swimming normally associated with schooling. It is apparent that rapid feeding and schooling are incompatible. Schooling promotes long-distance horizontal or vertical search patterns; rapid bout-feeding promotes efficient use of concentrated, patchy foods. *Euphausia superba*, therefore, does not randomly feed but actively forages. Krill schools resemble schools of juvenile clupeid fishes, and management of these resources must be planned accordingly.

Note added in proof: In our second season (January–February 1983) we dove eight times with *E. superba*. On seven dives all animals were in oriented schools, but on one dive all were in an unoriented swarm, rapidly feeding.

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4. A thread or glass rod glued to the dorsal carapace suspended individuals in a flow chamber (60 cm long, 10 cm wide, and 10 cm high) supplied with a constant laminar current of oxygenated seawater at ± 1°C. Suspended animals swam and fed normally in place. We used horizontally mounted stereoscopic optics, videotapes, and 35-mm macrophotography to analyze functional morphology of feeding.
5. Test substances, mixed with seawater and fluorescein dye, were injected through a pipette into the current flowing toward a tethered euphausiid (*4*). The full feeding bout, a stereotypic all-or-none response, was the bioassay. Euphausiids did not respond to fluorescein dye alone, Recent or Miocene diatoms (diatomaceous earth), sucrose, maltose, galactose, D(+)-mannose, fructose, L-glutamine, or EDTA. They performed full feeding bouts in response to live diatoms, Miocene diatoms mixed with citric acid, Maxi-Crop seaweed extract, Difco marine broth, dextrose, glycine, L-arginine, histidine, neopeptone, acetic acid, lactic acid, ascorbic acid, and citric acid. They actively rejected methionine and L-tyrosine.
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The Terminal Nerve: A New Chemosensory System in Vertebrates?

Abstract. *Ganglion cells of the terminal nerve in goldfish are located in the olfactory nerve and bulb and send peripheral processes into the olfactory epithelium and central processes to the supracommissural nuclei of the telencephalon as well as to the retina. Correlations between terminal nerve projections and neurobehavioral studies suggest that the terminal nerve mediates responses to sex pheromones.*

Pheromones, presumably detected by the olfactory system, influence a number of reproductive responses in fishes (*1*). The medial olfactory tract (MOT) is specifically implicated in several of these responses; electrical stimulation of the MOT in cod elicits behavioral responses similar to those observed in normal courtship (*2*); bilateral transection of the MOT in goldfish drastically reduces male responses to pheromones of reproductively active females (*3*); and stimulation of the MOT in reproductively active male goldfish elicits sperm release (*4*). However, the axons of another cranial nerve, the terminal nerve (TN), course centrally into the forebrain in association with the MOT in a wide range of vertebrates (*5–8*). This raises the possibility that pheromone-mediated responses are detected by the TN instead of, or in addition to, the olfactory system.

Descriptive studies of the TN in fishes (*5–8*) have led to the proposal that this cranial nerve consists of ganglion cells located within, or ventral to, the olfactory nerves and bulbs. The peripheral processes of these ganglionic cells are reported to course rostrally and become distributed among the epithelial tissues of the olfactory organs, whereas their central processes course into and terminate among several cell groups closely associated with the anterior commissure of the telencephalon (*5–8*).

Large neuronal cell bodies (Fig. 1A) do occur within the medial half of the olfactory nerves and implantation cones of the olfactory bulbs (area of entry of olfactory nerve fibers) in goldfish (*Carassius auratus*), a pattern that was described from observations of carp (*6*). In order to determine whether these cells have peripheral processes that ramify in the olfactory epithelium, small pledgets of Gelfoam soaked in horseradish peroxidase (HRP) enzyme (40 percent solution dissolved in 1 percent lysolecithin) were applied unilaterally onto the olfactory epithelium of six goldfish (7 to 10 cm in total length). Two to 4 days later the fish were perfused with 0.1*M* phosphate buffer and then with a solution of cold, buffered 4 percent glutaraldehyde in 0.1*M* phosphate buffer. The brains, including the olfactory bulbs and organs, were removed, embedded in gelatin, and sectioned horizontally at 40 μm. Sections were processed with tetramethylbenzidine in order to visualize the HRP (*9*).

In these cases, HRP-labeled olfactory nerve fibers terminate in the glomerular layer of the ipsilateral olfactory bulb, but no labeling occurred in the mitral cell bodies nor in the majority of the olfac-

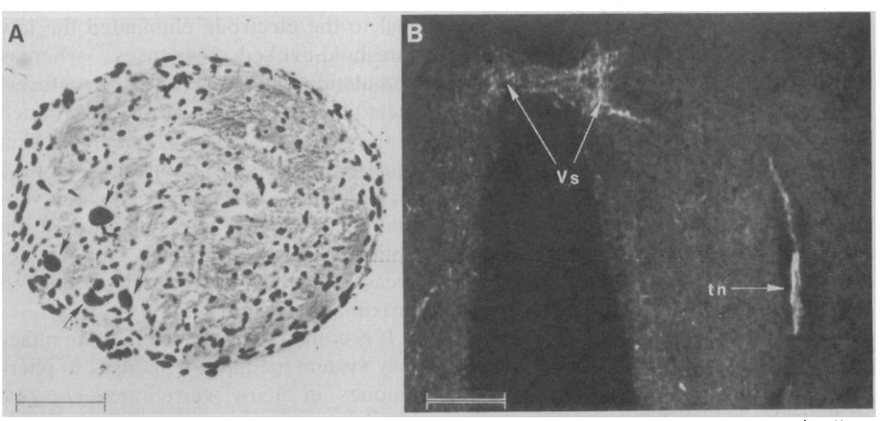

Fig. 1. (A) Transverse section of the right olfactory nerve of the goldfish stained by the Bodian method. The cell bodies of the terminal nerve are indicated by the arrows. Dorsal and medial surfaces are to the top and left of the figure, respectively (bar represents 50 μm). (B) Dark-field illuminated horizontal section through a ventral portion of the telencephalic hemisphere of the goldfish illustrating the central course of the terminal nerve fibers (*tn*) and their bilateral termination within the supracommissural nucleus of area ventralis (*Vs*) after HRP application to the left olfactory epithelium. Lateral and rostral planes are to the right and bottom of the figure, respectively (bar represents 100 μm).

tory pathways, an indication of the absence of transneuronal transport. However, a bundle of HRP-labeled fibers course more caudally within the ventromedial portion of the ipsilateral olfactory bulb and run in the most medial portion of the medial olfactory tract. On entering the telencephalon, these fibers course lateral to the ventral nucleus of area ventralis and, on reaching the anterior commissure, terminate bilaterally in the supracommissural nucleus of area ventralis (Fig. 1B).

These results confirm earlier descriptive reports that the peripheral processes of some ganglion cells of the TN end in the olfactory epithelium, and that the central processes of this nerve terminate in the ventral telencephalon. Similarly located cell bodies in several other piscine species have been labeled retrogradely after the application of HRP or cobalt unilaterally to the eye or optic nerve (*10, 11*). These cells and their retinopetal fibers contain luteinizing hormone–releasing hormone (LH-RH) and terminate in the inner nuclear layer of the retina (*10, 12, 13*).

In goldfish, unilateral injections (5 μl) of HRP (40 percent solution dissolved in 1 percent lysolecithin) into the eye or application of pledgets soaked in HRP to the transected optic nerve (five cases) causes bilateral labeling of many cell bodies in the olfactory nerve; we identify these as the ganglion cells of the TN. The majority of the labeled cells are contralateral to the HRP-injected eye or optic nerve. However, a few retrogradely labeled cells also appear in the ipsilateral olfactory nerve, suggesting that each terminalis ganglion projects bilaterally (Fig. 2). However, double-labeling experiments are needed to ascertain whether any single cell of the terminalis ganglion projects bilaterally. Whereas HRP injections into the eye retrogradely label many of the ganglionic cells of the terminal nerve, more distal processes, possibly coursing into the olfactory epithelium, were never labeled. Similarly, HRP applied to the olfactory epithelium never labeled fibers caudal to the anterior commissure. Thus, it is possible that our survival times or HRP concentrations were not adequate to label the entire processes of these ganglionic cells or that the TN contains more than one class of neurons, which has been claimed by earlier workers (*5, 6*).

If TN activation is responsible for the mediation of sperm release, then antidromic activation of the terminalis system by optic nerve stimulation could have similar effects. Accordingly, the optic nerves in several male goldfish were stimulated electrically. Fish were anesthetized in 2 percent urethane and then immobilized by an intramuscular injection of *d*-tubocurarine at 1.5 mg/kg. Suction and metal electrodes were placed on the orbital surface of the optic nerve; in one case this was done after enucleation. Consistent sperm discharge was evoked at thresholds ranging from 10 to 50 μA. Several experiments were performed to ensure that activation of the surrounding structures was not responsible for the responses. Either cutting the optic nerve or applying a local anesthetic (1 percent xylocaine) proximal to the electrode eliminated the low threshold-evoked responses, whereas stimulation of other orbital structures, including the superior ophthalmic branch of the trigeminal nerve, resulted in sperm release only when the current was very high (800 μA). The latter responses were undoubtedly caused by activation of the optic nerve as thresholds steadily decreased as the electrodes were moved proximal to the nerve.

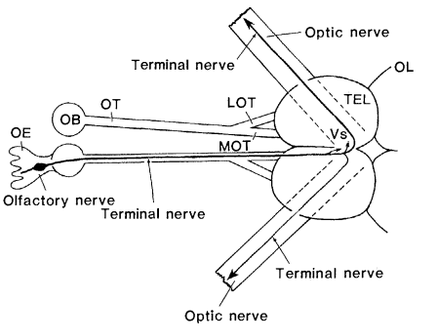

Fig. 2. Dorsal view of the goldfish brain illustrating the distribution of the terminal nerve and its central projections (terminal nerve) based on HRP transport. The terminal nerve ganglion cell shown embedded in the olfactory nerve represents a composite of probably more than one cell type since as yet no single ganglion cell has been demonstrated to have all of the processes indicated (see text for details). A heavier projection to the contralateral compared with the ipsilateral optic nerve is represented by the thicker line. Abbreviations: *LOT*, lateral olfactory tract; *MOT*, medial olfactory tract; *OB*, olfactory bulb; *OE*, olfactory epithelium; *OL*, optic lobe or tectum; *OT*, olfactory tract; *TEL*, telencephalon; and *Vs*, supracommissural nucleus of area ventralis.

It is commonly believed that the olfactory system mediates responses to pheromones in many vertebrates (*1, 14*). However, this contention must be challenged because experimental manipulations of the olfactory pathways in many studies also involve another pathway from the olfactory epithelium, the TN; moreover, studies in fishes (see below) provide support for TN rather than olfactory mediation of responses to sex pheromones.

In goldfish the MOT, the specific fiber bundle containing the TN axons, must be intact for chemosensory activation of male courtship (*3*) and TN fibers end, as we show here, in the supracommissural nuclei, a region in which small bilateral lesions drastically reduce this behavior (*15*). Our observations suggest that the TN is the major pathway for pheromonal triggering of sexual arousal. The TN fibers may also have a role in chemosensory modulation of sperm release in goldfish in that (i) MOT lesions block sperm release evoked by electrical stimulation of the undivided distal portion of the olfactory tract; (ii) stimulation of the MOT alone results in sperm release, whereas similar treatment of the lateral olfactory tract does not (*4*); (iii) TN fibers pass through the preoptic area, the major forebrain nucleus involved in sperm release (*16*), before joining the optic nerve to terminate in the retina (*10–12*); and (iv) as we show here optic nerve stimulation elicits sperm release in goldfish. Antidromic activation of TN fibers in the optic nerve with subsequent excitation of collaterals to preoptic terminal fields could account for this latter finding; verification of this hypothesis requires further study.

In summary, the data for goldfish favor the TN rather than the accepted olfactory system as the primary chemosensory pathway mediating responses to sexual pheromones. Similarities in the anatomy and biochemistry of the TN in many vertebrates including man (*5–7, 10, 13, 17*) suggest that our conclusions based on studies in teleosts may apply to a wide variety of species; in which case, many "olfactory mediated" responses to pheromones need to be reexamined in light of the TN and its central projections as a chemosensory system.

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Contiguity to Males in Utero Affects Avoidance Responding in Adult Female Mice

Abstract. *Female mice that had been situated in utero between two female fetuses displayed higher levels of active avoidance responding in adult life than females that had been located between two male fetuses and males for whom uterine position was without effect. Uterine position, therefore, influences acquired as well as species-typical behaviors.*

Clemens and co-workers (*1*) discovered that the position of the female rat fetus relative to its male siblings affects both its morphology and adult behavior. This seminal work and the subsequent efforts of others (*2*) studying rats and mice revealed that females located in utero between two males (mFm) have lengthened anogenital distances at birth and show more male-like copulatory and aggressive behavior than females not so situated. Such mFm animals are also less sexually attractive, have longer estrous cycles, attain puberty later, and become anovulatory earlier in response to postnatal testosterone challenge (*3*). That the effects of male contiguity can be generally classified as masculinizing, that perinatal exposure to testosterone yields similar effects, and that the fetal testis secretes androgens (*4*) have led to the view that the influence of contiguity is mediated, in some manner, by the transfer of testicular androgen from the fetal males to the female (*1, 2*).

Specification of the influence of uterine position on behavior addresses the issue of the genesis of individual differences in the display of behavior, especially behaviors dependent on particular concentrations of gonadal steroids. However, the behaviors thus far examined have not extended beyond the species-typical, unlearned, variety. The existence of gender differences in the display of various acquired behaviors (*5*) underscores the need to determine whether the uterine environment modulates the display of such behaviors. We have considered this issue and now report that uterine position significantly influences an acquired behavior, active avoidance responding.

Nulliparous Rockland Swiss albino mice (60 to 70 days old) (*6*), kept in groups with males, were housed singly upon the discovery of copulatory plugs which signified day 0 of pregnancy. The animals were kept in translucent cages (11 by 7 by 5 inches) containing pine shavings, provided with food and water in excess, and maintained on a cycle of 12 hours of light and 12 hours darkness with lights on at 0600 hours. On day 18 of pregnancy, 1 day prior to term, each animal was anesthetized with ether, the uterus exposed, and the fetuses expelled. They were placed on absorbant toweling in the order found in each uterine horn, cleaned with saline, and kept warm. Upon becoming motile and attaining the pink-red coloration characteristic of the full-term newborn, they were sexed and the following four groups of eight animals formed: (i) females located in utero between two males (mFm); (ii) females between two females (fFf); (iii) males between two males (mMm); and (iv) males between two females (fMf) (*7*). Each subject was fostered to a lactating animal that had delivered within the previous 24 hours and had been allowed to retain four pups of the sex opposite to that of the experimental animal, thus permitting us to identify the experimental animals at weaning.

Weaning was on day 21 and each of the 32 mice was housed with a like-sex and ear-punched conspecific. This arrangement was maintained throughout the experiment to obviate the potential confounding influence of long-term isolation. On day 60, each animal was placed into the testing apparatus (*8*) for a 30-minute habituation period followed by a single shaping session. They were trained by the method of successive approximations to terminate, by pressing a lever, a 0.25-mA scrambled electric shock delivered to the paws through the stainless steel grid floor (*9*). At the onset of the electric shock the houselights (three 4.75-W bulbs) were turned on, and the same lever that terminated the shock turned off the lights. If a response did not occur within 2 minutes, both the shock and the houselights were extinguished. The interval between each presentation of shock was 15 seconds. All subjects learned to escape, the criterion for which was ten successive escape responses in the absence of experimenter intervention.

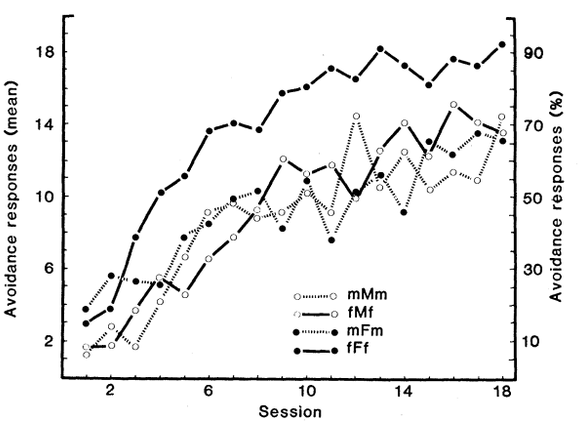

Fig. 1. Mean number and percentage of active avoidance responses made by adult female mice located in utero between two female fetuses (*fFf*) and two male fetuses (*mFm*) and males located between two females (*fMf*) and two males (*mMm*). Eight animals were assigned to each group. Twenty trials were given on each of the 18 test sessions.