the excess females might be sex-reversed males, as complete reversal (with achievement of egg-laying capability) has not been observed in experiments with any bird species.

Reproductive failure due to developmental suppression of male breeding behavior could remain unrecognized for years, especially in resident populations, because although birds are conspicuous throughout the year, nesting is usually secretive. Only in breeding colonies might the abnormality become evident and then perhaps only indirectly. The highly skewed sex ratio of gulls on Santa Barbara Island, for example, was discovered only because of questions raised by the unusual female-female pairing.

Abnormal development induced by DDT in birds could be more persistent than the pollutant itself. Breeding failure of unexplained origin in birds other than gulls may be the result of DDT contamination of eggs.

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Structural Correlates of Seizure Behavior in the Mongolian Gerbil

Abstract. *Hippocampi of seizure-sensitive and seizure-resistant Mongolian gerbils were examined in search of structural correlates of seizure behavior. In animals with well-established seizure histories, differences were found in both presynaptic and postsynaptic structures. Seizing animals had less dense dendritic spines, a greater proportion of mossy tuft area devoted to presynaptic vesicles, and a smaller proportion devoted to spines. The possible relationship of these findings to epilepsy is discussed.*

Attempts to characterize an anatomical substrate for epilepsy have yet to yield definitive results. Conclusions from qualitative studies on monkeys after application of toxic substances to the cortex and on humans undergoing temporal lobectomy for chronic seizure states (*1*) have been limited by the uncontrolled nature of tissue damage, while qualitative data from genetic models [photosensitive baboon (*2*); sound-sensitive mouse (*3*)] have not been reported. We have investigated seizure substrates in the Mongolian gerbil (*Meriones unguiculatus*), an animal that exhibits spontaneous seizures (*4*). Major advantages of this animal as a model for epilepsy—including the relative ease of eliciting

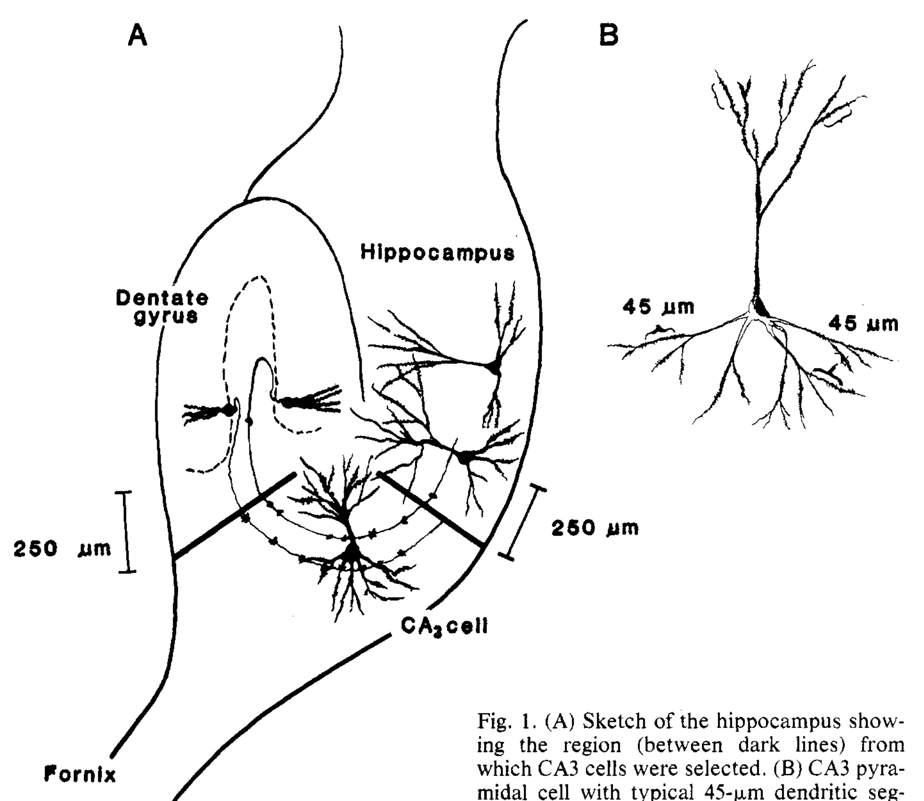

Fig. 1. (A) Sketch of the hippocampus showing the region (between dark lines) from which CA3 cells were selected. (B) CA3 pyramidal cell with typical 45-µm dendritic segments used for spine counts.

seizures, the resemblance of its seizures to human convulsions, and the consistency of the intensity of its seizures over many testing sessions (5)—make it possible to equate a known history and severity of ictal disorder with an observed morphological phenomenon.

Gerbils in our colony have been selectively bred into two "strains" (6), one of which has seizures [seizure-sensitive (SS)] and one of which does not [seizure-resistant (SR)]. Using rapid Golgi techniques, we examined selected brain areas of animals with well-established seizure patterns—gerbils that had consistently displayed the most extreme seizures and those that had never exhibited seizure behavior (5). Initial qualitative impressions, as well as evidence from a variety of other sources (7) implicating the hippocampus in seizure phenomena, led us to focus on that structure. These impressions included, in SS animals, an apparent reduction in spine density along basilar segments of hippocampal pyramidal cells and the presence of swollen, enlarged mossy endings. Since area CA3 (8) of the hippocampus is characterized by the presence of mossy tufts and a fairly uniform density of spines, our first quantitative investigations were performed there (Fig. 1).

To facilitate statistical analysis of spine counts, criteria were established for CA3 as seen in sagittal sections, for cells within CA3, and for acceptable dendritic segments (9). Four segments (two apical and two basilar) 45 μm long were chosen on each cell for spine counts. Counting [by the same investigator (L.P.) throughout the study] consisted of aligning a calibrated grid with the appropriate segment, viewing it as a two-dimensional structure, and enumerating the spines on both sides. Hippocampal cells were sampled from four SS (23 cells) and five SR (28 cells) gerbils.

In addition to these hippocampal cells, counts were made on neocortical pyramidal cells. Although we had had no subjective impression of spine differences between the two groups in this brain region, these data provided information about the specificity of spine differences to region CA3. Data were recorded for all stained pyramidal cells in layer III of the neocortical area dorsal to the hippocampus in the stained blocks, centering on sensory and motor cortex. Cells were sampled randomly according to the same criteria used for CA3 cells. Cell counts were made in three animals from each group (SS, 32 cells; SR, 39 cells).

Results substantiated our initial impressions. Fewer spines were found per

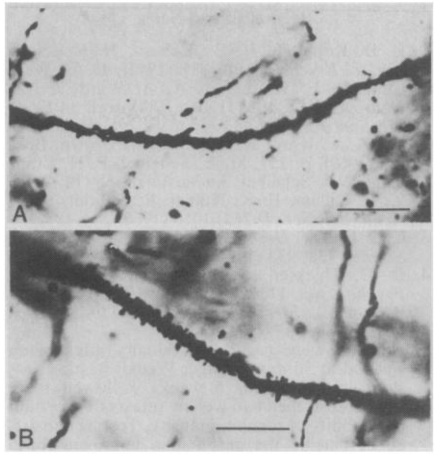

Fig. 2. Representative dendritic segments from SS (A) and SR (B) gerbils. Spine density of the SS segment is lower. Calibration bar, 5 μm.

45-μm segment in the hippocampus of SS than SR gerbils (Fig. 2). These differences were not found in the neocortex. The unequal number of animals in our groups, and of cells studied within each animal, necessitated using a statistical analysis based on a mixed, nested model with unequal replication. The BIMED program BMDP 3V, General Mixed Model Analysis of Variance (10), supplied the single degree of freedom likelihood ratio χ^2 tests and P values we report for testing the equality of group means. The SS animals differed from SR's in total spine density (χ^2 = 5.336, P < .025) in the hippocampus but not in the neocortex. Seizure-sensitive gerbils had fewer spines on both apical (χ^2 = 5.196, P < .025) and basilar (χ^2 = 5.027, P = .025) hippocampal dendritic segments than did SR animals.

The other major structure studied was the mossy tuft, the presynaptic structure on axons and axon collaterals projecting from dentate granule cells into hippocampal areas CA3 and CA4 (8). With the transmission electron microscope (TEM), we examined ultrathin sagittal sections from the strata radiatum and pyramidale of four SS and four SR gerbils (11). Differences between Golgi and TEM fixation procedures necessitated our using a different population of animals for this phase of the experiment. All quantitative analyses were performed on photographs of mossy tufts, selected according to strict criteria (12). From the acceptable photographs, seven tufts from four animals in each strain were randomly chosen for the preliminary quantitative analysis reported here.

We report results for four measures for each mossy tuft (Fig. 3): total tuft area (A_t), area occupied by vesicles (A_v), area occupied by spines (A_s), and area occupied by mitochondria (A_m). All areas were determined by planimetric measurement of tracings of the original tuft.

The proportion of total tuft area occupied by vesicles was larger in SS than in SR animals [$t(6)$ = 3.44, P < .025] (13) but the proportion of total tuft area occupied by spines was larger for SR animals [$t(6)$ = 2.46, P < .05]. Although vesicle density did not differ between the two strains, maximal packing of vesicles up to an average of 420 vesicles per square micrometer was often observed in tufts of SS gerbils. The two groups did not differ in total tuft area, in A_m/A_t, or in number of spines enclosed per mossy tuft.

Differences between gerbils with histories of seizure and those without were thus found in both presynaptic and postsynaptic structures. These findings resemble results from other investigators

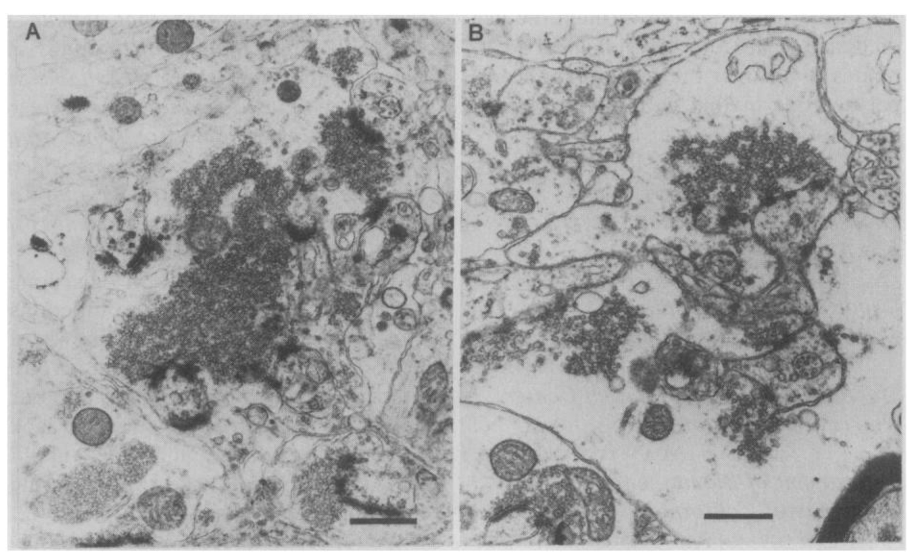

Fig. 3. Mossy tufts from SS (A) and SR (B) animals. The SS tuft has a greater proportion of total tuft area occupied by vesicles. Calibration bar, 1 μm.

studying the chronic irritative focus (*1*), the epileptic human temporal lobe (*1*), and the isolated cortical slab (*14*). Our studies differ in that we have used a naturally occurring behavioral model in which it is possible to control many seizure variables. Unlike researchers who detailed structural changes (*1, 14*), we did not examine tissue previously subjected to exogenous agents, chronic scarring, or long-term surgical manipulation. Further work is needed to clarify (i) the time course of the development of seizure pattern and spine density differences between SS and SR gerbils in ontogeny and (ii) whether the hippocampus, and area CA3 in particular, is a primary site in ictogenesis.

The spine decrease in SS strata oriens and pyramidale may represent a general loss of spines over the entire neuron. It could also imply that the receptive surface has been reduced for inputs of a certain character only, since CA3 contains afferents stratified according to both chemical content and site of origin (*15, 16*). The concept of balance between systems of different chemical content or regional origin with synapse on a common target is one with powerful explanatory potential for episodic phenomena such as seizures (*16*). One consequence of regional spine thinning on dendrites distal to the cell soma could be the functional enhancement of proximal inputs. Since the distributions of pre- and postsynaptic structures only partially overlapped, we can come to no firm conclusion regarding the interaction between spine and tuft findings; still, it is possible that the SS is distinguished from the SR preparation by different proportions of mossy tuft input relative to the postsynaptic spiny array.

Our findings provide a possible basis for further investigation through the use of dynamic anatomophysiological techniques to uncover the role of hippocampal neurons in this naturally occurring model of epilepsy (*17*).

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12. Criteria for tuft selection were (i) tuft diameter greater than 2.5 μm; (ii) tuft must enclose at least one spine; (iii) at least two synaptic plaques (postsynaptic darkenings) must be visible; and (iv) vesicles must be present within tuft boundaries.
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A Test for Responsiveness to Song Structure and Programming in Female Sparrows

Abstract. *Female song sparrows, primed with implants of estradiol, gave the solicitation display for copulation in response to acoustic stimulation with song. This technique demonstrated that female song sparrows respond more strongly to conspecific song than to alien songs, that they discriminate on the basis of both overall temporal pattern and syllabic structure, that they respond more to several song types than to repetitions of one song, and that they are most responsive to several song types if the songs are organized in bouts of a single type, as they are normally delivered by a male song sparrow. These results demonstrate a substantial correspondence between the structure and programming of the singing behavior of male birds and female responsiveness to song.*

Although mate attraction has long been thought to be one of the functions of male birdsong (*1*), little is known of effects of mate attraction on the evolution of singing behavior. This gap in our knowledge is a consequence of the lack of a sensitive, reliable, and widely applicable experimental test for measuring female preference for different songs (*2, 3*). We report on a technique for measuring the effects of several aspects of singing behavior on courtship intensity in female song sparrows (*Melospiza melodia*). The results demonstrate a close match between female responsiveness and the distinctive features of male song sparrow singing behavior.

After treatment with estradiol, female song sparrow response to songs was measured by number and intensity of copulation solicitation displays. King and West and their co-workers (*4*) used copulation solicitation display as a response measure in female brown-headed

