could preclude a necessity for regeneration of synaptic contacts per se), it was conceivable that (i) some regenerating fibers might have found their way to their central stumps and fused, or that (ii) fibers from roots 2 and 4 might have fused with the central stumps of root 3 to which they were tied.

Possibility (i) was evaluated at about 6 weeks by exposing the regenerating roots, attempting to cut all tissue connecting the peripheral with the central ends of the previously severed roots, and then retesting the ability of water drops to fire **A**. The situation encountered at the time of this "clean-up" surgery is summarized in Fig. 1B. Stumps of cut nerves other than 2 and 4 usually had smooth, clublike ends (see *C* in Fig. 1B), occasionally with small bundles of axons growing out of them. Growth out of the peripheral ends of roots 2 and 4 along the remnant of the central end of root 3 was sometimes obvious, but often the region was embedded in a mass of scar tissue. The stumps of the peripheral and the laterally tied central pieces (*R*) of roots 2 and 4 were frequently joined by a mass of vascularized scar tissue (*B*) in which regenerating axons could sometimes be seen and also sometimes by small bundles of stray regenerating fibers. The stray fibers and *B* or *R* of Fig. 1B were cut as necessary. This surgery commonly reduced the sensitivity of **A** to water drops but in no case abolished it. The average number of spikes produced after "cleanup" was 5.8 per 50 msec for experimental animals and 6.2 for controls. Upon fuller dissection at completion of testing we often found fibers joining the peripheral stump of root 3 to the region where 2, 3, and 4 were tied together. Some of these (*M* of Fig. 1B) could be seen by their course to be motor fibers growing out from the central end of root 3. But others (*S* of Fig. 1B) might have been sensory fibers from peripheral root 3 that could have fused with their counterparts in the central segment of 3. However, of the 12 animals with reactive **A**'s that were examined carefully, there were six with no indication of growth of sensory fibers that could have fused with their central stumps; moreover, the mean sensitivity of **A** in these animals (7.3 spikes per 50 msec after clean-up surgery) was actually slightly greater than that in the animals where there could have been fusion (5.2 spikes per 50 msec).

Possibility (ii) cannot account for recovery of excitability of **A**, because **A** was excited by water drops at 3.5 weeks after surgery in two animals in which roots 1, 3, and 5 were left intact until just before testing so that they did not provide cut central pieces with which regenerating roots 2 and 4 could have fused.

Finally, to rule out the possibility that our results might be accounted for by fusion of the severed neurite between **A**'s axon and soma, we removed a chunk of tissue containing **A**'s soma in six animals; in each animal regeneration of afferents to the somaless interneuron again occurred within 4 weeks. It remains conceivable that these somaless **A**'s joined with foreign somas, but in previous work in which we used the present operative techniques cobalt was not taken up by any soma when **A**'s axons and dendrites were filled with cobalt after 8 weeks of survival (*3*).

We therefore conclude that **A**'s return of sensitivity to water drop stimulation does indicate true regeneration of synapses between cut afferents and **A**, and that this regeneration is normal in time course and extent even though **A** lacks its cell body (*12*).

FRANKLIN B. KRASNE
SUN-HEE LEE

*Department of Psychology,
University of California,
Los Angeles 90024*

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3. See F. B. Krasne and S. H. Lee, *Brain Res.* **121**, 43 (1976), and references therein.
4. While it seems likely that the target cell plays an important role in the reestablishment of afferent synapses on itself, the precise nature of this role is uncertain. Cajal's evidence that target structures produce factors that promote growth or sprouting leads one to suspect that regeneration might require gene-dependent synthesis of substances that attract regenerating afferents or cause them to establish synapses, or both [see S. Ramon y Cajal, *Trab. Lab. Invest. Biol. Univ. Madrid* **17**, 181 (1919), L. Guth, Transl., in *Studies on Vertebrate Neurogenesis* (Thomas, Springfield, Ill., 1960), pp. 149–200; J. Diamond, E. Cooper, C. Turner, L. Macintyre, *Science* **193**, 371 (1976); M. H. Moscona and A. A. Moscona, *Science* **142**, 1070 (1963)]. On the other hand, there is some evidence that in crustacea synapses might be formed primarily by dendrites growing to meet and form synapses on the axis cylinders of presynaptic axons [see (*5*); and W. J. Davis, *Science* **168**, 1358 (1970)]; this would place an even greater demand on the target cell. Additionally, when afferents to a target are lost, there are often signs of morphological, physiological, or biochemical dedifferentiation of the target which must be reversed upon reinnervation [see (*6*); and J. Rosenthal, in *Handbook of Neurophysiology* (American Physiological Society, in press); S. Gelfan, T. H. Field, G. D. Pappas, *Exp. Neurol.* **43**, 162 (1974); T. Gentschev and G. Sotelo, *Brain Res.* **62**, 37 (1973); D. A. Matthews, C. Cottman, G. Lynch, *ibid.* **115**, 1 (1976)]. However, in rat superior cervical ganglia and septal nuclei, postsynaptic membrane thickenings persist without obvious change despite denervation, and therefore they might not have to be reconstituted upon reinnervation [see G. Raisman, in *Neural Mechanisms of Learning and Memory*, M. R. Rosenzweig and E. L. Bennett, Eds. (MIT Press, Cambridge, Mass., 1976), p. 384]; moreover, at vertebrate neuromuscular junctions some muscle changes that normally follow degeneration of motor neuron terminals appear not to occur in the absence of protein synthesis (*6*).
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10. Degeneration of cut sensory axons is reported to occur within 10 to 20 days [G. D. Bittner and A. L. Johnson, *J. Comp. Physiol.* **89**, 1 (1974)].
11. The possibility that contralateral or rostral afferents, which normally have no input to **A** (*5*), come to excite it in regenerates was ruled out by careful receptive field tests in all animals. In two experimental animals it was also shown that **A** could not be excited after severance of the apparently regenerated roots. In principle, it seems conceivable that regenerated afferents might gain access to **A** indirectly, by forming synapses on intact interneurons that excite **A**; however, we do not consider this a plausible possibility because intracellular recordings from **A** in normal animals reveal either no excitatory input whatever (*5*) or negligible input (our observations) from sensory interneurons; moreover, we have observed delays of less than 3 msec between electrical shocks to regenerated roots and appearance of extracellular spikes in **A**'s axon rostral to the last ganglion, which is inconsistent with a disynaptic pathway according to the criteria of Calabrese (*5*).
12. See (*3*) for a discussion of the possible meaning of survival of function in akaryotic neurons.
13. Supported by NIH grant R01-8108. We thank M. Letinsky for helpful discussions and P. Farel for commenting on the manuscript.

16 February 1977; revised 20 May 1977

Selective Vocal Learning in a Sparrow

Abstract. *Male swamp sparrows learn their songs; they fail to learn songs of the sympatric song sparrow. Syllables from tape recordings of both species of sparrow were spliced into an array of swamp sparrow–like and song sparrow–like temporal patterns. Swamp sparrows learned only those songs made of swamp sparrow syllables. They did so irrespective of whether the temporal pattern was swamp sparrow–like or song sparrow–like. Selectivity was retained by birds reared in total isolation from adult conspecific sounds.*

It is a long-standing premise of classical learning theory that any sensory stimulus can be attached through learning to any arbitrarily chosen response. Biological approaches to animal learning have called several assumptions of learning theory into question, including the principle of equipotentiality (*1*). Vocal learning is widespread in birds, and all oscine songbirds studied to date show some degree of song abnormality when reared in social isolation (*2*). A feature of

Table 1. Design plan for the "artificial" training songs each about 2 seconds in duration. The ten artificial songs of one set of training songs were created from 16 different song sparrow syllables. Another set was created of the same song patterns, but with 16 different swamp sparrow syllables. Examples of the patterns marked with asterisks are shown in Fig. 1. Each complete set of 20 artificial songs was supplemented by two additional fully synthetic songs, modeled after natural song and swamp sparrow songs created on the Pattern Playback Speech Synthesizer (Haskins Laboratories, New Haven, Conn.), making 22 songs per set in all. Five complete sets were created, all based on the same set of 32 different syllable types, but with each syllable type placed in a different pattern in each of the five sets. A given bird heard one set only, thus experiencing 32 natural syllable types, 16 of each species.

Overall pattern	Song type	Tempo	Syllable types (No.)
Swamp sparrow-like (one-part)	A	Steady, fast	1
	B	Steady, slow*	1
	C	Accelerated*	1
	D	Decelerated	1
Song sparrow-like (two-part)	E	Fast/slow*	2
	F	Slow/fast	2
	G	Decelerated/slow	2
	H	Decelerated/fast*	2
	I	Accelerated/slow	2
	J	Accelerated/fast	2

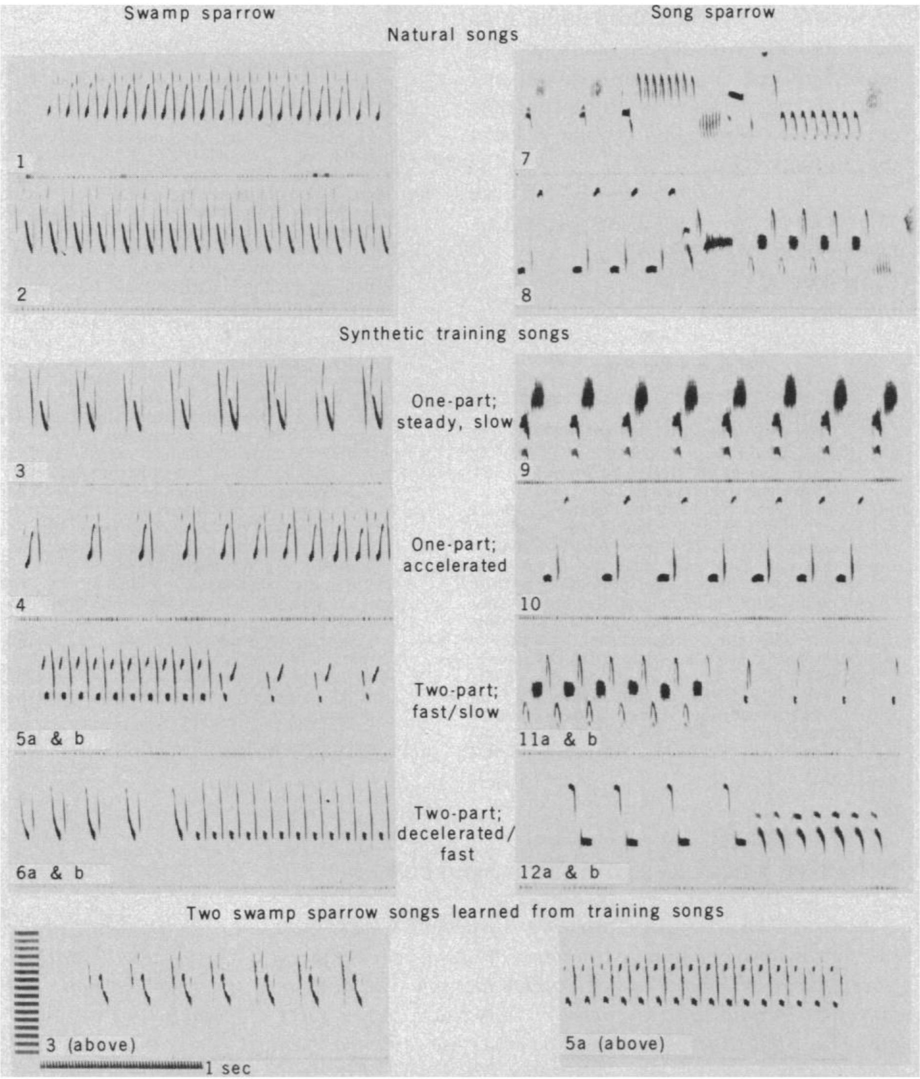

Fig. 1. Sound spectrograms of natural song sparrow and swamp sparrow songs and artificial training songs. Natural songs are shown at the top. Syllables from these and others were assembled in synthetic songs, some created from swamp sparrow syllables (for example, 3 to 6), some from song sparrow syllables (for example, 9 to 12), some in "swamp sparrow-like" patterns (for example, 3 and 9), some in "song sparrow-like" patterns (for example, 4, 5, 6, 10, 11, and 12); syllables from songs 1 and 2 can be seen in songs 3 and 4, syllables from song 8 in songs 10 and 11. Pattern B (see Table 1) is illustrated in songs 3 and 9, C in songs 4 and 10, E in songs 5 and 11, and H in songs 6 and 12. At the bottom are two songs of male swamp sparrows copied from training songs 3 and 5. A 1-second time marker is given at the bottom left, with a 500-hertz interval frequency scale.

the song-learning process in some, though not all, bird species is its selectivity, which is such that a male presented with a natural choice of songs to copy will selectively learn conspecific models (*3*). We present here a new example of selective vocal learning with evidence on some of the acoustical features on which the choice is based.

Song and swamp sparrows are closely related North American members of the genus *Melospiza*. The normal songs of males of the two species, although similar in duration, are very different in temporal organization (Fig. 1). The swamp sparrow song is simple, consisting of "a slow trill of similar slurred liquid notes." That of the song sparrow is complex, with several distinct parts, consisting "of many short notes and a trill near the end" (*4*). Within different, relatively stable, species-specific overall patterns, both species exhibit a great deal of individual variability in the acoustic structure of song syllables. Swamp sparrows engage in vocal learning, and songs of socially isolated males are significantly abnormal, with simpler syllables and fewer component parts than usual (*5*). Although their preferred microhabitats differ, the two species live within earshot of one another in the study area in Dutchess County, New York. Preliminary study revealed no evidence that the two species learn one another's songs in nature.

Our aim was to present male swamp sparrows with swamp and song sparrow songs to see whether selective learning occurs, and if so, to specify some of the acoustic parameters involved. We expected the major differences in overall temporal patterning of songs of the two species to provide the basis for any selective learning that might take place. In order to test this hypothesis, series of artificial songs were created. Distinctively different sound elements or syllables were edited out from tape recordings of normal local songs of both species. These were spliced together in a variety of simple temporal patterns, chosen to provide variants on some of the organization features by which normal songs of the two species differ (Table 1). "Swamp sparrow-like" patterns included sequences of identical syllables at various steady rates; "song sparrow-like" patterns included variable intervals between syllables (accelerating, decelerating) and a two-part structure. Song sparrows sometimes use two-part, never one-part, songs. Although three or more parts often occur in song sparrow songs (for example, Fig. 1, parts 7 and 8), we hypothesized that the contrast between one- and two-part patterns would suffice for the discrimination. Each set of ten song types (Table 1, A to J) was created in duplicate, once with 16 different swamp sparrow syllables and again with 16 different song sparrow syllables. Each syllable type was used only once in a set. These types were sufficiently distinct so that if imitation occurred we could determine from which temporal patterns they had been selected (Fig. 1). Two additional songs were created on the Haskins Laboratories speech synthesizer (see legend, Table 1), which were not learned and will not be mentioned further in this report. These 22 "artificial" songs were presented in song bouts at characteristic singing rates for these species. Each subject heard all 22 songs (*6*).

Anticipating the possibility that particular associations of syllable type and temporal pattern might influence the birds' choice, we prepared five sets of training tapes from the same 32-syllable types of the two species, but with each pattern assembled from a different syllable type in each set. A given bird heard only one of these five sets.

In the first experiment eight male swamp sparrows between 3 and 10 days of age were taken from wild nests and reared by hand with female siblings in small groups in acoustically shielded chambers. During rearing they could also hear song sparrows of a similar age present in the same chambers until the end of the song training period. A single set of tapes was presented to each group of subjects in varying order twice a day—morning and evening. Training continued for 30 days, when the sparrows were between 20 and 50 days old. We know that this included the sensitive period for vocal learning in this species (*5*). As with other songbirds, such as the white-crowned sparrow (*3*), male swamp sparrows learn to sing from memory. They came into song some months after training, while on an approximately normal photoperiod. The group of eight males produced 19 syllable types. As in nature, each male sang several songs, ranging from one to three types. We compared these syllables with the models experienced earlier in life, and judged 12 of the 19 to be close copies (see Fig. 1, bottom). These 12 represented eight different swamp sparrow syllables presented as models; no song sparrow models were copied. Thus the male swamp sparrows exhibited extremely selective vocal learning, accepting only conspecific syllables for imitation, and rejecting song sparrow syllables even when presented in swamp sparrow-like patterns.

The choice was clearly made at the level of components from which the song is constructed, and not the overall pattern of the song. Thus four of the 12 examples of learned syllables were extracted from one-part song (the normal swamp sparrow pattern) and eight from two-part models, which are closer to the song sparrow pattern. Five of the accepted models came from series with a steady rate (the normal swamp sparrow pattern) and seven from accelerated or decelerated series. Syllables presented in two-part models, or with variable rates, were usually transposed into one-part patterns, with a steady rate, typical of normal swamp sparrow song.

In order to explore further the developmental basis of this predisposition to learn songs selectively, swamp sparrows were reared under foster parents. Eggs were transferred early in incubation from wild nests to nests of canaries in the laboratory, and the nestlings were reared with the aid of supplementary feeding by the experimenter. Six males were exposed from 20 to 50 days of age to synthetic song patterns like those used in the first experiment. One-half of the songs were made from normal swamp sparrow syllables; the other half from song sparrow syllables that were either normal (two males) or subjected to a 13 percent upward transposition in frequency (four males) (*7*). Of ten syllable types developed, six matched the models closely—all swamp sparrow syllables. Thus it is clear that song syllables of these two sparrows are not equivalent stimuli as a basis for vocal learning by the swamp sparrow, even with subjects reared in complete isolation from all adult sounds of their species.

The many parallels between avian song learning and the development of the perception and production of speech in human infants lend added significance to these results (*8*). In particular, recent studies of auditory perception in infants suggest that young of our own species are predisposed to be responsive to particular aspects of speech sounds before speaking (*9*), just as some young songbirds are responsive to species-specific features of song before they themselves come into full song. Such perceptual predispositions are valuable as biological constraints on the vocal learning process, serving to focus the young organism's attention on an appropriate set of sounds and on particular features that they exhibit (*10*). The birds are guided to a set of conspecific models, thus reducing the potential hazards of learning the song of another species. Human infants stand to benefit (i) from being encouraged to attend closely to sounds of speech; (ii) from guidance, in embarking on the perceptual analysis of speech sounds, in the extraction of particular meaningful features from the multitude of cues of varying reliability that speech presents; and (iii) from the possession of mechanisms that can steer the processes of later vocal development from babbling to mature speech by auditory feedback, much as a bird passes from subsong to the fully crystallized patterns of adult song.

PETER MARLER
SUSAN PETERS
Rockefeller University Field Research Center, Millbrook, New York 12545

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17 March 1977; revised 15 June 1977