October. I therefore tested this hypothesis by examining seasonal variation in the outcome of confrontations between the two ant species at tuna fish baits (Table 1). In the absence of *Apocephalus*, *P. dentata* dominated most confrontations with *S. texana*; in the presence of phorids the outcome in most of the confrontations was reversed. Thus *Apocephalus* seasonally shifts the competitive balance between *P. dentata* and *S. texana* at large food sources.

Complex interactions among hosts, parasites, and competitors, similar to the ones described here, may be more common in ant communities than is generally realized (*4*). Such complex interactions may have profound effects on community organization and coexistence patterns. Parasitic phorids have been observed in all warm temperate woodlands in which careful searches have been conducted. In Texas, *Camponotus pennsylvanicus*, a common aggressive dominant ant species inhabiting many woodlands in the eastern United States, rapidly leaves baits at the appearance of the phorid fly *Apocephalus pergandei*. Baits abandoned by *C. pennsylvanicus* are normally quickly occupied by a variety of ant species, including *P. dentata*, *S. geminata*, and *Crematogaster punctulata* (*13*). Pasture and woodland nests of *S. geminata*, a fire ant native to the southern United States, are apparently heavily parasitized by several species of phorid flies (*14*). My observations in Austin, Texas, indicate that the presence of the phorid *Pseudacteon antiguensis* can prevent normal foraging behavior of *S. geminata* by forcing workers to assume defensive postures (*15*). In contrast, the notorious imported fire ant, *Solenopsis invicta*, appears free of phorid parasites in the United States, despite the diverse array of phorid flies this species and its close relatives support in South America (*16*). This freedom may partly explain the high densities of *S. invicta* and its competitive dominance over *S. geminata* in the southeastern United States.

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7. My observations were made at the University of Texas Brackenridge Field Laboratory in Austin between April and November 1976–78. I have made similar observations in Brazoria and Hardin Counties, Texas.
8. R. H. L. Disney, personal communication. Voucher specimens are deposited in both the author's and Dr. Disney's collections.
9. Specificity of phorids was determined by the number of ant species to which the flies were attracted and what species or castes elicited oviposition attempts. *Apocephalus* was attracted to more than 160 tuna fish baits occupied by *P. dentata* and to only two baits occupied by other species; both of the latter were within 10 cm of *P. dentata* workers. I have observed more than 50 oviposition attempts by *Apocephalus*. All of these attempts were directed at major workers of *P. dentata*. In no case were they directed at minor workers of *P. dentata* or the workers of other ant species.
10. Continuous observations for 2 hours on three separate occasions indicate that major workers stay in their hiding places as long as phorids remain within 10 to 15 cm of the hiding places. Repeated spot checking at 1- and 2-hour intervals on more than 100 separate occasions yielded similar conclusions.
11. Behavior of minor workers is never altered by the presence of one or two *Apocephalus*. However, minor workers may temporarily leave the area of a bait if five or more *Apocephalus* are present. This occurs in only 4 to 18 percent of the instances when *Apocephalus* are present. The response of the minor workers in these instances appears to be a generalized response to disturbance rather than parasite avoidance.
12. Laboratory experiments by D. Meyer demonstrated that colonies collected in Austin, Texas, respond by alarm-recruitment only in the presence of *Solenopsis*. Furthermore, addition of *Monomorium minimum*, a species of similar size and behavior to *S. texana*, did not provoke alarm-recruitment during field experiments concurrent with the ones described in my report.
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Individual Hippocampal Mossy Fiber Distribution in Mice Correlates with Two-Way Avoidance Performance

Abstract. *Mice systematically bred for randomization of their genotype show large individual differences when performing a two-way avoidance task (shuttle-box learning). Their behavioral scores correlate strongly* ($r = -0.80$, $P < .01$) *with the number of mossy fibers synapsing on basal dendrites of hippocampal pyramidal neurons, poor avoiders having relatively more such terminals. This confirms previous findings showing that rat and mouse strains known for genetically dependent poor avoidance learning have extended intra- and infrapyramidal mossy fiber projections.*

Recently we found evidence (*1*) confirming a previous hypothesis that variations in mammalian learning behavior are associated with genetically dependent variations in the connectivity of limbic and cortical areas (*2*). In mouse and rat strains characterized by high or low inherited performance levels in a two-way avoidance test, we observed that the poorly avoiding strains had more mossy fiber terminals on the basal dendrites of pyramidal neurons in regio inferior of the hippocampus as compared to the well-performing strains (*1*). Here we report for the first time that such a correlation occurs in individual mice of variable genotype: each animal was first tested for two-way avoidance, and then morphometrically for hippocampal mossy fiber distribution.

For the morphometry, we used Timm's silver sulfide stain for visualization of heavy metals, which are associated with synaptic enzymes (*3*). Where specific classes of synapses are arranged in laminae or clusters, as in the hippocampus, populations of synapses forming terminal fields are seen as colored bands or patches (Fig. 1, C and D). Most prominent among these populations are the clusters of the darkly staining giant boutons of the mossy fibers. These fibers originate from the granule cell layer in the fascia dentata and synapse predominantly on the proximal parts of the apical dendrites of the pyramidal neurons, forming a prominent band in Timm-stained sections: the suprapyramidal mossy fibers. A smaller projection occurs within or below the pyramidal layer on the proximal parts of the basal dendrites: the intra- and infrapyramidal (IIP) mossy fibers (*4*). Their presence is variable and genetically dependent (*5*). With-

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Table 1. Multiple regression analysis of hippocampal variables and two-way avoidance. The partial regression coefficients b_i and their standard errors show the apparent percentage change in avoidance performance after a 1 percent change in the relative size of a given hippocampal terminal field (for the regio inferior, after a change of 1/10 mm^2). Significance levels are based on two-tailed t values (b_i/standard error; d.f., 11) and, for the multiple correlation coefficient, on the F value from an analysis of variance.

Hippocampal variables	Partial regression coefficients (b_i ± standard error)
Regio inferior (1/10 mm^2)	1.4 ± 2.2
Stratum oriens (%)	0.6 ± 0.9
Stratum pyramidale (%)	−1.4 ± 0.8
Stratum radiatum (%)	0.7 ± 1.1
Stratum lacunosum-moleculare (%)	−2.4 ± 2.5
Mossy fibers CA4 (%)	0.1 ± 1.2
Mossy fibers suprapyramidal (%)	−0.1 ± 2.3
Mossy fibers intra-, infrapyramidal (%)	−6.2 ± 1.7*

*$P < .01$; multiple correlation coefficient: $R = .916$.

in the regio inferior of the hippocampus, we determined planimetrically in Timm-stained sections the areas covered by the different synaptic fields (Fig. 1A). The results were correlated with behavioral scores.

In successful two-way avoidance, the animal avoids an electric shock (preceded by a warning stimulus) by running to the other chamber of a two-compartment box. The number of successful avoidance responses after 5 days of training may vary between 10 and 90 percent. This level of performance depends strongly on genetic factors (*6*). Two-way avoidance does not necessarily measure a true (associative) learning ability since it depends on motivational mechanisms that may interfere with the acquisition of the task (*7*).

Twenty 3-month-old mice (ten females, ten males) from a strain bred for maximum genetic heterogeneity were tested for acquisition and performance of two-way avoidance (*8*) (Fig. 1B). The brains of all animals were processed for Timm staining according to the method of Danscher and Zimmer (*9*). Analysis was double-blind. Ten consecutive frozen horizontal sections from a level in the hippocampus corresponding to a horizontal plane through the habenula were studied (*10*). On drawings (×150) made with the help of a projection microscope, the areas of the various hippocampal fields were determined planimetrically through the use of a graphics tablet connected to a minicomputer (NOVA II) (Fig. 1A). The area covered by IIP mossy fiber terminals was determined by overlaying the regions in question with a point grid and counting the number of points over dark Timm-reaction product (*5*). For each animal, areas of the strata, of the mossy fiber terminal fields, and of the whole regio inferior [including CA4, the hilar region (Fig. 1A)] were then summed for ten sections and the relative sizes of the various measured areas were expressed as percentages of regio inferior (*11*). A correlation matrix was computed for the eight hippocampal variables [including the mean absolute size of the regio inferior (Table 1)] and the percentages of correct avoidance responses on day 5.

The results showed only two significant, negative correlations: the larger the relative area covered by IIP mossy fiber terminals (Fig. 1), or the larger the relative size of the pyramidal layer, the poorer the avoidance performance ($r = -.80$, $P < .001$ and $r = -.65$, $P < .01$, respectively). However, the data showed covariation between the morphological variables. In order to control for a masked relation of other hippocampal measures with IIP mossy fibers, which would create a spurious correlation between avoidance and mossy fibers, the data were analyzed by means of multiple regression (*12*). After the statistical correction of the covariation among the hippocampal variables, only the percentage of IIP mossy fiber terminals in the regio inferior showed a significant partial regression with behavior (Table 1).

Thus, the relative size of the IIP mossy fiber projection is perhaps not the only morphological characteristic associated with two-way avoidance, but so far the only variable permitting the prediction of a behavioral score. The negative association between avoidance performance and the number of mossy fiber terminals on basal dendrites of hippo-

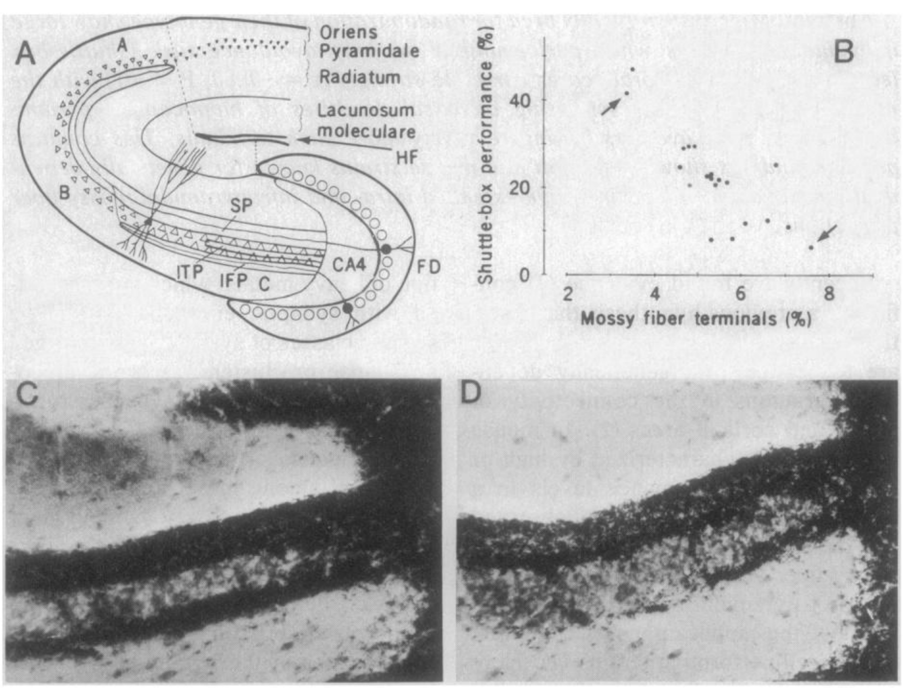

Fig. 1. Morphology and behavior. (A) Diagram of a Timm-stained horizontal cross section of the hippocampus. Stippled areas: supra- (*SP*), intra- (*ITP*), and infrapyramidal (*IFP*) and hilar (*CA4*) mossy fiber projections. Strata oriens and radiatum (*11*) contain the terminals of intrinsic hippocampal connections, and stratum lacunosum-moleclare receives entorhinal input from the cortex. Dotted lines: planimetric boundaries of the regio inferior to the regio superior and the fascia dentata. Abbreviations: *A*, *B*, and *C*, zones of the regio inferior; *FD*, fascia dentata; *HF*, hippocampal fissure. (B) Correlation plot of avoidance performance and relative size of the IIP mossy fiber projection ($r = -.80$, $P < .01$). Arrows: scores of animals whose hippocampi are shown in (C) and (D). (C) Zone C of a poorly performing animal. (D) Zone C of a good avoider.

campal pyramidal neurons appears to be a robust phenomenon, since it has been found among inbred strains of mice (*1*), in rat strains selectively bred for differential two-way avoidance performance (*1*) and, as shown here, in individual mice bred for randomization of their genotype. In all three studies, no other variable within the regio inferior showed such a constant relation to avoidance behavior. In view of the role of the hippocampus in the mediation of two-way avoidance [an intact hippocampus appears to interfere with good performance (*13*)], we hypothesize that the IIP mossy fibers play a role in this behavioral task. Further experiments must show whether this particular projection is directly involved in avoidance performance or whether it merely represents a neuroanatomical "marker" for an undetected correlation, perhaps in the target system—the regio inferior—or in the site of origin—the fascia dentata.

Since both the IIP mossy fiber distribution and two-way avoidance performance co-vary genetically and also after ontogenetic manipulations (*14*), the system that we have studied holds promise for future work on the interaction of genetics and environment in the establishment of neuronal circuitry underlying behavior.

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11. Stratum radiatum was defined as Cajal's stratum radiatum minus the suprapyramidal mossy fiber layer. Strata oriens and pyramidale included the IIP mossy fiber projection. Their inclusion or exclusion was irrelevant for our statistical results. The absolute size of the regio inferior refers to the mean surface of a section (grand total/10).
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15. Part of this work has been presented at the 13th annual meeting of the Union of Swiss Societies of Experimental Biology, Lausanne, March 1981 [H. Schwegler and H. P. Lipp, *Experientia* **37**, 14 (1981)]. We thank F. Vogel and P. G. H. Clarke for critically reading the manuscript; J. Beck, M. C. Cruz, M. Gaillard, M. P. A. Grisoni, and S. Methfessel for technical assistance; and C. Vaclavik for typing. The mice were a gift from the Institute of Biological and Medical Research Ltd., Füllinsdorf, Switzerland. This work was supported by the Deutsche Forschungsgemeinschaft (grant Schw-252/2) and by the Swiss National Science Foundation (grant 3.516).
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Early Experience Determines Song Dialect Responsiveness of Female Sparrows

Abstract. *In a laboratory experiment, female white-crowned sparrows responded almost exclusively to male songs taken from their home dialect region and usually not to songs taken from an alien dialect region. Song dialect populations may represent a level of genetic population structure below that of the subspecies and may play an important role in songbird evolution.*

Male white-crowned sparrows (*Zonotrichia leucophrys*) sing a song of stereotyped form and duration as part of their territorial defense and their behavioral display to attract females (*1, 2*). Each male usually has only one short (~ 2-second) song in his repertoire. The males in a local population share one or more syllables that differ from those of other local populations, resulting in a geographic mosaic of dialects (*3*).

In Colorado, the mountain white-crowned sparrow is a migratory subspecies with distinct dialect populations of various sizes. Our field experience indicates that some dialect populations may number as many as several thousand adults and others only a few hundred or less. Males learn their song during an early auditory-sensitive period; females also learn song but seldom sing (*4*). The usually monogamous male closely attends the female during the few days of egg laying and copulates with her after her solicitation display, in which she tilts her head upward, elevates her tail, squats slightly with wings fluttering, and emits a trilling vocalization (*5*). The posture, reminiscent of lordosis in small mammals, is termed a copulation posture in studies of female brown-headed cowbirds (*6*).

The biological role of the song dialect is of widespread interest (*7*), since a large number of songbird (oscine) species exhibit dialects. The speculation arose early in song dialect research that in some dialect systems a female may use the dialect markers in male song to select a mate from her natal area (*8*). In a field experiment in which tape recordings of songs representing local and alien dialects were played to territorial males, Milligan and Verner (*9*) counted the number of trill vocalizations by females and found that the response to the local dialects tended to be greater than that to the alien dialects, although "only occasionally did female white-crowned sparrows respond to playback during the breeding season." If females mate selectively with males from their natal dialect area, genetic adaptation to local environmental conditions could occur (*10*). The existence of partial barriers to gene exchange among local populations would fit the model of Wright (*11*) which suggests that this population structure is most conducive to rapid evolutionary change.

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