Receptive Fields of
Second-order Neurons in the
Olfactory Bulb of the Hamster

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ABSTRACT Electrical stimulation of nerve fibers emerging from different positions of the olfactory epithelium was used to determine the receptive fields for 52 olfactory bulb neurons in the hamster. The responses of olfactory bulb neurons were recorded extracellularly with metal-filled micropipettes. Suprathreshold stimuli (500 μA) were applied to each of eight standard epithelial positions spaced ~250 μm apart, and the position, or positions, which, when stimulated, produced a response in the bulb were taken as an index of the neuron’s receptive field. The results indicate that most bulb neurons have very localized receptive fields limited to only one or two stimulating positions. Furthermore, there was a statistically significant correlation between the location of a neuron’s receptive field in the olfactory epithelium and the recording depth of the neuron in the olfactory bulb (Spearman rank correlation coefficient, ρs, 0.67, P < 0.001). These findings demonstrate that in the mammalian olfactory system there exists a topographical projection of input from localized regions in the epithelium onto the second-order neurons in the olfactory bulb.

INTRODUCTION

In most sensory systems there is a spatial organization of projections from the receptor cells located in the periphery to the more centrally located cells in the brain. These projections are thought to play an important role in the coding and processing of sensory information. Recent evidence suggests that this may also be the case in the olfactory system. Adrian (1951, 1953, 1954) first suggested the concept that differential spatial and temporal patterning of neural activity was one of the basic mechanisms of olfactory discrimination. These spatial and temporal patterns were thought to originate peripherally as a result of the properties of receptor neurons in the olfactory epithelium. Furthermore, these patterns were thought to be transmitted centrally by a network of spatially organized projections of the olfactory nerve fibers.

Since Adrian’s initial proposal, several theories concerning the mechanisms
by which the olfactory system encodes and processes information from odorant stimuli have been proposed (Moulton and Beidler, 1967; Beets, 1970; Davies, 1971; Shepherd, 1972; Moulton, 1976). Several of these theories assume the existence of a spatially organized projection of receptor neurons onto the second-order mitral cells in the olfactory bulb. Evidence suggesting a spatial organization of projections has been reported in a number of studies (Le Gros Clark, 1951; Mozell, 1958; Land et al., 1970; Land, 1973; Land and Shepherd, 1974; Costanzo and Mozell, 1976). Anatomical studies such as those by Land (1973) and Land and Shepherd (1974) have shown that there are particular areas of the olfactory epithelium which project to localized regions in the rabbit olfactory bulb.

These anatomical studies, which depend primarily on degeneration techniques, do not determine whether the spatial organization of afferent inputs is transferred intact across the glomerular synapses and is thus preserved at the level of the second-order cells in the olfactory bulb. Fortunately, electrophysiological techniques are capable of dealing with this issue. Several electrophysiological studies suggest that the afferent projections of the olfactory system may be spatially organized at the level of the olfactory bulb (Mozell, 1958; Kauer and Moulton, 1974; Costanzo and Mozell, 1976; Moulton, 1976; Costanzo and O’Connell, 1978). For instance, Costanzo and Mozell (1976) have demonstrated that mitral cells in the olfactory bulb of the frog can be driven directly by electrical stimulation of small branches of the olfactory nerve which innervate localized regions of the olfactory epithelium. The results of this study, in which three widely separated olfactory nerve bundles were stimulated, indicate that some mitral cells (~30%) receive inputs from only one of the localized regions in the epithelium. Most of the remaining mitral cells sampled received inputs from several different regions of the epithelium. However, the relative effectiveness of inputs from the different regions did show an overall spatial bias because mitral cells in a particular part of the bulb always had their lowest electrical threshold to inputs from a particular epithelial region. This finding in the frog, where the geometry and structure of the nasal cavity is relatively simple, does not predict whether such spatial organization exists in the mammal, where the intricately folded turbinates result in a highly complex nasal geometry (Adams and McFarland, 1972). The hamster was selected as a suitable animal in which to study further the organization of olfactory nerve projections in the mammal.

A preliminary study of the hamster olfactory system using two widely separated stimulating positions in the olfactory epithelium suggests that afferent projections to second-order neurons are spatially organized, to the extent that all neurons examined received input from only one of the stimulating positions (Costanzo and O’Connell, 1978). The purpose of the present study was to determine in detail the extent and degree to which there is a spatial organization of projections in the hamster olfactory system by mapping the receptive fields of second-order neurons with stimulation of a large number of closely spaced afferent fiber bundles distributed across a continuous region of the olfactory epithelium.
METHODS

Experiments were performed on adult male hamsters *Mesocricetus auratus* (average wt, 130 g) obtained from Charles River Lakeview, Wilmington, Mass. (strain, Lak:LVG [SYR]). The animals were initially anesthetized with sodium pentobarbital (80 mg/kg, intraperitoneally) so that a tracheotomy could be performed. During the remainder of the experiment, gaseous anesthesia (halothane, 0.5–1.5% in air) was administered via a tracheal cannula. The animals were placed in a specially designed head holder that allowed free access to the nasal area. Surgical procedures included exposure of both the dorsal surface of the nasal bones overlying the olfactory epithelium and the anterior portion of the frontal bones overlying the olfactory bulbs. A dental drill was used to thin these bones so that sections could be removed with forceps. These procedures provided access to both the olfactory bulbs and the dorsal surface of the olfactory epithelium. The nasal septum, illustrated by the shaded area in Fig. 1, divides the two nasal cavities. A large section of the septum was exposed by removing most of the turbinates and olfactory epithelium from the left nasal cavity, leaving the right side completely intact. A vertical window was cut in the septal cartilage exposing small bundles of olfactory nerve which splay out along the medial (septal) side of the right olfactory epithelium. This window provided access to at least eight standardized epithelial stimulating positions spaced ~250 μm apart. The first three positions are in the dorsal aspect of the nasal cavity and are organized primarily in the lateral-to-medial plane. The remaining six positions are arranged in a linear array along the septal wall and are organized in the dorsal-ventral plane (Fig. 1 A). One additional stimulating position (Fig. 1, Lat), located in the recess just above the superior endoturbinate, was often used when it was desired to test a distant lateral region of the epithelium.

The dura overlying the right olfactory bulb was carefully removed before recording from bulb neurons. Metal-filled micropipettes plated with platinum black (Gesteland et al., 1956) were driven into the bulb with a hydraulic microdrive (David Kopf Instruments, Tujunga, Calif., Model 607). Single cells were identified for study by the presence of spontaneous activity. Once a single neuron was isolated, the depth of the microelectrode and its coordinate position in the bulb were noted. Coordinate recording positions were measured with a Zeiss operating microscope (×40) equipped with a calibrated ocular micrometer; recording depths were taken from the hydraulic microdrive readout. Histological verification of actual electrode positions was obtained in eight animals by making small electrolytic lesions at the end of a recording session. The resulting lesions were on the average within 100 μm of the recording position as predicted by coordinate position and depth in the bulb. This deviation (107 ± 32 μm, mean ± SE) does not take into account the effects of tissue shrinkage during histological preparation of the brains.

Electrical stimulation of the different epithelial positions was delivered with concentric bipolar suction electrodes fashioned from glass micropipettes. These electrodes had an internal diameter of 200 μm and an outer diameter of 250 μm, with a central cathode of Ag-AgCl wire and an annular anode consisting of a thin film of silver paint (Ernest F. Fullman, Inc., Schenectady, N. Y., no. 1481) applied to the outside of the glass tip, which was then plated with AgCl. A constant current stimulator (Frederick Haer & Co., Brunswick, Maine, Pulsar 4) was used to deliver single square pulses (0.5 ms in duration, 500 μA in intensity and isolated from system ground) in turn to each of the selected epithelial positions while both field potentials and single unit responses from the bulb were recorded with an ac-coupled amplifier (bandwidth, 0.02–5.3 kHz). The receptive fields of single neurons in the bulb were
FIGURE 1. Diagram of the hamster preparation illustrating the stimulating positions in the olfactory epithelium and the position of the recording electrode in the olfactory bulb. (A) Cross section of the nasal cavity showing the location of stimulating positions, 0–8, spaced ~250 μm apart and ~3,500 μm anterior to the anterior pole of the olfactory bulb. An additional position (Lat) was sometimes used to evaluate inputs from a distant region of the epithelium. Heavy lines indicate those areas where olfactory receptor cells line the nasal cavity. (B) Cross section of olfactory bulbs at the level of the recording electrode showing location of a neuron (filled circle) in the mitral cell layer. Open circles indicate the glomerular layer, and the solid lines within the outline of the bulb indicate the mitral cell layer.

determined by identifying those positions in the lamina propria of the olfactory epithelium, which, when stimulated, elicited a spike response in the olfactory bulb neuron.

In two animals the right nasal cavity was also opened to expose the mucosal surface of the right nasal septum so that it could be explored with a stainless steel wire electrode (60 μm in diameter, quadruply enameled). Stimulation of olfactory nerve fascicles on the lamina propria side of the epithelium elicits, in addition to orthodromic activation of mitral cells, antidromic volleys in those receptor neurons in the epithelium whose axons form the fascicle being stimulated. These antidromic volleys can be
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recorded with the wire electrode from the mucosal surface and serve to map the size and shape of the mucosal surface innervated by a particular nerve fascicle (Mozell, 1964).

RESULTS

Five separate antidromic maps of the mucosa were obtained. In each case, the fascicle being stimulated in the lamina propria contained axons from an elongated (in the anterior-posterior direction) elliptical area of olfactory epithelium. These areas were ~1,000 µm long and <400 µm wide. More ventrally located mucosal fields were longer and narrower (i.e., 1,500 µm long and <200 µm wide at position 6) than those in more dorsal positions in the mucosa (750 µm long and <400 µm wide at position 3). The width of these antidromically mapped mucosal fields suggests that the 500-µA stimulus current employed is not so strong as to preclude effective localization of the stimulating current to an area ~75 µm wide on either side of the stimulating electrode. In every case, the area within which responses could be obtained was regular in outline and, insofar as could be visualized through the mucosa, followed the course of the olfactory fascicle being stimulated. Because of the regularities in area observed in the peripheral maps for a given stimulating position, we operationally defined the receptive fields of olfactory bulb neurons as those positions in the lamina propria which, when stimulated, elicit driven spike responses in the bulb.

52 Neurons were sampled, primarily from the medial mitral cell layer of the right olfactory bulbs of 24 male hamsters. An example of a neuron located in this region is illustrated in Fig. 1 B (filled circle). Its coordinate position in the bulb was 600 µm lateral to the midline, 1,700 µm from the anterior pole of the bulb and 1,279 µm below the dorsal surface of the bulb (−600, +1,700, −1,279). The negative sign for lateral-medial dimensions (i.e., −600) indicates a location in the right olfactory bulb. The coordinate positions for the sample of 52 neurones described in this study ranged from −300 to −1,000 (median, −500 µm) in the medial-lateral plane, 1,000 to 3,200 µm (1,775 µm) in the anterior-posterior plane and −114 to −2,823 µm (−1,056 µm) in the dorsal-ventral plane. These locations were selected to allow thorough exploration of those regions of the bulb that have been shown to receive input from the dorsal recess and septal regions of the epithelium (Costanzo and O'Connell, 1978). These regions of the epithelium can be seen in Fig. 1 and contain the nine standard stimulating positions, labeled 0–8. In addition, we have tested 45% of these medial bulb units with stimulation of lateral (Fig. 1, Lat) positions in the epithelium to confirm the fact that they did not receive input from distant regions. We failed to observe any consistent relationship between the size or placement of receptive fields and the duration of the experiment. This indicates relative independence from progressive or cumulative anesthetic effects on field size.

Response Profiles

Response profiles giving the field potential responses and receptive fields were plotted for each neuron. Fig. 2 gives an example of the raw data (left) used to
construct a response profile \( \text{(right)} \) for a typical bulb neuron. The data shown are photographic records of single-sweep recordings from the bulb after electrical stimulation of each of nine epithelial stimulating positions (0-7, Lat). Both field potential and action potential (spike) responses can be seen in these records.

The field potential responses indicate active and inactive regions of the bulb. It has been demonstrated (Shepherd and Haberly, 1970; Costanzo and O'Connell, 1978) that the polarity of evoked field potentials in the partially activated olfactory bulb is different for active and inactive regions. When the recording electrode is in a region of the bulb (mitral cell layer) containing cells activated by stimulation, a negative field potential is observed; when it is in an inactive region, a positive potential is observed. Thus, the positive field potentials seen in Fig. 2 indicate that cells in the region of the recording electrode were not activated directly by stimulation of epithelial positions 0-3, 6, and 7. Presumably, these stimulating positions activate cells in other regions of the bulb. Additional evidence for this is the fact that there is a positive field potential after stimulation of the lateral (Lat) epithelial position, which has been shown (Costanzo and O'Connell, 1978) to activate distant cells in the lateral region of the olfactory bulb. Moreover, we have never...
observed a case in which stimulating positions that elicited negative field potentials bracketed a position that elicited a positive field potential. In contrast to positions 0–3, 6, and 7, stimulation of epithelial positions 4 and 5 produced activation of a population of cells in close proximity to the recording electrode, as indicated by the observed negative field potentials. Stimulation of these positions also activated the single neuron, as indicated by a driven spike on the leading edge of the negative field potential. Such driven-spike responses were always associated with negative field potentials and occurred with a fixed latency after stimulation. Spontaneously occurring spikes were easily distinguished from driven spikes because they occurred infrequently and had a variable latency. These driven-spike responses were used to determine the receptive fields for individual neurons. The receptive field of a neuron was defined by the electrode position or positions on the lamina propria of the epithelium which, when stimulated, produced spikes on the leading edge of a negative field potential.

Response profiles, such as the one illustrated in Fig. 2, provide a graphic representation of the magnitude of field potentials and the occurrence of spike responses (filled circles) for the different epithelial stimulating positions tested. The response profile shown in Fig. 2 indicates that this neuron had its receptive field at positions 4 and 5 in the epithelium. These positions occupy an intermediate or middle region of the septal portion of the epithelium, as indicated in Fig. 1 A. The location of this neuron in an intermediate region of the olfactory bulb is also indicated by the filled circle shown in Fig. 1 B. To summarize, these results show that this particular neuron located in an intermediate region of the bulb gets its primary input from an intermediate region of the epithelium and suggests that there may be a topographical or point-to-point organization of projections.

**Response Profiles at Different Bulb Locations**

Neurons sampled at different positions within the olfactory bulb were found to have receptive fields located in different areas of the olfactory epithelium. Fig. 3 shows how the receptive fields of three olfactory bulb neurons located at three different recording depths shift to more ventral position in the epithelium with increased electrode depth. Neuron A, located near the dorsal surface of the bulb (depth, 152 μm), was found to have its receptive field limited to the dorsal recess of the epithelium (positions 0–3). Neuron B, however, which was deeper in the bulb (1,257 μm), had its receptive field at a more ventral location in the epithelium (positions 3 and 4). Finally, the third cell, neuron C, located at a depth of 1,925 μm, had its receptive field at an even more ventral location of the epithelium (positions 5–7). This observation of a shift in receptive field location with increasing recording depth is a principal finding of this study and is consistent with the concept that there is a topographical organization of olfactory nerve projections onto cells in the olfactory bulb.

Of the 52 neurons studied, 39 gave driven-spike responses following electrical stimulation of one or more of the epithelial test positions. The bulb locations and receptive fields for these neurons are given in Fig. 4. The
remaining neurons were not driven by electrical stimulation, and their receptive fields were thus not determined. For the purpose of illustration, the location of each neuron is projected onto the nearest (in the anterior-posterior plane) of four arbitrarily selected cross sections of the olfactory bulb. The most anterior cross section, A, is ~750 µm posterior to the anterior pole of the bulb; subsequent sections are separated by 500 µm.

The results illustrated in Fig. 4 show that most of the neurons sampled were within, or close to, the mitral cell body layer of the olfactory bulb. The receptive fields for the different neurons varied in size. The smallest, indicated by the circled numbers, represent a single epithelial position not more than 250 µm in diameter. These results also show that the receptive fields of olfactory bulb neurons are spatially organized in a dorsal-ventral plane.

Figure 3. Response profiles of three olfactory bulb neurons showing a shift in receptive field with recording depth. Filled circles represent positions that excite the neuron (i.e., give a driven spike response) and thus define the extent of its receptive field. Recording depths: neuron A, 152 µm; neuron B, 1,257 µm; neuron C, 1,925 µm.

Neurons located superficially or dorsally in the bulb tend to receive input from the most dorsal positions of the epithelium, such as positions 0–3, whereas those neurons located at more ventral positions or deeper in the bulb receive input from the more ventral positions of the epithelium. Single electrode penetrations through the bulb in which multiple recording positions were obtained always demonstrated this organization (7 penetrations, 16 units). We have never observed an instance in which a superficially placed bulb neuron had a receptive field more ventral in the mucosa than a bulb neuron recorded deeper in the same electrode tract. The correlation coefficient calculated for recording depth and position in the epithelium of the center of a neuron’s receptive field was 0.67 (Spearman rank correlation coefficient, Rs; P < 0.001,
Figure 4. Olfactory bulb cross sections showing the coordinate positions and size of receptive fields for 39 bulb neurons. Filled circles indicate coordinate location of neuron in bulb. Numbers indicate epithelial stimulating positions that define the neuron's receptive field. Circled numbers indicate neurons with single position receptive fields. A–D represent arbitrarily selected cross sections 750, 1,250, 1,750, and 2,250 μm from the anterior pole of the olfactory bulb. Neurons are plotted on section closest to their actual anterior-posterior location in the bulb. Calibration, 1 mm.

Two-tailed test; Siegel, 1965). It should be noted that the data shown in Fig. 4 were obtained in 24 different animals and are superimposed onto a single set of standard cross sections. This pooling of data introduces an apparent variability that tends to blur the underlying organization of the projections.
In spite of this limitation, Fig. 4 gives strong evidence for a topographical organization of excitatory epithelial projections onto the mitral cells in the olfactory bulb.

Receptive Field Size

In addition to the finding that the position of a neuron's receptive field changes as a function of its depth in the bulb, Figs. 3 and 4 show that there are differences in the size of receptive fields. For example, the three neurons shown in Fig. 3 have receptive fields of different sizes. Neuron A has a receptive field spanning four epithelial positions located in the dorsal recess. Such neurons evidently receive substantial input from a relatively large area of the olfactory epithelium. Neuron B, on the other hand, has a smaller (two-position) receptive field. This cell obtains its major input from a relatively localized group of receptors. Finally, neuron C receives input from three ventrally placed epithelial positions.

When the 39 neurons from all locations in the bulb are analyzed together, there appears to be an inverse correlation between depth in the bulb and size of receptive field ($R_s = -0.45, P < 0.01$, two-tailed test). However this apparent relationship arises because neurons in the superficial (dorsal) layers of the bulb receive their inputs from the dorsal recess of the epithelium (positions 0-3), which is organized primarily in a medial-lateral plane, whereas the medial and more ventrally located neurons receive their inputs from the septal region of the epithelium, which is organized in a dorsal-ventral plane (see Figs. 1 and 4). Six of the seven dorsal recess neurons had receptive fields that were three or four positions wide. Their inclusion in the analysis with the remaining 32 neurons that receive input from the septum (primarily organized in the dorsal-ventral plane) results in an artificially inflated $R_s$ value. If the seven dorsally located neurons are eliminated from the analysis, the correlation between depth in the bulb and receptive field size is no longer significant ($R_s = -0.09$).

The different receptive field size categories found for the 52 bulb neurons studied are shown in Fig. 5. Thirteen of these neurons were not driven by electrical stimulation at any of the standard epithelial positions and are indicated by the category labeled 0. The significance of this category of neurons will be considered in the Discussion. It should be noted at this point that the stimulus current used for these neurons (500 μA), was clearly suprathreshold for activation of olfactory nerve fibers. The fact that the negative field potentials obtained were of the expected magnitude indicates that neurons in the vicinity of the recording electrode were in fact being activated. This was demonstrated in the case of multiple neuron recordings from the same electrode location in the bulb. For example, in one such experiment, one of the two simultaneously recorded neurons was driven by stimulation, and the size of its receptive field was determined. The second neuron, however, did not give a response and consequently was categorized as a zero receptive field neuron.

39 (75%) of the neurons studied have receptive fields ranging in size from...
only a single epithelial position to a maximum of four positions. The most common group consisted of those having receptive fields spanning two epithelial positions. Thus, the modal mucosal field size in the periphery is an area somewhere between 250 and 750 \( \mu \text{m} \) wide (in the dorsolateral-ventromedial plane), which is a relatively small region considering the extensive area covered by the olfactory epithelium in the hamster (see Fig. 1). Finally, although the most common receptive field was two positions wide, there was a considerable range of receptive field sizes. The presence of bulb cells with different receptive field sizes suggests the possibility that different types of information from the periphery are received by different neurons in the olfactory bulb.

**Receptive Field Size vs. Stimulus Current**

The receptive field measurements for bulb neurons reported in this study should be viewed as upper limits because they were all based upon responses to stimulation with constant current pulses of 500 \( \mu \text{A} \). Fig. 6 illustrates the fact that this intensity is considerably above threshold. For the neuron illustrated, the threshold for the occurrence of a spike is between 10 and 25 \( \mu \text{A} \). In a previous study (Costanzo and O'Connell, 1978) we determined that the mean threshold for the occurrence of a spike in bulb neurons is 108 \( \pm 100 \mu \text{A} \). Therefore, the use of suprathreshold stimuli (approximately five times threshold) should, if anything, reduce the probability of finding localized receptive fields. This raises the question of whether the receptive fields of some neurons might have appeared smaller had stimulus currents less than the standard 500 \( \mu \text{A} \) been used. This question was examined by testing a neuron with a near threshold stimulus in addition to the 500-\( \mu \text{A} \) stimulus. Fig. 7 shows the response of this neuron to both 500-\( \mu \text{A} \) and 50-\( \mu \text{A} \) stimulus pulses. To compensate for any variability due to the just liminal stimulus, we have superimposed three traces for each of the stimulating positions at the lower current level. With stimulus currents of 500 \( \mu \text{A} \), the cell is driven by three
positions (5–7). The center position (position 6) gives the largest number of spikes and has the biggest negative field potential. When the same positions are tested again with a stimulus current of 50 μA, approximately two times threshold for this neuron, a much smaller receptive field is obtained. The receptive field mapped under these conditions is now limited to a single epithelial position, i.e., position 6. These results suggest that the receptive fields reported in this study represent the maximum possible extent of the peripheral convergence onto olfactory bulb neurons and that there is a central zone in which the density or efficacy of the innervation is maximal. In neurons with receptive fields larger than one stimulating position, the effective positions were always contiguous. The stimulating position nearest the center of the field had the lowest threshold for spike initiation, and, at a fixed supra-threshold intensity, always gave the biggest negative field potential and the largest number of driven spikes. It is conceivable that under more physiological stimulating conditions, such as with odor stimuli or lower (near threshold) stimulus currents, the receptive fields for olfactory bulb neurons would be considerably more localized than was demonstrated in this study.

**DISCUSSION**

The results of this study demonstrate that there is a spatial organization of the mammalian olfactory system and that there exists a topographical projection of inputs from localized regions on the epithelium onto the second-order neurons in the olfactory bulb. At the present time, the significance of a spatially organized olfactory system is still unclear.

![Figure 6](image-url)
In a recent review, Moulton (1976) discusses the importance of spatial and temporal patterns of response for the coding of odor quality. He points out that there is a considerable amount of data both at the epithelial and bulbar levels demonstrating that spatiotemporal patterns of excitation are produced following odor stimulation. Furthermore, different patterns of response are reported for different odors. This evidence strongly suggests that there is a spatial component to odor quality coding. If spatial patterns are required for coding then the topographical organization of projections reported in our study could play an essential role in the processing of olfactory information. Perhaps the primary function might be simply to preserve the spatial and temporal patterns of activity generated in the olfactory epithelium and transfer them intact to the second-order neurons in the olfactory bulb. However, the finding that olfactory bulb neurons have receptive fields of different sizes suggests that a more complex process is involved.

Olfactory bulb neurons receiving input from only a single localized position may have a different function than those with large receptive fields receiving input from several different positions (Kauer and Moulton, 1974; Costanzo and Mozell, 1976). For example, there may be a qualitative difference in the response characteristics of these neurons. Neurons with small receptive fields might respond to a few different odor qualities and function primarily in the encoding of odor quality. On the other hand, neurons having large receptive fields receive input from a larger number of receptors, and therefore might be involved in encoding odor quantity.

In this study, the receptive fields for 39 of the 52 bulb neurons examined were mapped, and the degree of localization was found to range from one to four epithelial positions (250-1,000 μm). Thirteen of the neurons examined were not excited by electrical stimulation. These neurons were not damaged

![Figure 7. Stimulation of epithelial positions at two different intensities. With the standard suprathreshold stimulus (500 μA), the neuron's receptive field spans three positions, 5, 6, and 7. With near threshold stimuli (50 μA), the receptive field is localized to a single epithelial position, 6. Three repetitions for each position are superimposed for the 50-μA stimuli.](attachment:figure7.png)
because they had typical asynchronous spontaneous activity without obvious signs of injury discharge. Furthermore, electrical stimuli elicited negative field potentials of the expected magnitude from one or more of the standard stimulating positions, demonstrating that the electrical stimulation was activating some afferent inputs. There are at least three viable explanations for the lack of driven response in these cells. (a) The neuron's receptive field was outside the epithelial area that could be explored with the stimulating electrodes. If this were the case, one would expect to find most of these units in more lateral regions of the bulb. However, when the coordinate positions of these neurons were examined, they were found to be randomly distributed within areas of the bulb where the great majority of excited neurons were found, suggesting that they do not receive input from a very distant region of the epithelium like the endoturbinate III. However, they may represent neurons with inputs from epithelial positions that are on adjacent turbinates but still at the same dorsal-ventral location in the nasal cavity (e.g., the epithelium of the endoturbinate II). (b) Electrical stimulation produces an inhibition of the second-order neurons. This hypothesis awaits investigation with intracellular recording techniques because the neuron's spontaneous activity is too low to allow an adequate evaluation of inhibitory events by examination of variations in the frequency of extracellular potentials. (c) Maximal stimulation of any one epithelial position elicits only subthreshold excitation. Because of the difficulties associated with positioning two or more stimulating electrodes simultaneously on adjacent portions of the olfactory epithelium, we have not studied the convergence of inputs from two positions onto a single bulb neuron. The fact remains that in some cases supramaximal stimulation of single epithelial positions may evoke subthreshold excitation in bulbar neurons receiving input from several positions. Therefore, it is also possible that, in those cases in which a receptive field was mapped, interaction of two or more peripheral inputs would reveal a larger receptive field. Future studies on the interactions among multiple positions in the epithelium should provide useful data on the possible role of summation and lateral inhibition within the olfactory system.

Finally, a comment on the precision of localization of receptive fields observed for the hamster is in order. As mentioned in the introduction, the nasal cavity in most mammals is extremely complex. It consists of a series of intricately folded turbinates that project into the nasal cavity, resulting in a highly specialized structure (see Fig. 1). Yet, in spite of its anatomical complexity, we have been able to demonstrate that the topographical projection of the epithelium onto the bulb is relatively simple, at least for a contiguous accessible area like the septal region. A similar type of projection has been reported in the frog (Costanzo and Mozell, 1976). The nasal cavity of the frog is a simple cone-shaped structure, and the arrangement of nerve fibers is ideal for a spatial arrangement of projections. However, the projections in the frog are more diffuse than those in the hamster. In some cases, frog neurons receive input from the entire dorsal half of the epithelium, a distance of $\sim 10$ mm. This is ten times the width of the largest receptive field found in
the hamster, which spanned only four stimulating positions, representing a distance of only 1 mm. This difference in the precision of projections may be related to differences in the olfactory discrimination powers of the two animals.

In general, the olfactory capabilities of mammals, such as the hamster, are extremely well developed. On the basis of behavioral data it has been shown that mammals are sensitive to extremely low concentrations and can discriminate a wide range of odors (O'Connell et al., 1978 and 1979). Although there is little behavioral data on the frog, we believe that its olfactory capabilities are rather limited when compared with those of the mammal. It is important to note that the hamster's more sophisticated system, in spite of its complex anatomy, was found to have a simple yet precise topographical organization of its projections. This suggests the possibility that the precision of localized projections may play an essential role in determining the sensitivity and discrimination capabilities of the olfactory system. Future studies with controlled odor stimulation will be used to explore this possibility.

The authors wish to thank Drs. Michael Meredith and David Marques for their useful discussions and critical review of the manuscript and Dr. Carl Pfaffmann for the use of some of the equipment and laboratory space needed for these experiments.

This work was supported by National Institutes of Health Research Fellowship Award NS 00297 and National Institute of Neurological and Communicative Disorders and Stroke Research grant NS 14453.

Received for publication 11 May 1979.

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