Vertebrate Olfaction

Don Tucker
James C. Smith
Florida State University

INTRODUCTION

Olfaction does not appear to be very important to man as judged solely by the extent of anatomical development relative to that of the other senses, especially vision, audition, and somesthesia. Behaviorally, its greatest role seems to be in connection with eating, where its importance in the appreciation of flavor has been emphasized recently. There are also persistent suggestions that olfaction is important in sexual behavior, but the existing taboos render most such material rather anecdotal in character.

Familiarity with other animals, such as the bird or the dog, calls to mind different roles for olfaction. Since the days of Audubon, the bird has been considered as having poor, if any, sense of smell. The dog, in contrast, is an animal in which olfaction is thought to play a major role. In the literature regarding animal olfaction, the terms “microsmatic” and “macrosmatic” are often used. The classification of an animal into one of these two categories has traditionally been done on either anatomical or behavioral bases. The absolute or relative size of the olfactory bulbs, the number of olfactory ridges (conchae), area of olfactory mucosa, or color of the mucosa are some of the anatomical features used in such classifications. The behavior of an animal leading to a classification of either microsmatic or macrosmatic has been just as varied; i.e., whether tracking is observed, whether the nose is kept close to the ground, whether the animal digs for buried food sources, flies or swims toward an olfactory source, etc. In this review it will be seen that, on the basis of behavior,
INTRODUCTION

Olfaction does not appear to be very important to man as judged solely by the extent of anatomical development relative to that of the other senses, especially vision, audition, and somesthesia. Behaviorally, its greatest role seems to be in connection with eating, where its importance in the appreciation of flavor has been emphasized recently. There are also persistent suggestions that olfaction is important in sexual behavior, but the existing taboos render most such material rather anecdotal in character.

Familiarity with other animals, such as the bird or the dog, calls to mind different roles for olfaction. Since the days of Audubon, the bird has been considered as having poor, if any, sense of smell. The dog, in contrast, is an animal in which olfaction is thought to play a major role. In the literature regarding animal olfaction, the terms “microsmatic” and “macromsmatic” are often used. The classification of an animal into one of these two categories has traditionally been done on either anatomical or behavioral bases. The absolute or relative size of the olfactory bulbs, the number of olfactory ridges (conchae), area of olfactory mucosa, or color of the mucosa are some of the anatomical features used in such classifications. The behavior of an animal leading to a classification of either microsmatic or macromsmatic has been just as varied; i.e., whether tracking is observed, whether the nose is kept close to the ground, whether the animal digs for buried food sources, flies or swims toward an olfactory source, etc. In this review it will be seen that, on the basis of behavior,
one vertebrate class (birds) has historically been classified as microsmatic. In the other classes, a wide variety of species has been described, ranging from micro- to macrosmatic.

The evolution of olfaction must be deduced mainly through study of living forms. Anatomy, physiology, and behavior are principal sources of information. Embryology yields valuable information about anatomy and to the extent that "ontogeny recapitulates phylogeny," embryology bears directly on the question. A taxonomic scheme is sometimes said to be analogous to a genealogical tree, indicating evolutionary relationships. Current methods permit examination of only a few terminal twigs on such a tree. However, we are convinced that the tree is exceedingly complicated and that the living forms have arrived at the present through parallel, convergent, and divergent lines from which great numbers have become extinct during the course of evolution. Therefore, we cannot tell an evolutionary story. Our type of information may be usefully integrated into the store of knowledge that specialists may possess, however. We shall present a resume of anatomy for purposes of orientation, examine a question about the origin of the olfactory organ of tetrapods, and then go into more detail by vertebrate class.

ANATOMY

The cerebral hemispheres are generally believed to have begun as a paired correlation center for the special sense of olfaction. The concept of the ancient smell brain, to which Herrick (1921) has certainly given impetus, has been enthusiastically demolished. The limbic system incorporates most of the neuro-anatomical structures that are in the former system. However, recent results suggest that olfaction does influence the functioning of some limbic structures. The suggestion has even been made that it may be profitable to regard the olfactory system as having been derived from the limbic system and that the nervus terminalis (see below) may be peculiar to the latter system (Riss, Halpern, & Scalia, 1969a).

Olfaction seems to have been a prominent feature of the sensory equipment of the earliest vertebrates. Because such animals have lived only in water, the anthropomorphic view of olfaction as being mediated by a stimulus conveyed through air must always be avoided. The structure of the olfactory receptors is remarkably constant in all the living forms in which they are to be found. A century ago it was just being determined that there was no sensory ganglion of the olfactory nerve analogous to the ganglia of the other sensory nerves. The nerve fibers originate from primitive neuroreceptor cells in the olfactory mucosa. They are primitive because this is the general scheme of invertebrate receptor cells in general. The origin of the vertebrate olfactory receptor may therefore have been from any of the invertebrate Metazoa. Many arthropods are used in
studies of “olfaction” and “taste,” although some workers designate the receptors as distance and contact chemoreceptors.

The olfactory nerve is transmitted from the nasal cavity to the olfactory bulb in the cranial cavity where the first synapse in the nervous pathway occurs. Commonly, there is a specialized subdivision of the olfactory system known as the “vomeronasal organ,” or the “organ of Jacobson,” that embryologically arises from the nasal placode, as does the olfactory organ proper. The vomeronasal nerve connects Jacobson’s organ to the accessory olfactory bulb, which is typically located somewhere caudally relative to the principal olfactory bulb.

Jacobson’s organ in man was discovered 270 years ago by Ruysch (Van Wijhe, 1919; Negus, 1958). Jacobson independently discovered the organ in various mammals. He also discovered the vomeronasal nerve and felt that the organ must have an olfactory function. The work became known because of a report made by Cuvier (1811), in whose laboratory some of the work was done, to the Institut de France of a note by M. Jacobson, a surgeon serving in the army of the king of Denmark.

The nervus terminalis (nerve of Pinkus) was discovered in the lungfish Protopterus annectens by Pinkus (1895) in 1894 and shortly thereafter was described by Lacy (1905) in 20 genera of sharks and rays. At this time there was much confusion among the vomeronasal nerve, the terminal nerve, branches of the olfactory nerve, and even among branches of the trigeminal nerve, as discussed by Van Wijhe. The nerve has been found in many animals, especially in embryonic stages, where it appears only transiently in birds. The nerve has often been thought to have sensory and motor components but its distribution and function have never been adequately determined. The last major review is that by Larsell (1950).

The nasal cavity is also innervated by branches of the trigeminal nerve, which is generally believed to serve the modalities of tactile sense, temperature, pain, and proprioception. However, there are trigeminal fibers that respond well to odorants (Tucker, 1971). Parker (1922) popularized the concept of a common chemical sense mediated by “bare nerve endings” such as those of the trigeminal nerve fibers, being somewhat less sensitive in general than the gustatory sense, which of course is usually much less sensitive than the olfactory sense.

The olfactory (vomeronasal) sensory mucosa is recognized in almost all noses of tetrapods and the remainder of the nasal mucosa is commonly designated as “respiratory” mucosa. The respiratory mucosa typically has ciliated cells exhibiting a metachronal rhythm that propels a sheet of mucus. The trigeminal innervation seems to be denser in respiratory mucosa, although there are indications of trigeminal fiber endings in olfactory mucosa. The presence of nervus terminalis fibers has been claimed in both types of mucosa. The olfactory epithelium usually occupies a rather sheltered part of the nasal cavity and the respiratory epithelium may grade over into an indifferent nonmucosal type of epithelium. The geometry of the nasal cavity is extremely variable. The nasal
cavity of tetrapods is connected to the oral cavity by the internal nares or choanae, which have figured prominently in evolutionary studies. In most fishes, of course, such an oronasal connection does not exist. The vomeronasal sensory mucosa is most often enclosed within a structure called the "organ of Jacobson," which may open within the nasal cavity (many rodents), into the nasopalatine duct transmitted by the incisive foramen just behind the incisor teeth (characteristic of mammals), or directly onto the palatine surface (snakes and lizards). Adult birds and some other forms do not have the organ. Fishes, in particular, appear not to have any vomeronasal sensory mucosa. An accessory olfactory bulb has been described in some forms of fishes, but apparently in no such instance has the peripheral anatomy been investigated.

Nasal anatomy has been invoked as an aid in the study of phylogenetic problems (Parsons, 1959a). However, Parsons (1967) has forthrightly decided that no definite conclusions can be reached about evolution of nasal structure in the lower tetrapods. His (Parsons, 1959b) large work on comparative embryology of the reptilian nose is more comprehensive than is suggested by the title and the bibliography represents an extensive literature review. Bertmar (1965) has studied the nasal embryology of lungfishes and notes the ganglion of the terminal nerve, first discovered in a lungfish. The relations between fish and tetrapod noses, choanal connections to the mouth, accessory nasal sacs, possible homologs of Jacobson's organ, etc., have been discussed further by Panchen (1967) and Bertmar (1969).

**WAS THE TETRAPODAN VOMERONASAL ORGAN DERIVED FROM THE FISH OLFATORY ORGAN?**

As noted above, there is commonly a specialized subdivision of the olfactory system known as the vomeronasal organ, or Jacobson's organ, which embryologically arises from the nasal placode as does the olfactory organ proper. Histologists for a century referred to the olfactory cells of the sensory epithelium of Jacobson's organ. A diagnostic feature is that Bowman's glands, which are characteristic of most olfactory mucosae, are not present in any vomeronasal mucosae. The fact that there are no Bowman's glands associated with the olfactory organ of fishes has prompted Parsons (1970a) to revive the suggestion by Broman (1920) that the fish olfactory organ is the evolutionary precedent of the tetrapod vomeronasal organ. The medium for carrying stimulus molecules to the receptors would be glandular secretions, which would be transported by pumping movements in the mammalian organ and possibly by ciliary streaming in reptiles (Pratt, 1948; Bellairs & Boyd, 1950). Parsons' proposition is that the olfactory organ actually originated in connection with the transition to terrestrial conditions. This leads him to the conclusion that the olfactory bulb of
fishes is missing and what is actually present is the homolog of the accessory olfactory bulb, to which the vomeronasal nerve connects the vomeronasal organ of tetrapods.

Broman (1920) tried to support his proposition that the Jacobson’s organ was the old water smelling organ with the supposed association of the nervus terminalis with the vomeronasal organ of tetrapods and with the nasal sac of fishes. Although Kerkhoff (1924) supported Broman enthusiastically, Herrick (1921) rejected Broman’s suggestion that Jacobson’s organ was nothing other than the old water olfactory organ of vertebrates adapted for life on land; “an untenable position which he unfortunately attempted to support by reference to the nervus terminalis which reveals a total neglect of the recent contributions dealing with the innervation of this region.” Herrick evidently accepted the proposition of Seydel (1895) that the organ of Jacobson developed in connection with the establishment of a choanal connection from the nose to the oral cavity, a proposition that was enthusiastically supported by Bruner (1914). Thus, a more intimate relation between gustation and olfaction during the act of feeding was established and the physiological integration of all the associated sensory information led to the appearance of a primitive amygdala (Herrick, 1921). The transition to terrestrial life was presumably an independent development.

Current knowledge about the nervus terminalis is still very scanty and is only somewhat better in respect to the nervus vromeronasalis (Tucker, 1971). The existence of a separate projection from the frog accessory bulb to the primordial amygdala has been confirmed (Scala, 1972). However, there is every reason to believe that the gustatory system has persisted in parallel with the long existence of the olfactory system (Barnard, 1936). It seems likely that both are intimately involved in consummatory behavior of many representative types of living animals and that there must therefore be neural integration of the information arriving from the olfactory bulb at the front and from the bulb of the hindbrain, the medulla oblongata.

Parsons (1970a) indicated that the theories of Seydel and Broman were not necessarily in conflict, because Broman believed that the vomeronasal organ detected substances dissolved in glandular secretions, substances that likely came from the mouth. Parsons suggested that physiological evidence in the form of differential sensitivity to various kinds of chemical compounds might be decisive, because of the possibility that the vomeronasal organ of tetrapods represents the primitive nasal organ of fishes and still functions for chemoreception in an aqueous environment, whereas the olfactory organ of tetrapods is a new one adapted for chemoreception in air.

Another source of information that may bear on the question is ultrastructure. Until recently it has been thought that all olfactory receptors bear cilia, the olfactory hairs of the classical histologists, However, the vomeronasal receptors
have been shown to be free of cilia (Tucker & Smith, 1969; Kleerekoper, 1969; Graziadei & Tucker, 1970; Moulton, 1971; Altner & Müller, 1968; Altner, Müller, & Brachner, 1970; Kohnberger, 1971), except for one report (Luckhaus, 1969) that seems questionable. The presence of cilia on lamprey and fish olfactory receptors is an embarrassment to the theory being considered if electron microscopy of more forms continues to show vomeronasal receptors without cilia. However, Reese and Brightman (1970) found that the olfactory receptors of the nurse shark Ginglymostoma cirratum and the guitar fish Rhinobatus lentiginosus are nonciliated. The theory can be retained if it is posited that ancestral elasmobranchs have given rise to the tetrapods and that the other fishes have developed receptors like the tetrapod olfactory receptors, proper. However, the report that the Australian lungfish does not have olfactory receptor cilia (Theisen, 1972) suggests the possibility that the early pattern of results may fall to pieces.

CYCLOSTOMES

The living Agnatha are presumably degenerate forms (many are parasitic) that diverged very long ago from ancestral stock common to the extinct ostracoderms. In adults there is a single nasal opening and a large olfactory organ, which exhibits bilateral symmetry in Petromyzon marinus (Kleerekoper, 1969). The nervus terminalis is presumed to be present (Riss et al., 1969a). Taste buds and a lateral line system are present.

Shibuya (1960) has recorded electrically slow potential responses from the olfactory epithelium of Lampeetra japonica (Entosphenus japonicus) in response to aqueous extract of dried silk worm pupae, responses that are fundamentally the same as those recorded from several species of fish. Kleerekoper (1969) and associates have experimented extensively with respect to the behavior of the North American Great Lakes form of the sea lamprey P. marinus. The lamprey can discriminate one of the components of a prey fish “body odor,” which has been shown to be a complex mixture of free and bound amines, amino acids, and other compounds.

ELASMOBRANCHS

Sharks and rays are well known and their sense of smell is legendary. Their olfactory organs tend to be very well developed. Although the forebrain has been assumed to be dominated by olfaction, the olfactory bulb of the nurse shark has been shown to project to a restricted portion (Heimer, 1969). Electrical responses have been recorded from the forebrain of various sharks in response to nasal infusion of amino acids and tissue fluids of crabs, lobsters, fish,
etc. (see Kleerekoper, 1969). Behaviorally, locomotor activity increases when such stimuli are presented in the tank.

PISCES

A tagged steelhead fingerling was released at the Alsea River fish hatchery on the coast of Oregon and 5 months later was caught 2000 miles away in Alaska. Seventeen months later, the fish returned to the Alsea hatchery (Wright, 1964). It is well known that several species of salmon spawn in fresh water, go to the sea for several years, and then home to the stream where they have hatched. Olfaction particularly has been implicated in homing behavior of salmon by observations of the effects of sectioning the olfactory nerves (Craigie, 1926). Plugging the apertures to the nasal sacs has yielded results supporting a home-stream odor theory (Wisby & Hasler, 1954). Salmon fingerlings are thought to be conditioned to a characteristic odor in home water. Jones (1968) has developed an elaborate sequential hypothesis for home-stream detection in salmon. Other sensory systems seem to be involved also in the remarkable performance of salmon, in which adults return to spawn at or near the sites where they themselves have been spawned (Hasler, 1966).

Another type of fish behavior mediated by olfaction has been discovered by von Frisch (1938). Injury of the skin of a European minnow Phoxinus phoxinus causes a fright reaction of the other members of the school. The fright reaction caused by release of alarm substance from specialized cells of the skin has been shown to be confined to the order Ostariophysi, a very large group composed of cyprinid and siluroid (catfish) fishes, and the newly erected order Gonorynchiformes (Pfeiffer, 1962, 1967).

Schooling has also been shown to be partly mediated by olfaction in several fish species (Hemings, 1966). The German workers have been very active in studying the chemical senses of fishes, especially with behavioral methods. Teichmann (1959) has found the olfactory sensitivity of the common European eel to be much superior to that of the European minnow. Enormous dilutions are required to reach behavioral threshold concentrations for chemically defined substances commonly used in the flavor and perfume industry. About 1800 molecules of β-phenylethyl alcohol, a constituent of rose oil, are required per cubic centimeter of water. The threshold for the minnow is about $10^{10}$ times greater. After determining the size of the nose and the rate at which cilia propel a water stream through it, Teichmann has calculated that at threshold as little as one molecule per second in the nose of the eel is sufficient. For a biologically meaningful odor, Tubifex worms have been homogenized and diluted more than $10^{17}$-fold to reach threshold concentration.

Glaser (1966), Teichmann's student, determined the thresholds for Phoxinus of various sugars, saccharin, quinine hydrochloride, sodium chloride, and acetic
acid with a behavioral technique. The taste thresholds were less than 1 μM for saccharin and 0.04 μM for quinine hydrochloride. The thresholds ranged from 24-fold to 2500-fold lower than those determined for man. The quinine taste threshold was lower than the β-phenylethyl alcohol olfactory threshold that had been determined for the minnow and elimination of the sense of smell had no influence on the performance in response to quinine and acetic acid stimulation. It was therefore concluded that the secondary chemoreceptive cells, i.e., the ancillary taste receptors, were as sensitive as are the primary chemoreceptors, the olfactory neuroepithelial cells.

This surprising result has been supported by a study in the goldfish Carassius auratus (Zippel, Von Baumgarten, & Westerman, 1970) in which the fish have been conditioned to associate Tubifex worms as food with coumarin or amyl acetate. Then the primary olfactory nerves are sectioned and a functionally specific regeneration occurs within 10–14 days. Test fish before regeneration and control fish in which the olfactory bulbs have been removed exhibit behavioral “taste” thresholds slightly more than one log unit higher than the 10⁻⁶ v/v amyl acetate threshold of normals. The human catagorization of substances as taste and odor stimulants does not seem to hold up well for fishes (Bardach & Todd, 1970).

The eel has been determined macrosmatic (Teichmann, 1959) by virtue of its great olfactory acuity. Anatomically, this condition is manifested by the relatively great development of the nose, which contains a bilateral arrangement of many folds, or lamellae, supporting the olfactory epithelium. The ratio of olfactory mucosal area to the retinal area is among the greatest for fishes. The flow of water through the nose is repeatedly directed between the lamellae by the so-called “respiratory” cilia. The microstirring by the propelling cilia and the intimate contact of the odorous medium with a large sensory area are theorized to enhance the filtering out of odorant molecules. However, that the development of the eel’s nose is sufficiently greater than that of the minnow to account for a billionfold greater sensitivity is not intuitively evident, leaving the possibility of species differences at the receptor cell level.

Fishes from the family Polypteridae, found in Africa, have many olfactory lamellae in a radially symetric arrangement that Pfeiffer (1968, 1969a) has found resembles that of the living crossopterygian Latimeria. The noses of the lungfishes are much more like those of the Elasmobranchii and Actinopterygii, however. The morphology of the soft nasal tissue of Latimeria and the Dipnoi therefore militates against their grouping in Chonichthyyes and suggests an affinity between Latimeria and Polypteriformes. Whereas Latimeria has a large eye in addition to being a large fish, individuals of the Polypteridae have a ratio of olfactory to retinal areas equalling that of the eel. Accepting this as putative evidence for the macrosmatic condition, Pfeiffer (1969b) has tested behaviorally Polypterus palma, P. delhezi, Calamoichthys calabaricus, and, for comparison, Phoxinus laevis. Responses to a standard beefheart extract have been obtained at
dilutions of $10^{10} - 10^{11}$ for *Polypterus*, $10^7 - 10^8$ for *Calamoichthys*, and $10^3 - 10^4$ for *Phoxinus*.

In long-term studies fish exhibit seasonal variation of olfactory acuity. The behavioral threshold concentration of the eel increases by several orders of magnitude during late fall and early winter (Teichmann, 1959). The range cannot be so great, of course, for a relatively insensitive fish, such as *Phoxinus*. The seasonal variation of behavioral olfactory sensitivity is suspected to be under hormonal control. The olfactory system may feed information back to the neurohormone system of the hypothalamus. Kandel (1964) has shown that electrical stimulation of the goldfish olfactory tract synaptically activates neuroendocrine cells that originate in the preoptic nucleus and terminate in the neurohypophysis. Perfusion of the gills, through the mouth, with tap water containing a fewfold increase of the 0.3 mequiv sodium ion per liter found causes suppression of neuroendocrine cell baseline activity. These concentrations of sodium ions are near the beginning of the response range determined by electrical recording from taste and lateral line nerve preparations (e.g., Sutterlin & Sutterlin, 1970; Katsuki, Hashimoto, & Kendall, 1971). A quantitatively similar curve for sodium stimulation of the olfactory system has been obtained by EEG-type recordings from the olfactory bulb of the carp *Cyprinus carpio* (Satou, 1971). Olfactory bulb responses of the thyroidectomized lungfish *Protopterus annectens* are highly dependent on the level of injected thyroxine (Dupé & Godet, 1969). Unitary activity of cells in the olfactory bulb of goldfish has been recorded with stainless steel microelectrodes (Oshima & Gorbman, 1966). The nose is stimulated with 60 µM sodium chloride and pretreatment of the fish with estradiol, progesterone, testosterone, and thyroxine all cause changes in the types of responses recorded.

Unit activity from single-fiber recordings was obtained from the olfactory tract of goldfish (Nanba, Djahanparwar, & Von Baumgarten, 1966) and crucian carp *Carassius carassius* (Sato & Suzuki, 1969) in response to amyl acetate, coumarin, and morpholine in the former study and isooamyl acetate, butyl acetate, isooamyl alcohol, butyl alcohol, and sodium chloride in the latter. Many patterns of response were observed. In the goldfish mechanical sensitivity was seen in response to water flow or probing of the olfactory mucosa with a small bristle, and temperature sensitivity of some units was observed in the carp. Sodium chloride caused a tonic type of response and had no inhibitory effect from 6 to 500 µM. Similarly, single-fiber recordings were obtained from the olfactory tract of the burbot *Lota lota* (Döving, 1966). Twenty-three chemical compounds were used, all at the relatively high concentration of 1 mM. Of 281 stimulations, 32% of the responses were an increase in the rate of firing, 21% were inhibitory, and 47% were without effect.

EEG-type recordings from the olfactory bulbs of adult migrating salmon in response to stream water samples from various locations have been of much interest. Initially, it seemed that water from the locations nearer to the spawning
site evoked larger responses with the culmination being that from the spawning site (Ueda, Hara, & Gorbman, 1967). A larger study of homing Pacific salmon from three spawning groups has not yielded such a simple pattern of results. The largest responses are evoked by the home waters, but a pattern of increasing response with approach to spawning location does not appear (Oshima, Hahn, & Gorbman, 1969). The nature of the stimulating compounds in river water is unknown, but there are some indications of nonvolatility. Olfactory receptor responses have been recorded directly from the nasal epithelium of young Atlantic salmon, *Salmo salar* (Sutterlin & Sutterlin, 1971). Amino acids as a class of compound are by far the most stimulatory of those tested. Suzuki (Suzuki & Tucker, 1971; Tucker & Suzuki, 1972) has remembered that catfish exhibit the fright reaction behavior and skin as well as other tissue extracts have been found to be highly stimulatory for the olfactory receptors. From this clue the common amino acids have been found to be extremely effective, with the lowest threshold concentration lying between $10^{-8}$ and $10^{-7} \text{M}$. The potency of amino acids for Pacific salmon *Oncorhynchus nerka* and *O. kisutch* and rainbow trout *Salmo gairdneri* has been confirmed by olfactory bulb EEG recording (Hara, 1972).

Recently, gustatory receptors of catfishes have been found to be at least as sensitive as olfactory receptors to amino acids (Caprio & Tucker, 1973; Tucker, 1973; Oakley, 1971). Perhaps catfishes are unique in this regard, in correlation with the great numbers of taste buds present on the external body surface, concentrated especially on the barbels. The distinction between taste and smell in fishes has been discussed (Bardach & Atama, 1971), with emphasis on taste. Similarly, Kleerekoper (1969) has reviewed the literature with emphasis on olfaction. A very broad range of roles of the chemical senses, olfaction, taste, and others, has been discussed for a variety of fishes (Bardach & Todd, 1970). Atama (1971) has concluded that, at least for the yellow bullhead *Ictalurus natalus*, food is found by taste only. The facial nerve portion of the taste system is thought to function as a true distance receptor, by virtue of its sensitivity, and also controls the picking up of food. The vagal and glossopharyngeal nerve portion of the taste system is essential for the swallowing of food. The sense of touch (trigeminal) combines with the sense of taste to control normal feeding behavior. The function of the olfactory system is essentially different and is involved in behavioral interaction with other yellow bullheads.

**AMPHIBIA**

Salamanders and newts, the Urodela, tend to have fairly simple noses. Frogs and toads, the Anura, have the most complicated noses, usually with three recognizable interconnecting cavities. Noses of the least familiar amphibians, Gymnophiona (= Apoda), are probably intermediate in complexity. A homolog of Jacobson's organ is usually recognized in all these three orders. Parsons (1959b)
has discussed the literature on embryology and adult anatomy of the nose and Jacobson's organ of these forms, which cannot be arranged in a phylogenetic series. An accessory olfactory bulb with a more or less distinguishable vomeronasal nerve is commonly situated on the caudal, ventrolateral aspect of the olfactory bulb, which contrasts with the more familiar mediadorsal placement of mammals and reptiles. Bowman's glands are never found associated with the presumed vomeronasal epithelium and also are commonly missing from the olfactory epithelium of neonatal urodeles, i.e., those that do not undergo metamorphosis.

Homing behavior of the newt *Taricha rivularis* appears to be mediated largely through olfaction (Grant, Anderson, & Twitty, 1968). Blinded animals have performed successfully over mountainous terrain. Some salamanders make breeding migrations during rainy nights and therefore are not expected to orient visually, a feat of which some newts and frogs have been shown to be capable. Occasionally toads, and especially frogs of the genus *Rana*, have been very popular for electrical recording studies of olfaction and there has therefore been interest in the possibility of finding olfactorily mediated behavior, apparently without fruit. However, the well-known African clawed toad *Xenopus laevis* has been successfully conditioned to respond to odorants with food reward of *Tubifex* worms (Altner, 1962). The animals have been blinded by enucleation and the lateral line system of these highly aquatic anurans plays an important role in their behavior. The threshold concentration for β-phenylethyl alcohol is close to that found for the minnow by Teichmann (1959), but the threshold for the next higher homolog, γ-phenylpropyl alcohol, is about tenfold higher, being $3 \times 10^{14}$ molecules per cubic centimeter (dilution ratio 1:1.5 $\times 10^7$). The highest sensitivity has been found for β-ionone, $1.5 \times 10^{13}$ molecules per cubic centimeter (dilution ratio 1:2 $\times 10^8$). The value for citral is slightly higher and conditioning has not been successful with terpineol. Altner (1962) has examined the physiological anatomy of the nose of *Xenopus laevis* and has concluded that the olfactory mucosa, with Bowman's glands, is always covered by water and that the animal smells in an aqueous medium. The presentation of *Tubifex* extract on a brush near the nasal entrance during respiratory exchange of air elicits no search reaction in response to the airborne food odor. Typical frogs are thought to normally have air in their nasal and oral cavities. The mechanism of breathing has been analyzed (Gans, De Jongh, & Farber, 1969) and a comparison made with that of lungfishes. The buccal oscillation should be important in bringing stimuli to the olfactory organ, and even in the lungless salamanders buccal oscillations are commonly observed.

Since publication of Ottoosn's (1956) monograph on the recording of slow potential changes recorded from the exposed olfactory mucosa of the frog in response to odorous stimulation, there has been much activity in recording the electroolfactogram, or EOG, as this type of response record is named. Müller (1971) has also obtained EOG's from the vomeronasal mucosa of frog in
response to amyl acetate, propionic acid, propanal, and heptanal. The eminentia olfactoria in the floor of the horizontally expanded anuran nose is the usual recording site and is well illustrated in Figure 36b of Negus' (1958) book. Workers in laboratories scattered all over the world have published many papers on recording the EOG with macro— and microelectrodes from the frog olfactory mucosa, microelectrode recording of receptor unit activity from the olfactory mucosa, microelectrode recording of secondary or postsynaptic neural responses in the olfactory bulb, macroelectrode surface recordings from the olfactory bulb, and some other techniques that cannot be categorized this way. Much of this literature can be found in various symposium volumes, notable among these being the *Olfaction and Taste* series I—IV (edited by Zotterman, 1963; Hayashi, 1967; Pfaffmann, 1969; and Schneider, 1972). A review of the voluminous literature in this area is outside the purview of this chapter. Much of the work can be characterized as attempts to determine the nature of neural coding of odor qualities. The comparison of electrical recording results from frogs with human odor quality judgment must be based on the assumption of an essential similarity of the two odor "worlds." Actually, the results from both directions have been so variable that it appears that definitive statements cannot safely be made at this time. There seems to be growing agreement that electrically recorded data indicate a conspicuous lack of specificity at the receptor level and at secondary neural levels in the olfactory bulb (Tucker & Smith, 1969). Although in the gustatory field the idea of four primary qualities is strongly entrenched, many electrical recording data have been interpreted as supporting an across-fiber pattern theory rather than the older concept of specific taste qualities (see symposia cited above).

There have been questions about the degeneration and regeneration of olfactory mucosa for many years and retrograde degeneration of the receptors after sectioning of the primary olfactory nerve has been used as an experimental tool (Takagi, 1971). The use of tritiated thymidine, the pyrimidine precursor unique to DNA or deoxyribonucleic acid, has revealed that new olfactory receptors are continuously being formed in the frog's olfactory mucosa (Graziadei & Metcalf, 1971; Moulton & Fink, 1972). Autoradiography combined with electron microscopy leaves no doubt that in adult animals there is a continuous turnover of receptor cells and apparently a much slower turnover of supporting cells. Such findings are not confined to amphibia, of course; they have been reported in forms from lampreys (Thornhill, 1970) to mice (Moulton & Fink, 1972).

**REPTILES**

Turtles are the most primitive reptiles and their nasal structure differs considerably from that of the other reptiles. There is no nasolacrimal duct. The olfactory organ tends to be well developed and the vomeronasal mucosa is not
housed in a separate cavity so as to form a distinct Jacobson's organ. Instead, the vomeronasal epithelium appears more or less ventrally within the principal nasal cavity. Tucker (1963a) has mistaken the medial nasal gland in the tortoise *Gopherus polyphemus* for the organ of Jacobson and has published a correction (Tucker, 1971). This problem has been discussed well by Parsons (1959b). A distinct accessory olfactory bulb is not clearly evident in many species of turtles. In histological sections of the olfactory bulb of three turtles, Riss, Halpern, & Scalia (1969b) have found that only in the painted turtle, *Chrysemys picta*, does the bulb appear clearly divided into a dorsal and ventral half. Noting the view of Crosby and Humphrey (cited by Riss *et al.*, 1969b) that the dorsal portion constitutes the accessory olfactory bulb, Riss *et al.* have stated that "if indeed true, the painted turtle offers an excellent opportunity to explore distinctive projections of the main bulb and the accessory bulb." The accessory bulbs are distinct and much smaller and are located on the dorsocaudal aspect of the main bulbs, and the vomeronasal nerves are quite distinct from the olfactory nerves in *Gopherus polyphemus* and *Terrapene carolina*. A paired Jacobson's organ opening onto the roof of the mouth is characteristic of the Squamata, the lizards and snakes, and it reaches its peak of development in many snakes with an accompanying elaboration of the accessory olfactory bulb. There tends to be a close association of the opening of the nasolacrimal duct and the opening of Jacobson's organ (Pratt, 1948; Bellairs & Boyd, 1950). Adult Crocodilia lack a Jacobson's organ and all the reptiles except the turtles have at least one true concha (Parsons, 1970b).

The red-eared terrapin, *Pseudemys scripta*, has been trained to associate the odor of amyl acetate with food. Animals that have had the olfactory nerve sectioned regain the discrimination in 5–6 weeks (Boycott & Guillory, 1962). Manton, Karr, & Ehrenfeld (1972) have developed an operant method for the study of chemoreception in the green turtle, *Chelonia mydas*. The young sea turtles have detected under water the odors of β-phenylethyl alcohol, isoamyl acetate, triethyl amine, and cinnamaldehyde at approximately $5 \times 10^{-6}$ to $5 \times 10^{-5} M$. The amino acids serine and glycine are not effective at a concentration of about $10^{-4} M$. A reversible disruption of the behavioral performance has been obtained by intranasal perfusion with 0.35 $M$ zinc sulfate solution, with recovery taking place in a variable period of 1–5 days. The discrimination may have been mediated by olfactory or vomeronasal receptors. Recordings from small twigs of the nerves have shown that olfactory, vomeronasal, and trigeminal receptors of the gopher tortoise and the box turtle respond to airborne and waterborne odorants and that there is much overlap in responsiveness of the different types of receptors (Tucker 1963a; Tucker & Shibuya, 1965; Tucker, 1971).

The box turtle and the gopher tortoise have been used for studying the relations between the electrically recorded neural response, unit receptor responses led off with microelectrodes, and the EOG or slow potential response of the olfactory mucosa. An "underwater" EOG has been routinely recorded in
turtle preparations as has likewise been done in fish preparations (Tucker & Suzuki, 1972). The location of the turtle olfactory organ in a dorsal diverticulum suggests that an air bubble can be trapped in it when water is drawn into the naris, and because of its exposed, ventral location the vomeronasal mucosa should be in direct contact with the water. These differences have been suggested of possible importance in the behavioral utilization of these two kinds of olfactory receptors, which are freely exposed in the turtle's nasal cavity. Electron microscopy has revealed that the olfactory receptors proper are ciliated and that the vomeronasal receptors instead bear rather elaborate microvilli (Graziadei & Tucker, 1970). It may be of interest that when eating, these land turtles first touch their nose to the food, open their mouth, touch the food with their tongue, and then bite into it.

There is a large literature showing that lizards and particularly snakes can track prey and members of their own species. In some instances the olfactory organ or Jacobson's organ alone is sufficient, but in many both seem to be used. Wilde (1938) has shown that the garter snake Thamnophis sirtalis does not feed, that is, grasp and swallow, if the vomeronasal nerves are sectioned. The forked tongue tips seem to be relatively important in nerve-intact animals. Earlier experimenters had shown the importance of the tongue and suggested the probability that the tips were inserted into the openings to the paired Jacobson's organ (reviewed by Wilde, 1938; Burghardt, 1970; Tucker, 1971). Jacobson's organ has been implicated in recent studies of innate food preferences of newborn snakes (Burghardt, 1970).

Müller (1971) and co-workers have recorded EOG's from the exposed vomeronasal mucosa of lizards and snakes, using a wide variety of compounds at unspecified but probably rather high concentrations.

BIRDS

In 1826, John James Audubon wrote

as soon as, like me, you shall have seen the Turkey Buzzard follow, with arduous closeness of investigation, the skirts of the forests, the meanders of creeks and rivers, sweeping over the whole of extensive plains, glancing his quick eye in all directions, with as much intentness as ever did the noblest of Falcons, to discover where below him lies the suitable prey; when, like me, you have repeatedly seen that bird pass over objects calculated to glut his voracious appetite, unnoticed, because unseen; and when you have also observed the greedy Vulture, propelled by hunger, if not famine, moving like the wind suddenly round his course, as the carrion attracts his eye; then will you abandon the deeply rooted notion, that this bird possesses the faculty of discovering, by his sense of smell, his prey at an immense distance.

The controversy regarding avian olfaction existed before Audubon (Scarpa, 1789) and continues to the present (Wenzel, 1971). Owen (1837) has described
the olfactory anatomy of the turkey vulture, although it has been claimed that Audubon's remarks reveal that he was often observing the black vulture Coragyps instead of Cathartes (Stager, 1967). Several other investigators have studied the olfactory anatomy of birds (e.g., Ariëns-Kappers, Huber, & Crosby, 1936), but it has not been until the work of Cobb (1960) and Bang (1960) that "the long overdue job of putting olfaction in context in avian ethology is now under way" (Bang & Cobb, 1968).

All birds appear to have the appropriate anatomy for odor perception, but the variation in that anatomy suggests the likelihood of significant differences among species. Bang and Cobb (1968) have measured the greatest diameter of the olfactory bulb and compared it to the greatest diameter of the cerebral hemisphere in 108 species of birds. They have found, for example, that the kiwi, Apteryx australis, has the largest bulb–hemisphere ratio at 38%; the turkey vulture Cathartes aura has a ratio of 28.7%; the domestic fowl Gallus gallus, 15%; and the house sparrow Passer domesticus, 4%. In all species studied, the anatomy of the avian olfactory bulb is similar to the mammalian forms, consisting of a glomerular layer, a mitral cell layer, and an internal granule cell layer (Wenzel, 1971). Not much is known about the neural projections from the olfactory bulb.

The nasal region in birds is sometimes said to be similar to that in reptiles (Portmann, 1961), except that no organ of Jacobson is present in adults. There are three conchae or turbinals in the nasal cavity, in which three chambers can be recognized. A transverse threshold separates the first from the second or main chamber, which extends to the choana. Above the main chamber is the olfactory chamber containing a prominent tubercle or a more highly developed turbinal system, such as is seen in Cathartes. True olfactory epithelium covers the olfactory tubercle or concha and may also lie along the roof and on the posterior and ventrolateral walls and the upper portion of the septum nasi of the olfactory chamber in some species (Bang, 1960). With the anatomy described, the question next arises of the physiology. Portmann (1961) has written that

the physiological evidence for the function of true olfactory structures is contradictory ... the unsettled state of current knowledge invites a re-examination of the whole problem. The wide, open secondary choana provides a special pathway for olfactory stimuli; choanal smell is probably a fact in many birds and particularly in groups where the external nasal openings are small or even closed. The role, and interaction, of vision and smell in orientation must be more carefully studied. The morphological facts testify strongly against the simple conclusion that birds are completely anosmatic. The development of the olfactory part of the nasal cavity, and the well-marked variation in the proportion of the olfactory bulbs of the brain, are in favor of an opposite view.

A reexamination was accomplished with the publication of electrophysiological evidence for olfaction in 14 species of birds (Tucker, 1965) and the recording of receptor unit responses in vultures (Shibuya & Tucker, 1967). Among the
birds used for olfactory nerve recording were the house sparrow, chicken, and
turkey vulture with bulb-hemisphere ratios of 4, 15, and 28.7%. An interesting
point was the lack of obvious species differences noted. Sieck and Wenzel (1969)
recorded with chronically implanted macroelectrodes in the olfactory bulbs of
pigeons. Thresholds were estimated for a variety of odorants, and bulbar re-
sponses were shown to cease if the olfactory nerve was sectioned, if the bird
breathed through the mouth, or if the nostril was plugged. Bulbar responses were
recorded from chicken, mallard duck *Anas platyrhynchos*, black-vented shear-
water *Puffinus puffinus opisthomelas*, and black-footed albatross *Diomedea
nigripes*, the latter two having a bulb-hemisphere ratio of 29% (Wenzel, 1971).
Wenzel (1971) concluded that “regardless of the many gaps in our knowledge,
however, it is perfectly clear that some birds, if not all, show the kind of activity
in the olfactory system that is seen in other vertebrates whose olfactory ability
has never been questioned.”

The behavioral literature up to the middle of this century depicted a rather
negative opinion about the sense of smell in birds; see Walter (1942) for a
comprehensive review. Then a series of papers began to yield positive results
more frequently (Wenzel, 1971). A response-contingent reinforcement pro-
cedure was used by Michelson (1959), working under the guidance of Stanley
Cobb and B. F. Skinner, to train two pigeons to discriminate sec-butyl acetate or
isooctane from air-only control trials. Calvin (1960) criticized this study on
several grounds, the most important of which was the possibility that the
discrimination was not truly olfactory but was instead mediated by the trigem-
nal system. Michelson (1960), in response to Calvin, reported that he performed
bilateral sections of the olfactory nerves and that neither bird could discriminate
isooctane postoperatively. sec-Butyl acetate was discriminated by one
of the lesioned birds, indicating possible trigeminal activation. The postmortem
examination revealed a total section of olfactory nerves. No histology was
reported.

Pigeons were employed in a series of olfactory behavioral studies in which a
modification of the conditioned suppression technique was used; see Smith
acetate discrimination in three birds that lost the response when the olfactory
nerves were bilaterally sectioned and regained the response when the concentra-
tion of amyl acetate was raised. Henton (1969) demonstrated thresholds to amyl
acetate, butyl acetate, and butyric acid; demonstrated discrimination of amyl
acetate from butyl acetate in normal pigeons; and demonstrated the odor quality
discrimination in olfactory nerve sectioned birds at high concentrations, pre-
showed that pigeons could make intensity discriminations with amyl acetate. In
terms of vapor saturation, 7% was reliably discriminated from 2% but not from
3%. In summary, the only problem left appears to be whether birds employ
olfaction in normal behavior and, if so, to what extent, which undoubtedly can be expected to vary greatly over species.

MAMMALS

Mammalian nasal anatomy is exceedingly variable but generally involves a maxilloturbinal invested with respiratory mucosa, a highly variable nasoturbinal of which part may bear olfactory mucosa, and an ethmoturbinal system of which most is covered with olfactory mucosa. The ethmoturbinals originate at the cribriform plate, through which foramina transmit the fila olfactoria (collectively, the olfactory nerve), and most often the anterior ends are connected together to form a continuous plate of bone covered with respiratory mucous membrane. These specialized projections of the ethmoid bone vary greatly in number among mammalian forms. For example, in man there is only one and in Echidna, the spiny anteater, there are 12. The nasal turbinates are conchal structures, of course, that have been variously homologized with the conchae of the other amniotes (Parsons, 1970b, 1971). Negus' (1958) book contains a wealth of illustrations of mammalian material and comparisons are made with other forms. Although this is an excellent source for gross and histological anatomy, many of the functional interpretations made are certainly questionable today. For example, Negus makes an argument to explain the greater acuity of macrosmatic mammals by describing the subethmoidal shelf or lamina transversa (= lamina terminalis?) that helps to recess the olfactory organ. This subethmoidal shelf is said to be well developed in typical carnivores, present in marsupials, and small in ungulates, rodents, and rabbits. His argument is difficult to follow, because recessing the olfactory organ excludes most of it from the air currents.

Jacobson's organ in mammals is typically a tubular structure with glands emptying into the caudal aspect. A small pore at the anterior end opens either within the nasal cavity near the infundibulum of the nasopalatine duct or directly into the duct somewhere over its course. The mystery has been how stimuli can be conveyed to the receptors within and whether stimulus compounds are necessarily volatile (Broman, 1920; Negus, 1958; Tucker, 1971). Ruysch, Jacobson, and Cuvier thought that the organ had a secretory function; yet the obvious innervation in nonprimate forms compelled consideration of an olfactory function. However, “quel agent extérieur pourroit [sic] aller se faire percevoir dans un réceptacle si caché, si profond, si peu accessible?”

1 What outside agent could provoke perception from a receptacle so concealed, so deep, so inaccessible?
that the accessory olfactory bulb of rabbit projects to the mediocortical complex of the amygdala (Winans & Scalia, 1970). The old ideas of possible roles in feeding and sexual behavior are given new credence because of the projections of the cortical amygdaloid nucleus to the anterior medial hypothalamus and the ventromedial nucleus of the hypothalamus. The projections of the main bulb provide a separate, parallel route of influence to the hypothalamus. A large literature exists on the behavioral effects of olfactory bulb ablation and it is worth reemphasizing that in virtually all such experiments both of the olfactory bulbar systems as well as the nervus terminalis have been interrupted.

Comparison of the ratio of the largest cross-sectional area of Jacobson's organ to that of the olfactory organ suggests a great range for vertebrates, with the mammalian carnivore's ratio becoming very small, because of the large olfactory organ (Negus, 1958). Such a measure is reminiscent of the ratio of olfactory bulb to hemisphere diameters employed for birds (Bang & Cobb, 1968) or of the ratio of retinal to olfactory areas used for fish and mammals. Such relative measurements partly represent an effort to remove the confounding influence of the size of the animal. An elephant, for example, may not need an organ system any larger than that of the mouse in order to do the same job, although the elephant olfactory bulb is relatively large with multiple layering of the glomeruli. An interesting allometric approach relates brain structure volumes of simians, prosimians, and "progressive" insectivores to those of "basal" insectivores (Stephan & Andy, 1969). The only structure that clearly decreases on this basis with ascent of the primate scale is the olfactory bulb. There seems to be an enlargement of higher centers of the amygdaloid complex. The accessory olfactory bulb is well developed in prosimians, highly variable in new world monkeys, and very small or absent in old world monkeys. The human accessory olfactory bulb reaches its peak during fetal development at about the time movement begins and then regresses greatly (Humphrey, 1940). Still later, during fetal development, the main olfactory bulb seems to reach a peak and then to regress somewhat.

Electrophysiology of the mammalian olfactory system has been investigated extensively. Adrian (1956), a pioneer in this field, has written a highly readable account of methods of electrical recording from the rabbit olfactory bulb. Mitral cell (second-order neuron) responses are grouped according to the relative sensitivity displayed to the stimulating compounds, which continues to be the typical finding for both the receptor and secondary cell responses. A regional variation in the olfactory bulb of sensitivity to various kinds of compounds is also found. The theory that the bulbar waves (EEG-type recordings) originate in the peripheral organ has been retracted (Adrian, 1957).

Electrical recording from the receptor axons of responses to natural stimuli was first achieved in opossum and rabbit (Beidler & Tucker, 1955). Conventional methods of nerve recording were adapted to this smallest caliber of fibers and the response of a small population of receptors was shown to be determined
primarily by the kind of odorant, odorant concentration, and inspiratory flow rate of the odorized air. This result was generalized to nonmammalian forms for both olfactory and trigeminal responses to odorants and to turtles for vomeronasal responses (Tucker, 1963b). Although responses were often recorded from rabbit vomeronasal receptors under unusual conditions, it was felt that anesthetization precluded the animal's exploitation of normal methods of stimulus transport to the interior of the long tubular organ (Tucker, 1963a).

Comparison across species of amphibian, reptile, bird, and mammal olfactory nerve twig responses indicates that if an odorant is efficacious for one it is for all the others. The lack of obvious species differences in olfactory responsiveness is puzzling when it is noted that in taste studies prominent differences are found within mammals and even within salts as stimuli. However, the olfactory recording results from fishes indicate a major difference between air- and water-breathing vertebrates. The odorants effective for air breathers can be applied in aqueous solution by nasal perfusion with similar effectiveness and the way is therefore open for testing air breathers with amino acids. However, the solutions must be carefully purified of "odorous" contaminants that come with the commercially available compounds, contaminants that appear to be quite ineffective in comparison with amino acids on fish olfactory receptors. Observations on newts that can live on land or in water can perhaps be taken up again with profit (Shibuya & Takagi, 1963). The point should be emphasized that comparisons of stimulatory effectiveness in electrical recording preparations are in general only relative, e.g., a ranking of compounds for a given preparation is obtained. The uncertainty derives from the unknown amount of stimulus attenuation between the input at the naris and the small population of receptors, localized somewhere in the olfactory organ, that is monitored. (Tucker, 1963b; Moulton & Tucker, 1964). Exceptionally, the effective stimulus concentration can be deduced at the receptor level. The curve fitted to such data for olfactory response of the gopher tortoise to amyl acetate extrapolates toward zero at about $10^{-5.5}$ of vapor saturation. Behavioral threshold determination with the conditioned suppression technique of the laboratory rat has yielded a value of $10^{-5.58}$ vapor saturation (Pierson, 1974), which is less than a factor of two smaller than the preceding value. However, the lowest amyl acetate threshold concentration found for the pigeon is $10^{-3.6}$ of vapor saturation.

Mammals are customarily credited with a good sense of smell. By far the most evidence regarding mammalian olfactory behavior is anecdotal and lacks objective demonstration. From the literature of the naturalists (e.g., Bedichek, 1960; Millen, 1960) information gathered from hunters, trappers, guides, pet owners, and kennel club devotees indicates that dogs, cats, foxes, sheep, rabbits, deer, hedgehogs, zebras, elephants, rhinoceroses, and bush babies are prominent among the mammals endowed with fine olfaction. Moncrieff (1967) has said "it is a matter of frequent observation that many of the mammals have a much keener sense of smell than man. . . . There is a correspondence between the
amount and intensity of the nasal pigmentation and the acuteness of smell.” Milne and Milne (1962) refer to the relative “odor blindness” of humans. Burton (1961), in explaining why “smell animals” get much more information from odors than man, has said “there are two reasons for this. The first is that their smelling-membrane is so much larger than ours. The second is that they have, as we say, a much finer discrimination for the various scents.” He goes on to say “there is a third reason why we cannot use the sense of smell as efficiently as the smell-animals do. Our sense of smell readily tires.” Matthews and Knight (1963) have said “hedgehogs are very discriminating in their sense of smell and will ignore ground beetles which have an unpleasant odour, while eating greedily those beetles and other insects which have not.” Finally, Wilentz (1968) has said the change that distinguishes man from these highly olfactory-oriented species occurred in the course of evolution. Man’s ancestors moved from sea to land, and then to trees. It was here that vision and hearing took over as the prime distance senses. Monkeys are not good sniffers as rats or rabbits. So man exists today, between the birds and four-footed beasts, far superior to the whales and porpoises that have no sense of smell at all, but still inferior to many others.

For man the sense is non-intellectual. We have great difficulty in describing smells—except as similes with other smells. But perhaps that very degree of weakness in the intellectual quality of smell explains why its emotional impact is so profound. Smell can conjure up the past or quicken the present; it can nauseate or excite, repel or entice us.

Although the above statements are based almost entirely on anecdotal evidence, there is good reason to believe that mammals do use olfaction to a great extent in their behaviors. The variety of mammalian scent glands, present in at least 15 of 18 orders (Mykytowycz, 1972), and the behavior known as “scent marking” (Ralls, 1971) quickly lead to such a conclusion. From hunters and dog trainers have come anecdotal records of fantastic feats of retrieval, tracking, and rescue work with a variety of canine species (see McCartney, 1968, p 15–77, for an excellent historical review). Perhaps the most quoted report is that of Romanes (1887), in which he refers to the “almost supernatural capabilities of smell in dogs” and concludes that his dog

distinguishes my trail from that of all others by the peculiar smell of my boots (1 to 6) and not by the peculiar smell of my feet (8 to 11). No doubt the smell which she recognizes as belonging distinctively to my trail is communicated to the boots by the exudations from my feet; but these exudations require to be combined with shoe-leather before they are recognized by her. Probably, however, if I had always been accustomed to shoot without boots or stockings, she would have learnt to associate with me a trail made by my bare feet.” (The parentheses refer to experiments.)

More objective studies were conducted on dog olfaction in the middle of this century by Neuhaus in Germany, Moulton and associates and Kalmus in England, and Becker and associates in the United States (see Wright, 1964, for a comprehensive review). Neuhaus (1953) found, on the one hand, that human subjects could identify the sheets of paper on which people had stepped and, on the other, that dogs were a millionfold more sensitive than humans to the fatty
acids present in sweat from foot glands. Neuhaus reasoned that if only a thousandth part of the 16 cm$^3$ sweat released per day from a man’s foot were to penetrate the sole of the shoe, there would be $2.5 \times 10^{14}$ molecules left behind in each footprint. This quantity is so much in excess of the minimal amount required that there is nothing “supernatural” at all about the dog’s ability to track humans, according to Neuhaus. Moulton, Ashton, & Eayrs (1960), however, have found the dog to be only about 100 times more sensitive than man to butyric acid. The differences in breeds tested, training methods, apparatus, and odor concentration estimation techniques in some way must account for the four log unit difference in the threshold results from Neuhaus’ and Moulton’s work. A series of laboratory experiments by Becker, King, and Markee (1962) has involved a method for testing olfactory thresholds in dogs in a “free-ranging laboratory environment.” Dogs have been able to accurately select a “slightly fingerprinted” glass slide as long as 6 weeks after the print has been deposited (King, Becker, & Markee, 1964). They can even detect such a slide that has been weathered up to 1 week. These observations suggest the importance of care in handling odor stimulating equipment in such experiments with dogs. However, Lord Adrian (1956), who pioneered in electrical recording of olfactory responses from fishes, hedgehogs, and rabbits, said that “I do not think there is any direct evidence to show that the absolute sensitivity of the organ to various pure substances is greater in a dog than in a man” in his discussion of how a large olfactory organ may give better discrimination than a small one.

A large body of literature is available on many behavioral roles of olfaction in rodents, especially laboratory rats and mice. Pheromones of the inducer type have been implicated in the reproductive physiology of mice, in which three well-known effects are recognized (e.g., Dominic, 1969; Gleason & Reynierse, 1969). Pheromones are often thought to be involved in sexual attraction, alarm behavior, trail and territorial marking behavior, and individual recognition. Literature on the olfactory control of behavior in rodents has been reviewed by Schultz and Tapp (1973), with four main divisions being (1) movement in the living space, (2) feeding behavior, (3) rodent societies, and (4) fixed patterns and heredity. Reviewers are unanimous in emphasizing the importance of maintaining a heightened awareness of the importance of olfaction in behavioral and physiological studies.

The suggestion is frequently made that biologically significant or relevant odors should be used in the studies with electrical recording methods. After all, the insect sex pheromones have been shown to be highly specific for specialized receptor cells. Pfaff and Gregory (1971) have compared urine odors from rats of various endocrine status and nonurine odors, such as amyl acetate and phenylethyl alcohol. They have made single-unit recordings from neurons in the olfactory bulb and from the preoptic region of the hypothalamus, which has been shown to respond to olfactory input and which has been linked to hormonal control of reproductive function. They have found no evidence for a
simple mechanism of coding in the sense of highly specific responding of any cells to a given type of odor. However, “differential response analyses, taking into account the direction and magnitude of response, showed that cells in the preoptic area gave more differential responses to female urine odors than cells in the olfactory bulb, even though the opposite was true for nonurine odors.” The effects of testosterone injection have been nonspecific on preoptic units. As has been seen above, androgens and other hormones have been found to augment fish olfactory bulb responses.

ACKNOWLEDGMENTS

The authors’ research was supported by the United States Public Health Service, grant NS-8814; by the United States Atomic Energy Commission, Division of Biology and Medicine, contract AT-(40-1)-2903; and by the Psychobiology Research Center, Florida State University, through the following grants: PHS NS-7468, PHS MH-11218, and NSF GU-2612.

REFERENCES


Adrian, E. D. Electrical oscillations recorded from the olfactory organ. *Journal of Physiology*, 1957, 136, 29P.


Audubon, J. J. The black vulture or carion crow, *Cathartes Jota*, Bonap., In J. J. Audubon, *Ornithological biography, ... or an account of the habits of the dogs of the United States of America accompanied by descriptions of the objects represented in the work entitled the birds of America and interspersed with delineations of American scenery and manners*, Vol. II. Edinburgh: Adam & Charles Black, 1834, P. 33.


2. VERTEBRATE OLFCTION


Glaser, D. Untersuchungen über die absoluten Geschmaeksschwellen von Fischen. Zeit-


Humphrey, T. The development of the olfactory and the accessory olfactory formations in human embryos and fetuses. Journal of Comparative Neurology, 1940, 73, 431–468.


Locy, W. A. On a newly recognized nerve connected with the forebrain of selachians. Anatomische Anzeiger, 1905, 26, 33–63, 111–123.


Oakley, B. Public communication at the Fourth International Symposium on Olfaction and Taste, Starnberg, Germany, August 2–4, 1971.


Satou, M. Electrophysiological study of the olfactory system in fish I. Bulbar responses with special reference to adaptation in the carp. *Cyprinus carpio L. Journal of the Faculty of Science, University of Tokyo*, 1971, 12 (Section IV), 183–218.


2. VERTEBRATE OLFACTION 51


