Only in early adulthood, a time of rapid testicular growth and waxing androgen production, do they begin transforming portions of the memorized material into matching sound patterns.

Previously it was implicitly assumed that adult song is a reliable register of what a male bird has learned. The analysis of plastic song reveals that the birds developed much more than was needed for adult song. As already indicated, crystallized song repertoires in swamp sparrows typically consist of three syllables per male. The plastic song recorded only 1 week before crystallization incorporated an average of six different syllables per bird. Earlier in development there may be as many as 19 distinct syllables per male, with an average maximum of 12. Thus in plastic song a male swamp sparrow produces four times more syllables than are needed for the mature repertoire (Fig. 2). A total of 199 different syllables were identified in plastic song from the 16 males. Only 45 survived the crystallization process.

Comparison of the syllable types produced in plastic song with those heard in infancy was also revealing. Only 59 syllables—less than a third of those produced—were judged to be accurate copies of models. Of the remainder, 36 were construed as poor copies, perhaps modified by improvisation. This left 104 syllables unaccounted for. We conclude that these were inventions. Four of the 16 birds sang only invented and improvised syllables and 12 sang a mixture of imitated syllables. Invented and copied syllables mingle freely in plastic song, and a facility for syntactical rearrangement is evident in the many syllable recombinations that occur. Of the 45 syllables that were finally crystallized, 19 were copies of training songs, 19 were invented, and the rest were improvised or poorly copied. Thus, both inventions and imitations are winnowed as song develops.

Although imitation plays a crucial role in swamp sparrow song development, it evidently is not the only process involved. So far as we can determine, the invented syllables originated independently of the imitations and were not produced by progressive improvisation upon learned themes. They differed from the learned syllables in the smaller number of notes from which they were constructed (1.4 per syllable versus 2.8 for learned syllables). However, they were more complex than the innate song syllables of untrained swamp sparrows, which average 1.1 notes each (Fig. 1).

The process of singing from memory described here almost certainly occurs in wild swamp sparrows. A similar process probably occurs in the first year of life in many other songbirds. Temporal separation of the perceptual and sensorimotor phases of vocal ontogeny may be important in allowing cognitive mechanisms to operate on the memorized material. In sparrows these mechanisms appear to parse learned song material into syllabic multinote units that can then be recombined in novel syntactical arrangements by processes equivalent to phonological syntax in human speech (*7*). Finally, vocal invention makes a major contribution in birdsong ontogeny, even in a species such as the swamp sparrow, in which the impact of learning is pervasive. Many more syllables, both imitated and invented, are used in plastic song than in the final song patterns. This may be analogous to the overproduction of diverse speech sounds in the prespeech babbling of human infants (*8*).

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Electrotonic Coupling Between Pyramidal Cells: A Direct Demonstration in Rat Hippocampal Slices

Abstract. *Intracellular recordings from pairs of neurons in slices of rat hippocampus directly demonstrated electrotonic coupling between CA3 pyramidal cells. When two neurons were impaled simultaneously (as verified by subsequent double staining with horseradish peroxidase), current pulses injected into one cell caused voltage changes in other cells. These interactions were bidirectional. Fast prepotentials, historically thought to represent spike activity in dendrites, resulted from action potentials in other electrotonically coupled pyramidal cells. These data directly demonstrate electrotonic coupling between neurons in the mammalian brain and indicate that some fast prepotentials are coupling potentials. Coupling between pyramidal cells could mediate synchronization of normal rhythmic activity and of burst discharges during seizures.*

Several lines of evidence indicate that electrotonic coupling occurs between neurons in some areas of the mammalian central nervous system (*1*). The evidence has been indirect, however: (i) physiological results showing short-latency, collision-resistant depolarizations after antidromic activation of neurons coupled to the impaled cell (*2*) and (ii) observations of gap junctions (*3*), which are considered the ultrastructural substrate of electrotonic coupling. A direct demonstration of electrotonic coupling requires simultaneously impaling two neurons with two microelectrodes and injecting current into first one and then the other neuron to cause a voltage change in the uninjected neuron. Previously this has not been done in mammalian brain because of the difficulties of simultaneously impaling two coupled neurons. Electrotonic coupling in the hippocam-

pus could be relevant to questions concerning the generation of seizures and fast prepotentials (FPP's) (*4*). Hypothetically, electrotonic transmission could account for neuronal synchronization during seizures. Fast prepotentials are small rapid intrasomal depolarizations, which are thought to represent remote action potentials at dendritic "hot spots" (*5–8*). A neglected but still tenable hypothesis is that FPP's are electrotonic coupling potentials.

In a previous study with intracellular injections of the fluorescent dye Lucifer yellow (*9*), we showed that CA3 pyramidal cells are dye coupled, probably via somata and dendrites, and that the somata of dye-coupled cells are usually within 50 μm of each other (*4*). We now report a direct demonstration of electrotonic coupling between CA3 pyramidal cells through the use of simultaneous intracellular recordings in slices of rat hippocampus in vitro. We also present direct evidence that some FPP's are coupling potentials generated by action potentials in other pyramidal cells.

Transverse hippocampal slices, prepared from adult rats (200 to 300 g), were maintained as described elsewhere (*6, 10*). Intracellular recordings were made with micropipettes containing horseradish peroxidase (HRP) for intracellular staining (*11*).

Simultaneous impalements of CA3 pyramidal cells were obtained as close together as possible (< 100 μm) in the cell body layer. In 47 of > 400 simultaneous impalements, current injected through either electrode caused a voltage change at the other (*12*). Two lines of evidence were used to show that some of these recordings were from two electrotonically coupled cells rather than two parts of the same cell. First, simultaneous impalements with low coupling ratios (< 0.3) (*13*), and thus apparently from two electrotonically coupled cells, were occasionally encountered near impalements with high coupling ratios (~ 1.0) (Fig. 1, A to D). These latter recordings were apparently from the same cell, thus indicating that the former recordings were from two coupled cells (*14*). Second, after the observation of weak coupling (Fig. 1, E and F), injections of HRP through both electrodes (*15*) showed two stained cells (Fig. 2) in four cases. When the coupling ratio was low, action potentials in one recording were usually associated with FPP's in the other recording (Fig. 1, A and C). Therefore, simultaneous impalements from pairs of cells, which were corroborated by double staining with HRP, indicate that some CA3 pyramidal cells are electrotonically coupled to other pyramidal cells and some FPP's are electrotonic coupling potentials.

For nearly 20 years, FPP's in hippocampal pyramidal cells have been interpreted as representing dendritic spike activity (*16*). Field potential studies (*17*) and intradendritic recordings (*18*) have shown that the dendrites of pyramidal cells are excitable, but there is no direct evidence that FPP's represent remote spike activity in the impaled cell versus an electrotonically coupled cell (*19*). Our correlation of FPP's in one pyramidal cell with action potentials in other electrotonically coupled pyramidal cells indi-

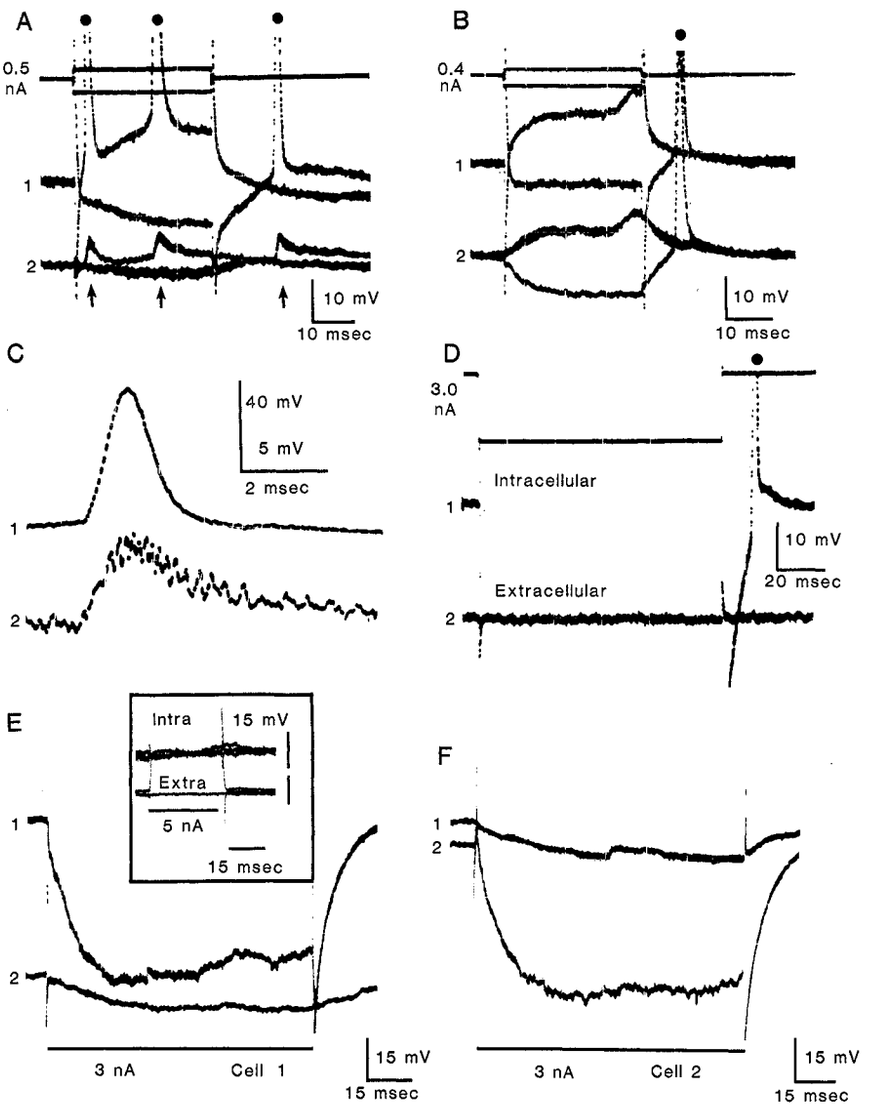

Fig. 1. Electrotonic coupling between hippocampal pyramidal cells. (A) Current pulses depolarized or hyperpolarized the injected cell (A1) and caused similar but smaller voltage changes in the coupled cell (A2). Electrotonic interactions were demonstrated in both directions by injecting current alternately in both cells, and the coupling ratio was approximately 0.2. Recordings in (A) were not obtained from different parts of one cell (for example, soma and dendrite), because the electrodes had already impaled the same cell in the same track (B). (B) When both electrodes were apparently in one cell, current injection caused approximately equal voltage changes at either electrode. Then one electrode was advanced 16 μm and impaled another cell that was weakly coupled to the first cell (A). When the electrodes were in two coupled neurons (A), action potentials in one cell (truncated and marked by filled circle, A1) were usually detected as FPP's (arrows, A2) in the coupled cell. (C) An action potential from current injection in one cell (C1) and the FPP that is evoked in the coupled cell (C2) are illustrated at higher gain and sweep speed. (D) After one impalement was lost and the microelectrode was in the extracellular space, current injected into one of the coupled cells (D1, voltage trace off scale) was not detected extracellularly as a voltage change (D2), nor did action potentials (truncated and marked by closed circle) evoke FPP's. (E and F) Demonstration of electrotonic coupling between two pyramidal cells that were subsequently stained with HRP (Fig. 2). Hyperpolarizing current (indicated by bars) injected into either cell [(E) cell 1; (F) cell 2] caused a smaller voltage change in the other pyramidal cell. (Inset) After one of the electrodes was withdrawn from the cell (*Extra*), strong current pulses through this electrode (which caused bridge imbalance) were not detected intracellularly (*Intra*) in the other cell.

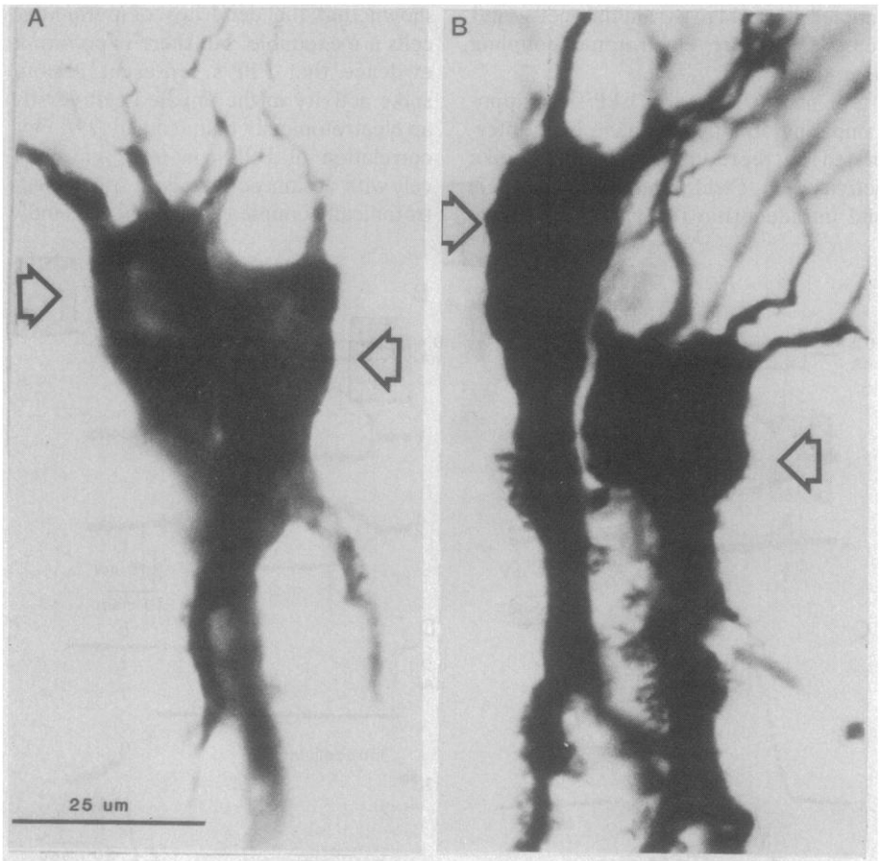

Fig. 2. Electrotonically coupled pyramidal cells separately injected with HRP. Electrotonic coupling was first demonstrated with reciprocal current pulses during simultaneous intracellular recordings. Horseradish peroxidase was injected through both electrodes to show that the impalements were obtained from two separate neurons. Recordings from the pair of cells shown in (A) are shown in Fig. 1, E and F. Two adjacent cell bodies (arrows) were subsequently visualized with possible soma-somatic contacts. In another similar experiment, HRP staining showed that the somata (arrows) of two electrotonically coupled neurons were separated (B). In this case, the contacts appeared to be dendro-dendritic.

cates that some, if not all, FPP's are coupling potentials. Since FPP's occur more frequently during penicillin-induced seizures (*7*), the spread of action potentials through electrotonic junctions could be an important factor in generating epileptiform activity.

Electrotonic coupling between pyramidal cells could have several important implications for hippocampal physiology and epilepsy. (i) Electrotonic junctions function as low-pass filters (*1*) and would preferentially transmit the relatively slow potential changes associated with synaptic input and burst discharge (*20*). (ii) Synchronous synaptic input within coupled pyramidal cells would effectively evoke spike bursts, whereas asynchronous input would be shunted throughout the network (*1*). (iii) Increased membrane conductance during recurrent inhibition shunts junctional transmission (*21*) and would uncouple pyramidal cells. Conversely, those convulsive agents (such as penicillin) which reduce recurrent inhibition (*22*) would enhance coupling. (iv) Some electrotonically coupled networks behave as reverberating circuits (*1*), so that positive feedback from the spread of action potentials between coupled neurons could lead to prolonged bursting. Therefore, electrotonic coupling in mammalian cortical structures (*23*), particularly when combined with recurrent excitation (*24*), could contribute to synchrony and spread of normal brain rhythms and epileptiform events.

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12. No voltage change occurred during current injection at these intensities when one or both electrodes were just outside the cells.
13. Coupling ratio was defined as the amplitude of the voltage change in the noninjected cell over the amplitude of the voltage change in the injected cell. Coupling ratios were rough estimates because of the technical limitations of the bridge circuit for measuring the voltage change in the injected cell, particularly when strong currents were injected through HRP electrodes.
14. Previous measurements of the electrotonic length of hippocampal pyramidal cells range from 1.0 for CA3 [D. Johnston, *Biophys. J.* **25**, 304a (1979)] to ~ 2.0 for CA1 [D. A. Turner and P. A. Schwartzkroin, *J. Neurophysiol.* **44**, 184 (1980)], which indicate that the space constant of these cells is too long for two electrodes separated by < 100 μm to be in the same cell and have a coupling ratio of < 0.3.
15. In 15 control experiments, small injections (for 30 seconds) of one cell consistently stained only a single cell. The quality of the impalement was monitored electrically throughout the injection to ensure that no HRP was ejected extracellularly.
16. The main reason for this belief has been that in the original work of Spencer and Kandel (*5*), FPP's could be evoked orthodromically but not antidromically. However, under their experimental conditions the majority of pyramidal cells probably could not be activated antidromically. They recorded from 70 cells and their table 1 [E. R. Kandel, W. A. Spencer, F. J. Brinley, *J. Neurophysiol.* **24**, 225 (1961)] shows that 23 of the first 40 of their cells could not be activated antidromically by fornix stimulation and were therefore classified as "unidentified." Nonetheless, their unidentified cells had the same properties as identified pyramidal cells and probably were pyramidal cells, especially in light of the difficulty and rarity of impaling other types of cells in the hippocampus [P. A. Schwartzkroin and L. H. Mathers, *Brain Res.* **157**, 1 (1978)]. Antidromic stimulation techniques are much less likely to reveal electrotonic coupling potentials when the percentage of antidromically activated cells is small. Furthermore, P. A. Schwartzkroin and D. A. Prince [*Brain Res.* **183**, 61 (1980)] have recently reported that antidromic stimuli can elicit FPP's in pyramidal cells, especially in penicillin-treated slices.
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23. Dye-coupling and short-latency depolarizations

to antidromic stimulation have also been observed in dentate granule cells [B. A. MacVicar and F. E. Dudek, in preparation] and neocortical neurons [M. J. Gutnick and D. A. Prince, *Science* **211**, 67 (1981)].
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Recruitment in a Sea Anemone Population: Juvenile Substrate Becomes Adult Prey

Abstract. *Populations of the sea anemone* Anthopleura xanthogrammica *(Brandt) occur in tide pools and surge channels below intertidal mussel beds where they capture mussels dislodged by wave action and by sea star foraging. Dense concentrations of small juvenile anemones occur only within mussel beds and are probably the result of larval settlement or differential survival in that habitat. Areas experimentally cleared of anemones showed that recruitment was primarily by migrating juveniles and that the rate of immigration over a 2-year period was much higher in experimental removal areas near mussel beds than in those further away. Mussel beds thus function as an important juvenile habitat (refuge and nursery); juveniles later migrate downward and are then in a position to capture dislodged mussels and grow to adult size.*

Intertidal marine organisms often disperse planktonic larvae over great distances. It is thus necessary that larvae have mechanisms to locate, recognize, and settle in habitat types appropriate for juvenile growth, survival, and adult reproductive success. Specific substratum selection by invertebrate larvae has been demonstrated for species in a variety of phyla (*1*), but the process of secondary habitat selection by settled individuals has received less attention. Completely sessile species cannot change their location if it proves unsuitable, therefore the habitat selected by a larva is also that of the adult. The juvenile habitat of more mobile animals, however, can be distinct from that of adults (*2*). Sea anemones, for example, can move several centimeters per day (*3*) and thus have the option to alter location throughout their lifetime.

The anemone *Anthopleura xanthogrammica* (Brandt), a dominant member of the North American west coast intertidal community, preys primarily on mussels and other intertidal invertebrates dislodged by wave action and by sea star foraging (*4*). Anemone offspring face the problem of locating a suitable habitat for early growth and survival and later establishing themselves where dislodged mussel capture is a predictable event. Dense concentrations of small juvenile *A. xanthogrammica* (≦ 2 cm in diameter) occur only in mussel beds (*Mytilus californianus* Conrad), a physically protected microhabitat with a predictable prey resource.

At an average diameter of 3.3 ± 1.4 cm (standard deviation), juvenile anemones migrate downward from the mussel beds, thus finding sites where later mussel capture is likely. Juveniles (individuals ≦ 6.5 cm in diameter do not produce gonads) move frequently within mussel beds, around the bases of adults in tide pools, and along the sides of channels (*5*). Adult anemones (6.5 to 25 cm in basal diameter) are long-lived (several decades) and rarely move from their position in tide pools and surge channels. *Anthopleura xanthogrammica* is dioecious and reproduces by epidemic spawning of gametes followed by the development of feeding (planktotrophic) larvae that remain in the plankton for at least several weeks (*6, 7*). Larvae are difficult to culture and have not been induced to settle in the laboratory (*7*). Although larval cohorts may move together in the same water mass, their settlement site is likely to be far from the location of their parents. Unlike the sympatric congener *Anthopleura elegantissima, A. xanthogrammica* never reproduces asexually (for example, by longitudinal fission) (*8*).

The present study is part of an investigation of population dynamics, reproductive ecology, and habitat selection in *A. xanthogrammica* (*5*). Its objectives were to (i) measure rates of immigration into areas cleared of all anemones, (ii) quantify the sizes of individuals recruiting into several intertidal habitat types, and (iii) examine the role of mussel beds as juvenile habitat and as sources of recruitment into adult habitats.

Population monitoring sites were located on Tatoosh Island and at Shi Shi Beach, Washington (*5*). Both sites are on wave-exposed outer coast, the former with extensive mussel bed cover and the latter with few mussel beds. Quadrat sampling for size-frequency distributions of populations was also carried out at both sites, at Mukkaw Bay, Washington, and at several other sites along the west coast (*9*). Mapped control populations of marked individuals were established at three intertidal levels at each of the two sites and followed for 2 years (*5*) (September 1974 to October 1976). Seventeen areas were cleared of anemones (intertidal height, 0.2 to 2.2 m) above the mean lower low water between March 1973 and January 1975 and followed until June 1977. Before removal, all anemones were mapped, photographed, and measured (basal diameter) in each of the discrete tide pool or channel areas (0.3 to 0.9 m^2 per removal; 14 to 36 anemones). Anemones adjacent to the removals were marked with neutral red dye spots (*10*) as were immigrants found on subsequent visits. Sites were monitored bimonthly and all immigrants into the areas were also photographed, drawn on maps, and measured.

Anemones within mussel beds (both on mussel shells and on rock surfaces) were consistently smaller than those in tide pools and channels; at both sites the mean size increased as the intertidal height decreased (Fig. 1). Samples taken in large contiguous mussel beds at Mukkaw Bay (~ 5 km north of Shi Shi Beach) had the densest population of small individuals at any site—58 anemones in an area of 3 m^2 (diameter, 1.5 ± 0.9 cm). Another sample taken in extensive beds at Cape Arago, Oregon, had 41 anemones in a 4-m^2 area (diameter, 2.9 ± 1.5 cm). Such concentrations of small individuals were found only in mussel beds and in no other habitat type examined (Fig. 1B). Most mussel bed areas had only a few individuals per square meter, and dense concentrations were extremely patchy. A massive settlement of the congener *Anthopleura elegantissima* (Brandt) occurred on Tatoosh Island in the winter of 1972–1973 (to 600 individuals per square meter) and was monitored until 1977 (*5*), but no such obvious settlement of *A. xanthogrammica* occurred at either site between 1973 and 1977. Larval settlement of *A. xanthogrammica* is thus not a predictable annual event and is probably very patchy in time and location.

The mean diameter of anemones immigrating into all cleared areas on Tatoosh Island was 3.8 ± 2.4 cm (N = 112); that of immigrants into control areas on Ta-

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