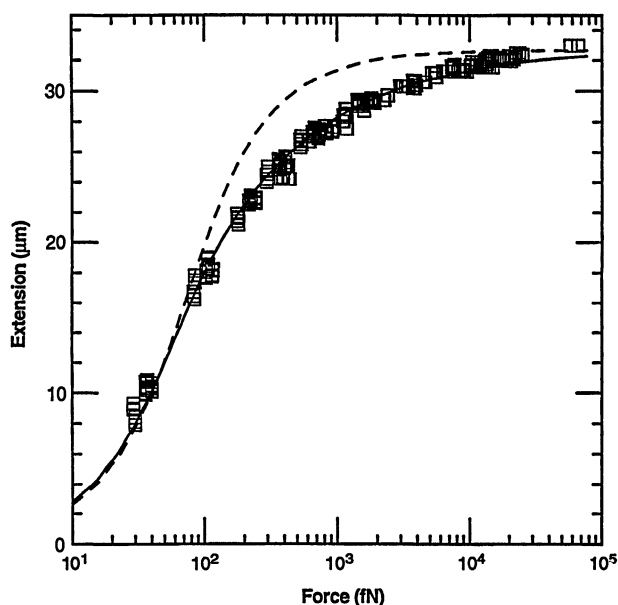


Fig. 1. Squares are experimental force versus extension data for 97 kb λ -DNA dimers from figure 3 of (2); solid line is a fit of the entropic force required to extend a worm-like polymer. The fit parameters are the DNA length ($L = 32.80 \pm 0.10 \mu\text{m}$) and the persistence length ($A = 53.4 \pm 2.3 \text{ nm}$). Shown for comparison (dashed curve) is the freely jointed chain model (2) with $L = 32.7 \mu\text{m}$ and a segment length $b = 100 \text{ nm}$ chosen to fit the small- x data.



rate method for determination of L and A for DNA in solution, in part because the interpretive theory is simple. For example, excluded volume effects are minimal for unstretched DNA with $L \leq 100 \text{ kb}$, and are further reduced by extension. The systematic underestimation of F for $x > 31 \mu\text{m}$ may signal the breakdown of the conventional bending elasticity, because beyond that point the correlation length $(kTA/F)^{1/2}$ becomes less than the double helix period. Further mechanical studies of DNAs that are supercoiled, single-stranded, intrinsically bent, or in contact with proteins should prove even more interesting.

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Explicit and Implicit Learning and Maps of Cortical Motor Output

Alvaro Pascual-Leone *et al.* (1) report that cortical motor output maps change systematically as subjects practice a reaction time task when a sequence of stimuli is patterned, but not when the sequence is random. Implicit learning, measured by comparing improvement in reaction time in patterned conditions with that in random conditions, was correlated with growth in the maps. Pascual-Leone *et al.* assessed explicit learning every 120 trials by asking subjects to try to describe the pattern; by their definition, explicit learning had occurred only when the subject could describe the pattern with complete accuracy. The maps returned to baseline conditions about the time explicit learning occurred. Pascual-

Leone *et al.* suggest that the growth in the maps reflected implicit learning and that the return to baseline reflected some kind of transfer from implicit to explicit learning. This conclusion is post hoc and is inconsistent with other research on implicit learning.

Implicit and explicit learning can occur independently (2, 3), whereas Pascual-Leone *et al.* seem to regard the former as a precursor of the latter. In their experiment (1), subjects were asked to recall the pattern after every block of 120 trials, a procedure that is likely to have induced an explicit learning strategy. Assuming that implicit learning is automatic, both forms of learning probably occurred simultaneously under these conditions. If so,

the changes observed in the maps could reflect a number of stages in implicit learning or explicit learning, or both, and not necessarily a shift from one to the other.

But the maps may not reflect implicit learning at all. Pascual-Leone *et al.* apparently assumed that implicit learning in the reaction time task is a motor process, but that assumption is suspect. Implicit learning is evident in this task even after the mapping of effectors to responses is changed (4) and when subjects are first exposed to the repeating pattern only by watching it without making a response (5). Without a specific rationale for relating implicit learning to the cortical motor output maps, it is not clear that the growth in the maps is related to implicit learning.

It seems more likely that explicit learning caused the growth in the maps. Mean reaction time was about 200 ms five blocks before explicit learning supposedly occurred and was under 100 ms two blocks before. Such fast reaction times suggest that subjects knew in advance what stimulus to expect, which suggests explicit learning had occurred. Reaction times faster than 100 ms have previously been regarded as anticipations, and such responses are strongly correlated with, although perhaps not completely diagnostic of, explicit knowledge (3). The subjects in the study by Pascual-Leone *et al.* had apparently acquired explicit knowledge well before they were so classified, perhaps because the procedure induced an explicit learning strategy. Thus, the greatest growth in the maps was strongly related to explicit learning. Moreover, implicit learning has been shown to begin early in practice, in the first 100 trials (3, 6). At that stage of the experiment of Pascual-Leone *et al.*, there was little, if any, change in the maps. Both the growth in the maps and the return to baseline were most likely caused by explicit learning. Perhaps the growth is caused by increments in explicit knowledge and the return to baseline by overlearning or automatization.

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Response: Stadler criticizes our interpretation of the relationship between implicit learning, explicit learning, and changes in the cortical motor output maps (1). The main issue raised is whether the growth in maps of cortical motor output reflects explicit or implicit learning.

The serial reaction time task (SRTT), as defined in our research design, involved visual afferent input, motor efferent demand, and somatosensory afferent feedback. The role of these different components in the generation of implicit and explicit learning is unclear; however, it seems unlikely that any given component can be neglected. In a task that demands a motor output, there is by definition a motor process that constitutes an integral part of the network associated with the learning process. Modulation of the motor outputs will be necessary to optimize performance of the task regardless of the underlying kind of learning. Therefore, both implicit and explicit learning might be related to changes in cortical motor output maps.

Initially, subjects' performance in the SRTT improved despite their unawareness of the repeating nature of the sequence of trials. Explicit learning might only be inferred when a subject is aware of the repeating character of the sequence of trials. In our study, subjects were asked after each block of trials: "Were the trials presented in random order or was there

any repeating component?" Only if the subject answered "repeating" did we ask the subject to recall the pattern. Therefore, changes in cortical motor output maps that took place before the subject's recognition of a repeating sequence must have been associated with implicit learning. Subjects 1, 3, and 4 recognized the repeating character of the sequence after the fourth block of trials; subject 2 after the third block; and subject 5 after only the second. However, the mean peak amplitude of the cortical motor output to the forearm finger flexors had already increased 160% above the baseline in the last block in which subjects believed that the trials were presented in a random order (Fig. 1). The size of the motor output maps was similarly modulated.

After the subjects knew that the trials

were presented in a repeating sequence, performance was certainly conditioned by aspects of implicit as well as explicit knowledge (2). At that point, the modulation of the cortical output maps may well depend on a combination of implicit and explicit learning. The requirement that subjects learn the entire sequence (1) might be considered an "artificial" cut-off point. However, only such complete explicit knowledge of the task is likely to result in a change in performance strategy (2), as only then does the subject have the capability to use a predictive, anticipatory strategy for the entire sequence. This hypothesis is supported by the dramatic change in the cortical output maps at that point. The change was consistent across subjects despite having occurred after six blocks of trials in subjects 1 and 3, after block 7 in subject 2, after block 8 in subject 4, and only after nine blocks of trials in subject 5 (Fig. 1).

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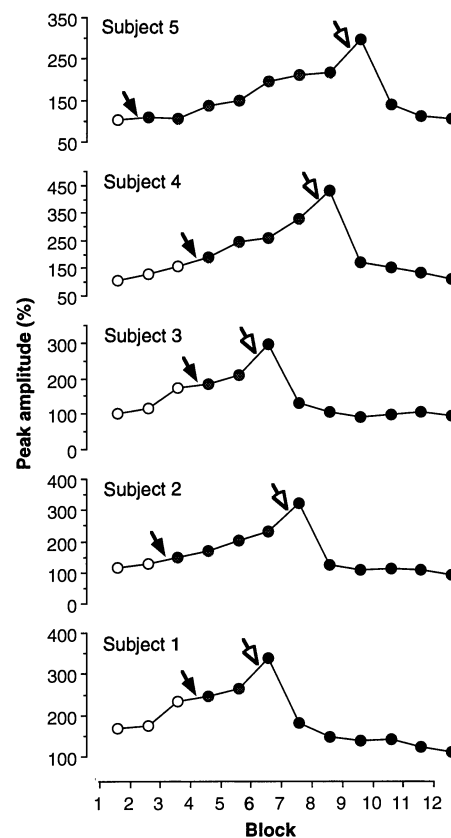
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Fig. 1. Peak amplitude (in percentage of baseline) of the cortical motor outputs to the forearm flexor muscles after each block of trials in the SRTT in all five subjects (7). Filled arrows mark the points at which each subject recognized the repeating order of the sequence of trials. Open arrows mark the point of complete explicit knowledge of the sequence in each subject. Open symbols indicate responses to transcranial magnetic stimulation after blocks of trials when the subject still believed that the order of trials was random. Gray symbols indicate results after blocks where the subject knew that the trials were presented in a repeating order, but before complete explicit knowledge of the sequence was present. Filled symbols indicate results after development of complete explicit knowledge of the sequence.



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