Use It or Lose It. Focus on: “Sequential Learning From Multiple Tutors and Serial Returning of Auditory Neurons in a Brain Area Important to Birdsong Learning”

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What is the long-term vocal effect of that year spent in France at the impressionable age of 2 yr? Will you be able to order a meal in French when you return to Paris 20 yr later? Yazaki-Sugiyama and Mooney (this issue p. 2771–2788) have looked at the neurophysiological correlates of such early auditory and vocal experiences in a songbird, the zebra finch, that was raised with two successive tutors during the most plastic period of its vocal learning phase. They recorded the neural activity of single neurons in a sensory-motor brain area called lateral magnocellular nucleus of the anterior nidopallium (LMAN) that has been shown to be crucial for song learning (Bottjer et al. 1984; Scharff and Nottebohm 1991). After exposure to the first tutor song, neurons were selective for the sound of the bird’s own immature song and, to a lesser extent, the sound of the tutor song. This selectivity, however, disappeared after the birds were exposed to a second tutor and learned to sing this song exclusively. At that point, the neurons became tuned to the sound of the new song. If the selectivity of these neurons is a neural correlate of the memory of either the vocal program or the sensory tutor experience, these memories seem to be completely erased and replaced by new ones. In other words, on your return trip to Paris, you would have forgotten all the French sentences that you could produce fluently as a 3 yr old.

Tutor-driven vocal learning is a complex task that involves the interaction of a purely sensory task, the recognition and memorization of the tutor’s vocalization, with a sensory-motor task, the production, perception, and modification of the pupil’s own vocal output. For learning to occur, both the motor program and the sensory template must be stored in the brain. Whether these memories are stored in distinct brain areas and how these templates interact remain a puzzle. If one adds the additional complication of multiple sensory and vocal learning experiences, the problem becomes daunting. Thus, to study how multiple auditory/vocal memories are stored and the extent to which such memories persevere requires particular care both in the experimental design and in the interpretation of the results.

The study by Yazaki and Mooney makes a considerable effort in both respects. First, the behavioral training paradigm was cleverly designed to clearly define two nonoverlapping periods of sequential learning. This is particularly challenging in the zebra finch, where the vocal learning period lasts approximately 60 days and where early learning is often difficult to assess. To overcome the time constraint, the authors used a combination of isolation and short tutor exposure that resulted in condensed motor learning. To surpass the difficulty in assessing the quality of copying in very young birds, the authors used a cross-fostering technique, which first exposed the young zebra finches to a Bengalese finch tutor before exposing them to a second (zebra finch) tutor. They could then convincingly show that the bird’s own immature song resulted directly from early copying of the Bengalese finch song. The result of their behavioral paradigm was unequivocal: zebra finches were able to learn the two songs sequentially, and there were no observable effects of the first learned song in the adult song.

Another strength of the study is the use of intracellular recordings to assess the neurophysiological responses. By doing so, they were able to show that the memory of the first song in the adult bird was neither in the spiking output nor, in a latent form, in the subthreshold potential of single cells. This is an important control because, in other systems, it has been shown that early experience that has been overwritten can leave neural traces that might be masked in the spiking output (Bickley SG et al. 1994; Zheng and Knudsen, 1999).

Finally, this study also provides further insight on exactly what is being stored in LMAN. In both the young bird and the adult bird, neurons were more selective for the bird’s own (current) song than for the tutor song. In the young bird, this difference in selectivity is revealing because the immature bird’s own song is clearly acoustically different from the desired stored tutor template. In the adult bird, the strength of the selectivity for the tutor song was correlated with the acoustical similarity between the tutor song and the bird’s own song. Previous studies have also shown that, in young birds, neurons in LMAN become selective for the plastic song that the bird is producing (Solis and Doupe 1997), even when this song is highly distorted and distinct from the tutor song (Solis and Doupe 1999). Taken together, these results suggest that the selectivity can be interpreted as a memory for the produced vocalization, a sensory-motor template for the current song output, and not a sensory memory of the tutor song. In a complicated twist, the degree of selectivity of the neurons has been shown to be affected by the quality of the match to a desirable tutor song (Solis and Doupe 2000). The memory stored in LMAN might therefore be a motor memory in auditory coordinates that reflects the quality or the stage of learning. How this memory is used to guide vocal learning and whether a separate brain area is involved in storing the tutor template remain unknown.

As pointed out by the authors, the zebra finch model for speech learning or vocal learning in other songbirds has limitations. Early language experience in humans is known to have lasting effects on perceptual and vocal performance later in life (Hansen et al. 2002). Furthermore, zebra finches represent only one species of songbird, a species that sings no more than one
song elements that were learned during early vocal development can be absent in the mature song produced the first year but re-emerge in following years (Marler and Peters 1982). It would be very revealing to repeat the experiments of Yazaki-Sugiyama and Mooney in such a species and determine whether or not the memory of the absent song elements can be found in LMAN. If not, one could conclude more strongly that LMAN is in fact storing the current vocal program and that previously learned vocal programs or the sensory memory of the tutors’ sounds are found elsewhere. Similarly, it would also be interesting to examine behaviorally whether the adult zebra finches trained with two songs sequentially have any perceptual memory of the first song. A positive result would also suggest the involvement of a separate brain area in perceptual memories.

REFERENCES


