neuronal types[7]. This result suggests an escape network that is distributed across several segments in the hindbrain.

Such data call for a distributed motor control system with built-in redundancy. However, the current study and previous zebrafish studies suggest a more dedicated, discrete command system for motor control. Although touch stimuli cause widespread activation of reticulospinal neurons, the fast, large-angle turn can be eliminated by abolishing the Mauthner cell and its homologs[10]. A slow, large-angle turn persists and may be generated by the rest of the escape network. The fast C-start responses to touch or acoustic stimuli seem to be generated by a dedicated control system, the Mauthner array. Adding credence to this view, the Mauthner neuron is not necessary for generating large-angle turns in response to dark flashes[11], thus indicating that the response of the Mauthner array is specific to certain sensory modalities. Also, two neurons in a midbrain nucleus, the nucleus of the medial longitudinal fasciculus (nMLF), are involved in generating another form of swimming behavior, prey-capture swimming, but are not required for spontaneous swimming or optomotor behavior[12]. Together these results suggest the presence of dedicated micronetworks for specific motor patterns. It is certainly possible that the control systems for some behaviors are distributed across several hindbrain segments, such as is seen for forward swimming in the current study, whereas other behaviors, perhaps those that require robust short-latency responses, have dedicated control elements.

Like any well-done scientific study, this work raises several questions and ideas. For example, although the optic tectum is not required for the optomotor response[13], little else is known about the upstream circuit elements mediating this behavior. With the advent of new techniques to trace monosynaptic connections[14], it should be possible to delineate this circuit. Further, the reticulospinal neurons that respond during the optomotor stimulus send their axonal projections to the spinal cord as early as 31 h after fertilization[15], but the optomotor behavior only matures by 6 d after fertilization[2]. What processes are responsible for the delayed appearance of the optomotor behavior? Finally, given that at least some reticulospinal neurons participate in multiple behaviors, future experiments investigating the role of neuromodulators in sculpting the activity of reticulospinal neurons will shed more light on the selection of motor patterns for different behaviors.

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# Malleable templates: reshaping our crystallized skills to create new outcomes

Scott T Grafton

**Even well-practiced skills show trial-by-trial variations. A study in *Nature* suggests that such variability may be adaptive, allowing for plasticity in apparently crystallized skills, which should therefore be considered more like templates.**

Every morning I get up and tie my shoes the same old way. Like a robot, I dutifully play out a familiar motor program that I learned as a child. The program is crystallized in that it is resistant to forgetfulness, fatigue, distraction and interference from all the other exotic knots I have learned since. Yet there is a problem with this view. If my tying really is a rigid 'program', akin to a computer program, why can I flexibly adapt my performance to stiff laces, gloved hands or tying my son's skates? This tension—between what is prescribed by a scripted program versus what is adapted—strikes at the heart of understanding what constitutes a motor memory. How is it that the nervous system can learn to represent extremely precise action patterns that remain stable over decades, yet at the same time can adjust them on the fly as needs arise?

To address this question, two key insights are gaining support in learning research: that skills are organized around goals rather than movements, and that adjustments to a skill are constantly made in a never-ending balancing act between exploratory and exploitative behavior. The latter idea comes from computational machine learning theory. Intended for the training of robots, this theory is potentially applicable to nervous systems as well[1]. For any motor behavior where a successful outcome is rewarded, actors can adopt either of two policies. They can take their reward and try to reconstruct whatever they did on previous trials as closely as possible, to assure a similar future reward, or they can explore their situation by adding some variety into each movement. In the latter case, they may find a new action that leads to an even greater reward. Clearly, the policies defining how much they exploit versus explore can have profound influences on the rate, generalization and retention of what is learned. Although it is straightforward to generate computational models that demonstrate the utility of incorporating variability for enhancing learning and reducing error[1], evidence that the nervous system does something similar is thin on the ground. In an elegant study of birdsong in the bengalese finch, Tumer and Brainard now provide evidence for the utility of motor variation[2].

Previous studies in people, monkeys and other mammals have provided only limited experimental evidence for this idea, as there is so much noise in the musculoskeletal apparatus[3,4]. Unlike the robot on the assembly line that can generate the same movement to micron precision, our clumsy motor apparatus can never do anything quite the same from trial to trial. Thus, it is very difficult to distinguish central variability from peripheral noise.

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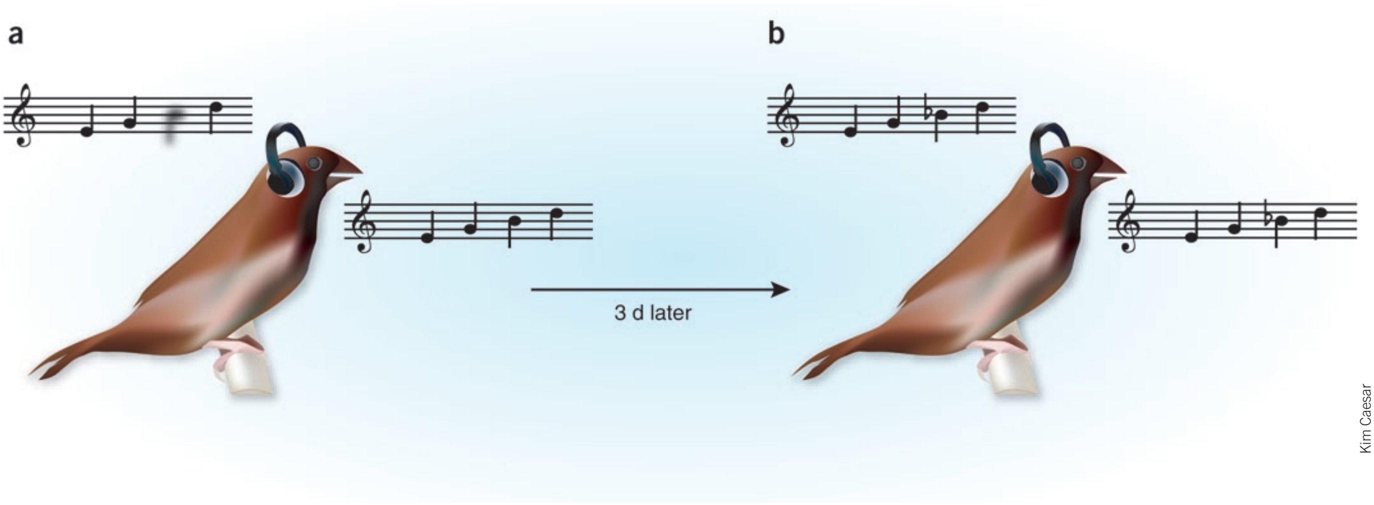

**Figure 1** The birdsong of the bengalese finch can be reshaped by selective adaptation. Whenever the bird sang a target note in its upper range of normal, a burst of white noise was introduced that obscured feedback for only that particular note. With training, the bird learned to adjust the target note to a lower pitch. The sensory consequences of the action drive the adaptive change.

A key requirement in demonstrating the role of central variability in animal learning is to examine a very tightly controlled musculoskeletal apparatus. This is where the extreme precision the bird's nervous system comes in useful. Tumer and Brainard used it to induce adaptation in specific elements of a motor program[2]. The bengalese finch acquires a specific song during development that is learned by auditory feedback: birds must hear what they sing to acquire a motor memory. Once acquired, the song is crystallized into a stable form. Although crystallized, each syllable in a birdsong has a variable but very narrow range of acceptable pitches, on the order of 1.5%. Some level of auditory feedback is needed throughout life to maintain this precision, as deafness can lead to gradual declines in overall performance.

Rather than disrupting feedback for the entire song, Tumer and Brainard tested if they could change the pitch of a single syllable in the song by disrupting feedback only when this syllable was being produced in the upper or lower range of normal (**Fig. 1**). What if the bird only hears white noise when the target syllable is generated with a pitch in the upper range of acceptable and hears normal feedback when the pitch is in the lower range? Within about 600 trials or a half a day of singing, the song had changed so the new central frequency of that syllable was lower. Alternatively, by applying white noise feedback when the target syllable was sung in the lower range of normal, the pitch could be moved to a higher frequency. These pitch shifts reached asymptote within 3 days of training. This result shows that the bird nervous system knows the centrally generated variance of the pitch it is trying to produce for each syllable on a trial-by-trial basis and can selectively adjust a syllable based on relatively crude, binary feedback. For the bird, this variance is normally extremely narrow, and the default control policy emphasizes exploitation over exploration. Nevertheless, the nervous system maintains remarkable capacity to adapt an already crystallized motor program in the face of new performance criteria.

In theory, reinforcement learning can take place whether feedback is immediate or delayed[5]. We are all familiar with delayed gratification for our hard work. This is not the case for birdsong learning in the finch. Tumer and Brainard found that delaying the negative feedback so that it did not overlap with the target syllable did not lead to pitch adaptation. For the signal to have an effect, the relevant feedback had to be provided within the time frame of the expected sensory consequences of the motor action, less than 70 ms in this system. In other words, unlike the delayed reward systems typically associated with the dopaminergic system of the basal ganglia in mammals, the adaptive response in the finch requires a tight coupling between the internal representation of the song as generated by premotor neurons and the expected sensory consequences of that action.

The temporal specificity of effective feedback in the bengalese finch underscores the need to revise conventional notions of how a motor program should be defined. The traditional view—that a motor program represents a set of fixed motor elements organized in space and time, modified only by global parameters such as rate or force—is an incomplete model that only captures sequential and macroscopic features of a task[6]. The Bengalese finch shows that the local elements of a program are organized around the immediate sensory consequences of their execution. Altering the feedback for a single element of a program can lead to a new motor output and more importantly, a new outcome.

The concept of a motor program has always been conflated by analogy with the rigidity of a computer program. What is clear from the new study by Tumer and Brainard is that crystallized motor skills are more like templates that are organized around desired sensory consequences. This idea is concordant with a range of human studies that frame motor skills in terms of action outcomes or goals rather than motor primitives[7]. In these models, cerebellar and parietal circuitry are essential to the integration of motor efference copy and sensory information with a desired motor outcome[8,9]. A range of computational approaches, including Bayesian approaches, are now considering how variability in planning and motor commands can be integrated with inherent sensorimotor noise to achieve desired outcomes across multiple time scales of learning[10].

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