Saline-indomethacin blanks, extracted and assayed concurrently with the samples, were below the limits of sensitivity of the assays (80 pg for PGF and 100 pg for PGE-A).

The amounts of PGF and PGE-A in groups of 144-hour blastocysts are shown in Table 1. When expressed as PG per blastocyst, the amount was highest in sample No. 5 (1.16 ng of PGF per blastocyst) and lowest in sample No. 6 (0.16 ng of PGF per blastocyst). This rather wide variability could have been caused by differences in blastocyst volume which ranged from 4 to 32 mm^3.

Each of the two uteri of pregnant and pseudopregnant rabbits was flushed with 5 ml of saline-indomethacin. The amount of PG's in these flushings is shown in Table 2.

Prostaglandins have been demonstrated in practically all tissues that have been investigated. The present results demonstrate, for the first time, PG's in a preimplantation embryo—the rabbit blastocyst. Because the blastocyst has the capacity to synthesize a wide range of compounds, we suggest that it synthesizes the PG's it contains. However, since synthesis has not been proved yet, we have to consider that the PG's may be transferred from the uterine lumen into the blastocyst. A gonadotropin similar to hCG or luteinizing hormone has been demonstrated in rabbit blastocysts (*9*). It was suggested that this gonadotropin stimulates steroidogenesis in the blastocyst (*4*). We now propose that one or more of the PG's found act as mediators in blastocyst steroidogenesis.

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10. Supported in part by the Ford Foundation. We thank D. C. Beuving for excellent technical assistance.

16 June 1975; revised 25 August 1975

Neuroplasticity in the Sparing or Deterioration of Function after Early Olfactory Tract Lesions

Abstract. *Mating behavior in male hamsters depends on the sense of smell. Thus, complete transection of the lateral olfactory tract in adults eliminates mating. If the cut is made early in life, however, mating is spared. Partial section of the tract in adults does not affect mating, but similar cuts in the neonate lead to impaired mating performance later in life. Observed postsurgical rearrangements in the connections of axons in the lateral olfactory tract may explain both the sparing and the deterioration of function.*

Infants often show a remarkable degree of functional sparing after brain lesions that are devastating when they occur in adults (*1*). Neuroanatomical plasticity has been proposed as one possible way of accounting for such sparing (*2*), but strong evidence for this has only recently been found in mammals. Using a behavioral marker for visual function, Schneider and Jhaveri (*3*) described how axonal rearrangement after early lesions can have either adaptive or pathological consequences depending on the nature of the new connections formed. The present experiments extend this principle to the aftereffects of transection of central olfactory fibers, a neural system that likewise offers simple behavioral markers for the presence of functioning anatomical connections.

The axons from the olfactory bulb run caudally on the surface of the olfactory cortex, where most of them are collected into a compact bundle, the lateral olfactory tract (LOT) (*4, 5*). In the adult male hamster, bilateral transection of the LOT eliminates mating (*6*), a behavior that is dependent on the sense of smell (*7, 8*). Partial LOT section in adulthood, however, does not cause this deficit (*6*). The present experiments show that after complete LOT section in the neonate, mating capacity later in life is spared. After partial LOT section in the neonate, however, mating capacity later in life is impaired. Both behavioral sparing and behavioral deterioration apparently depend on the postoperative rearrangement of cut and neighboring uncut axons in the olfactory tract.

The experiments were performed in two stages. First, the LOT was cut unilaterally and the normal development of mating behavior was confirmed. Then, the contralateral olfactory bulb was removed so that any residual functional contribution of the previously cut side would be uncovered. This procedure was followed because even some normal, unoperated hamster pups fail to mate when they reach sexual maturity. It was thus necessary to confirm that all the experimental animals were capable of mating before they were subjected to a bilateral lesion of the olfactory system.

In 27 male golden hamster pups 3 days of age, and in 14 adults 6 weeks of age, the LOT bundle was exposed unilaterally and transected either completely or partially (*9*). The hamsters were then allowed to grow to sexual maturity, and they were given extensive sexual experience beginning 5 to 15 weeks after surgery. In these mating tests a sexually receptive female was placed in the male's home cage (*8*), and the vigor of the male's sexual behavior was rated on a four-point scale (legend, Fig. 1A). Each test was ended after 5 minutes or after the first ejaculation, and successive tests were separated by at least 2 days. All of the animals mated vigorously (legend, Fig. 1A), an expected result since previous studies showed that neither unilateral LOT section nor unilateral bulbectomy performed in adulthood affects mating (*6–8*).

Next, the functional contribution of the previously cut LOT was assessed by removing the olfactory bulb on the intact side (main and accessory parts) and then giving an additional series of up to 17 mating tests over the next 2 to 28 weeks (*10*).

After this period of behavioral analysis, the distribution of olfactory bulb efferents that survived the original LOT cut or became rearranged because of it (or both) was traced by using either silver-staining or autoradiographic techniques (*11*). The anatomical analyses were done with knowledge of the animal's age at the time of the first operation but without knowledge of either its behavioral performance or the completeness of the LOT cut.

In the eight hamsters that underwent complete LOT section (first operation) at 6 weeks of age, subsequent contralateral bulbectomy essentially eliminated mating behavior (Fig. 1A). This is consistent with the earlier demonstration of severe deficits in mating behavior following bilateral LOT cuts in adulthood. In animals tested as long as 6 months after the bulb lesion no recovery was evident, nor did mating appear when the duration of tests was extended from 5 to 30 minutes.

In contrast, all but two of the hamsters that underwent complete LOT section at 3 days of age continued to mate after the contralateral bulbectomy. And while postoperative mating performance was not consistently vigorous from test to test as it had been previously (Fig. 1A), the loss was significantly less severe than that of animals whose first operation was complete LOT section at 6 weeks of age ($P < .001$) (*12, 13*). Thus, complete LOT section in the neonate leads to a relative sparing of function later in life (*14*).

Unilateral bulbectomy following partial LOT section at 6 weeks of age left mating essentially intact (Fig. 1A), consistent with the data obtained after partial bilateral LOT section in adults (*6*). Surprisingly, unilateral bulbectomy in the animals that underwent partial LOT section at 3 days of age rendered mating behavior significantly less vigorous and consistent than it had been preoperatively ($P < .01$) (*12*). That is, these animals showed a functional deterioration ($P < .01$) (*12*) relative to the animals with partial LOT cuts made later in life (Fig. 1A). Thus, complete LOT section has its most severe consequences when it occurs in adulthood; partial LOT section has its most severe consequences when it occurs shortly after birth.

The anatomical data, summarized in Fig. 1B [for further documentation see (*4*)], suggest a possible explanation for these behavioral results. In the normal hamster, olfactory bulb efferents run caudally in the LOT, and throughout their length distribute widely overlapping collaterals to a broad area of olfactory projection cortex (*4, 5*). The olfactory tubercle and terminal fields on the medial wall of the hemisphere, however, receive bulbar input along medially placed fibers that do not join the LOT bundle. These medial bulb efferents were not cut even in the complete LOT transections, and are apparently insufficient in and of themselves to support mating behavior (*6*).

After complete LOT section at 6 weeks of age, the olfactory tubercle and medial fields retained their normal input from the bulb, but the remainder of the cortical areas distal to the cut was completely denervated. This extensive denervation presumably accounts for the loss of mating in these cases (*6*).

Following complete transection at 3 days of age, bulb efferents reinnervated at least part of the cortex distal (caudal) to the cut (Fig. 1B), either by traversing the cut on the cortical surface (four cases) or by sprouting laterally from the olfactory tubercle (nine cases). This partial reinnervation may well account for the partial sparing of function seen in these cases. Rostral to the cut, proximal branches of LOT axons also sprouted new collaterals. This was reflected in a thickening of the normal stratum of terminals and the spread of terminals medially and sometimes laterally beyond their normal cytoarchitectonic boundaries into the infralimbic cortex and the neocortex which forms the dorsal bank of the rhinal sulcus [Leonard's "sulcal cortex" (*15*)]. The sprouting that occurs in these rostral fields, however, is insufficient to account for the observed functional recovery. This is suggested by results obtained from the two animals with complete neonatal cuts which failed to mate. Both showed substantial sprouting proximal to the cut but almost no reinnervation of the olfactory cortex distally. Animals in which the LOT is sectioned at 7 to 10 days of age also show this more restricted pattern of sprouting (*4*). Correspondingly, when the behavioral experiment was repeated in nine animals in which the LOT was completely transected in this age range, mating ceased in eight of them after the contralateral bulbectomy. Thus, when the LOT is cut in hamster pups only slightly older than those described above, the results are different both neurologically and behaviorally.

Partial LOT section in adult hamsters causes complete denervation of only a small wedge of cortex immediately behind the cut; the rest of the bulb's caudal distribution, although reduced in density, maintains its normal size (Fig. 1B). This is expected, because each part of the olfactory bulb and LOT contributes to each of these projection areas (*4, 5*). Thus, the remaining widespread bulbar distribution is apparently sufficient to maintain vigorous, consistent mating behavior.

After partial LOT section at 3 days of age, evidence of sprouting in areas rostral to the cut was similar, if less prominent, than that seen following complete LOT cuts. Collaterals must also have sprouted into the area immediately behind the cut, because no wedge of completely denervated cortex could be found there. In compensation, however, the most distal (caudal) part of the bulb's distribution was foreshortened (Fig. 1B), by an amount inversely proportional to the cross-sectional area of LOT cut (*4*). In cases in which one-third or more of the LOT was cut, for example, the bulb's terminal distribution did not extend caudally beyond the level of the nucleus of the LOT. Thus, there is a substantial reduction in the total area of olfac-

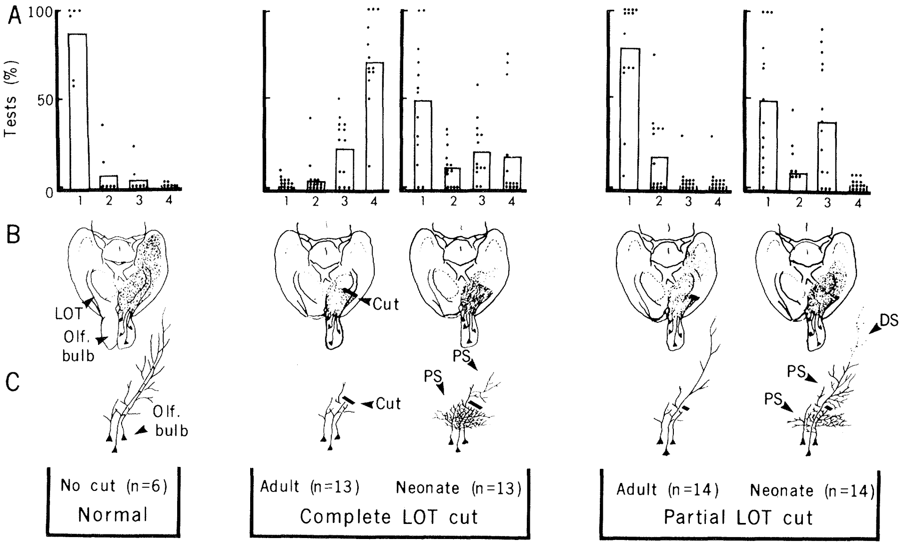

Fig. 1. (A) Distribution of postoperative mating test scores into behavior categories 1 to 4. The bars represent group means. Every animal is represented in each behavior category by one point. Thus, an animal may have rated 1 on 60 percent of tests, 2 on 30 percent, 3 on 10 percent, and 4 in no tests. The behavior categories were as follows: 1, vigorous, regularly patterned mating sequence with latency to first intromission ≤ 2 minutes; 2, some mounts but irregular patterning or intromission latency > 2 minutes; 3, no mounts but moderate investigatory interest in female (that is, ≥ 30 seconds of sniffing and licking); 4, no mounts, no interest in female (that is, < 30 seconds of investigation). Since the behavior of animals in which the LOT was cut bilaterally in adulthood was directly comparable to that of the animals described here, some of the earlier data were included in the present analysis (five complete cuts, eight partial). During the period after the LOT cut and before the bulb removal, each of the animals scored 1 or 2 on at least 10 consecutive tests. These data were identical for the control group and the four experimental groups ($P > .02$) (*12*). (B) Chartings of the distribution of olfactory (*Olf.*) bulb efferents in normal hamsters and in animals that sustained prior complete or partial LOT cuts. The density of stippling in the olfactory cortex represents the density and laminar thickness of the bulb's projection. At the time of experimental behavior testing, the animals had only one intact olfactory bulb, that on the same side as the prior LOT cut. (C) Proposed interpretation of the anatomical data in (B). Complete LOT transection in neonates severs ("prunes") the distal branches of the axons. In compensation, collaterals that branch off of the tract proximal to the cut form new sprouts (*PS*). Similarly, after partial LOT transection in neonates the cut fibers undergo proximal sprouting (*PS*). Proximal (midlevel) branches of the uncut fibers, however, also sprout new collaterals (*PS*), these to refill the vacated terminal sites just behind the cut. But since these axons have not been severed, the growth of their more distal branches is stunted (*DS*) in compensation for the accelerated growth of the midlevel branches. The extent of the resulting foreshortening of the bulb's projection was proportional to the number of LOT fibers cut (*4*).

tory cortex continuing to receive some bulbar input after partial LOT section performed in neonates but not in adults. This may well account for the relative deterioration of mating behavior in this group of animals. Thus, in all four experimental groups, mating behavior appears to depend on the extent of the olfactory bulb's projection, either total cortical area innervated or input into caudal structures specifically (Fig. 1, A and B) (*6*, *16*).

The postsurgical rearrangement of transected LOT axon populations suggests that individual axons grow much like trees (Fig. 1C). When all of the axons' distal branches are severed ["pruned" (*3*)] by complete LOT section at 3 days of age, their proximal branches compensate by sprouting new collaterals, some of which apparently reinnervate part of the denervated cortex behind the cut. After partial LOT section at this age, the cut fibers undergo similar compensatory sprouting. The distribution of the uncut fibers, however, also becomes rearranged; their mid-level branches proliferate to fill in the otherwise denervated wedge of cortex just caudal to the cut, and, apparently in compensation, the most distal axonal branches become foreshortened. This may reflect the retraction of these distal arborizations (*17*). It is more likely, however, that in response to the abnormal occupation of terminal sites vacated as a result of the cut, growth of the most distal branches of the uncut fibers is stunted so that they can no longer keep pace with the ballooning size of the underlying cortex. Thus, by undergoing compensatory sprouting and compensatory stunting, growing axons would tend to conserve their total amount of axonal arborization (*3*, *4*). Furthermore, while in some circumstances the sprouting of new connections may lead to functional recovery, the compensatory stunting of normal connections elsewhere may have pathological consequences.

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7. In hamsters, mating is eliminated by bilateral bulbectomy, destruction of the olfactory epithelium, or nostril occlusion, and is not restored by testosterone injections. The odor of female hamster vaginal discharge elicits mating [M. R. Murphy and G. E. Schneider, *Science* **167**, 302 (19[illegible] R. D. Lisk, J. Zeiss, L. A. Ciaccio, *J. Exp. Zool.* **181**, 69 (19[illegible] R. L. Doty and J. J. Anisko, *Physiol. Behav.* **10**, 395 (1973); M. R. Murphy, *Behav. Biol.* **9**, 367 (1973); R. E. Johnston, *ibid.* **12**, 111 (1974); E. M. Darby, M. Devor, S. L. Chorover, *J. Comp. Physiol. Psychol.* **88**, 496 (1975)].
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9. Cuts were made at the level of the olfactory tubercle and usually extended through cortical layer II. Completeness was assessed by histological examination. Surgical details are given in (*4*).
10. The second lesion was made at 101 to 177 days of age. Interlesion intervals of the four groups overlapped widely.
11. Residual debris from the prior LOT cut disappears quickly. Thus, it does not obscure one's view of the fibers that survived the cut and were present during the period of behavioral testing, and were later visualized by the histological procedure. Silver staining was done by the first metho[illegible] R. P. Fink and L. Heimer [*Brain Res.* **4**, 369 (1967)], with 4-day survival after bulbectomy. For the autoradiographic determinations, animals were killed 1 day after intrabulbar injection of ^{35}S-labeled methionine tracer [A. M. Graybiel, in *The Use of Axonal Transport for Studies of Neuronal Connectivity*, M. Cuénod and W. M. Cowan, Eds. (Elsevier, Amsterdam, 1975), pp. 175–216, and (*4*)].
12. Mann-Whitney U test, 1-tailed.
13. Odor perception remains critical, however, inasmuch as (i) nostril occlusion (*7*, *8*) or removal of the remaining bulb eliminated mating; (ii) mating was not spared in cases in which the order of the lesions was reversed, with unilateral bulbectomy followed by contralateral LOT cut; and (iii) mating is not spared after bilateral bulbectomy in neonates [S. S. Winans and J. B. Powers, *Behav. Biol.* **10**, 461 (1974)].
14. This sparing might represent the recovery of olfactory function lost after the cut, rather than the preservation of a function never lost. Thus, normal pups 3 days of age show strong preferences for certain odors (*18*). When such pups are given complete unilateral LOT sections combined with contralateral bulbectomy, however, they show a severe odor-preference deficit when tested at 7 to 12 days of age (*18*). Neonatal LOT section apparently disrupts the sense of smell, which only subsequently recovers. This conclusion is tentative, however, because the pups' responsiveness to sex-related odors (*7*, *8*) was not investigated.
15. C. Leonard, *Brain Res.* **12**, 321 (1969).
16. A small accessory olfactory bulb projection to the corticomedial amygdaloid complex persisted in only some of the cases of complete LOT section.
17. Many bulb efferents have already reached the caudal fields (area 28b and the caudal half of area 51) by 3 days of age (*4*) (C. Leonard, *J. Comp. Neurol.* in press).
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27 January 1975; revised 9 June 1975

Niche Analysis of a Zooplankton Community

Abstract. *The division of the niche hyperspace has been demonstrated for the limnetic zooplankton community of Mirror Lake, New Hampshire. The niche structure of the zooplankton community is conceived as an intensive or intracommunity population continuum corresponding to the niche hyperspace. The community of zooplankton is a system of interacting populations whose adaptive centers do not overlap and have evolved toward dispersion in relation to the complex gradients of food size, depth, and time.*

The limnetic zooplankton community of oligotrophic Mirror Lake, New Hampshire, consists of at least 18 species of Cladocera, Copepoda, and Rotifera. If a vertical tow with an appropriate net were made, most of these species would be found to coexist in the lake on any given day during summer. Is this coexistence of 18 species of zooplankton a refutation of the competitive exclusion principle?

The competitive exclusion principle contends that no two species can coexist in the same niche; that is, complete competitors cannot coexist (*1*). Unfortunately, the term niche has been used in more than one sense. The functional niche has been defined as the position or role of a species within a given community (*2*), and the spatial or habitat niche may be thought of as the distributional relation of a species to a range of habitats (*3*). Furthermore, the fundamental niche of a species has been defined as a multidimensional hypervolume bounded by species tolerance limits in relation to environmental variables (both physical and biological) within a given biotope and community (*4*).

In a recent attempt to clarify the use of the terms niche and habitat, Whittaker *et al.* (*5*) restricted the term habitat to intercommunity variables, that is, environmental variables with an extensive spatial component. The term niche (*5*) was restricted to intracommunity variables, that is, intensive or local environmental variables. To complete the definition of niche, some measure of the population response to environmental variables is added, for it is the response of the range of genotypes in the population to the complex of environmental variables that is of concern. The niche variables may be viewed as axes of an *n*-dimensional coordinate system defining the niche hyperspace. That part of the hyperspace that each species in the community (*6*) utilizes, occupies, or is affected by is the niche hypervolume. Within this hypervolume the species' response to niche variables is expressed by population measurements, and the population response surface to the niche variables provides the best characterization of the niche. This concept of niche is used in the study reported here.

Mirror Lake represents a discrete eco-