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The Cognitive and Neural Architecture of Sequence Representation

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The authors theorize that 2 neurocognitive sequence-learning systems can be distinguished in serial reaction time experiments, one dorsal (parietal and supplementary motor cortex) and the other ventral (temporal and lateral prefrontal cortex). Dorsal system learning is implicit and associates noncategorized stimuli within dimensional modules. Ventral system learning can be implicit or explicit. It also allows associating events across dimensions and therefore is the basis of cross-task integration or interference, depending on degree of cross-task correlation of signals. Accordingly, lack of correlation rather than limited capacity is responsible for dual-task effects on learning. The theory is relevant to issues of attentional effects on learning; the representational basis of complex, sequential skills; hippocampal- versus basal ganglia-based learning; procedural versus declarative memory; and implicit versus explicit memory.

The ability to produce and learn sequential actions is one of the hallmarks of human cognition. Indeed, this ability has been hypothesized to constitute a fundamental adaptation that characterizes what makes human cognition so extraordinary (Corballis, 1991). Sequential representation in human memory is responsible for the production and perception of phonemes that compose words, for the production and perception of musical notes, and for a myriad of other human skills based on the varied sequential ordering of small numbers of elements.

In this article, we present a theory of sequential representation extracted from both behavioral and neural analyses of sequencing. We propose that the human brain supports two broad systems of sequence learning. These systems are based on different neural pathways extending from posterior to frontal cortex and can operate in parallel when circumstances allow. The systems differ in their attentional requirements, their access to awareness, and in the form with which they represent sequential knowledge.

The ubiquity and ease with which humans learn and perform sequential actions have motivated researchers to seek model tasks to analyze such behavior. Our theoretical work draws primarily on such a model task, serial reaction time (SRT). In this task, participants respond as quickly as possible to signals of various types, such as auditory tones or visual locations. Reaction times (RTs) are compared between conditions in which the signals occur in a predictable, repeating sequence (hereafter simply called *sequence*) and in which they occur in a random order. A difference between the two conditions emerges with practice and provides an index of learning (Nissen & Bullemer, 1987; see Bahrick, Noble, & Fitts, 1954, for a related, pioneering study). It is important to note that this RT difference index allows the assessment of learning under circumstances in which subjects may be unaware that the signals occur in a repeating sequence. Given the relative simplicity of the task, combined with a performance-based measure of learning, the SRT task has proven an important tool for research in studies involving neurological populations (e.g., Curran, 1997; Knopman

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This article synthesizes ideas that have grown out of several years of studies from our different laboratories. Despite the different laboratory origins, the studies shared a remarkably similar methodology, allowing the synthesis. We are grateful for the collaborative work, insights, and comments provided by Michael Anderson, Ben Clegg, Asher Cohen, Tim Curran, Scott Grafton, Thomas Goschke, Laura Helmuth, Arthur Reber, and Volker Schmidtke. Scott Grafton also was instrumental in supplying additional PET analyses regarding awareness of learning.

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& Nissen, 1991; Nissen, Willingham, & Hartman, 1989; Reber & Squire, 1994; Willingham & Koroshetz, 1993), normal subjects under the influence of drugs (Nissen, Knopman, & Schacter, 1987), neuroimaging techniques (e.g., Grafton, Hazeltine, & Ivry, 1995), and conditions in which attention is distracted by the inclusion of a secondary task (e.g., A. Cohen, Ivry, & Keele, 1990). This literature forms the basis of our theory. Although our use of other sequencing tasks, such as artificial grammar tasks, has been more limited, we draw on this literature and the analysis of natural sequential behaviors (e.g., speech) when it is relevant to the theoretical issues we raise.

We begin by presenting our theory in a nutshell. Then we present the empirical evidence behind it. In the Discussion section we draw comparisons with other theories and examine some implications of the theory.

Core Tenets of the Model

Our core assumption is that the representation of sequential regularities is dealt with by two distinct learning systems. One system, which we call *multidimensional*, builds associations between events from different dimensions or modalities. The cross-dimensional property greatly enhances context and facilitates the learning of relatively complex sequences. For example, intonation, temporal pauses, or visual–manual gesture may help segment phonemes into words, facilitating the learning of phoneme strings.

The second system, which we call *unidimensional*, is composed of a set of modules, with the input to each module restricted to information along a single dimension. This encapsulation allows the independent learning of predictable series of events within individual dimensions even when concurrent dimensions lack correlation with one another. For example, when driving a car on a familiar route while listening to the radio, one is able to make sense out of two independent streams of at least partly regular, sequential information: visual–spatial information related to maneuvering the car and auditory information from the radio.

The issue of what constitutes a dimension is contentious and is reminiscent of an older issue in psychology about whether dimensions are separable or integral (e.g., Garner & Felfoldy, 1970). 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, similar to the way in which visual attention studies have described fundamental dimensions for perception (e.g., Treisman, 1988). Moreover, distinctions within the motor system (e.g., hands vs. feet) may also constitute dimensions. We expect that similar principles will apply across these various situations. The dimensions examined for present purposes, however, are ones that most would recognize as distinct. Associations within the multidimensional system involve integration across shapes and spatial position, across shape and auditory frequency, and across visual-spatial positions and auditory dimensions such as pitch. Despite uncertainties regarding the term *dimension*, the present endeavor establishes a viable framework for analysis, including the delineation of experimental methodologies (e.g., assessment of multidimensional learning via phase-shift probes), which may prove useful for dimensional specification. Later, in the section on system differences in representational code, we consider that the two systems differ in terms of their dimensional codes, the unidimensional system associating relatively uninterpreted stimuli and the multidimensional system associating categorized stimuli.

One important distinction between the two systems is based on their hypothesized attentional requirements. The unidimensional modules are not susceptible to potentially disruptive information from other dimensions because they form associations only among events that occur along a single dimension. The formation of the associations within these encapsulated modules should be automatic, even when information along other dimensions is relevant for the task at hand.

Learning within the multidimensional system also occurs automatically. Similar to classical conditioning, associations are formed when a signal in one dimension reliably predicts an immediately following event in either the same or another dimension. A lack of reliable prediction prevents association. Real-life settings typically involve simultaneous, uncorrelated modalities of stimulation—for instance, as one walks down the street talking with a friend, one also may hear the songs of a bird, the sounds of traffic, and other voices in the background as well as see a variety of sights. Such uncorrelated streams of events might render the multidimensional system helpless, making us unable to understand the friend. In our model, the operation of the multidimensional system is protected by an attentional constraint. Only signals specified as relevant by the current task sets—that is, attended signals—gain entry to the multidimensional associative system. If this information includes correlated events, associations will be formed even in the presence of random but unattended events. However, if the random events are also attended, as in a dual-task situation, the secondary-task events will disrupt learning.

An important point to emphasize here is that under this hypothesis, a secondary task interferes with cross-dimensional learning not because it taxes limited resources or causes distraction, but because it disrupts coherence between successive events. Should events in an attended secondary task predict intertwined events in another attended dimension, even though relevant to a different task, automatic association occurs. A novel aspect of our theory, therefore, is that attention plays a critical role in the selection of task-relevant information rather than via capacity limitations. This selection process is hypothesized to be relevant only for the multidimensional system. Each unidimensional module automatically extracts regularities in its input.

The assumption that the multidimensional system operates on categorized stimuli, rather than uninterpreted stimuli, is essentially a corollary of the task-relevance selection constraint. Task relevance is based on instruction of what to select (e.g., letters or digits), and is an inherently categorical procedure.

Related to these hypotheses concerning attention, our theory offers a new perspective on the distinction between explicit and implicit learning. Because the unidimensional system operates outside attention, learning here is entirely implicit. Learning is also hypothesized to occur implicitly within the multidimensional system in the sense that its associative mechanism will automatically operate on those signals that gain entry to the system. However, because such events are attended, they are accessible to processes underlying awareness and thus these representations can become explicit. It is important to note that the multidimensional system can support the formation of associations between events from a single dimension when there is no additional task-relevant information to disrupt associations. As with cross-dimensional learning, we would attribute any emergence of awareness of single-dimension sequences to the operation of the multidimensional system. Thus, our critical distinction is between two systems with different computational capability—cross-dimensional association or not—rather than between implicit and explicit systems.

Although both systems operate on similar association principles, the cross-dimensional capability of the multidimensional system may greatly enhance the learning of sequences with inherent ambiguity. An example of this would be when within-dimension relationships vary as a function of their position within the sequence. Of course, this is a fundamental problem in learning such things as the order of phonemes in words. In such a case, a second dimension that correlates with position, providing context, might serve to segment and make less ambiguous subsequences composed from the first dimension.

When considered together, the two systems provide the basis for a powerful sequence-learning device. Each unidimensional module is able to extract regularities along a single dimension even when information on other dimensions is not predictive. However, when reliable cross-dimensional contingencies are available, a second, parallel system can extract these correlations as long as both dimensions are attended.

In the next section, we review evidence suggesting that these two systems are dissociable from one another. Our review draws on both behavioral and neurological evidence.

Evidence for Two Sequence-Representation Systems

The empirical cornerstones that imply two dissociable systems for sequence learning are provided by three SRT experiments. In this section, we review two of these, one behavioral and one involving positron emission tomography (PET) scanning; we supplement this discussion with reference to related imaging and patient studies. The third cornerstone study provides critical evidence regarding the unidimensional versus multidimensional character of the two learning systems. We turn to a review of this study in a subsequent section.

Initial Behavioral Evidence for Two Systems

Curran and Keele (1993) provided initial evidence for dissociable systems. On each trial in their study, a stimulus appeared at one of four visual positions and the participants responded on one of four keys, aligned in correspondence with the stimulus positions. Figure 1 shows the learning functions for three groups of subjects. One group was explicitly told that the four spatial positions of the stimuli would follow a repeating six-element sequence, and the sequence was described. The other subjects were presented with the same sequence, but they were not informed of its presence. As determined by postexperiment assays, some uninformed subjects became aware of the sequence on their own, whereas others demonstrated minimal or no awareness. RTs became shorter, with practice, for all three groups, although the improvement was less marked for the unaware subjects. When the event order was randomized on a probe block of trials, RT increased for all subjects, especially for the aware groups, indicating the magnitude of sequence learning associated with awareness.

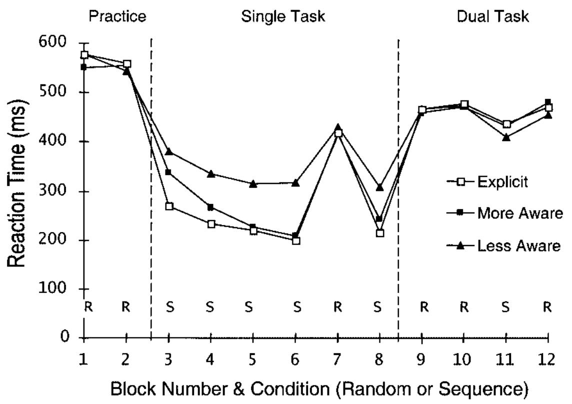

Figure 1. Reaction time as a function of number of blocks of practice. Blocks 1 and 2 involved random (R) orders of visual stimuli and a secondary task. Blocks 3–6 and Block 8 involved stimuli that occurred in a particular sequential (S) order: During these blocks, there was no secondary task. The slowing of reaction time to an inserted block of random events, Block 7, indicates that the sequence had been learned. The secondary task was reintroduced on final blocks, and sequential knowledge was probed by the contrast of Random Blocks 10 and 12 with Sequence Block 11. Subjects receiving explicit knowledge and those becoming aware of the sequence showed more sequence knowledge during single-task learning than did less aware subjects, but when the secondary task was added, all subjects showed equivalent sequence knowledge. Adapted from "Attentional and Nonattentional Forms of Sequence Learning," by T. Curran and S. W. Keele, 1993, *Journal of Experimental Psychology: Learning, Memory, and Cognition, 19,* p. 192. Copyright 1993 by the American Psychological Association.

Following these single-task trial blocks, a secondary task was introduced. A high-or low-pitch auditory tone was inserted between each of the visual stimuli, and at the end of each block, the subjects reported the number of high-pitch tones. The effects of the secondary task on already acquired sequential representations were assessed by keeping the sequence of visual events the same on one trial block as during the prior single-task phase. On surrounding blocks, the visual events occurred at random. As can be seen in Figure 1, the magnitude of the learning score (difference in RT between random and sequence blocks) was smaller in the dual-task blocks, averaging about 60 ms. This reduction from the single-task score was seen even in the performance of the unaware subjects. Most interesting, the amount of sequence learning expressed in the dual-task phase no longer differed among groups despite the fact that the aware groups had exhibited greater learning during the initial single-task training compared with the unaware group.

These results suggest the operation of two forms of learning that operate in parallel during the initial single-task training. One type is accessible by awareness, accounting for the better learning of the aware subjects. In our two-system theory, we assume that this form of learning was also operating implicitly for the unaware subjects. With the introduction of the secondary task, this form of learning was no longer viable in either its explicit or its implicit form. Nonetheless, some residual effect of learning persisted, an effect attributed to learning that had occurred within the unidimensional system (Curran & Keele, 1993). The comparable performance of the three groups during the dual-task blocks was interpreted as resulting from the sole operation of this latter system.

The two-forms-of-learning hypothesis is supported by two other experiments reported by Curran and Keele (1993). In one, subjects were initially trained under either single-or dual-task conditions. Learning during this phase was greater for the former group. However, when transferred to a dual-task phase, the two groups performed comparably. These results suggest that the secondary task not only blocks one form of learning but also prevents the expression of that form of learning even when it has already been established.

In Curran and Keele's (1993) final experiment, the secondary task was used during the initial learning. This was expected to restrict learning to only one system. To test this hypothesis, they removed the secondary task during a transfer phase. As predicted, the degree of learning exhibited during the initial single-task sequence block was comparable to that observed under dual-task training.

As we argue subsequently, the system isolated by dual-task conditions corresponds to the unidimensional system of our theory. The additional learning that occurs under single-task conditions corresponds to the multidimensional system. Despite its multidimensional capability, this latter system also can learn associations within the single dimension of single-task learning as long as there is no interference from a secondary task.

A study by Frensch, Lin, and Buchner (1998) claimed failure to replicate the last of the Curran and Keele (1993) studies, reporting instead immediate improvement in learning score upon transfer from dual to single task. As pointed out more recently by Frensch, Wenke, and Rünger (1999), however, the earlier Frensch et al. experiments confounded transferred learning with new learning. First block transfer data are less contaminated by new learning, and close examination of that block in Figure 1 of Frensch et al. (1999) reveals results consistent with those of Curran and Keele: The single-task learning score immediately after transfer and before new learning is equivalent to the prior dual-task learning score. We cite those data later in Table 2, in which we include additional results that replicate Curran and Keele's and other's results relevant to the current theory. Frensch et al. (1999) also used a regression analysis to argue in a new way that performance, not learning, is suppressed by a secondary task. They argued that subjects who exhibited no evidence of dual-task learning have more learning on the second trial of single-task transfer than can be accounted for by new learning. In the Appendix we detail their regression approach and show that their estimate of the amount of actual learning when the dual-task learning score is zero is subject to an over-estimation (see Klauer, Greenwald, & Draine, 1998, for another example of this kind of error). We conclude that behavioral results, including those of the Frensch group, are consistent with our two-system view (see also Shanks & Channon, 2002, for further supporting data). This view is bolstered by neuroimaging results that reveal distinct brain systems for learning under the dual-task and single-task conditions. We turn now to review our core neuroimaging evidence.

Neuroimaging Reveals Distinct Neural Architectures for Single- and Dual-Task Sequence Learning, Supporting the Existence of Two Systems

The hypothesis that single- and dual-task learning engage distinct association systems is supported by a series of neuroimaging studies with the SRT task. Our second foundation study, Grafton et al. (1995), which used the PET procedure, measured changes in regional cerebral blood flow (rCBF) while subjects were trained on the SRT task with either the presence or absence of a secondary task. For the dual-task condition, visual signals occupying one of four locations alternated with randomly ordered low- and high-pitched tones. Subjects silently counted the number of low-pitched tones and responded with key presses to the visual signals. Tones were also presented in the single-task condition, but they were all high-pitched and the subjects were instructed to ignore them. Rather than use a fixed response-to-stimulus interval (RSI), the interval between successive visual signals was fixed at 1,500 ms. This modification ensured that the rate and number of responses did not change over the training blocks as RTs improved. Such performance changes would make it difficult to determine whether the neural changes were associated with sequence learning per se or with increased motor activity.

Comparisons between the last block of trials with the sequence and a subsequent random block showed a learning score of about 50 ms in the dual-task case and 170 ms in the single-task case, consistent with results of our previous core study (i.e., Curran & Keele, 1993).

PET scans were obtained on the first, fourth, and seventh sequence blocks. To assess the neural correlates of sequence learning, Grafton et al. (1995) looked for neural regions exhibiting a monotonic increase in rCBF over the course of these training blocks. As a control for generic hemodynamic changes, regions were excluded that showed a similar monotonic change across a series of random blocks. An activation map is shown in Figure 2, and Table 1 provides a listing of neural regions exhibiting rCBF increases correlated with sequence learning.[1]

Three points stand out. First, increases in rCBF during sequence learning in both the single- and dual-task conditions were observed in a distributed set of regions spanning posterior and anterior cortex. Second, the foci during dual-task learning were mostly in the left hemisphere, contralateral to the responding hand. In contrast, the prominent foci during single-task learning were mostly in the right hemisphere. The third and, for the present theory, most important finding is that different regions within both frontal and posterior cortex were associated with the single- and dual-task conditions.

Brain regions correlated with dual-task learning generally were located more superior to those correlated with single-task learning. During dual-task learning, rCBF changes were observed in left occipital cortex (Brodmann's Area 18) as well as at the junction of the parietal and occipital lobes bilaterally. These areas likely reflect the visual nature of the signals. Moving anteriorly, dual-task learning was associated with activation in Areas 40 and 7, areas linked to spatial representation and visually guided actions (e.g., Desmurget et al., 1999; Ungerleider & Mishkin, 1982; Van Essen & Maunsell, 1983). Within frontal regions, learning-related changes were restricted to the supplementary motor area and motor cortex in the left hemisphere.

The motor cortex activity that accompanied learning likely reflects priming from the upstream sources of sequence knowledge

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[1] The reader should consult the original references for a listing of regions that exhibit decreases in rCBF.

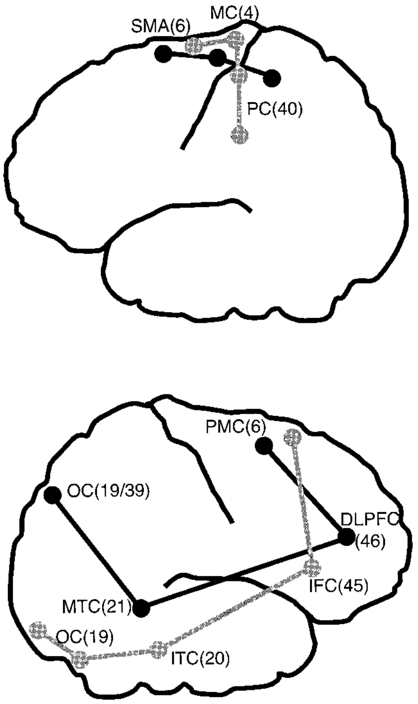

Figure 2. Major cortical regions showing increased blood flow correlated with dual-task sequence learning (top) and single-task learning (bottom). Black lines refer to learning of visual–spatial sequences based on Grafton et al. (1995); gray lines refer to learning color sequences based on Hazeltine et al. (1997). Under dual-task conditions, learning-related increases in regional cerebral blood flow (rCBF) were observed in the parietal (PC), supplementary motor area (SMA), and primary motor cortex (MC). We refer to this network as the "dorsal pathway" for sequence learning, capable of forming intradimensional associations. In contrast, learning-related increases under single-task conditions were restricted to the occipital (OC), temporal (MTC and ITC), prefrontal (IFC and DLPFC), and lateral premotor (PMC) cortex. This network is referred to as the "ventral pathway" and is hypothesized to support the formation of interdimensional associations. Numbers in parentheses indicate Brodmann's Areas.

in the supplementary motor area and parietal cortex together with specification of the relevant motor effector. Grafton, Hazeltine, and Ivry (1998) used a transfer design in which the responses were initially made with the fingers and then switched to arm movements. Following this switch, motor cortical activity showed an immediate shift in topography. The immediate shift in locus with no prior practice with the arm suggests that motor cortex activity reflects priming rather than learning per se. In contrast, supplementary motor activity failed to shift with transfer (see also Grafton, Mazziotta, Woods, & Phelps, 1992).

A very different picture was observed in the single-task condition. Within posterior cortex, learning was associated with increased rCBF in inferior aspects of the parietal–occipital lobe (Brodmann's Area 40/19) and in the temporal lobe of the right hemisphere (Area 21). In the frontal lobe, learning-related increases in rCBF were observed in Area 8 and inferior prefrontal cortex (Areas 10 and 46) and lateral premotor cortex (Area 6).

In summary, the neural correlates of sequence learning under single- and dual-task conditions formed two nonoverlapping sets, one more dorsal and the other more ventral. This dissociation in terms of neural activity is in accord with the behavioral results suggesting that these conditions engage distinct learning systems.

Hazeltine, Grafton, and Ivry (1997) conducted a similar study, but with different visual stimuli. All of the visual events occurred at fixation, with spatial–manual responses based on the color of the stimuli. In this way, potential eye movement artifacts were avoided and the effect of an arbitrary stimulus–response map could be examined. Despite these changes, the results were remarkably similar to those reported in Grafton et al. (1995). Again, dual-task learning was primarily restricted to the left hemisphere with rCBF increases observed in parietal cortex, supplementary motor area, and primary motor cortex. The neural correlates of single-task learning were in the right hemisphere, including occipital and temporal foci in posterior cortex and lateral prefrontal and premotor foci in frontal cortex.

The similarities across the two studies can be seen in Figure 2. The SRT task, as well as some related sequencing tasks, has been used in other imaging studies, always under single-task conditions. Comparisons with the Grafton et al. (1995) and Hazeltine et al. (1997) studies are difficult because these studies have relied on a

Table 1
Brain Regions Showing Changes in Visual–Spatial Sequence Learning (Grafton et al., 1995)

Brain region	Secondary task	No secondary task
Frontal cortex	Left anterior 10 (−12, 55, 9)	Right dorsolateral 46 (31, 39, 22)
	Left sensorimotor 3/4 (−36, −18, 55)	Right premotor 6 (37, 1, 54)
	Supplementary motor area 6 (−1, 1, 57)	Right superior 6/8 (24, 15, 49)
		Right middle 10 (28, 51, 13)
Posterior cortex	Left parietal 40/7 (−36, −37, 57)	Left parietal/occipital 19/39 (−36, −73, 36)
	Left lingual gyrus 18 (−12, −79, 1)	Right parietal/occipital 19/39 (36, −81, 30)
		Right middle temporal 21 (55, −43, 0)
Subcortical	Left putamen of basal ganglia (−27, −15, 12)	Right putamen and nucleus accumbens of basal ganglia (15, 15, −7)
	Right putamen of basal ganglia (25, −15, 9)	

Note. Numbers outside parentheses denote approximate Brodmann Areas; numbers inside denote *x*, *y*, and *z* coordinates in Talairach space. From "Functional Mapping of Sequence Learning in Normal Humans," by S. T. Grafton, E. Hazeltine, & R. Ivry, 1995, *Journal of Cognitive Neuroscience, 7*, pp. 501, 503. Copyright 1995 by MIT Press. Adapted with permission.

subtractive methodology, usually involving the reintroduction of a random block after sequence training. Nonetheless, the general pattern indicates that anterior activation during sequence learning is centered in lateral prefrontal cortex (Berns, Cohen, & Mintun, 1997; Doyon, Owen, Petrides, Sziklas, & Evans, 1996; Honda et al., 1998; Rauch et al., 1995; Rauch, Whalen, et al., 1997; Salidis, Willingham, & Gabrieli, 2000).[2] The exact location within prefrontal cortex varies across these studies, likely reflecting specific details of stimulus and task. In addition, Rauch et al. (1995) and Rauch, Whalen, et al. (1997) reported activation in premotor cortex, consistent with our core studies. With respect to posterior brain regions, the picture is less consistent. Temporal lobe activity is reported only in one experiment, a study in which subjects used trial-and-error learning to determine the sequence (Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994). Parietal activations are reported in all of the SRT studies. As in the Grafton et al. (1995) and Hazelitne et al. (1997) studies, this activation is more inferior than is observed for dual-task learning, generally falling within Brodmann's Areas 19, 39, and 40, rather than the more superior Area 7. Rauch et al. (1995) and Rauch, Whalen, et al. (1997) also reported activation in visual cortical Areas 17, 18, and 19, again consistent with our core studies.

Using transcranial magnetic stimulation, Pascual-Leone, Wassermann, Grafman, and Hallett (1996) provided converging evidence for a role of prefrontal cortex in sequence learning. Stimulation of this area disrupted SRT learning under single-task conditions. It is interesting to note that a similar disruption was not found following stimulation of supplementary motor cortex. The involvement of lateral prefrontal cortex during single-task learning is also supported by studies of individuals with brain injuries.[3] A. R. Marks, Cermak, and Grafman (1997) and A. R. Marks, Wild, Higgins, Massaquoi, and Grafman (1997) reported that patients with lesions of right prefrontal cortex were impaired in sequence learning. Patients with left prefrontal lesions were not impaired. Thus, the patient studies also point to a central role for right prefrontal cortex during sequence learning in the absence of secondary tasks.

Regarding patients with posterior impairment, Curran (1997) examined single-task learning in subjects who had damage to hippocampal-temporal lobe brain systems. Such damage should impair our hypothesized ventral system, leaving the dorsal system intact. Curran found considerable preservation of single-task learning in these patients that on the surface suggests intact learning within our theorized ventral system. However, the patients demonstrated subtle deficits involving associations among nonadjacent items. Subsequently in the Discussion section when we consider the problem of sequence ambiguity, we argue that the dorsal (unidimensional) system, reflected in brain regions correlated with dual-task sequence learning, is less robust than the ventral (multidimensional) system in learning remote associations. The latter system makes better use of context to achieve its capability. Thus, we think that Curran's results reflect impairment of our hypothesized multidimensional system, and are, therefore, consistent with our two-system view. We further predict that hippocampal-temporal patients would retain normal dual-task learning but would be impaired in cross-dimensional learning. These predictions remain to be tested.

The Two Systems Learn in Parallel but Are Competitive in Control of Performance

The behavioral data of Curran and Keele (1993) indicate that learning occurs in parallel within the two systems under single-task conditions. When a secondary task was added after training, residual learning scores were attributed to a representation that had already developed within the dorsal unidimensional system.

The PET data on the surface, however, are not entirely consistent with the behavioral data. During single-task learning, no changes in rCBF were observed in those areas that were implicated during dual-task learning. Thus, the PET data suggest that the two systems operate exclusively rather than in parallel. To reconcile this discrepancy with the behavioral results, we suggest that whereas learning under single-task conditions occurs in parallel within the two systems, PET primarily reveals the system that is in current control of performance.

A PET study reported by Jenkins et al. (1994) is relevant to this point. Subjects used a trial-and-error procedure to explicitly learn the order in which to press four keys in a repeating eight-element sequence. In one condition, the PET data were collected during the phase in which the sequence was being discovered and initially practiced. In a second condition, the PET data were obtained after the sequence was well practiced.

Activation during the discovery portion of early learning was prominent in premotor and dorsolateral prefrontal cortex, a result that corresponds to that of the single-task SRT studies reviewed above. After substantial practice, however, frontal activation shifted to the supplementary motor area. Instructing the subjects to "think about the movements" (Jueptner et al., 1997; see also Passingham, 1996) led to an immediate return of the lateral prefrontal activation and reduction in the supplementary motor area activation.

These PET results suggest that brain systems compete to control performance without necessarily impacting learning. When acquired knowledge within the multidimensional system controls behavior, lateral prefrontal cortex and inferior regions of posterior cortex become active. Brain structures that support the unidimensional system become less active, and perhaps even suppressed (Grafton et al., 1995), despite their continued accrual of knowledge. Such accrual becomes manifest as the supplementary motor area and superior regions of posterior cortex, all regions of the unidimensional system, become engaged. When this occurs, the

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[2] Honda et al. (1998) reported two parietal foci in Brodmann's Area 40 that are correlated with accuracy and RT indices of learning. On reexamination, one of these areas (26, −70, 32) appears closer to the border of Areas 39 and 19. The other (−30, −60, 40) is on the border of 40 and 19. Thus, this study is also consistent with our claim that single-task SRT learning tends to activate Areas 39 and 19.

[3] Doyon et al. (1997) reported that patients with lesions of frontal lobes are not impaired in sequence learning, but this conclusion is problematic. Sequence learning was indexed by improvements in RT over several sessions rather than by comparison of RTs to sequenced events with random events. Factors other than sequence learning are likely to be involved in session-to-session improvements (see Willingham, 1998). Moreover, the lesions for some of the patients were restricted to ventromedial frontal regions or left hemisphere, regions not implicated by imaging and other patient studies for single-task sequence learning.

more ventral regions of the multidimensional system recede in activity but can be reconstituted by attention, demonstrating that they continue to retain sequential knowledge.

The Two Sequence-Learning Systems Differ in Cross-Dimensional Connectivity: The Schmidtke and Heuer (1997) Study

We turn now to the third of our foundation studies, Schmidtke and Heuer (1997). This study introduced a novel procedure that led to three primary insights. The results first provided a confirmation of the two-system hypothesis. Second, they made clear the need for a distinction between unidimensional and multidimensional learning. Third, they led to a new explanation of interference effects resulting from a secondary task.

We begin with the last of these three interconnected issues. The conventional view of dual-task interference, at least within the SRT literature, has been that the secondary task diverts attentional resources from the primary sequencing task (e.g., A. Cohen et al., 1990; Curran & Keele, 1993; Nissen & Bullemer, 1987; but see Stadler, 1995, and Goschke, 1997, 1998, for challenges). Schmidtke and Heuer (1997) proposed instead that dual-task interference is caused not by capacity limitations but by eliminating the correlation between adjacent, successive events. In their view, associative mechanisms are designed to extract coherence that may exist between stimuli, subject to constraints related to the degree of predictability and contiguity. In most dual-task SRT studies, the secondary task required tone counting, and the pitch of each tone was randomly determined. This randomization procedure reduces the degree of predictability from one stimulus to the next when the combined sequence of auditory and visual events is considered. Schmidtke and Heuer hypothesized that the reduced correlation in dual-task conditions would disrupt the operation of an associative mechanism. Correlation would still exist across the successive events of the primary task, but within a multidimensional system, the association between such noncontiguous events is likely to be weak (Ebbinghaus, 1885/1913).

Whereas a secondary task consisting of random events will severely limit the utility of the multidimensional system, our theory proposes that modules of the unidimensional system would be impervious to the disruptive influence of secondary tasks that have no access to the modules. Assuming other task characteristics such as the interstimulus interval are held constant, sequenced events to which the unidimensional modules are sensitive would remain contiguous and learnable.

Schmidtke and Heuer (1997) predicted that if the secondary-task stimuli were correlated with the primary-task stimuli, associative learning within the multidimensional system would once again be viable. Cross-dimensional learning should not only be possible but also as large as single-task learning if the correlation between successive events is similar. “Capacity” plays no role in this view.

To test this prediction, Schmidtke and Heuer (1997) introduced a slight modification of the standard dual-task version of the SRT task. The responses to the visual stimuli were based on their spatial position, and in sequence blocks the stimulus positions followed six-element sequences, similar to our other foundation studies. Pitch discrimination was used, as before, as the secondary task. However, rather than maintaining an internal count of the number of low-pitched tones, subjects pressed a foot pedal following each target tone, a go/no-go task. This procedural change provides an RT measure of performance on the secondary task.[4] Concern might be expressed that the change in response mode to the secondary tones would produce critical differences in outcomes. As we discuss below, however, the results from all comparable conditions replicate those of our other core studies. Moreover, as described in the next section, we replicated results from the novel features of the Schmidtke and Heuer study in a previously unreported study (Hazeltine, Ivry, & Chan, 1999), a study that returns to the tone-counting procedure.

Because Schmidtke and Heuer (1997) used a number of different conditions, Table 2 provides a summary of learning scores from their various conditions. Their usage of the same six-item visual–spatial sequences used in our other core studies and by Frensch et al. (1999) prompts the inclusion of data from those studies as well. The scores are organized according to whether the conditions are hypothesized to affect the dorsal, unimodal system alone or the ventral system in addition to the dorsal system. Two distinct groups of values emerge, supporting the hypothesized distinction.

For a baseline measure of learning, Schmidtke and Heuer (1997) included a single-task condition in which only the visual stimuli were presented. After several sequence blocks, the order of the events was randomized. This led to an increase in RT of 139 ms, comparable to single-task learning scores obtained in related studies (e.g., Curran & Keele, 1993).

There were two dual-task conditions. In the first one, the visual sequence alternated with random auditory tones, similar to previous studies. When the visual stimuli were randomized on a probe test, the visual RTs increased by 64 ms, about the same as in Curran and Keele (1993), Grafton et al. (1995), and Frensch et al. (1999). Note that this cost is much less than that observed in the single-task condition. Moreover, when learning of the visual sequence was probed in blocks in which the tones were eliminated (following dual-task learning), the cost was a similar 70 ms. We earlier attributed such dual-task learning to the more dorsal system we hypothesize to be unidimensional in character. Removal of the secondary task should not immediately improve the learning score because, by our theory, no learning has occurred in the more ventral system. Thus, we assume the 70-ms cost observed in the dual-task probes is less than the 139-ms cost in the baseline condition because in the latter learning has taken place in both systems. Thus, despite the methodological changes, the results for conditions with random secondary-task events replicated our earlier core studies in all essential aspects.

The novel condition in the Schmidtke and Heuer (1997) study involved a situation in which the auditory tones were presented in a 6-element sequence. Given that this sequence is the same length as the visual sequence, the auditory–visual events now constituted a multidimensional sequence 12 elements in length. Although one

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[4] Auditory tones, when present, occurred within a 200-ms interval between the response to a visual stimulus and the onset of the next visual stimulus. For tones requiring a foot press, RTs to the next visual signal were elongated and highly variable. We focus, therefore, on visual RTs in the dual-task conditions for trials in which the visual stimulus was preceded by a nontarget auditory tone (i.e., responses following no-go tone trials).

Table 2
Learning Scores (in Milliseconds) Analytic to Hypothesized Unidimensional and Multidimensional Sequence-Learning Systems

Learning condition	Unidimensional system	Multidimensional system
Single-task learning		
Schmidtke & Heuer (1997)		139
Curran & Keele (1993)		154
Grafton et al. (1995)		~170
Dual-task learning (secondary task random)		
Schmidtke & Heuer (1997)	64	
Curran & Keele (1993)	63, ~75	
Grafton et al. (1995)	~50	
Frensch et al. (1999)	~65	
Dual- to single-task transfer		
Schmidtke & Heuer (1997)	70	
Curran & Keele (1993)	69	
Frensch et al. (1999)	~45	
Single- to dual-task transfer		
Curran & Keele (1993)	~50	
Correlated visual–auditory sequences		
Schmidtke & Heuer (1997)		
Visual prephase shift		153
Auditory prephase shift		135
Visual postphase shift	44	
Auditory postphase shift	68	
Not correlated visual–auditory sequences		
Schmidtke & Heuer (1997)		
Visual	85	
Auditory	83	

Note. All learning scores reflect performance on either a six-item visual–spatial sequence or, where noted, a tonal sequence. Scores from Curran and Keele (1993) are averages of data from unaware and aware subjects who were not instructed about the sequence. Visual scores from Schmidtke and Heuer (1997) are from trials not requiring a response to the auditory signal. Learning is predicted to be restricted to the unidimensional system if signals on a secondary task are either random or uncorrelated with the primary task. Otherwise, the multdimensional system also learns. If two intertwined dimensions are correlated, allowing learning within the multidimensional system, shifting their phase subsequent to learning is predicted to express learning only within unidimensional modules.

might be concerned that increasing sequence length by itself would disrupt learning, previous studies have found substantial learning with unidimensional sequences of this length (Heuer & Schmidtke, 1996; Reed & Johnson, 1994). More important, the subsequent probes revealed substantial learning. A probe of randomized visual signals yielded a learning score for the visual sequence of 153 ms. A probe in which the auditory signals were randomized yielded a learning score for the auditory sequence of 135 ms. Both values are comparable to what was found in the single-task baseline condition.

These results clearly indicate that if the secondary-task stimuli follow a fixed sequence that is predictive of events on the other dimension, significant sequence learning occurs for both dimensions. Does such learning represent cross-dimensional learning? An alternative hypothesis is that independent learning within each dimension may have occurred. To compare these two hypotheses, Schmidtke and Heuer (1997) introduced a new type of learning probe in which the phase relationship of the visual and auditory events was shifted after the training blocks. This phase shift altered the interdimensional order of events while preserving the intradimensional sequences. RTs to the visual and auditory events increased by 109 ms and 63 ms, respectively. Residual learning can be estimated by subtracting the phase-shift deficits from the random deficits, yielding scores of 44 and 68 ms for the visual and auditory dimensions. We attribute the phase shift cost as reflecting disruption in the associations within the multidimensional system. Residual learning following phase shift is assumed to reflect the fact that learned representations remained intact in the unidimensional modules, one sensitive to visual position and the other to the pitch of auditory events.

Further evidence of dissociation between unidimensional and multidimensional learning comes from a control condition in which the auditory sequence was only five elements long. Because the lengths of the stimulus cycles for visual and for auditory events are uneven in this case, the order of interdimensional events changes with each cycle. On the one hand, multidimensional learning is not possible under such conditions because of lack of correlation between dimensions. On the other hand, unidimensional learning should still be possible because of intradimensional coherence. The results confirm this prediction. A random probe for the visual signals revealed an 85-ms learning score; a random probe of the auditory sequence an 83-ms score. Both of these values are substantially less than the learning scores obtained when the visual and auditory sequences were each of equal length, allowing multidimensional predictability. In fact, these learning scores are comparable to that found for dual-task visual sequence learning when the auditory task always involves randomized events.

The results of Schmidtke and Heuer's (1997) study make a strong case for the two-system view, adding information about dimensional constraints on learning. Unidimensional modules extract separate representations, each sensitive only to information along a single dimension. These modules are encapsulated in the sense that they are only sensitive to input along a specific dimension. The degree of learning within these modules is independent of whether training occurs under single-task conditions or under dual-task conditions. For the latter, the amount of learning in a unidimensional module will be similar regardless of whether secondary events excluded by the module are random, follow a sequence of unequal length, or follow a sequence of equal length. We identify these modules with the superior brain regions associated with dual-task learning in the imaging studies reviewed above (Grafton et al., 1995; Hazeltine et al., 1997), although we recognize that specific locations of the modules may vary depending on modalities in which learning occurs.

Learning within the multidimensional system is more limited. For this system to extract sequential associations, the successive events must either be from a single dimension or, when task-relevant information is present on multiple dimensions, the successive interdimensional events must be predictive. We identify this multidimensional system with the ventral brain regions that were correlated with learning under single-task conditions in the PET studies of the SRT task.

It is important to note that the Schmidtke and Heuer (1997) study challenges the view that sequence learning is capacity dependent. From a subject's perspective, the tasks with correlated dimensions were essentially the same as in other dual-task SRT studies when the pitch of the tones was randomly determined. Nonetheless, when the events for the two tasks were amenable to the formation of cross-dimensional associations, learning was actually comparable to that found in the single-task baseline condition. We assume that the multidimensional system is always operative. In single-task learning, its associations are intradimensional because there is no other task-relevant information. In dual-task experiments, the task-relevant events from both channels gain access. Predictability among these events will promote interdimensional learning; randomness among these events will discourage such learning.

Converging evidence for parallel learning in distinct dimensional modules has been reported by Mayr (1996). He showed that subjects implicitly learned two uncorrelated sequences, one associated with objects requiring response and the other with locations at which objects occurred. Correlational evidence suggested that learning of the one sequence was not associated with learning the other.

Recently, Rah, Reber, and Hsiao (2000) further examined Schmidtke and Heuer's (1997) contention that the effect of a secondary task is related not to capacity constraints but rather to the contingencies between this task and the primary task. As in many SRT studies, Rah et al. combined a visual–manual task with a tone-counting task. However, the visual stimuli did not form a sequence. Rather, the location of a visual signal was partially predicted by the preceding tone. The subjects were not informed of these contingencies. On probe blocks, the contingencies were eliminated such that the auditory–visual pairs were randomly selected. Visual RTs increased on these blocks, indicating that the prior cross-dimensional contingency had been learned. A second experiment showed that when the visual signals followed a 12-element sequence, a contingent, although nonsequenced, tone task enhanced learning compared with noncontingent tones. These and additional experiments by Rah et al. support the contention that when secondary-task events are correlated with primary-task events, a multidimensional representation develops even when the events from the two dimensions are relevant to different tasks.

Rah et al. (2000) suggest that sequence learning involves "scanning the environment for potentially coordinate patterns of covariation" (p. 313). Although this hypothesis is similar to our theory in terms of the interpretation of secondary-task influences, it does not entail a two-system hypothesis. We have argued that there is a set of unidimensional modules separable from a multidimensional system. Within the multidimensional system, random, task-relevant events of any dimension can obscure patterns of covariation among any other dimensions. That is, in our theory there is no system that "scans" each and every dimensional combination. We next report an experiment that examined this issue directly.

Further Confirmation of the Integrative Nature of the Multidimensional System

It could be argued that in the Schmidtke and Heuer (1997) study, unidimensional learning persists in the presence of a random secondary task because the visual sequence is so short, repeating every six events. By this hypothesis, learning should occur for comparably short cross-dimensional sequences, regardless of whether there are intervening random events from a third dimension. In contrast, our theory would argue that the presence of random events would disrupt learning even for short cross-dimensional sequences, although independent unidimensional associations could still develop. In our theory, all task-relevant information gains access to the multidimensional system; there are no modules for pairwise combinations of dimensions.

To test this prediction, we devised a new experiment involving two very short intradimensional sequences (Hazeltine et al., 1999). One sequence consisted of a repeating series of three tones, two low-pitched and one high-pitched. A second intradimensional sequence consisted of a series of three shapes, two triangles and a square. Successive events alternated between the two dimensions, creating a cross-dimensional sequence of six events. For example, the interdimensional sequence might be high–triangle–low–square–low–triangle. Vocal responses were made to the tones ("low" or "high") and key presses were made to the shapes.

To prevent integrative learning, a red or green circle, randomly determined, was presented in the 1,500-ms interval between each sequence element (thus there were twice as many colored circles as there were shapes or tones). Subjects kept an internal count of the number of green circles during each block of trials. In effect, subjects were performing three concurrent discrimination tasks: Vocally responding to pitch, manually responding to shape, and internally counting the number of color targets.

Our theory predicts independent learning of the three-item tone sequence and the three-item shape sequence within their respective unidimensional modules. Because the intervening colored circles are randomly specified, no cross-dimensional learning should occur despite a cross-dimensional sequence. After six sequence blocks, intradimensional learning was probed by inserting a trial block in which either the tones or shapes were randomly determined. The probability for each element within these sequences was maintained to control for the possibility that the learning might consist of sensitivity to stimulus probability rather than reflect associative mechanisms. Cross-dimensional learning was probed by shifting the phase relation of the two sequenced dimensions. The results supported the predictions of the two-system hypothesis: RTs were significantly longer during the random blocks but showed no change in the phase-shift block. These results suggest intradimensional learning but no integration across dimensions.

In a control condition, the experiment was repeated but the subjects were told to ignore the colored circles. With this change, an increase in RT was seen for both the random probes and phase-shift probe, with the latter indicating that cross-dimensional learning had occurred. As in the Schmidtke and Heuer (1997) study, however, the phase-shift cost was smaller than the costs observed during the random blocks, implying that some benefit of learning was still present during the phase-shift probe. This residual effect, we suggest, reflects the preservation of unidimensional learning. Such learning is impervious to the phase-shift manipulation.

The results of this experiment (Hazeltine et al., 1999) provide four notable contributions:

1. Learning of even short, cross-dimensional sequences is blocked by intervening random events of another task, arguing that the critical factor allowing multidimensional

learning is the absence of interleaved task-relevant events that are not predictive of succeeding events.

2. The failure of cross-dimensional learning despite the presence of two short sequences argues, at least on the surface, against a view that a "scanning" system searches for patterns of correlation across all combinations of dimensions (Rah et al., 2000). Instead, the results are consistent with our view of two systems, one that is sensitive only to within-dimension contingencies and a second that is sensitive to all task-relevant information. A modified view that reconciles the two perspectives is possible, however, and is considered more fully in the Discussion section. In this view, a secondary task impairs primary-task learning to varying degrees, depending on temporal relationships between primary and secondary tasks. A corollary of this view is that correlated dimensional combinations may be learned even in the presence of a random-events third task given either proper temporal relationships or extensive learning. Nonetheless, the distinction between a unidimensional system and a multidimensional system, which exhibit different properties, remains paramount in our view.

3. The effect of randomness in one dimension on learning sequential dependencies in another depends on whether the random information is task relevant or not.

4. Our prior conclusions about cross-modal learning were based on experiments involving spatial position of visual stimuli and pitch of auditory tones. Given the prominent role of spatial information in theories of visual attention and cross-dimensional binding (e.g., Treisman, 1988), it is important to assess the generality of our ideas with nonspatial dimensions. This experiment demonstrates that a nonspatial visual dimension, shape, can be integrated with auditory events. The experiment (Hazeltine et al., 1999) also demonstrates that color, when random, can disrupt associations between two other dimensions.

Neurophysiological Basis of Cross-Dimensional Integration

Although we lack neuroimaging data for the cross-dimensional case, similarity of behavioral results with single-task learning leads us to propose that the multidimensional learning system is associated with the same neural network observed in single-task learning of lateral prefrontal and premotor cortex and with a relatively ventral stream within parieto-temporal cortex. We also predict that during phase-shift probes, one would observe an immediate increase in activity in regions supporting the independent unidimensional representations, presumably more dorsal in location at least for spatial dimensions.

Despite the lack of relevant neuroimaging studies, neurophysiological evidence obtained during single-cell recording in primates supports the hypothesis that ventral regions of posterior cortex are sensitive to multidimensional inputs. Perhaps the most commonly cited multimodal region is the superior temporal sulcus (STS). Single neurons within STS can be driven by visual, auditory, and somatosensory stimuli (Hikosaka, Iwai, Saito, & Tanaka, 1988; Seltzer & Pandya, 1994; Watanabe & Iwai, 1991). Similarly, the parietal–occipital–temporal junction is considered a multimodal association region (e.g., Kupfermann, 1991).

Multimodal neurons have also been identified in lateral frontal cortex. Graziano, Reiss, and Gross (1999) have reported that neurons in lateral prefrontal cortex respond to the location of a stimulus and that the location can be cued by either an auditory or a visual stimulus (see also Vaadia, Benson, Hienz, & Goldstein, 1986). It appears that the frontal cortex not only generalizes across modalities to extract location information but also abstractly codes actions. For example, neurons within ventral premotor cortex respond during the execution of particular actions such as grasping, with different cells tuned for specific actions (Rizzolatti & Arbib, 1998). The same neurons respond when the animal observes the action performed by other primates or their human caregivers. Even more impressive, these neurons are activated when the animal hears the sounds produced by the action. For example, a cell responsive when an animal breaks a stick by twisting will respond when the sounds are replayed later on (G. Rizzolatti, personal communication, September, 2000).

Such results attest to the cross-dimensional sensitivity within regions closely related to or nearby those observed in neuroimaging analyses of single-task sequence learning. In contrast, we know of no physiological evidence indicating that neurons in the more dorsal aspects of parietal lobe are polysensory. It is not clear whether the critical studies have yet to be conducted or whether the lack of such reports reflects a bias against publishing null results. There is certainly an extensive literature describing the physiological properties of cells in superior parietal lobe. In general, these studies have emphasized dimensional specificity. For example, studies of the perception of space (Bushara et al., 1999) and motion (Lewis, Beauchamp, & DeYoe, 2000) have indicated dimensionally-specific regions lying within the superior parietal cortex. We assume these regions correspond to parts of a unidimensional learning system.

Functional Differences Between the Two Systems

System Differences in Awareness

The relationship of awareness to learning has been a contentious issue (for discussion, see A. Cohen & Curran, 1993; Goschke, 1997, 1998; Perruchet & Amorim, 1992; Shanks & St. John, 1994; Willingham, Greenley, & Bardona, 1993). Nonetheless, we believe our two-system hypothesis provides useful insights regarding this controversy by providing dissociations. Specifically, we have proposed that the uni- and multidimensional systems differ in terms of their access to awareness. Learning within the unidimensional system is entirely implicit, a proposition that follows from its encapsulated nature. Explicit learning, by its very nature of expressing knowledge in modes different from initial learning, depends on the multidimensional system. Although instructed attempts to discover a sequence (e.g., through trial-and-error learning) may use the multidimensional system from the beginning, we assume that this system also is capable of forming associations implicitly. However, such representations may become accessible to awareness. Thus, a novel component of our theory is to challenge the idea that the implicit–explicit distinction

Table 3
Number of Subjects Able to Report 0–2, 3–4, or 5–6 Successive Elements of the Visual Sequence (Schmidtke & Heuer, 1997, Experiment 1)

	Number reported			
Learning condition	0–2	3–4	5–6	Total
Single-task learning	7	3	6	16
Dual-task learning				
V6/AR	13	0	3	16
V6/A5	13	2	1	16
V6/A6	4	6	6	16

Note. "5" and "6" refer to sequence length for visual (V) or auditory (A) sequences. "R" refers to random order. Equal visual and auditory sequence length (V6/A6) results in a repeating interdimensional sequence 12 events long. Unequal lengths (V6/A5) result in uncorrelated visual and auditory sequences. From Table 3 of "Task Integration as a Factor in Secondary-Task Effects on Sequence Learning," by V. Schmidtke and H. Heuer, 1997, *Psychological Research, 60,* p. 59. Copyright 1997 by Springer. Adapted with permission.

provides a fundamental way to characterize the distinction between the dorsal and ventral learning systems (see also Chun & Phelps, 1999). Rather, we emphasize a representational distinction between the two systems.

Awareness is rarely observed when subjects are initially trained under dual-task conditions (A. Cohen et al., 1990), suggesting that associations formed within the unidimensional modules are inaccessible to awareness. We assume that the neural instantiation of these modules primarily involves superior brain regions activated during dual-task learning. Other researchers also have noted that actions generated within these regions may be dissociated from awareness. For example, Goodale, Milner, Jakobson, and Carey (1991) described a patient who can successfully orient her hand when reaching for objects, even though she is unable to explicitly report the required orientation.

The relationship of awareness to the multidimensional system is more complex. Expressed learning under single-task conditions is greater when accompanied by awareness (see Figure 1), but the fact that learning is greater in single-task conditions compared with dual-task conditions, even for subjects lacking discernable sequence awareness, suggests that implicit learning can occur within the multidimensional system. Schmidtke and Heuer (1997), in one of the core studies we discuss here, carefully assessed awareness at the end of their experiments and sought to determine its relationship to performance under conditions in which cross-dimensional learning was either possible or not. As can be seen in Table 3, when the auditory secondary-task stimuli were either random or uncorrelated with the sequenced visual events, sequence learning occurred, but awareness of the visual sequence was largely lacking. Again, this outcome is consistent with the idea that learning within the unidimensional system is not accessible to awareness. When the two sequences were correlated, cross-dimensional learning occurred and awareness was relatively high for many of the subjects. We would attribute the emergence of awareness to the multidimensional system.

In a second experiment, awareness was assessed for both the visual and auditory tasks. Again, when the two sequences were uncorrelated, awareness was low and likely no more than what would be expected on the basis of guessing rates. Moreover, a contingency analysis revealed no relationship between reported awareness of the auditory and visual sequences (for a similar result, see Mayr, 1996). In contrast, when the two sequences were correlated, allowing development of an integrated representation, awareness was much higher and the contingency analysis showed awareness of one sequence was likely to be accompanied by awareness of the other.

It is important to note that integrated representations within the multidimensional system also can occur in the absence of awareness. About half of the subjects in the correlated condition of the Schmidtke and Heuer (1997) study expressed little or no sequence awareness. Nonetheless, the phase-shift manipulation revealed cross-dimensional learning for these subjects. We have obtained similar results in the experiment cited above (Hazeltine et al., 1999) involving integrated three-element sequences. The lack of awareness for some subjects is especially striking here given that the intradimensional sequences were so short.

The most compelling evidence that the multidimensional system is able to learn implicitly, as well as explicitly, comes from the core neuroimaging studies of Grafton and colleagues (Grafton et al., 1995; Hazeltine et al., 1997). None of the subjects in the dual-task conditions of either study reported any awareness of the sequence, providing a direct link between purely implicit learning and the more dorsal neural areas of the unidimensional system. More interesting, the subjects in the single-task conditions were approximately evenly split between those who reported at least some awareness and those who did not. When PET analyses were performed separately for these two groups, areas showing learning-related changes—areas that we characterize as forming the multidimensional system—were essentially the same, although the magnitude of the effects was greater in the aware subjects (Grafton et al., 1995; Hazeltine et al., 1997).[5] A direct comparison on the aware and unaware subjects revealed that awareness was associated with increased rCBF in the right anterior cingulate and left temporal lobe, two areas not correlated with sequence learning. These regions have been linked to awareness in other imaging studies (e.g., Posner & DiGirolamo, 1998; Posner & Raichle, 1994). The enhanced activation for aware subjects of areas related to sequence learning corresponds to prior findings that attention to particular stimulus attributes enhances activity of brain regions sensitive to the attributes whether attended or not (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Posner & Raichle, 1994, p. 147).

Salidis et al. (2000) provide further evidence that what we have called the multidimensional system can be engaged during implicit sequence learning. Using functional magnetic resonance imaging, activation in dorsolateral prefrontal cortex and ventral regions of posterior cortex was correlated with sequence learning under single-task conditions. As in the Grafton et al. (1995) study, these regions did show higher activation when sequence knowledge became explicit. Likewise, the anterior cingulate became active

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[5] Data indicating that aware and nonaware subjects show similar areas of activation to be correlated with single-task sequence learning does not appear in the Grafton et al. (1995) study but were kindly supplied to us by Grafton.

with the development of awareness. Finally, Berns et al. (1997) and Rauch, Whalen, et al. (1997) also reported prefrontal and premotor activation even though subjects were unaware of a learned single-task sequence.

In contrast to our claims, Doyon et al. (1996) argued that activity in dorsolateral prefrontal cortex during single-task learning occurs only when awareness is achieved. However, close scrutiny of their PET results supports our position that prefrontal dorsolateral brain regions are associated with sequence learning regardless of awareness. Subsequent to sequence learning but prior to the emergence of awareness, prefrontal activity increased reliably on a probe block of random events. We suggest that such increased activity with the introduction of random events is a result of mismatch with what has already been learned even though awareness is not triggered. Thus, we believe the Doyon results are in accord with our hypothesis.

Mesulam (1998) reviewed the progression of sensory information throughout the cortex, delineating between unimodal and transmodal regions. Although focusing on different behavioral phenomena than the present theory, the review suggests that associations within unimodal structures support implicit learning, whereas explicit learning is dependent on transmodal structures. This proposal is consistent with the present framework if it can be amended with the proposition that implicit learning can occur within transmodal structures as well.

It is not clear why awareness would be restricted to the multidimensional system. We suggest that lack of awareness in the unidimensional system reflects the encapsulation of its modules. Another hypothesis centers on the idea that the unidimensional, dorsal system reflects a fast, relatively automatic system designed to support immediate action (e.g., Goodale, 1996). The more ventral multidimensional system, although capable of guiding current responses, is fundamental to a system essential for forming the complex representations that enable flexibility (e.g., Eichenbaum, 2000).

Our theory can, at this point, be compared with a sequencing theory presented by Willingham (1998). As in our case, Willingham proposes two systems, a dorsal and a ventral cortical learning system. His proposed ventral system is restricted to explicit learning only. It operates by the passage of goal knowledge from dorsolateral prefrontal cortex to posterior temporal lobe where successive target locations are activated in allocentric space (as opposed to body-centered space for the dorsal system). In contrast to Willingham's view, substantial evidence now favors the view that the ventral system supports implicit learning from which explicit knowledge might or might not emerge. In the Discussion section, we point out that recent views of hippocampally based memory converge on a similar conclusion. Although Willingham's suggestion that the ventral system codes locations in allocentric space is related to our view of a ventral system specialized for multidimensional binding (and object recognition—see the Discussion section), our emphasis on multidimensional sequential representation is new. Moreover, as will be developed now, we propose a substantially different view of attentional constraints for both ventral and dorsal systems than does Willingham, who essentially postulates capacity constraints.

System Differences in Attentional Constraint

The natural environment presents a flux of information from multiple sources, most sources uncorrelated with one another. A system that is sensitive to all such information would generally be useless, with the signal contained in correlated events swamped by the noise from the unrelated events. To ensure functionality of the multidimensional system, it is necessary to postulate a selective mechanism that restricts access to information relevant to the tasks at hand. Such insulation is not required for the unidimensional system because these modules are sensitive only to information along single, matching dimensions.

To solve the many-sources problem, our theory proposes a novel view regarding attention in sequence learning: The multidimensional system establishes relationships among attended dimensions only; the unidimensional system can extract regularities among events along single dimensions, attended or not. Neither system, by this view, requires attentional "capacity" for learning. It is possible that attention can be devoted to a dimension by virtue of its salience or its sudden onset. In the SRT experiments that we've been concerned with, however, attention is dictated by task relevance. That is, we assume that if signals are both relevant and necessary for performing some task, they are attended.

One of our primary messages prior to this point speaks against a capacity interpretation of primary- and secondary-task interactions. If a secondary task siphons capacity from the primary task, interference would be expected even when they were correlated. Schmidtke and Heuer (1997) showed, however, that a change in primary- and secondary-task relationship from uncorrelated to correlated produced a change from interference to coordinate learning. Moreover, such cross-dimensional learning was robust, yielding learning scores as large as for single-task learning. Similar conclusions come from studies by Rah et al. (2000) that we previously described.

What about the contention that the multidimensional system is selective? This view predicts that even random information from unattended dimensions—that is, dimensions not relevant to any task—will fail to disrupt cross-dimensional learning among attended dimensions. As reviewed above, a repeating six-element sequence composed of tone and shape subsequences was learned even when random colors of no task relevance were presented between each of the tones and shapes (Hazeltine et al., 1999). When the subjects had to count the number of target colors, however, cross-dimensional learning was disrupted, even though unidimensional learning was unaffected.

A related but second prediction is that an ignored dimension also will fail to be integrated with an attended dimension, even if the two are correlated. Jimènez and Mèndez (1999, 2001) reported data relevant to this prediction. On each trial, one of four possible shapes appeared at one of four locations. Unknown to the subjects, the successive locations followed a probabilistic sequence. In addition, there was a contingency between shape and the following location. For the primary task, the subjects' responses were based on the location of the stimulus. In one condition, the subjects were also required to keep track of the number of occurrences of two of the four shapes. In the other condition, the shapes were ignored. The results showed that all subjects exhibited a spatial learning effect. However, only that group of subjects who had to count shapes exhibited shape–location learning; those subjects for whom shape was irrelevant exhibited no shape–location learning. This result is similar to the finding of Schmidtke and Heuer (1997), who found that cross-dimensional learning between tones and visual position occurred when tones were counted but not when they were ignored. In sum, these studies confirm that attention modulates the access of information to the multidimensional system.

What about the other side of our hypothesis, specifically, a prediction that access to the unidimensional system is not affected by attention? A study by Mayr (1996), which we described earlier in support of extraction of regularities in independent unidimensional modules sensitive to dimensions in each of two noncorrelated sequences, might be deemed relevant to this prediction. Subjects responded to sequenced shapes on one task. The locations at which successive shapes occurred also was sequenced but in a manner not correlated with the shape sequence. Both sequences were learned independently. Although there was no instruction to respond to locations, it is possible that fixation on shapes at locations constituted a kind of location attention. Thus, an experiment reported in Schmidkte and Heuer (1997), which we've not previously described, is relevant here. During training, subjects were required to attend only to the visual signals; sequenced tones intervening between visual signals were ignored. In a test phase, the subjects were required to perform the go/no-go task with the tones by themselves. When the tone sequence used in training was maintained, RTs were marginally faster than when the pitches were selected randomly. Although the effect fell short of significance, it is consistent with a conclusion of a learned unidimensional sequence of tones despite lack of attention. Unfortunately, tone-sequence learning, even if reliable, may have reflected test-phase learning rather than transfer from the training phase. Clearly, more investigation is needed regarding the role of attention (or lack thereof) on unidimensional learning. Later in the Discussion section, however, evidence from a non-SRT study will be presented that provides confirmation of the prediction of unidimensional learning of nonattended sequences.

System Differences in Representational Code

The proposal that the unidimensional and multidimensional systems operate under different constraints of attention has corollary implications regarding representation. Task sets specify relevant stimulus and response categories to the multidimensional system. For example, a set may require responding to letters and not digits. Categorical specification of information entering the multidimensional system may in turn result in categorical representation. In contrast, unidimensional learning might include precategorical, "raw" stimulus or response features.

The just-described SRT studies of Jimènez and Mèndez (1999, 2001) illustrate this point. Recall that in a task-relevant condition, two of four shapes constituted targets of the secondary task. Because target count did not distinguish between the two, targets were defined categorically. Of particular relevance to the current issue of representation is a manipulation in which, following association of shapes to locations within a multidimensional sequence, the shape targets interchanged across blocks. This manipulation would disrupt the multidimensional sequence in terms of specific shape–location associations. But it would leave unchanged the association between targets, categorically defined, and locations. It is interesting to note that cross-dimensional learning was unaffected by the exchange of the target shapes, consistent with the idea that it is the category defined by the task set that enters the associative process of the multidimensional system.

In contrast, we predicted that precategorical stimuli, attended or not, can contribute to learning via the unidimensional system. The prediction concerning precategorical representation has not been tested in the SRT literature. However, the prediction that task relevance is not necessary for learning in the unidimensional system is consistent with the results reported in our core study by Schmidtke and Heuer (1997), which indicated sequence learning of a nonattended tone sequence. Because this study failed to rule out new learning during a test phase, a non-SRT study designed to capture critical aspects of language learning may be even more germane (Saffran, Newport, Aslin, Tunick, & Barrueco, 1997). While engaged in a drawing task, subjects were exposed to an auditory stream of meaningless syllables, syllables defined on the basis of first-order contingencies. Following this incidental exposure, the subjects were significantly better than chance in classifying previously experienced syllables as "legal" or "illegal." The fact that unattended syllables were meaningless suggests not only that the unidimensional system is able to extract contingencies between unattended events but also that the representation is precategorical.

Discussion

Our two-system theory of sequence learning derives primarily from studies that used the SRT task. Although this task is designed to capture critical aspects of skill acquisition, the resulting literature may also provide novel insights into topics of learning and memory. We turn to these topics here, relating our theory based on sequence learning with general principles of associative learning as well as with memory theories derived from the analysis of nonsequential learning tasks. Points of convergence can suggest general principles of cognitive and neural organization; points of difference can outline issues for future investigation. Comparisons to other theoretical frameworks can also inform the evaluation of the SRT task as a model task for understanding skilled performance, a topic to which we subsequently turn.

Relationship to Learning Theory

Our theory posits that the association of successive events occurs automatically, that is, without capacity constraint. Within the multidimensional system, we assume the associative mechanisms are subject to selection constraints, however. Considered in this manner, SRT learning can be loosely viewed as a form of classical conditioning whereby the repeated and reliable occurrence of one stimulus before another results in their association. Assuming this analogy is reasonable, it follows that variables that affect conditioning should also affect SRT learning.

Perhaps most similar to conditioning tasks are dual-task SRT paradigms. In dual-task studies, successive stimuli alternate between two dimensions (e.g., spatial SRT stimuli and auditory frequencies for secondary task). This dimensional alternation is analogous to a typical conditioning task in which two stimuli of different type are paired (e.g., tone and food or light and shock or, in sensory preconditioning, tone and light). Over a series of conditioning trials, these stimuli, too, alternate. In the SRT task, when secondary-task events are sequenced and correlated with primary-task events as in the Schmidtke and Heuer (1997) study, the same pairings of stimuli from two dimensions occur repeatedly. Thus, one could consider this a case in which conditioning is occurring for several different pairings at the same time.

An important factor in conditioning is the temporal relationship between the conditioned stimuli (CS) and unconditioned stimuli (US). Traditional views of conditioning (e.g., Kimble, 1961), suggest that, except for very short intervals, the ease of association declines as the interval between CS and US increases. In most SRT studies, this issue has not been addressed because the interval between successive events was typically fixed. In an exception by Shin and Ivry (2002), however, three different intervals—200 ms, 500 ms, and 800 ms—were used to separate different event pairs within an eight-element sequence of spatial stimuli, the same event pairs always separated by the same interval. In conformity with expectations from the conditioning literature, learning was greatest for the shortest interval.[6]

We've argued that on the one hand, when signals of a secondary task fail to correlate with primary-task signals, integrative learning fails because successive signals within the ventral multidimensional system no longer predict one another. On the other hand, when primary- and secondary-task signals are correlated, integrative learning (i.e., cross-dimensional association) develops. An elaboration of this view is that the system attempts to form associations between all task-relevant inputs. When these are not correlated, the system learns about this lack of predictability. By this view, we would expect that the same temporal relationships that favor cross-dimensional learning within the ventral system would also maximally interfere with primary-task learning within the ventral system when primary and secondary tasks lack correlation. In contrast, some primary-task learning could occur within the ventral system even with a noncorrelated secondary task under temporal intervals that are not favorable for cross-dimensional association.

A study by Hsiao and Reber (2001) is particularly relevant here. In their experiment, a 12-element sequence was formed by the ordering of 4 different spatial stimuli. Randomly ordered high-or low-pitch tones were inserted in the 200-ms interval between the response to one visual stimulus and the onset of the next such stimulus, and the subjects were required to count the tones of a target pitch. Rather than randomly vary the timing of the tones, Hsiao and Reber used three different fixed intervals in a between-group manipulation. For separate groups of subjects the tones occurred either 50 ms, 100 ms, or 150 ms after primary-task responses. Sequence learning is, of course, not possible for the tone-counting task because the pitch of the tones was determined randomly. However, by the interference perspective we've just described, one would expect that the tones should disrupt primary-task learning (within the multidimensional system) not by distraction but by providing poor predictions of the forthcoming visual events.[7] That is, the tone is a poor CS for the following spatial stimulus. Interference would be expected to be greatest for the 150-ms group, because in this condition the tone is closest in time to the following visual signal (i.e., akin to the prediction that learning would have been greatest in this group should the tones have predicted the visual signals).

Indeed, this is exactly what Hsiao and Reber (2001) observed. Primary sequence learning, as measured by the difference between sequenced and random blocks and estimated from Hsiao and Reber's Figure 3, was 41 ms, 27 ms, and 10 ms for the 50-, 100-, and 150-ms groups, respectively. Although not tested, our analysis predicts that intervals that produce minimal learning scores (i.e., maximum interference) when primary and secondary events are not correlated would produce maximum learning scores when the cross-dimensional events correlate. Thus, as with conditioning, the timing between successive events appears to influence both learning (Shin & Ivry, 2002) and interference (Hsiao and Reber, 2001), suggesting common associative principles.

If our analysis is correct, the Hsiao and Reber (2001) study mandates a modification of how we conceptualize association in the multidimensional system. Until this point in the article, we have emphasized that learning of the primary-task sequence is blocked by uncorrelated, secondary-task events. However, the notion that associative tendencies depend on temporal relationships suggests that this view is too strong. Associations might still form between the primary events, but these would be diminished the more proximate nonpredictive secondary events are to primary events.

Recent theorizing in the conditioning literature has emphasized relative time over absolute time (Gallistel, 1990; Gallistel & Gibbon, 2000). Thus, cross-dimensional association (or interference) in SRT may be a function not of absolute time intervals but of the ratio of the interval between successive primary-task stimuli to the interval between each secondary-task stimulus and the following primary-task stimulus. To date, no SRT study has disentangled relative and absolute timing. Such investigation would be very welcome.

Two caveats should be kept in mind, however. First, the recent theorizing regarding relative timing in conditioning rests heavily on a study by Gibbon, Baldock, Locurto, Gold, and Terrace (1977). That study involves time scales an order of magnitude longer than those used both in SRT tasks and in many classical studies of conditioning, such as those involving eye-blink conditioning (see Kimble, 1961). Second, despite our earlier arguments to the contrary, it is possible that late occurring secondary-task events interfere not with learning of the primary task per se, but with the expression of the learning, an interpretation not clearly ruled out in the one study of temporal relationships.

Nonetheless, consideration of the SRT task as a form of conditioning leads to a number of novel predictions about sequence learning within the ventral multidimensional system, as detailed below:

1. Whether a secondary task produces interference or learning will depend on the degree of correlation between the task-relevant stimuli. The two outcomes reflect the operation of a common associative mechanism and as such should be sensitive to the same variables.

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[6] We thank Jackie Shin for reanalyzing the data from Shin and Ivry (2002) for these post hoc analyses based on the RSIs.

[7] We assume that tonal influences on primary-task learning occur within the multidimensional system. By our theory, learning within the unidimensional system is uninfluenced by a secondary task because the module in which learning occurs in not receptive to stimuli of the secondary task.

2. The degree of learning or interference should depend not on the absolute temporal interval between secondary- and primary-task events but on the relative positioning of secondary events within the intervals between primary-task events.

3. If the primary- and secondary-task events are correlated, primary-task sequence learning, assessed by phase shift of the two sequences, will be greatest when the secondary-task stimuli lead the primary-task stimuli by a relatively short interval. Correspondingly, when the secondary events closely follow the primary events, learning will be greatest for the secondary sequence. Thus, a time-dependent asymmetry in the learning of two correlated sequences should be observed.

Comparison to Other Theories of Learning, Memory, and Brain Organization

The hypothesized multidimensional learning system that is central to our theory bears considerable similarity to recent proposals about the hippocampal learning system,[8] a system claimed to support cross-dimensional binding (e.g., Sutherland & Rudy, 1989; see N. J. Cohen et al., 1999, and O'Reilly & Rudy, 2001, for reviews). O'Reilly and Rudy (2001) suggested that cross-dimensional binding can occur in the absence of hippocampal involvement when training is extensive. Such protracted learning allows the extraction of stable associations, embedded in a variable context. The hippocampus, in contrast, is essential for the formation of associations that are learned with little experience and for forming engrams that are isolated from other similar but partially conflicting experiences. These features favoring hippocampal learning are similar to what happens within SRT learning absent an uncorrelated secondary task. Subjects in SRT studies typically learn only a single sequence within a single experimental session. The sequences usually are deterministic rather than probabilistic, at least when higher order associations are considered.

One notable difference between hippocampal theories of cross-dimensional memory and our theory of cross-dimensional sequence learning concerns the precise brain regions involved. Neuroimaging studies of sequence learning suggest involvement of lateral regions of temporal lobe (Brodmann's Areas 20 and 21). The only evidence of hippocampal system involvement in sequence learning is provided by Rauch, Savage, et al. (1997) and then only for subjects with obsessive–compulsive disorder. In contrast, the medial temporal lobe region, part of the hippocampal system, is emphasized in more general theories of memory and learning. One possible interpretation of the discrepancy reflects our inferential identification of lateral temporal region with cross-dimensional sequence learning. Lateral temporal cortex is activated in single-task (i.e., one-dimension) sequence learning. We've argued, on the basis of polysensory receptivity of the temporal lobe and on the basis of similarities in performance between single-dimension and cross-dimensional sequence learning, that the temporal lobe is also involved in the cross-dimensional case. Cross-dimensional sequence learning might activate temporal regions more medial than has been observed during single-task learning. That is, the precise foci of learning within the ventral stream might differ depending on particularities of the input dimensions, similar to differences that have been observed for single-task learning of spatial and color sequences (see Hazeltine et al., 1997). This point underscores the need for neuroimaging studies of cross-dimensional sequence learning.

In addition, failures to detect hippocampal activation during learning and memory studies in which hippocampal activity is expected have been described in the imaging literature, especially in studies involving PET (see N. J. Cohen et al., 1999, for a review of this issue). Thus, relative failure to observe hippocampal activation in SRT learning may not be particularly diagnostic of the role of hippocampal function.

Neuropsychological studies have provided an alternative way to assess the role of the hippocampus in sequence learning. Early reports suggested that amnesic patients with medial temporal lobe damage exhibit SRT learning under single-task conditions (Nissen et al., 1989). It is noteworthy, however, that learning by the amnesic patients did not appear normal, showing an approximate 40% reduction in the measure of sequence learning compared with control subjects. Although not reliable, this reduction is consistent with residual learning in our hypothesized unidimensional system and impaired learning in the multidimensional system.

A more recent neuropsychological study has implicated the hippocampal system in SRT single-task learning (Curran, 1997). Although the amnesic patients in this study again showed substantial preservation of learning, they were impaired in learning higher order associations in which a current event is predicted not by the preceding event but by the context of two preceding events. In essence, context utilization was reduced in the patients, a function typically associated with hippocampus. As we elaborate later, we propose that context enhancement is a primary feature of a sequential system capable of multidimensional learning.

The role of the hippocampus in sequence learning has also been explored in neurophysiological studies. Woods, Dudchenko, Robtsek, and Eichenbaum (2000) trained rats to run a T maze in which the animals were required to alternate between left and right turns on successive runs. Such a case can be conceptualized as a series of actions, the first always occurring down the stem of the maze (Action 1) and the second sometimes involving a turn to the left (Action 2) or a turn to the right (Action 3). Indeed, because the rats followed different return paths to the starting point (Actions 4 and 5), the general sequence can be schematized as 124135124135. . .. Such sequences have a syntax that is analogous to the ambiguous sequences in human SRT studies (A. Cohen et al., 1990), with certain transitions being dictated by a context defined by remote events. Cellular activity in the hippocampus was correlated with such contextual associations. For example, when the animal was in the stem (Action 1), some cells were activated when the forthcoming action required a left turn; other cells only became active when the context specified a right turn (but see Bower, Euston, Gebara, & McNaughton, 2001). These results indicate that the context of prior movements was used together with the current movement to code for the upcoming direction of turn.

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[8] The hippocampal system typically refers not only to the subcortical hippocampus itself but includes surrounding cortical regions, sometimes called *parahippocampus*, that are critical to hippocampal functioning (e.g., N. J. Cohen et al., 1999).

Thus, although additional investigation would be useful, some evidence does suggest hippocampal involvement in SRT learning under conditions that invoke our proposed multidimensional, ventral system. Such conclusion raises questions about other issues associated with discussions of the hippocampal system—representational similarities between the hippocampal and ventral systems, explicit versus implicit memory, declarative versus procedural memory, and competition with striatal- (basal ganglia) based learning.

Comparison of hippocampus-based coding and ventral system coding. Although we've emphasized the ventral system's capability for cross-dimensional association, we've also pointed out that this system can learn single-dimension associations as long as no events relevant to a different task produce lack of correlation between successive events. Our conclusion that ventral system representation rests on task-specified events—that is, categorized events—adds a new perspective about the code for single-dimension learning. We presume that this code involves association of events that are in some manner interpreted with respect to other events in the world. For spatial stimuli we suggest, in accord with Willingham (1998), that ventral system representation is allocentric. Such a code specifies object locations in relation to other objects in the external world rather than with respect to egocentric (i.e., body-centered) coordinates. This kind of categorical representation may be a special case of cross-dimensional learning. For example, allocentric representation may be one in which object identities are bound to different external locations. It is these bound entities that then may be associated one with another in the course of sequence learning.

The claim of categorical representation for the ventral system bears additional similarity to current views about the nature of hippocampal coding. For the hippocampus, the claim is not that it just creates cross-dimensional association but that it creates relational associations. N. J. Cohen et al. (1999), for example, suggest that "the hippocampal system is critically involved in . . . relational memory processing. This system binds together converging inputs from various processors, permitting it to mediate representations of the relationships among various objects and events" (p. 94). The apparent similarity of code between our proposed ventral system and the hippocampal system constitutes an additional reason for assuming these two are congruent.

Implicit versus explicit learning. According to our theory, the multidimensional system, although being critical for the emergence of explicit awareness, is capable of implicit learning. This hypothesis is at odds with theories of the hippocampus that emphasize a role limited to explicit memory (see N. J. Cohen et al., 1999, for a critical review). A recent study by Chun and Phelps (1999) provides new evidence consistent with our proposals. In their view, the hippocampus provides contextual learning, or multidimensional binding, and at least in some circumstances does so implicitly.

Their task involved detection of a target shape among nontargets. The shapes appeared at various locations across trials. Control participants not only became faster across trials at detecting the target when present, but they exhibited an additional benefit when the target appeared in familiar contexts as defined by color–location combinations of the background nontargets. This form of learning is indicative of cross-dimensional binding between shape, color, and location information. Patients with amnesia resulting from medial temporal lobe damage also showed a reduction in RT across trials. However, they failed to exhibit any benefit from the context. It is important to note that from the view of our theory, the context benefit shown by the control subjects was entirely implicit: On a recognition memory test, the controls were unable to discriminate between familiar and unfamiliar contexts.

N. J. Cohen et al. (1999), reviewing a range of memory tasks involving words, nonsense words, objects, and scenes, further challenged a link between hippocampal function and explicit memory. In accord with their review, as well as the Chun and Phelps (1999) study, we suggest that the more fundamental distinction is between a system that is restricted to learning within-dimension relationships and a system capable of multidimensional association. Although a multidimensional learning system may confer the possibility of transfer to new modes of expression, which is the essence of awareness, such a system by no means requires that learning be explicit. We see these developments as representing a shift from what we call a "descriptive" distinction between two memory systems (implicit vs. explicit) to a "computation-based" distinction (unidimensional vs. cross-dimensional association).

Procedural versus declarative memory and associated subcortical brain regions. A second major characterization of memory systems has been a distinction between procedural and declarative memory (see Gupta & Cohen, 2002, for an elaboration). This view is closely related to the implicit–explicit distinction, with the declarative system hypothesized to be dependent on a hippocampal learning system. Procedural memory, in contrast, has been associated with subcortical structures of the basal ganglia (e.g., Eichenbaum & Cohen, 2001). Procedures, by their nature, involve a series of events or actions across time. As such, SRT learning has typically been viewed as a form of procedural learning.

At a conceptual level, we believe the term *procedural* fails to provide a useful characterization between memory systems. We've distinguished between a system of modules located in dorsal brain regions that are restricted to the formation of unidimensional associations and a system located in more ventral brain regions capable of multidimensional associations. The term *procedural* appears appropriate not only for the former but also for the latter. Both systems are responsible for representing a series of events from which action flows.

Regarding subcortical brain involvement, PET studies of SRT learning have, as we've described in our core studies, shown that activation changes within the basal ganglia are associated with learning in both the dorsal and ventral cortical systems (Grafton et al., 1995; Hazeltine et al., 1997). Rauch and colleagues (Rauch, Whalen, et al., 1997; Rauch et al., 1998) also report basal ganglia activation during single-task learning: That activation co-occurs with activation of ventral system cortical regions. Such results seem at odds with proposals that declarative and procedural systems are dependent on different cortical and subcortical systems.

Until this point in the article, we have not emphasized the role of the basal ganglia within sequence learning. Nonetheless, the presence of basal ganglia activity even in ventral-based sequence learning raises important issues about its computational role in memory.

Why, therefore, might the basal ganglia be involved with both learning systems? Consider a study by Hayes, Davidson, Keele, and Rafal (1998) that examined set shifting by patients with

Parkinson's disease. An explicit cue, the word *Color* or *Shape*, was used to indicate the task-relevant dimension. The time to shift set is revealed by the difference in RTs on trials requiring a set shift and those trials not requiring a shift. Patients with Parkinson's disease exhibited an increase in shift time compared with control subjects, a result replicated by Cools, Barker, Sahakian, and Robbins (2001) for shifts between letter naming and digit naming. Hayes and colleagues also examined shifting in the production of sequential movements. Subjects were taught two different key-press sequences, each sequence three key-presses in length and each cued by a different letter, *A* or *B*. After practicing each sequence alone, subjects were given explicit, compound cues (*AA*, *BB*, *AB*, or *BA*) that described two successive sequences to be performed in rapid order. Patients with Parkinson's disease exhibited increased transition times between the two subsequences when their identity changed.

The results of Hayes et al. (1998) and Cools et al. (2001) suggest that the basal ganglia provide a change or transition function that is invoked for both cognitive tasks (see also Owens et al., 1993) and motor tasks, including sequence learning and/or production. Typically, a sequence is internally represented as a series of actions, hierarchically arranged (see Keele, Cohen, & Ivry, 1990, for a review). We propose that the basal ganglia provide a "proceduralization" function in the real-time conversion from one segmental representation of a sequence to another.

The neuroimaging results suggest that this function can be applied to representations supported within both the dorsal and ventral systems of the cortex. Single-cell recordings in the basal ganglia of the primate provide converging evidence that this structure is important for linking sequential representations and supporting transitions through the sequence (Brotchie, Iansek, & Horne, 1991; Kermadi, Jurquet, Arzi, & Joseph, 1993). This observation mirrors similar observations in supplementary motor cortex (Tanji & Shima, 1994), part of the dorsal system, and in prefrontal cortex (Barone & Joseph, 1989), part of the ventral system. When coupled with neuroanatomical evidence for interconnections of both supplementary motor cortex and prefrontal cortex with basal ganglia (e.g., Alexander, Crutcher, & DeLong, 1990), the neural evidence is compelling and consistent with our neuroimaging observations that the basal ganglia participate in both dorsal and ventral sequence-learning systems.

A case study regarding procedural versus declarative memory. It has been argued that procedural and declarative memory systems, based respectively on basal ganglia and hippocampal systems, should be viewed as competitive processes (e.g., Poldrack et al., 2001). Indeed, the lack of overlap in the imaging studies with the SRT task could be seen as consistent with this view. However, we favor a hypothesis that the two systems can be engaged in parallel, consistent with our prior analysis of the behavioral data. We suggest that evidence supporting the competition hypothesis reflects the fact that the contribution of different computational systems will vary as a function of task demands (see Gupta & Cohen, 2002, for a similar view).

Let us examine from this viewpoint a recent imaging study reported by Poldrack et al. (2001). These researchers contrasted hippocampal and basal ganglia brain activity during the learning of two different versions of a "weather" prediction task. In the feedback version, a label, *Rain?* or *Sunshine?,* was paired with a complex visual pattern on each trial, the question mark indicating to subjects that they should judge whether the label was correct for that pattern. Four seconds later, feedback was provided by the correct pairing. In the paired associate version of the task, only the correct pairings of pattern and label (rain or sunshine) were presented, and each pairing was repeated after 4 s. When memory of the pairings was tested at the end of the scanning session, subjects achieved about 85% accuracy for each of the two task versions.

Despite this similarity in performance, the pattern of brain activation was quite different for the two conditions. For the feedback version, medial temporal cortex was activated early in the learning period. As learning progressed, this activation regressed and activity within the basal ganglia increased. Moreover, across subjects there was a negative correlation between amount of medial-temporal activity and caudate activity. In contrast, for the paired associate version, there was little activation of the basal ganglia.

Why did basal ganglia activity increase only in the feedback condition? Poldrack et al. (2001) proposed that only this version led to the development of procedural memory. The reduction in medial temporal lobe activity as basal ganglia became more active was interpreted as reflecting competition between the two systems. They assumed that this shift is lacking in the paired associate version because this task solely engages declarative memory. However, this hypothesis is of limited explanatory value without a description of task features and computational processes that underlie procedural versus declarative memory. Lacking such description, there is no way to assess whether one brain system is specialized for one form of memory or the other.

As an alternative to the competition hypothesis, we propose that the increased basal ganglia activity in the feedback condition reflects the operation of the "switch" function outlined above. In the feedback version, a label and a pattern must be retained in working memory until feedback is provided 4 s later. If the initial label was correct, then this information should be bound into long-term memory with the pattern. If the initial label was incorrect, then the information in working memory must be shifted, one label being purged and the correct one installed before association can occur. We hypothesize that such transitions would involve the basal ganglia, similar to how this structure is involved in the transition from one sequence representation to another or from color set to shape set. Note that it is not simply that a new representation is required in working memory. Rather, we assume that the basal ganglia shifting operation is invoked when the new representation must replace an existing, incompatible representation (Cools et al., 2001). Such switches are not required for the paired associate version of the weather task because only correct associations are presented on each trial. Given the absence of representational change, basal ganglia activation would not be expected.

At first glance, it seems that the switching hypothesis would predict reduced basal ganglia activity over time. As learning improves, the need to re-map associations in working memory becomes reduced. However, the visual patterns were complex and unfamiliar, consisting of clusters of different shapes. Under such conditions, the initial stages of the experiment would center on learning to recognize these patterns, and such learning would involve the cross-dimensional binding of shapes to locations, a process we associate with the hippocampal system. Thus, the shifting operation between response categories becomes prominent only after an extended initial learning phase. Indeed, Poldrack et al. (2001) subscribe to this two-phase learning process.

In sum, we suggest that change in activation brain patterns over the course of learning reflects not a shift in balance between two competitive systems but rather results from changes in the computational requirements over time. In imaging studies of SRT learning, stimulus values have been simple (e.g., stimulus location or color). The multidimensional associative system of ventral posterior cortex and the sequence production mechanisms of the basal ganglia may be recruited in a cooperative manner.

On the basis of our analysis of the computational function supplied by the basal ganglia, we predict that activity in those structures would be observed in memory tasks, implicit or explicit, that require the purging of representations that are incompatible with current demands. For example, in one version of directed forgetting, an item is held in working memory for a variable period of several seconds until an instruction is received regarding whether it should be remembered for later use or forgotten (Woodward, Bjork, & Jongeward, 1973). Recent work (W. Marks & Dulaney, 2001) provides no evidence for inhibition of items directed to be forgotten. Presumably, items not to be remembered simply decay from working memory. We predict, however, that in directed forgetting circumstances in which information in working memory must be actively purged, as when it conflicts with current demands on working memory, basal ganglia activation will be correlated with the frequency of the countermanding requirement. Similarly, basal ganglia activation might be observed in so-called "*n*-back" assessments of working memory, when in recall a previous item must be skipped over to allow retrieval of a preceding item.

We readily acknowledge that our hypotheses concerning subcortical contributions to cortical associative systems are tentative. Nonetheless the preceding example, together with new predictions about when basal ganglia activation will be observed in memory tasks, illustrates the utility of a functional approach for disentangling contributions of brain networks to tasks associated with procedural and declarative memory.

Perspectives on Skill

An influential two-system view of cortical function is based on a distinction made by Ungerleider and Mishkin (Ungerleider and Mishkin 1982; see also Van Essen & Maunsell, 1983) concerning the "what" and "where" pathways. As in our theory, the neural division is between a dorsal and a ventral cortical pathway. Although the what–where distinction emphasizes the representation of different perceptual attributes, Goodale and colleagues (Goodale, 1996; Goodale et al., 1991) argued that, computationally, these attributes differ in how they serve cognition and motor skill. They characterized the dichotomy as "what" versus "how." The former, the ventral pathway, is conceptualized in a similar way to how Ungerleider and Mishkin conceptualize it, forming representations that are essential for object identification. Applying the label "how" to the dorsal pathway, emphasizes that this system is essential for visually guided action.

There are some obvious similarities between our theory and the what–where and what–how ideas. These similarities are seen not only in terms of a similar segregation of neural systems, but also in terms of computation. We've proposed that the unidimensional system is composed of encapsulated modules that are immune to interference from secondary tasks. Similarly, Goodale et al. (1991) have argued that the "how" pathway is part of a system involved in directly specified actions. In their view, this system supports automatic motor performance, for example, the processes that allow people to fluently reach and grasp objects (Pisella et al., 2000). Indeed, key sources of evidence for this system come from studies showing dissociations between direct and indirect measures of perception and performance. For example, the widely discussed patient D.F. is able to shape her hand to match a reached-for object but is unable to perceive by conscious report the orientation of the object (Goodale et al., 1991). Also, just as we've suggested that the dorsal, unidimensional system is composed of independent modules, neuropsychological evidence suggests that Goodale's (1996) postulated dorsal system is divisible into modules that support different spatial dimensions such as grasp orientation and reach direction (e.g., Perinin & Vighetto, 1988).

Similarly, the role of the ventral pathway in object recognition emphasizes processes involved in binding information across multiple channels, a central tenet of our theory. Goodale (1996) had assumed that these associations are consciously accessible. Indeed, it is the conscious reports of ventral-based representations that reveal their differences with dorsal representations.

Our two-system theory extends the "what"–"where/how" distinction in a number of novel ways. Whereas Goodale (1996) had focused on the role of their dorsal system in visually guided reaching, we've hypothesized a more general role for this system, proposing modules that provide the representations for an organized series of actions. With respect to the ventral system, our theory emphasizes not its accessibility to consciousness (as opposed to necessity) but its computational character. We suggest this route implements cross-dimensional learning in support of action sequences, in addition to the binding of separate form features into objects. As such, our theory postulates a role for both dorsal and ventral pathways in motor control, and indeed, in the development of skilled behavior, topics to which we now turn.

Implications of a distributed cortical network. On the basis of the data of our core neuroimaging studies (Grafton et al., 1995; Hazeltine et al., 1997), we have proposed distributed cortical networks for sequence representation that extend far beyond traditional "motor" areas. The multidimensional system includes not only premotor cortex but also more anterior regions of prefrontal cortex and posterior cortical regions of the temporal and occipital lobes. The unidimensional system includes supplementary motor cortex and various loci within the parietal lobe.

Although activity in motor cortex is correlated with sequence learning under dual-task conditions (Grafton et al., 1995; Hazeltine et al., 1997), we've suggested that such activity reflects priming from upstream sources of sequence representation in supplementary motor cortex and parietal cortex. The focus of activation within motor cortex that accompanies initial learning exhibits immediate shift with change to finger movements from arm movements or vice versa (Grafton et al., 1998). In contrast, activation focus within the supplementary motor area remains constant across effector change (see also Grafton et al., 1992). Behavioral evidence based on the SRT task as well as other movement tasks also supports the conclusion that sequential representation, both for the unidimensional and the multidimensional system, is relatively abstract, developing prior to the specification of motor effectors (e.g., Chan, Ivry, & Hazeltine, 2000; Fendrich, Healy, & Bourne, 1991; Hazeltine, in press; Keele, Jennings, Jones, Caulton, & Cohen, 1995; Willingham, Wells, & Farrell, 2000).

How relevant are these ideas for real sequential skills such as knitting, speaking, or playing the violin? The evidence in favor of abstract, effector-independent representations derives from SRT experiments that use only short training periods. Real skills, however, often develop over the course of many years. Intuitively, it may seem that these are not effector independent (e.g., ask a violinist to reverse the roles of his or her left and right hands). Considerable evidence, however, both behavioral and neuropsychological, indicates that speech, writing, and musical productions are all represented abstractly and prior to motor specification.

In a classic study with bilingual speakers, MacKay and Bowman (1969; see also MacKay, 1982) observed perfect transfer of practice-induced speed between English and German when meaning and concept order was preserved. Given that the articulatory requirements were vastly different for the two languages, the transferred learning implies a representation more abstract than the specificity of the motor system. Similar conclusions arise from the analysis of handwriting. Writing style is very similar across motor systems of the same person as diverse as fingers, hand, arm, shoulder, foot, or head (Bernstein, 1947, as cited in Keele et al., 1990; Wright, 1990). Lindemann and Wright (1998) examined the improvement in writing with practice by the nondominant hand. They found complete transfer of practice effects to letters that used the same strokes as practice letters, although in different sequential arrangement. No transfer was found to letters composed of unpracticed strokes. Thus, whereas the learning of elementary strokes is hand specific, the sequential arrangement of several strokes to produce unique letters is represented abstractly and prior to the specification of specific hand. A similar conclusion, with the exception of limited co-articulatory representation, applies to typing (Jordan, 1995). With respect to musical production by accomplished pianists, Palmer and Meyer (2000) found transfer of a practiced piece of music to a conceptually similar piece independent of whether hands and fingers were changed.

Thus, it appears that skill acquisition involves the development of abstract representations of successive elements, not only in short-lasting SRT tasks but also in highly practiced skills as diverse as speech, writing, typing, and instrumental music production. Neuropsychological studies also point toward a level of abstract representation for skills using different output modes. For example, typing, writing, and oral spelling rely on a common orthographic code (see Margolin, 1984, and Keele et al., 1990, for reviews). Such results are consistent with observations from our core studies of distributed cortical foci for sequential representation that extend beyond putative "motor" regions.

Evidence from real skills, however, is largely mute on whether abstract, distributed coding reflects dorsal or ventral systems. We've mentioned neuropsychological evidence in support of the modularization of the dorsal system into separable dimensions supporting actions such as reaching and grasping. Of particular concern, however, is whether the ventral system itself is operative in the production of consolidated skills. At present, we do not know of any direct neuropsychological evidence. However, when considering the computational power of the multidimensional system, especially in terms of providing a disambiguating context, the role of such representations for skill learning becomes clearer. We now turn to this issue.

Multidimensional context and the ambiguity problem in sequence learning. At least from an intuitive view, it appears that input from a variety of dimensions aids in the control of the sequential movements that make up a variety of skills. Dribbling a basketball is made easier by visual input of ball motion, the repetitive contact of the ball with the fingertips, and the sounds generated as the ball bounces off the floor. A violinist in an orchestra uses visual information from the written score and from the conductor's movements both in combination with the kinesthetic and auditory information from the just-played passage to determine time and content of succeeding actions. Even as fundamental a skill as speech perception is enhanced under multimodal conditions (e.g., McGurk & McDonald, 1976).

Each of these cases lends credence to the supposition that our proposed multidimensional system is important in the conduct of actual skilled performance. But what accounts for any benefit provided by multidimensional representation? One reason is that the different dimensions provide redundant information and that this redundancy helps ensure that the correct intent is conveyed. Visual observation of articulatory gestures, for example, can be a powerful tool for clarifying speech sounds that differ in subtle ways (Massaro, 1987).

A related reason is that additional dimensions may provide context that helps in learning otherwise very difficult sequences arising out of sequential ambiguity. The problem of ambiguity has long been recognized as one of the core problems for learning and performing complex action series (e.g., Lashley, 1951). For example, the consonants *t* and *r*, combined with the long *i* sound, can yield either *rite* or *tire* depending on their ordering. How is it that the same fundamental units can be associated unambiguously in different order?

A central claim of our theory is that context provided by one dimension can reduce confusion about ambiguous sequence order in another dimension. That is, context may not only yield a representation integrated across dimensions but may ease learning. The critical role of context for reducing ambiguity has been emphasized by many theorists (e.g., Wicklegren, 1979). For example, in MacKay's (1987) model, a word-level concept is differentiated into syllable-level representations, and these in turn are divided into phonological levels. In essence, cues such as the pauses between certain elements in the sequence can help define representational units and serve as a context that helps specify subsequent elements in the sequence. In a somewhat similar manner, Jordan's (1997) connectionist model includes both "state" and "plan" units, with the former representing currently active elements and the latter providing the context within which these elements are invoked. The two sources combine to codetermine the next element.

In our view, the most important source of context in resolving ambiguity is not the context provided by memory of preceding events but context provided by other dimensions. For example, prosodic fluctuations, silent pauses, and visual gestures can provide important segmentation cues for parsing a speech segment. Indeed, cross-dimensional sequential representation might have evolved as a solution to the fundamental ambiguity problem, providing a precondition for the highly intelligent and creative sequential actions that characterize human behavior.

Although limited in number and scope, some SRT studies support the contention that context contributes to disentangling an ambiguous sequence. For example, spatial sequence learning in the SRT task is greater when the intervals between the successive visual–spatial events form a correlated pattern (Shin & Ivry, 2002). Koch and Hoffman (2000) not only found that a temporal pattern of intervals between successive events aided SRT learning when correlated with the SRT sequence but also found an uncorrelated temporal pattern impaired learning (see also Stadler, 1995).

To date, studies of facilitatory contributions of context in the SRT paradigm have generally been limited to temporal context. However, the role of context as a scaffold for learning has been emphasized in one study of language acquisition (Weinert, 1992). Participants were initially exposed to acoustic strings generated from a set of artificial phrase structure rules. In a test phase, they were asked to judge the grammaticality of new and old strings. The critical experimental manipulation was whether each phrase had been presented with a characteristic prosody during the training period. Only children of normal language-learning capability and who were exposed to the prosodically enriched input were able to learn the grammatical structure. We interpret these results as indicating that prosodic information constitutes a dimension of context, which if integrated with word information, enhances learning. Note that the context in this experiment was introduced implicitly and the subjects did not become aware of the prosody manipulation.

Missing from studies of context is a direct test of our prediction that the utility of cross-dimensional context for disambiguation is limited to the multidimensional system. We predict, for example, that adding a color sequence that is correlated with an ambiguous visual–spatial sequence should enhance learning beyond that of the ambiguous visual–spatial task by itself. Such context should not aid learning the ambiguous sequence in the presence of an additional random task, given our assumption that such learning would be restricted to isolated modules of the unidimensional system.

We further predict that the contextual benefit for single-task learning would occur only if the context itself were relevant to some task, that is, if it were attended. However, in each of the studies cited as providing evidence of contextual enhancement of learning, including the language-learning study of Weinert (1992), the temporal or prosodic context was incidental. One possibility is that temporal and prosodic contexts are special because they may not be separable from the dimensions they modify (Garner & Felfoldy, 1970). Indeed, Shin and Ivry (2002) showed that learning of a visual–spatial sequence could occur independently of the temporal sequence. The reverse was not true. A temporal pattern, therefore, seems inseparable from the events that it marks. Prosody, although being defined over a series of acoustic events, is a product of the same auditory dimension that identifies each individual event. Thus, attending to acoustic events of individual speech elements may unavoidably allow access of prosody to a learning mechanism.

Final Comments

One of our major goals for this article has been to bring together findings from different disciplines in an effort to understand sequential representation and acquisition. Although we recognize limitations associated with our focus on the SRT task, a rich literature based on behavioral, neuropsychological, and neuroimaging studies allows for a synthesis unique among sequence-learning paradigms. The SRT methodology also has provided fertile ground for developing a theory based on functional concepts. We believe that our emphasis on functional differences that characterize different learning systems will serve as an important springboard for future experiments on the cognitive and neural mechanisms of skilled behavior.

A second goal has been to place sequence learning within a broader context of human cognition. The learning and production of sequential action is a hallmark of human cognition. As revealed by the neuroimaging studies, a broad network of neural regions is implicated in the control and acquisition of sequential actions. We have described a division between two general learning systems. The unidimensional system can extract regularities along a single channel of information, using this limited information to generate predictions for future actions. This encapsulation is similar to how motor control theorists have conceptualized the operation of a dorsal pathway for the direct control of action (e.g., Goodale, 1996).

In contrast, the multidimensional system spans a network that includes regions associated with many aspects of higher cognition, suggesting that sequential behavior is not readily separable from cognition. Notable among these are prefrontal cortex and the temporal lobe, regions implicated in executive control and context-dependent learning (see Eichenbaum, 2000; Monsell & Driver, 2000). Executive processes constrain behavior to be consistent within a hierarchy of goals rather than subject to constantly changing environmental influences (e.g., Norman & Shallice, 1986). We suggest that the activation in the prefrontal cortex reflects the need to assure coherence of lower level sequential activity to higher level goals. Such associations may be essential for behaviors as disparate as sequence learning, problem solving, and analogical reasoning. In the case of sequence representation, we speculate that interactions between prefrontal cortex and ventral regions of posterior cortex support hierarchical representations that are critical for solving the ambiguity problem. Through this form of complex, context-dependent representation, actions are prevented from branching into inappropriate behavior that might be triggered by similarity of sequence components to those in other sequences.

In his analysis of comparative intelligence, Rozin (1976) argued that simpler cognitive systems are dominated by relatively isolated processing mechanisms, similar to the encapsulated modules proposed by Fodor (1983). The unidimensional learning system of our theory is composed of such modules. Note that these modules can support quite sophisticated behaviors such as depth perception, reaching, and grasping; indeed their computational efficiency may benefit from their encapsulation (e.g., Arbib, 1990). In Rozin's view, the emergence of interactions between these modules is a signature of more complex cognitive processing capabilities. For example, reading was only possible once processes associated with the analysis of visual symbols were able to access representations of the phonemes of speech. The multidimensional system of our theory likely confers this advantage for learning and memory across multiple domains including the representation of complex sequential behaviors.

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Appendix

Comments on Frensch, Wenke, and Rünger (1999)

Frensch, Wenke, and Rünger (1999) reported some findings they claimed to contradict our theory. They examined learning scores from dual-task and single-task tests immediately following initial dual-task practice. According to our theory these learning scores should be identical because during dual-task learning, only the unidimensional system is involved. Lacking single-task experience that would enable the second system, only knowledge from one system is available at initial transfer and prior to the opportunity for new learning. A distinguishing feature of Frensch et al.'s study was the addition of a random-control group in which a repeated sequence was introduced only after the dual-task test. This group offers a control for sequence learning that might have occurred after transfer to single-task conditions but prior to assessment of single-task learning. The control is needed in part because the single-task transfer assessment in the Frensch et al. study made use of the second, not first, block of single-task sequence learning. The mean learning scores and the (interindividual) standard deviations are given in Table A1 for the hybrid sequence used for two groups of participants, a sequence very similar to that used in our core behavioral and neuroimaging studies.

In a first analysis, Frensch et al. (1999) showed that the mean single-task learning score (95 ms) from the second assessment block was larger than the prior dual-task learning score (70 ms). However, the larger single-task score could be accounted for by new learning, which could have occurred in the first and second test blocks following dual-task learning. In this regard, it is useful to estimate from their Figure 1 the amount of expressed learning on the first block of single-task trials. We estimate this to be about 45 ms, a value less and not more than the 70-ms dual-task score. Thus, it is quite plausible that the substantially larger second-block score of 95 ms is attributable to new learning.

New learning that has occurred by the second transfer block can be estimated by the single-task score in the group that had random events during prior dual-task learning, experiencing the sequence only at transfer to the single-task condition. This new-learning score is estimated, at second block, to be 42 ms. The larger single-task score in the sequence group (95 ms), by our theory, could be due to a compound of transferred learning from one system and new learning in a second system. If, as in the Frensch et al. (1999) view, there is only a single system of learning, in which the secondary task suppresses some expression of learning, the fully expressed learning following secondary-task removal should be larger than the sum of new learning plus learning assessed under dual-task conditions. Such is not the case. The sum of the two learning scores, 42-ms new learning and 70-ms pretransfer learning, is more and not less than the 95-ms single-task score of the second trial block. Regardless of view, therefore, this analysis leads to the conclusion that after dual-task practice, dual-task tests and single-task tests give equivalent results, as implied by our theory.

Frensch et al. (1999) ran a second kind of analysis motivated by the consideration that the single-task test following random dual-task training might give too high an estimate of the learning that could have occurred following secondary-task removal for the sequence group. This consideration was based on the typical shape of practice curves in which increments would be expected to be large for a group with no prior practice and small for a group with already substantial practice, albeit under dual-task conditions. The second kind of analysis led to the conclusion that single-task tests give higher scores than dual-task tests (or reflect learning that finds no expression in dual-task tests). However, artifacts plague this second analysis.

Table A1
Means (and Standard Deviations) of Learning Scores, in Milliseconds

Group	Dual-task test	Single-task test
Sequence	70 (64)	95 (49)
Random	0 (44)[a]	42 (33)

Note. "Sequence" refers to a group that received a systematic hybrid sequence during dual-task training. "Random" refers to a group that received randomly ordered events during dual-task training.

[a] The data for this cell are not reported by Frensch et al. (1999) but were kindly provided by Peter Frensch. The individual learning scores in this test, which was a dummy comparison between random blocks, should deviate from zero only by chance.

This second analysis intended to compare single-task scores in the systematic and random groups under conditions of zero scores in the dual-task tests. The argument is that even when there is zero expressed dual-task learning, some learning nonetheless exists, which will be revealed when the suppressing effect of the secondary task is removed. On the basis of this rationale, Frensch et al. (1999) computed the linear regressions of single-task scores on dual-task scores for both the systematic and random group and compared the intercepts, which they took as estimates of single-task scores when dual-task scores had been zero. Intercepts were larger in the systematic group (79 ms) than in the random group (42 ms). This finding, however, is caused not necessarily by differences in learning but by, first, the effects of measurement errors on intercepts (see Klauer et al., 1998) and by, second, the restriction of these effects to the systematic group.

Let X be the dual-task learning scores, with X_T being the true scores and X_e the measurement errors; similarly, let Y, Y_T, and Y_e be the observed scores, true scores, and measurement errors of single-task learning scores, respectively. Then, for observed values, the slope of the linear regression is $b = \mathrm{cov}(X, Y)/\mathrm{var}(X) = \mathrm{cov}(X_T, Y_T)/\mathrm{var}(X)$ and the intercept is $a = \mu_Y - b\mu_X$, with $\mu_Y = \mu_{YT}$ and $\mu_X = \mu_{XT}$ because $\mu_{Ye} = \mu_{Xe} = 0$. For the true scores the slope is $b_T = \mathrm{cov}(X_T, Y_T)/\mathrm{var}(X_T)$, with $b_T \geq b$ for $\mathrm{cov}(X_T, Y_T) > 0$ because $\mathrm{var}(X_T) \leq \mathrm{var}(X) = \mathrm{var}(X_T) + \mathrm{var}(X_e)$; the intercept is $a_T = \mu_Y - b_T\mu_X$, which for $\mu_Y \geq 0$, $\mu_X \geq 0$, and $b_T \geq 0$ is at most as large as a; whenever $\mathrm{var}(X_e)$ is larger than 0, a will overestimate the true intercept a_T, provided that $\mu_X > 0$. Thus, the overestimation of the true intercept will be present in the systematic group with $\mu_X > 0$, but not in the random group with $\mu_X = 0$. This accounts for the results obtained by Frensch et al. (1999) in principle, which otherwise seem to contradict the results of their first kind of analyses.

Of course, an account in terms of an artifact resulting from measurement errors does not really exclude the possibility that there is a difference in true intercepts in addition. Therefore, one might ask whether the measurement error needed to account for the difference in intercepts is of a reasonable size. In the random group the intercept was estimated as 42 ms; the slope was essentially 0. Thus $\mathrm{cov}(X_T, Y_T) = 0$, which is expected because in the dual-task test all deviations from 0 should be measurement errors. If, for the systematic group, we take the means of Table A1 as parameters $\mu_X = 70$ and $\mu_Y = 95$ ms, the true slope b_T should be 0.76 to obtain an intercept of 42 ms. This contrasts with the slope b of 0.23 reported by Frensch et al. (1999). The ratio b/b_T is equal to the reliability $\mathrm{var}(X_T)/\mathrm{var}(X)$. With a total variance of 64^2 ms^2 in the systematic group (see Table A1), we obtain as estimates $\mathrm{var}(X_T) = 1240$ ms^2, $\sigma(X_e) = 53$ ms. This error variance is well within the confidence interval of the estimate of the measurement error given by the variability of the learning scores in the dual-task test of the random group; when the 95% confidence limits for the true variance are given as standard deviations, they are 36 and 58 ms. Thus, there seems to be no really good reason for the claim that the second kind of analysis, in contrast to the first one, contradicts the present theory of two learning systems.

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