of approach was 17 cm/sec. The object was hung from the shadow-casting apparatus and displayed in a three-sided visual corridor made of bamboo curtains. Its run was 75 cm in length and ended about 15 cm in front of the infant. The object was not rotated but remained frontal parallel to the infant seated at the end of the run, in the same fashion as in the shadow-casting procedure. Infants started with either hit or miss sequences in a balanced design across subjects. Three trials of each sequence were again attempted, and a video tape recording was made of the sessions.

Because the form of the infant's response is fundamental to the experiment, a qualitative description will be given before the quantitative results. Infants generally began the session slumped in the chair with their arms down. During a hit sequence, the infant moved his head back and away from the screen and brought his arms toward his face. This was the full avoidance response. Sometimes the infant finished by facing toward the ceiling. The coming back of the head was usually observed only after the shadow had begun to fill the field or when the object came close. It was never observed before the transformation began. The person holding the infant often reported a "stiffening" of the infant's body during looming phases, followed by a relaxation during the recession phase. The response during the miss trials was dramatically different. There was commonly a slow turning of the head and eyes along the path of the shadow or object. The arms tended to come up, but the head did not come back as it did in hit trials, nor did the infant stiffen. Strikingly, visitors with no knowledge of the stimulus conditions, who observed the tapes, commented that the baby seemed to be either avoiding or following something in the respective conditions.

For the quantitative analysis, counts were made of the movement of the head backward, of the arms upward, and of the head tracking to the side; counts were also made of fussing (primarily vocalizations from low cries to wailing). Each of these events was scored and analyzed separately, and a combined measure of two out of three components produced a tracking or upset index. The quantitative results support the qualitative descriptions.

In the shadow-casting experiment, hit and miss trials were significantly different ($\chi^2 = 16.8$, d.f. $= 1$, $P < .001$) for the combined upset measure. The difference was accounted for by a significant difference between the movement of the head (movement backward versus tracking) in the two conditions ($\chi^2 = 82$, d.f. $= 1$, $P < .001$). There were no differences in any of the measures for the different age groups or for the solid as compared with the flat sequences. The recession trials did not produce the above components at all. The results in the case of the real object were similar. Hit versus miss was significantly different on the combined upset measures (Fisher exact test, $P = .003$), and the difference was accounted for by the head-movement measure.

The qualitative and quantitative results support the interpretation that infants can detect object qualities of direction and relative depth of approach and collision for both real objects and their optical equivalent. Neither kinetic depth in the optical displays nor the real display appeared to produce a stronger response than the simple expansion pattern. It may be that the infants are unable to process all the information available simultaneously or that expansion alone is a sufficient elicitor of the response with or without additional information. The lack of age differences over the age range studied indicates that learning (either to detect the event or, in the shadow-casting case, to detect that it is *not* a real object) does not play a major role in the phenomenon.

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Competition between Species: Frequency Dependence

Abstract. *Whether two species competing for the same limited resources can stably coexist has been subject to controversy for several decades. The relative fitnesses of two species of* Drosophila *under competition in laboratory populations are shown to be inversely related to the relative frequencies of these species. This frequency-dependent fitness leads to a stable coexistence of the two species in spite of their competition for limited resources.*

The question of whether two or more related species competing for the same limited resources—such as food, places to live, or places to nest—can coexist has long been debated among ecologists. The "principle of competitive exclusion," or Gause's principle, postulates that no two species are likely to be exactly identical in their efficiency to exploit any given resource; one species or the other will be at a relative advantage. If the two species compete for the same resource existing in limited supply, no matter how small is the difference between the two species in their efficiency to exploit it, the less efficient species will eventually be eliminated. For as long as the competition continues, the more efficient species will gradually increase in number relative to the less efficient species, until the latter becomes extinct (*1*).

This reasoning ignores, however, the complexities of the process of ecological competition. Physical and biotic environments of organisms are heterogeneous both in the spatial and in the temporal dimension. Species are not monolithic entities composed of identical copies of the same model; rather, in species that experience sexual outbreeding, no two individuals, with the trivial exception of monozygotic twins, are likely to be genetically identical. Moreover, the frequencies of genes and genotypes of a population are continually changing through natural selection which promotes adaptation of the population to its environment. For these reasons, it can be argued that species competing for the same limited resources may, under certain conditions, coexist in a more or less stable equilibrium (*2*). The proponents of this position failed, however, for many years to obtain decisive and convincing evidence from either observations or experiments. But, recently, it has been demonstrated in an experimental system that two species of *Drosophila* coexisted at equilibrium frequencies while competing for limited resources of food and space (*3*).

A necessary requirement for a stable equilibrium between two competing species is that their relative fitnesses be frequency-dependent. Environmental fluctuations and chance events are likely to alter the relative frequencies of the competing species. The system will be stable only if the competitive fitness of one species relative to the other species is less than unity when the species is above its equilibrium frequency and greater than unity when its frequency has fallen below the equilibrium level. At the equilibrium frequency the competitive fitnesses of the two species are, of course, identical. But equal fitness is not a sufficient condition for a stable equilibrium; it may also be compatible with an unstable or neutral equilibrium. The experiments reported here were undertaken to ascertain in an experimental system whether the fitnesses of two coexisting and competing species are frequency-dependent.

At 21.5°C *Drosophila willistoni* and *D. pseudoobscura* flies competing for the same limited resources may coexist at frequencies that depend on the genetic constitution of the strains used. Two series of experiments were carried out. In the first series, mixed populations of the two species were started at three different frequencies and allowed to breed under controlled conditions, the amount of food, the amount of living space, the temperature, and so on being kept constant. These populations were maintained by "serial transfer" (*4*). Adult flies were introduced into a half-pint (0.24-liter) milk bottle, along with a measured amount of food; egg laying was allowed for 7 days; every week the population was etherized, counted, and then transferred to a new bottle with fresh food. When adult flies began to emerge in the bottles where the eggs had been laid, they were collected and counted under anesthesia, and then added to the bottle containing the adult population. The bottles were discarded 5 weeks after the adult flies had been first introduced. A population consists, then, of five bottles. One bottle contains the ovipositing adult flies, whereas the four other bottles contain eggs, larvae, pupae, and newly emerged adults. The following parameters were measured: the number of flies surviving after 1 week in the bottle containing the adult flies ("survivorship") and the number of flies emerging per week ("productivity"). The sum of the number of flies surviving from the previous week plus the number that had emerged during the week ("total") constitutes the initial number for the new week.

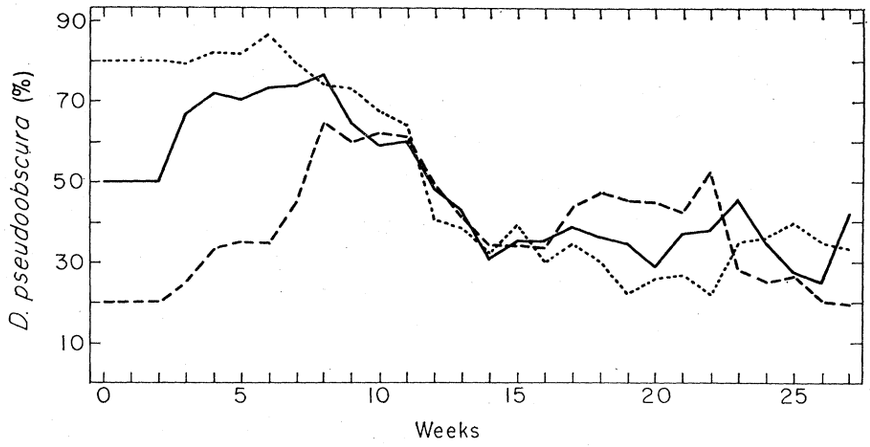


Fig. 1. Results of the competition of *Drosophila pseudoobscura* with *D. willistoni* M11 in three experimental populations started at different initial frequencies.

The strains of *Drosophila* used have been described elsewhere (*5*). All experiments were made in two sets, one with the M11 strain and the other with the RP3 strain of *D. willistoni*. The same strain, 211, of *D. pseudoobscura* was used in all experiments. The experimental populations were started with 1000 flies of both species. The initial frequency of *D. pseudoobscura* was 20 percent in one population, 50 percent in a second, and 80 percent in a third. The frequency of *D. pseudoobscura* among the total number of flies is shown in Fig. 1 for the populations involving the M11 strain of *D. willistoni*. The frequencies of *D. pseudoobscura* rapidly converge. From week 13 on, or after

Table 1. Mean number of flies and standard error for survivorship, productivity, and total, at three initial frequencies of two species of *Drosophila*. *N*, number of replications.

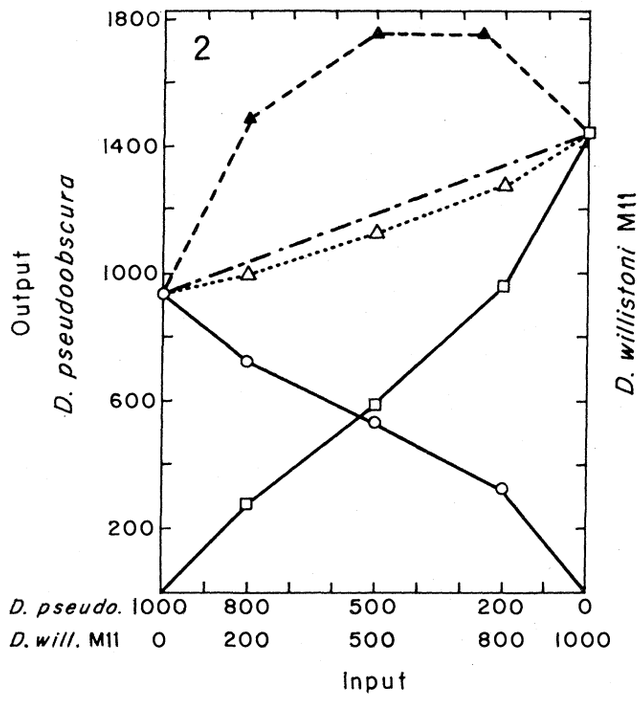
Species	Initial number	*N*	Survivors after 1 week	Flies produced per culture	Total	Percentage
D. willistoni M11	200	54	101 ± 4	186 ± 10	287 ± 3	28.3
D. pseudoobscura	800	54	563 ± 11	164 ± 15	727 ± 8	71.7
D. willistoni M11	500	52	277 ± 8	315 ± 19	592 ± 2	52.2
D. pseudoobscura	500	52	359 ± 8	183 ± 14	541 ± 9	47.8
D. willistoni M11	800	54	465 ± 14	501 ± 23	966 ± 41	75.1
D. pseudoobscura	200	54	152 ± 2	168 ± 11	320 ± 8	24.9
D. willistoni RP3	200	54	99 ± 3	114 ± 9	214 ± 7	21.6
D. pseudoobscura	800	54	596 ± 9	179 ± 9	775 ± 9	78.4
D. willistoni RP3	500	51	250 ± 8	254 ± 18	503 ± 15	48.1
D. pseudoobscura	500	51	380 ± 7	163 ± 8	543 ± 4	51.9
D. willistoni RP3	800	54	454 ± 13	418 ± 13	872 ± 14	74.6
D. pseudoobscura	200	54	158 ± 2	138 ± 7	296 ± 8	25.4

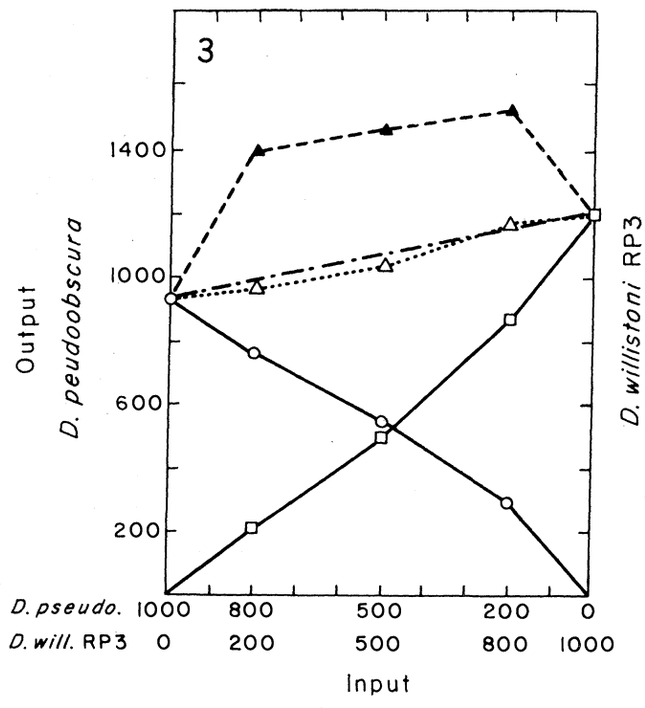
Table 2. Mean number of flies and standard error for survivorship, productivity, and total, in single-species cultures of *Drosophila*. *N*, number of replications.

Species	Initial numbers	*N*	Survivors after 1 week	Flies produced per culture	Total
D. willistoni M11	200	24	154 ± 5	491 ± 25	645 ± 25
D. willistoni M11	500	24	363 ± 14	725 ± 38	1088 ± 39
D. willistoni M11	800	24	547 ± 26	728 ± 55	1276 ± 59
D. willistoni M11	1000	20	650 ± 26	768 ± 28	1419 ± 38
D. willistoni RP3	200	24	146 ± 4	407 ± 21	553 ± 21
D. willistoni RP3	500	24	335 ± 15	465 ± 24	800 ± 27
D. willistoni RP3	800	24	504 ± 19	555 ± 34	1059 ± 38
D. willistoni RP3	1000	20	651 ± 28	559 ± 43	1210 ± 51
D. pseudoobscura	200	24	161 ± 4	306 ± 21	467 ± 20
D. pseudoobscura	500	24	397 ± 7	260 ± 22	656 ± 23
D. pseudoobscura	800	24	606 ± 16	231 ± 24	837 ± 28
D. pseudoobscura	1000	20	759 ± 20	172 ± 18	931 ± 27

about four generations, the frequency of *D. pseudoobscura* oscillates around a mean value of about 35 percent. The RP3 populations converge in a similar manner. The average frequency of *D. pseudoobscura* from week 13 on is about 50 percent.

In a second series of experiments an attempt was made to estimate the changes in numbers after 1 week at the same three initial frequencies as in the first series. As before, 1000 flies of both species were placed in a culture bottle and egg laying was allowed for 1 week. The proportion of *D. pseudoobscura* flies was 20 percent in one population, 50 percent in a second, and 80 percent in a third. After 7 days the survivors were counted and discarded. The flies emerging from each bottle until the end of week 5 were also counted. The sum of the number of survivors plus the number of flies emerging from the bottle gives the expected total number of flies after 1 week under the conditions of the first series of experiments. This second series of experiments was also carried out with the two strains, M11 and RP3, of *D. willistoni*. From week 6 to week 23 of the populations of Fig. 1 each combination of strains and initial frequencies was replicated three times a week. All cultures were kept in the same constant-temperature room, distributed among the shelves at random. The results are summarized in Table 1. It seems evident that, within the range studied, the competitive fitness of each species is inversely related to its initial frequency. In the M11 populations, if the initial frequency of *D. pseudo-*





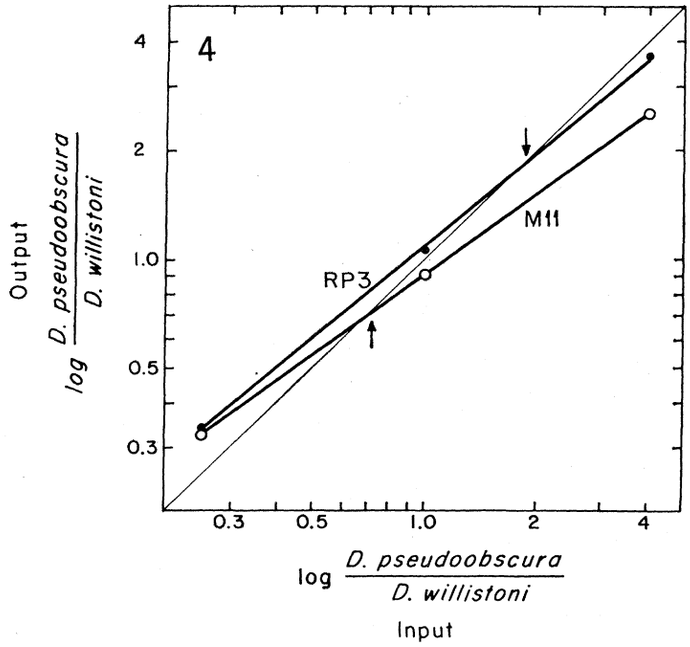


Fig. 2 (top left). Replacement series diagram for the M11 populations showing the change in the number of flies for any given initial combination. (Solid lines) Numbers of *Drosophila pseudoobscura* (circles) and *D. willistoni* (squares) in the two-species populations; (dotted line) numbers of both species in the two-species populations; (dashed line) numbers of both species in the single-species populations; (dashed and dotted line) expected numbers of both species in the two-species populations on the assumption that there will be complete sharing of limited resources. Fig. 3 (top right). Replacement series diagram showing for the RP3 populations the change in the number of flies for any given initial combination. The meaning of symbols is explained in Fig. 2. Fig. 4 (left). Ratio diagram showing the linear regression of the logarithmic output ratio on the logarithmic input ratio of *Drosophila pseudoobscura* to *D. willistoni* flies. (Open circles) M11 populations; (solid circles) RP3 populations. The intersects indicated by the arrows give the ratios at which the frequencies of the two species will remain stable. The numbers on the axes are the actual ratios.

obscura is 80 percent, the frequency is expected to decrease to 72 percent after 1 week. On the contrary, if its initial frequency is 20 percent, the frequency will increase to 25 percent after 1 week. Qualitatively identical results are obtained with the RP3 populations.

In an effort to measure the intensity of the competition between the species, single-species populations were studied. The initial numbers of flies were 200, 500, 800, and 1000. Survivorship after 1 week and the number of flies emerging from each bottle until the end of week 5 were scored as before. Each initial frequency for each strain was replicated once a week, contemporaneously with the two-species populations. They were also kept in the same constant-temperature room with similar amounts of food, living space, and so on. The results are summarized in Table 2. In the *D. willistoni* populations the number of flies produced per bottle increases as the number of parents increases from 200 to 500 in the M11 strain and from 200 to 800 in the RP3 strain. The number of progeny does not change significantly as the initial number of flies increases from 500 to 1000 in the M11 populations, and from 800 to 1000 in the RP3 populations. With *D. pseudoobscura* the situation is quite different; the number of progeny gradually decreases as the number of parents gradually increases from 200 to 1000. Under the experimental conditions the number of *D. pseudoobscura* parents which maximizes the number of progeny is below 500 and may be lower than 200.

Comparison of Tables 1 and 2 provides evidence of competition between the two species. For any given initial number of flies of one species, the number of survivors and the number of flies produced per culture are always greater in the single-species than in the two-species cultures. Some additional facts are worth noticing. For any given density, the M11 populations produce more flies than the RP3 populations both in single-species and in two-species cultures. Furthermore, the M11 flies generally survive better than the RP3 flies, although the differences are frequently not significant. *Drosophila pseudoobscura* survives better, but at two densities this species produces fewer offspring in competition with the RP3 than in competition with the M11 strain.

The overall effect of the competition between the two species is best shown by the replacement series diagrams (*6*) in Figs. 2 and 3. The initial numbers of flies are given on the abscissa. The total number of flies after the competition is given on the ordinate. The solid lines show the total number of flies of *each* species in the two-species cultures. The total numbers of flies of *both* species in these competition cultures are indicated by the dotted line. The dashed line represents the total number of flies of *both* species in the single-species cultures. On the assumption that there are no cooperative or disoperative interactions between the species other than possible sharing of the same resources, the expected location of the dotted line would be as follows: If each species exploits different resources with no competition between them, the dotted and dashed lines should coincide; that is, the total number of flies of both species would be the same in the two-species as in the single-species cultures. This result is clearly not the case. If the two species compete for some resources, but each species exploits some additional resource not exploited by the other, the dotted line should fall between the dashed line and the alternating dashed and dotted line. If the two species fully compete for the same limited resources, the dotted line and the alternating dashed-and-dotted line should coincide. This is, indeed, the case for the RP3 populations (Fig. 3), within the limits of experimental error. However, for the M11 populations (Fig. 2) the total number of flies of both species in the two-species cultures is lower than the value expected on the assumption of the complete sharing of resources (although at the initial frequency of 800 *D. willistoni* and 200 *D. pseudoobscura* the difference is not statistically significant). This observation seems to indicate that some other disoperative interaction, in addition to competition for limited resources, occurs between the two species in these populations. This observation brings into question the interpretation of the outcome of the RP3 populations as due to the complete sharing of limited resources. It is clear that the total number of flies of both species could as well coincide with the expected number on the assumption of complete sharing of resources if the species share only some resources but interact disoperatively also in some other way.

Table 3. Regression coefficient b and standard error of the output on the input ratio of *Drosophila pseudoobscura* to *D. willistoni*, with significance ratio t and level of significance P for the significance of the difference between unity and the regression coefficient.

Parameter	$b \pm$ S.E.	t	P
	M11 populations		
Survivorship	1.023 ± 0.020	1.2	$>.40$
Productivity	0.348 ± 0.026	24.8	$<.05$
Total	0.733 ± 0.002	126.8	$<.01$
	RP3 populations		
Survivorship	1.026 ± 0.022	1.1	$>.40$
Productivity	0.561 ± 0.046	9.6	$<.10$
Total	0.864 ± 0.005	25.2	$<.05$

Linear regressions of the output on the input ratio of the two species are given in Table 3. The regression coefficients are significantly less than unity for the total number of flies. There is an inverse relationship between the initial frequency of a species and its competitive fitness. This frequency dependence would lead to stable equilibrium at the initial frequencies indicated by the intersect of the regression lines and the diagonal line whose slope is 1. The intersects are indicated by the arrows in Fig. 4. The expected equilibrium frequencies of *D. pseudoobscura* are 42 percent and 65 percent for the M11 and the RP3 populations, respectively. The expected equilibrium frequencies agree reasonably well with the observed ones in the first series of experiments (Fig. 1 for the M11 populations). The equilibrium density in the first experiment was about 1200 flies while the second series of experiments was conducted at a density of 1000 flies.

The outcome of larval competition, as measured by the number of flies emerging per bottle, is strongly frequency-dependent; the survivorship of the adult flies is not (Table 3). Within the range of frequencies tested, *D. pseudoobscura* flies survive better than *D. willistoni* flies. At the equilibrium frequencies, the advantage of *D. pseudoobscura* as adults is exactly compensated by their disadvantage at the larval stage. Previous experiments have demonstrated that competitive fitness is in some cases frequency-dependent; this is true, for instance, for larval competition between two genotypes (*7*) or two species (*8*) of *Drosophila* and for the number of spikelets produced by two species of *Avena* (*9*). However, only some stages of the life cycle were studied in those experiments. In the experiments reported here, the competition involves all stages of the life cycle. Frequency-dependence leads, therefore, to a stable coexistence of the two competing species.

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Recurrent Excitation of Secondary Olfactory Neurons: A Possible Mechanism for Signal Amplification

Abstract. *Secondary neurons of the olfactory bulb can be excited monosynaptically after activation of neighboring secondary neurons by antidromic and orthodromic volleys. Recurrent collaterals of secondary neurons are proposed to synapse with other secondary neurons, thus forming a direct recurrent excitatory pathway. Such a positive feedback system could strengthen the original input signal.*

One of the most striking features of the olfactory system is its high degree of acuity. It has been estimated that as little as a few molecules of an odorant can be detected by some species (*1*). Thus one might expect the olfactory system to contain neuronal mechanisms for signal amplification. Although the concept of signal amplification in sensory systems has been proposed by a number of investigators (*2–4*), there is little physiological evidence for the presence of such a process. The results presented below suggest one possible mechanism in olfaction which might also function in other sensory systems.

The olfactory bulb is well suited for the study of sensory processing because the afferent and efferent pathways are easily accessible for stimulation and the neuronal elements are organized into discrete layers. Olfactory nerves arise from bipolar receptor cells in the nasal mucosa and terminate in the glomeruli of the olfactory bulb (Fig. 1). Secondary neurons of the olfactory bulb, mitral and tufted cells, receive synaptic excitation from olfactory nerves and send axons to the lateral olfactory tract (LOT) (*5–7*). Cajal showed anatomically that both mitral and tufted cells have axon collaterals that terminate in the external plexiform layer, and he proposed that such pathways might spread excitation to "an increasing number of conductors (avalanche conduction)" (*2*). I report here evidence for the monosynaptic recurrent excitation of secondary neurons; this would provide a positive feedback system that could strengthen the input signal.

Experiments were performed on rabbits with transected olfactory peduncles. Such a lesion would remove the centrif-

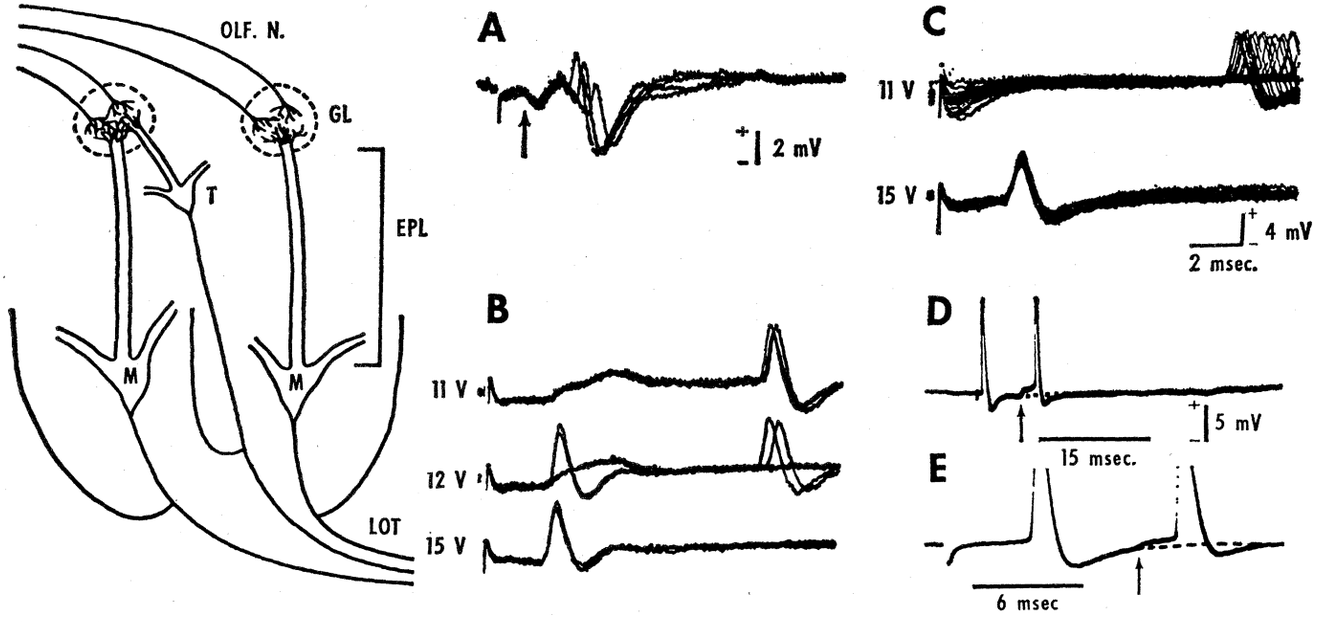

Fig. 1. Diagram at left illustrates basic anatomical features of the olfactory bulb. Olfactory nerves (*Olf. N.*) run along the surface of the bulb to form excitatory synapses with dendrites of mitral (*M*) and tufted (*T*) cells in glomeruli (*GL*). Axons of both cell types travel in the lateral olfactory tract (*LOT*) and send recurrent collaterals to the external plexiform layer (*EPL*). (A) Extracellular records of a presumed tufted cell showing variable latency to threshold stimuli to the LOT (five superimposed traces). Arrow shows onset of negative field that indicates antidromic invasion of the mitral cell. The time scale is the same as in C. (B) Extracellular recording from a mitral cell. The LOT was stimulated with 11 volts, 12 volts, and 15 volts as indicated (three to five superimposed sweeps). (C) Upper record: the LOT was stimulated with 11 volts at a frequency of 110 cycle/sec. Lower trace: the LOT was stimulated with 15 volts at a frequency of 110 cycle/sec. (D) Intracellular recording from a mitral cell responding to LOT volley (stimulus artifact just precedes first spike). Arrow indicates beginning of EPSP. (E) Intracellular record from another mitral cell at faster sweep responding to olfactory nerve volley (stimulus artifact at beginning of trace). Lack of inhibitory postsynaptic potential is presumably due to Cl^- leakage from the electrode.