Ipsilateral sensorimotor regions and motor sequence learning

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Recently, Boyd and Winstein tested three groups of individuals with damage to unilateral sensorimotor areas on a version of the serial reaction time task performed with the ipsilesional hand. Only when the individuals were provided in advance with explicit knowledge of the motor sequence were they able to benefit behaviorally from the sequence. Despite aspects of the experimental procedure and the subject selection that make it difficult to draw strong conclusions, these results add to growing evidence that sensorimotor structures contribute to the formation of abstract representations that affect more than ipsilateral effectors.

One of the most productive insights of modern cognitive psychology is the distinction between implicit and explicit memory. This schism has helped to define many of the questions posed by psychologists and to establish thriving subfields of research. Implicit learning itself is an umbrella term for many phenomena, including motor learning. Investigations probing the neural substrate of motor learning have reshaped our understanding of the brain structures critical for motor control. A recent study by Boyd and Winstein continues this tradition, as well as exploring the relationship between implicit and explicit learning.

The SRT task

Boyd and Winstein used a motor sequence learning task called the serial reaction time (SRT) task, first introduced by Nissen and Bullemer. The SRT task has been frequently used to assess implicit learning and also to investigate the relationship between implicit and explicit learning. It involves a series of choice-reaction-time trials that require either a random series or a repeating sequence of responses. Typically, subjects are trained for several minutes with blocks of trials that require sequential responses and are then tested on probe trials that require random responses. The increase in reaction times for the random trials compared with the preceding sequence trials provides a measure of sequence learning. It has been demonstrated that subjects can show robust learning scores (between 30–100 ms) but at the same time report that they have no awareness of the sequence and perform at chance on tests of explicit knowledge.

Boyd and Winstein tested twelve individuals on the SRT task who had chronic stroke affecting unilateral sensorimotor areas. There was considerable heterogeneity among the locations of the strokes: seven of the subjects had cortical lesions in the left hemisphere, including the parietal lobe, whereas the remaining five had lesions that involved subcortical structures on either side. How the location of the lesion affected performance was not addressed by the study. This omission is unfortunate because, although both cortical and subcortical structures are involved sensorimotor processes, it is unlikely that their roles are identical.

The subjects were divided into three groups of four subjects, with the subcortical lesions distributed as evenly as possible, and each group received a different experimental protocol. The ‘unaware’ group performed the task for a single session and was exposed to 24 cycles of the sequence. The ‘explicit knowledge’ group was explicitly taught the sequence before performing the same version of the task. This teaching procedure did not include producing any responses but instead consisted of schematic representations of the sequence, and pre-tests to assess when this information had been explicitly learned. The ‘extended practice’ group repeated the same procedure used by the unaware group on three consecutive days, without the explicit training. All subjects performed the SRT task with the hand ipsilateral to the side of lesion.

After the SRT task, the groups completed three tests to assess their explicit knowledge of the sequence. No learning without explicit knowledge

The most prominent finding from the study was that neither the unaware nor the extended-practice group showed any evidence of sequence learning. These individuals showed nearly constant reaction times throughout training regardless of whether the responses occurred in a random order or a sequence. By contrast, the explicit knowledge group demonstrated robust learning, with the increase in RT for the random trials being nearly 50 ms. Explicit knowledge appeared to be restricted to this group as well, as only these subjects were able to recognize the sequence consistently.

Several aspects of this study, however, suggest that these findings should be evaluated with caution. First, the three groups were heterogeneous in terms of the stroke locations and were small, comprising only four individuals each. Second, except in the case of the extended practice group, exposure to the sequence was fairly limited, less than is typical in SRT experiments. This could be particularly important given that most of the subjects performed the task with their left hand, which was likely to be non-dominant before the stroke. Moreover, the sequence used by the researchers was fairly complex, potentially slowing the acquisition of sequence knowledge. Finally, the absence of age-matched controls makes it difficult to place the observed levels of performance in context.

The neural substrate of sequence learning

Despite these caveats, Boyd and Winstein’s results have some important implications for theories about the neural substrate of motor sequence learning. Many researchers, relying mostly on evidence from neuroimaging studies, have proposed that complex networks of brain structures support motor sequence learning. However, few, if any, have posited a significant role for ipsilateral sensorimotor structures. In fact, studies that have specifically investigated the role...
of the ipsilateral primary motor cortex in the control of one-handed movements have characterized this structure's primary contribution as being related to planning rather than learning or execution (e.g. Ref. 4).

One potential explanation for the surprising results found by Boyd and Winstein relates to the consistent laterality of the parietal lesions, all of which occur within the left hemisphere. The left parietal cortex is frequently activated during sequence learning in imaging studies. Damage to the left parietal lobe, in contrast to the right parietal lobe, is strongly associated with apraxia, the inability to produce learned movements5,6. Moreover, there is growing evidence that for right-handed individuals, left-hemisphere brain regions are recruited for movements that involve either hand, whereas right-hemisphere regions are recruited primarily for movements involving the left hand7. Thus, the predominance of left-sided damage in this study complicates the interpretation of lack of implicit learning. The subcortical damage was not restricted to the left hemisphere, but there was only one right-hemisphere lesion in each group. The subcortical damage included the basal ganglia and thalamus, which are both associated with sequence learning in the SRT task. In summary, the observed learning deficits might result from the dysfunction of regions other than ipsilateral sensorimotor cortex.

If this hypothesis can be ruled out, then researchers will have to rethink the role of ipsilateral sensorimotor areas in the control of movement. Behavioral studies of the SRT task indicate that the learned sequence representation is sufficiently abstract to transfer to conditions in which novel effectors are used to perform the task. Thus, it is unlikely that this region is involved in the formation of representations that specify particular muscle groups. In this respect, Boyd and Winstein's results challenge accounts that assume sensorimotor areas serve primarily to program and process motor commands for contralateral effector systems. On the other hand (so to speak), their findings might prove useful for developing an understanding of the phenomenon of intermanual transfer, in which learning a sequence with one hand benefits performance with the other.

**Interactions or independence of implicit and explicit learning?**

Along with the learning deficits observed in the unaware and extended-practice groups, the learning ability in the explicit knowledge group is revealing. The intact learning demonstrated by these subjects indicates that the task is sufficiently sensitive to measure the acquisition of sequence knowledge and emphasizes the importance of explicit knowledge in determining the patterns of behavior. Many neuropsychological studies overlook this variable in their assessments of behavioral learning. Such findings would probably not be observable in motor learning tasks that measure individuals' abilities to achieve explicitly learned goals. For example, in canonical versions of the mirror drawing and rotor pursuit tasks, the contributions of explicit learning to performance are not easily identified.

Boyd and Winstein propose that the explicit knowledge possessed by the individuals in the explicit-knowledge group benefited their implicit learning. Further work will be necessary to determine whether the distinct learning patterns demonstrated by the three groups resulted from interactions between implicit and explicit learning systems or from their independence. One might suppose that the development of implicit representations is facilitated by explicit knowledge. Alternatively, the results might reflect deficits in implicit learning for all subjects. Despite volumes of research supporting the distinction between explicit and implicit memory systems, identifying the contributions of each during performance on a given task remains a difficult and controversial endeavor. In particular, that both explicit and implicit learning can contribute to reaction-time improvements in the SRT task has been recognized since the task was first used. Therefore, a plausible account of the reaction-time costs for the random blocks demonstrated by the explicit-knowledge group is that they reflect explicit learning.

Although the findings of Boyd and Winstein do not constrain theorization about the relationship between implicit and explicit learning systems, they do add to the evidence that sensorimotor regions contribute to complex representations that encompass more than contralateral effector systems. How such findings might change our understanding of the roles of the various motor structures remains to be seen.

**References**


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