard of automaticity, has been shown to be reduced or eliminated under some conditions (e.g., Tzelgov, Henik, & Berger, 1992). In this respect, Deroost and colleagues (e.g., Deroost & Soetens, 2006a; Deroost et al., 2008) have recently provided some interesting findings with respect to how unidimensional sequence learning could depend on the fulfillment of certain constraints. We will here briefly discuss these findings because of their strong relevance to the dual-system model.

As was noted above, Deroost et al. (2008) observed negative priming when a sequence of locations of a task-irrelevant stimulus (presented simultaneously with the imperative stimulus during training) was later imposed on the locations of the imperative stimulus in a test phase (i.e., participants were now responding to a sequence of stimuli they were previously to ignore). However, no such negative priming was observed when the imperative stimuli were presented in random order during training (and thus no response sequence could be learned). This is a complicated set of findings, especially when considering the proposed automaticity and unselectivity of the unidimensional system: Why was the task-irrelevant, unidimensional regularity not detected and utilized by a unidimensional module when no response sequence was being learned?

One may argue that one particular unidimensional module is tuned to stimulus location information overall, regarding both the relevant and irrelevant location information, and thus unable to detect regularity in the irrelevant information when it is interspersed by random information from the relevant stimulus (rendering the pattern as a whole to be irregular). However, Deroost et al. (2008) themselves provided evidence against this account: In their Experiment 2, the authors found that a similar amount of negative priming occurred independently of the synchronization (i.e., running in phase or not) between the relevant and irrelevant sequences, whereas out-of-sync relevant and irrelevant sequences also produce an irregular overall sequence of stimulus locations. Hence, in the design of Deroost et al. (2008), the relevant and irrelevant stimuli seem to provide independent, unidimensional sequential structures to be learned, and not one overall unidimensional sequence of (combined relevant and irrelevant) stimulus locations. Then, how to explain the absence of learning of the irrelevant, single dimension in a unidimensional module when the imperative stimuli were presented in random order?

Deroost et al. (2008) provided an answer to this question. They explained their findings in terms of attentional processing: Responding to predictable stimuli may have released attentional capacity that could be used to process the task-irrelevant sequence (in line with the Lavie model of selective attention; Lavie, 1995; Lavie & Tsal, 1994). Such a dependence on attentional processing is a characteristic assigned to the multidimensional system, and this explanation therefore implies that the irrelevant, unidimensional sequence was not learned within the unidimensional system, thus opposing true unselectivity of the latter system.

Further results that reinforce this suspicion were provided by Deroost and Soetens (2006a). They replicated the study of Mayr (1996), in which participants showed learning of a sequence of task-irrelevant stimulus locations when responding to a different dimension of the stimuli (e.g., color). Interestingly, and in strong analogy with the study by Deroost et al. (2008), learning about the sequence of task-irrelevant locations occurred only when the imperative stimuli were also sequentially structured. Again, this could well be explained by released attentional capacity due to the fixed sequence of task-relevant stimuli (see Deroost et al., 2008). However, from the dual-system model outlined by Keele et al. (2003), one would have expected the unidimensional system to automatically pick up on the fixed series of (task-irrelevant) locations. Clearly, this was not the case, once more suggesting that learning of task-irrelevant information does not occur within the unidimensional system, even when it involves just a single dimension.

Overall, the findings by Deroost and colleagues (Deroost & Soetens, 2006a; Deroost et al., 2008) at the very least indicate that learning in the unidimentional system does not arise immediately from any interaction with a structured environment and, thus, highlight the importance of assessing the conditions that constrain sequence learning about unidimensional relations. A possible way to approach this issue might be to restrict the unidimensional system, as described by Keele et al. (2003), to information that is strongly action related, which would be in line with the view that the dorsal processing route is mainly involved in online action control (e.g., Glover, 2004). Learning about task-irrelevant regularity, then, would be confined to the multidimensional system and, thus, would be dependent on attentional processing. However, further exploration and contemplation is needed in order to justify such a strong claim.

Determinants of Learning: Task Set

From the notion that qualitatively different sequence representations can develop in the SRT task, an important question arises on what precisely determines the effective nature of the sequence representation in a specific condition. It seems clear that not all the different kinds of learning depicted in the literature (i.e., perceptual, response effect, and response location learning) always develop in parallel: Many examples are known of studies in which the sequential order of at least one of these three levels is maintained over a transfer test but, nevertheless, no reliable transfer is observed (e.g., Abrahamse, 2010, chap. 7; Jiménez et al., 2006; Willingham et al., 2000). Hence, instead of developing multiple sequence representations in parallel, as predicted by Keele et al.'s (2003) unidimensional system, the brain typically tailors a specific sequence representation to the task at hand (cf. Memelink & Hommel, 2006). This may be individually determined—for example, on the basis of visuo–spatial ability or personality variables such as "openness to feelings" (a subscale of the NEO-PI-R personality inventory; see Norman, Price, Duff, & Mentzoni, 2007). However, probably more relevant in accounting for the equivocal findings across the literature is the concept of task set: The precise representation that is ultimately formed may depend mainly on the regularity that is present in events that are part of the task set.

Task set can be loosely defined as the set of cognitive processes that are actively maintained during task performance (e.g., Sakai, 2008) and that include both the overall processing goal and a more detailed specification of relevant stimulus features, response features, and their mapping (e.g., Monsell, 2003). These internal control settings are important because, in our interaction with the environment, one (path of) action typically has to be selected from multiple alternatives. Although, to the best of our knowledge, the concept of task set has not been used explicitly to account for differences in sequence-learning results, the prediction that task set should constrain sequence learning arises directly from the view of implicit learning as an obligatory result of active processing (e.g., Jiménez & Méndez, 1999; Logan, Taylor, & Etherton, 1996). If, as Logan et al. put it, "people will learn what they attend to and express what they learned in transfer if they attend to the same things in the same way" (p. 620), then probably it would simply not be accurate to ask what is learned in a sequence-learning paradigm, but rather, we should ask how the acquisition and the expression of sequence learning are affected by the specific processing priorities stressed by a given task set.

The notion that the current task set is important for the precise development of sequence learning is already implied by the crucial role of selective attention in sequence learning, as discussed above (e.g., Jiménez & Méndez, 1999), since selective attention may be seen as a direct consequence of a particular task set. We here discuss a number of studies that further illustrate the importance of task set in determining implicit sequence-learning effects.

In a study by Koch and Hoffmann (2000), the use of spatial and symbolic information was systematically varied for both the stimulus and the response set. It was observed that perceptual and response-based learning can develop in parallel but that the development of each is heavily dependent on the availability of spatial information to be learned. In other words, perceptual learning was observed mainly as stimuli were presented across different locations, whereas response-based learning was observed mainly when stimuli were mapped onto multiple response locations.

Another example of the importance of spatial processing as part of the task set in sequence learning was provided in a study by Deroost and Soetens (2006c). As was noted above, they explored the influence of processing spatial information on implicit sequence learning in an adapted version of the SRT task. In their study, responses were based on the identity of stimuli, and the stimuli were presented at a fixed sequence of task-irrelevant locations. Responses to the target could depend either on a single feature of the target (i.e., its color) or on the spatial relation between two of its features (i.e., "xo" vs. "ox"). Learning about the task-irrelevant sequence of locations was observed in the latter case, when the task-relevant information required spatial processing, but not in the former one, when the response was determined independently of any spatial feature. These results suggest that spatial processing of relevant information sets the stage for learning about regularity across spatial features of the stimuli.

A similar line of reasoning may apply to the directional features of movement. In a study by Richard et al. (2009), participants performed a standard four-choice SRT task with either one or four fingers. A simple pattern of alternating directions (right–left–right, etc.) was embedded in the stimuli, whereas the precise stimulus and response locations were not predictable. Implicit learning of this pattern of directions was observed only for the group of participants that used one finger across all possible response locations, whereas the group using four fingers—one for each response location—did not show such learning. This may very well be explained by assuming that the direction of the stimulus was much more important for task execution for the one-finger group than for the four-fingers group, since the former needed to move around their finger on the basis of this direction, whereas the latter group could simply rest their fingers on the four response buttons.

Another pattern of results that might be reinterpreted in terms of specific task demands is that reported in Willingham et al. (2000, Experiment 1). In this study, the authors failed to obtain transfer between different response location configurations, even though the stimulus sequence on the screen remained unchanged over the transfer phase. Given that there is now ample evidence in favor of the existence of a perceptual component in sequence learning and that the large number of participants tested precluded any power concerns, one may wonder why perceptual-learning effects did not arise under the particular conditions in their study. Again, the specific task set established in this experiment could provide us with a useful approach to this question. When participants are told to respond using a set of neatly defined response locations on a fixed keyboard, and when they are instructed to use only one finger to act on all of these response locations, task demands could be taken to strongly emphasize the processing of the response locations (simply because the task requires moving the finger between these response locations), hence rendering a representation of the sequence in terms of the series of response locations to be most effective.

But what could be expected if the task did not have such well-defined response locations, such as when it required keeping track of a moving target with a mouse cursor (Chambaron, Ginhac, Ferrel-Chapus, & Perruchet, 2006) or, even more realistically, responding with a racquet, as in playing a game of tennis? Would procedural learning in these tasks also be based on representing a sequence of response locations? There is no need to say that this would render the underlying skill extremely rigid and dysfunctional. One may even wonder whether the dominance of response locations in the study by Willingham et al. (2000) could already be changed after a small change in task set, such as performing the SRT task with four fingers (one for each response button), instead of one, during practice. In this case, the task of executing a response no longer strongly emphasizes the programming of a movement to a specific response location, because the fingers are already in place. We surmise that, in such a design, reliable transfer could be observed over changes of specific response locations, at least when the spatial S–R compatibility is not radically altered between training and transfer, as it was in Willingham et al. (2000, Experiment 2).

Focusing on the impact of the task set could also be useful in explaining why, under some conditions, one can fail to obtain evidence for an allocentric representation of a sequence, despite the fact that allocentric coding has been proposed as the default representation mode for the multidimensional learning system (cf. COBALT; Willingham, 1998). Witt et al. (2008) and Liu et al. (2007) reported this failure to find evidence for an allocentric representation of a sequence in conditions in which participants were instructed to use a single effector (either a single finger or a mouse cursor) to act upon all response locations. Here again, we surmise that this task set emphasizes the coding of response locations, thereby reinforcing learning about that aspect of the task. Obviously, for such a task set, an egocentric reference frame is the most useful, since, otherwise, a translation from allocentric to egocentric codes would be needed to effectively act upon these locations. It would be interesting to see whether allocentric coding can be observed when participants learn about a sequence of stimulus locations in conditions in which these locations do not coincide with the response locations. For example, in the spatial sequence-learning designs employed by Mayr (1996) and Deroost and Soetens (2006a), where participants responded to the color of a stimulus appearing on each trial at one of a predictable series of locations, it is an open question whether the spatial sequence would be learned within an allocentric or an egocentric frame of reference.

Finally, precise task characteristics and the type(s) of processing that they stress may be an important predictor of the amount of sequence awareness that develops with practice. For example, as was noted above, Destrebecqz and Cleeremans (2001) showed that the development of explicit knowledge can be (partly) controlled by manipulating the length of the RSI. Furthermore, whereas Deroost and Soetens (2006b) and Koch (2007) observed that learning of deterministic sequences benefits from employing incompatible S–R mappings, Abrahamse (2010, chap. 7) showed that such a benefit is absent when using probabilistic sequences (which are known to hinder the development of explicit knowledge). Abrahamse (2010, chap. 7) reasoned that the use of incompatible S–R mappings stimulates the development of explicit learning through more demanding S–R processing. These types of finding motivate a more direct exploration of the task characteristics that modulate the development of sequence awareness.

In sum, there is growing evidence that sequence learning in the SRT task may be highly sensitive even to seemingly trivial task parameters, such as the response effectors used, the response-to-stimulus interval (see Destrebecqz & Cleeremans, 2001), and spatial processing of task-relevant information. Acknowledging this may be important in order to deal with the frequently observed equivocal or even conflicting findings in the literature. To finish this section, it is worthwhile noting that, just as the training conditions may affect what is learned in a sequence-learning task, the conditions in which learning is tested may also determine how learning is expressed during a transfer phase. Again, by relying on Logan et al.'s (1996) quote, people not only learn what they are effectively processing for the task at hand, but they also "express what they learned in transfer if they attend to the same things in the same way" (p. 620). This implies that in addition to comparing the amount of sequence learning obtained in a training procedure, it is important to assess the impact of manipulating certain parameters over a transfer task on the expression of the previously acquired knowledge.

CONCLUSION

The ability to represent sequential order in various ways is in line with the notion that sequential behavior is fundamental to human functioning and is supported by both neuropsychological and behavioral findings. In the present article, we have presented a review of the various themes and challenges that relate to the representational base of sequence learning. First, we discussed some of the major issues with respect to the topic of sequence awareness. Second, and more important, we provided an assessment of the type of associations underlying implicit sequence learning in the SRT task, which showed that strong empirical support exists for the formation of associations between successive stimulus features (perceptual learning), successive response features (response-based learning), and successive response-to-stimulus compounds (response effect learning). We propose that the strong oppositional thinking, usually between response-based and perceptual learning, should be replaced by a more dynamic, integrative approach that takes into consideration how the task set and task context modulate the acquisition and the expression of sequence learning. According to what may be called an overall principle of activation, we assume that the associations that underlie sequence learning are not predetermined with respect to one particular type of information but, rather, develop from the most active representations from ongoing S–R processing. Moreover, a similar role for task set and task context could be reserved for the development of awareness. Hence, the representations that are most relevant (and thus most active) for current purposes (on the basis of task set and/or task context) ultimately determine the nature of sequence learning.

Substantiating an integrative approach with respect to the different types of learning that have been proposed across the literature can be achieved by a synthesis with the dual-system model as depicted by Keele et al. (2003). This has mutual benefits. First, integration of existing, smaller scale forms of sequence learning is provided by a well-known multilevel model, the development of which is firmly grounded in major SRT studies. Second, the proposed reframing directly links the dual-system model to recent findings on sequence learning as obtained in the SRT task, thereby introducing new questions and predictions and enhancing the overall testability of the model. However, it must also be noted that the present review modifies the initial framing of the unidimensional system as fully automatic and unselective: As was noted above, we believe that some preliminary support has been reported for the notion that even the unidimensional system is restricted by the current task set.

Crucially, a multilevel approach shifts the emphasis from the old question "what is the nature of sequence learning?" to a whole new set of questions concerning what precisely determines the nature of sequence learning and its dynamics. Future research faces the challenge of trying to understand and classify the rules of this complex dynamics.

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NOTES

1. A notable indication that implicit learning should be distinguished from its explicit counterpart is the observation that implicit learning is spared in amnesic patients (e.g., Knowlton & Squire, 1996; Vandenberghe, Schmidt, Fery, & Cleeremans, 2006).

2. For pragmatic purposes, Seger (1994) added as a third criterion for implicit learning that it necessarily involves "information that is more complex than a single simple association or frequency count" (p. 164).

3. Sometimes, the stimulus feature on which regularity (i.e., sequential order) is imposed differs from the stimulus feature that is to be responded to.

4. Related studies employed instructions in which participants were required to respond only to the stimulus appearing at one particular location, and not other locations (e.g., Berger et al., 2005; Vakil, Kahan, Huberman, & Osimani, 2000). This revealed results similar to those in studies in which no responding was required at all: Sequence learning takes place independently of responding.

5. In this unpublished study, no transfer was observed from a compatible to an incompatible stimulus-to-response mapping, even though the response (location) sequence was maintained. In line with the study by Willingham (1999), however, reliable transfer was observed the other way around.

6. Within the paradigm of laboratory experiments in cognitive psychology, it has become common practice to refer to clearly distinguishable stimulus characteristics such as shape, color, and stimulus location and to response characteristics such as response location and effector used. Here, we choose to adhere to this practice. For present purposes, then, an example of a "type of feature" may be color or effector, whereas red and index finger may be considered examples of specific features.

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