Journal Club

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Does Fast Learning Depend on Declarative Mechanisms?

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Review of Keisler and Shadmehr

A skilled pianist can verbally report a particular piece's sequence of notes or she can execute the sequence with her fingers. There are two types of memory processes involved here: a memory that can be declared (naming the notes) and a procedural memory that can be implemented (pressing the keys in the correct order). The study of patients with medial temporal lobe lesions, such as HM, provides compelling evidence that these processes are neurally distinct. Patients such as HM are able to learn new motor skills and maintain those skills over time, without being aware that they have learned the skill (Scoville and Milner, 1957; Corkin, 1968). These studies were foundational in cognitive science, helping set forth productive literature exploring the domain and mechanisms associated with declarative and procedural learning.

The serial reaction time task (SRTT) was developed as a tool to examine the operation of procedural and declarative processes simultaneously (Nissen and Bullemer, 1987). In the SRTT, participants are presented a series of visual cues at different spatial locations and instructed to press corresponding buttons. The series of stimuli can be random or can follow a repeated sequence. When the series follows a sequence, participants show behavioral evidence of learning, in that their reaction time (RT) decreases. Improvements in RT occur even when participants are unable to verbalize what they learned, or even to be aware that the stimuli followed a sequence. Subjects also can gain explicit knowledge of a sequence if subtle changes are made to the task, such as increasing repetitions or the regularity of the stimulus pattern.

A cognitive task cannot be taken as a pure measure of a single cognitive mechanism (Jacoby, 1991), however, and SRTT is no exception. In the example of sequence learning, both declarative and procedural processes are in operation. These differing components can interact at different stages during encoding, storage, consolidation, and retrieval. The degree to which each process contributes to a given task can only be teased apart with careful experimental manipulations. In the case of the SRTT, the involvement of distinct memory systems suggests that introducing a competing memory task (for either system) after the initial learning should lead to competition with the corresponding component of the sequence learning task, and would therefore lead to decreased performance at later stages. In practice, the memory tasks are performed only after the motor task is complete, suggesting that any interaction found is due to an effect on consolidation of the memory, rather than on attention or encoding demands of a dual task.

In a series of experiments using the SRTT and word list learning, Brown and Robertson (2007) showed that there is an interaction between declarative and procedural memories during consolidation, and that this effect was bidirectional. In these studies, the SRTT had a substantial declarative component. Participants could verbally report the sequence of button presses, just like a skilled pianist can report the notes of a piano piece. Was the interaction reported by Brown and Robertson (2007) a direct result of a verbal rehearsal process? Moreover, are procedural motor tasks without a clear declarative component also susceptible to interference?

In a recent issue of *The Journal of Neuroscience*, Keisler and Shadmehr (2010) provided strong experimental evidence that the antagonism between declarative memory and motor learning is not limited to tasks that involve a seemingly direct verbalizable component. Rather, they show similar interference between a verbal learning task and force-field adaptation. The authors had subjects perform reaching movements to a single target while grasping the handle of a robotic arm that introduced one of two velocity-dependent force fields. Depending on the experiment, subjects received a different combination of force fields. Immediately following the reaching blocks, an interfering 3 min word task was administered; either word-pair learning or a vowel-counting task (Keisler and Shadmehr, 2010, their Fig. 1). Word-pair learning was chosen to tax the declarative memory network, and vowel counting was assumed to not require this system. This 3 min secondary task was then followed by reaches in an error clamp, a technique for quantifying the memory of motor adaptation. This is achieved by measuring the aftereffect of

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reach trajectories without subjects experiencing an error.

Motor adaptation is thought to engage two learning mechanisms that operate on different time scales and act in concert to achieve the desired skill (Smith et al., 2006). It is as yet unclear which neural circuits underlie these two learning components, but the fast process is thought to be dominant at the start of adaptation, whereas the slow process gradually builds over time and eventually accounts for the majority of learning. Previous work has shown that the slow process also decays more gradually, producing aftereffects over much longer intervals. Therefore, one can probe the amount of learning that the slow system has achieved long after the learned force field has been removed.

In their first experiment, Keisler and Shadmehr (2010) had subjects perform 384 reaches in one force field (A), followed by 19 reaches in a force field with forces in the opposite direction (B). Participants then performed one of the two interfering tasks (word-pair learning or vowel-counting task) and, finally, performed reaches in an error clamp. This combination of conditions (hundreds of reaches in A, 19 in B) will show up in the error clamp as a summation of an aftereffect for the slow process from field A and the fast process from field B. The results (Keisler and Shadmehr, 2010, their Fig. 2) showed that the word-pair learning task selectively abolished the aftereffect from the fast process of field B, while retaining the memory trace formed by the slow process.

These results more clearly delineate the processes involved in the interaction between declarative and motor systems. Specifically, the interaction is limited to the fast system, a process that primarily operates when subjects are aware of the perturbation and are making substantial changes in behavior to compensate for large errors. This is quite different from a task in which a visuomotor rotation or force field is introduced gradually, such that participants are not aware of the environmental change. Under such conditions, motor adaptation follows a curve that indicates that only slow process learning is occurring. We would expect that, if the word-pair task followed adaptation under gradual conditions, the motor memory would not be affected.

One interpretation of these results is that word-pair learning interferes with the fast process of motor adaptation by increasing competition for a resource that is shared by both the declarative and motor memory networks. An alternative explanation is that the fast process is a verbalizable component of motor adaptation that is encoded within the declarative memory system itself. Under normal conditions, this verbalizable fast component is used to rapidly compensate for large motor errors, whereas the slow process gains momentum with training. Once the error is reduced and the slow process can stabilize the adapted skill, the verbalizable, fast component is no longer necessary. Consequently, this may help lead to new ideas concerning the difficulty of verbalizing well learned motor skills.

This hypothesis could help explain the differences in learning of abrupt and gradual perturbations, which are with and without awareness, respectively. For instance, it could be that following an abrupt perturbation (and a large error), subjects adopt a verbalizable compensatory strategy (e.g., more to the right) that is maintained and updated by the declarative system. If this, or something like it, is true, the question remains as to what type of declarative knowledge it is and what neural circuits are involved. Korsakoff's patients and amnesiacs, aside from some results with HM, have not been reported to have decrements in the initial stages of motor learning that correspond with the fast system (Weiner et al., 1983; Shadmehr et al., 1998). These patients have intact language, but impaired memory processing. It remains to be seen if patients with severe language problems or impairments of verbal working memory show evidence of the fast process during adaptation.

It would be surprising if encoding any declarative memory could interfere with motor memory. Future work should focus not only on what motor tasks are susceptible, but also what types of declarative memory tasks interact with the consolidation of motor adaptation. To date, studies on interactions of consolidation in motor skill learning have tended to rely on verbal tasks. It would be interesting if nonverbal declarative tasks, such as learning fractal patterns, failed to produce interference during consolidation of force-field learning. Also, the bidirectional interaction seen in Brown and Robertson's (2007) studies has yet to be established with this paradigm.

Keisler and Shadmehr's (2010) article is an important contribution to the literature because it suggests that the retention of motor memories may be best when a participant cannot report learning, and that the fast process may be a declarative mechanism. These results are intriguing and potentially challenge a great deal of established thought on the taxonomy of memory. No matter what the subsequent work on this topic discovers, it is bound to be of interest to a diverse group of neuroscientists.

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