Response Patterns of Single Neurons in the Tortoise Olfactory Epithelium and Olfactory Bulb

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ABSTRACT The responses to odor stimulation of 40 single units in the olfactory mucosa and of 18 units in the olfactory bulb of the tortoise (Gopherus polyphemus) were recorded with indium-filled, Pt-black-tipped microelectrodes. The test battery consisted of 27 odorants which were proved effective by recording from small bundles of olfactory nerve. Two concentrations of each odorant were employed. These values were adjusted for response magnitudes equal to those for amyl acetate at -2.5 and -3.5 log concentration in olfactory twig recording. Varying concentrations were generated by an injection-type olfactometer. The mucosal responses were exclusively facilitory with a peak frequency of 16 impulses/sec. 19 mucosal units responded to at least one odorant and each unit was sensitive to a limited number of odorants (1–15). The sensitivity pattern of each unit was highly individual, with no clear-cut types, either chemical or qualitative, emerging. Of the 18 olfactory bulb units sampled, all responded to at least one odorant. The maximum frequency observed during a response was 39 impulses/sec. The bulbar neurons can be classified into two types. There are neurons that respond exclusively with facilitation and others that respond with facilitation to some odorants and with inhibition to others. Qualitatively or chemically similar odorants did not generate similar patterns across bulbar units.

INTRODUCTION

Studies of the neural basis of the sense of smell have delineated three ways by which information about odor quality may be coded. Adrian (1950 a, b; 1953) was the first to observe that olfactory bulb neurons displayed varied temporal and spatial patterns. Spatial patterning was the greater sensitivity to water-soluble substances in the anterior portion of the bulb and to oil-soluble compounds in the posterior area. The temporal patterning which he observed was characterized by differences in the latency, duration, the rise, and the fall time of the response. He later (1953) provided evidence for the differential sen-
tivity of single neurons as a possible code for odor quality. This specificity was observed only around threshold; it was lost at higher concentrations.

In addition to demonstrating that the ratio of the response magnitudes of amyl acetate to heptane was always greater in the anterior portion of the rabbit bulb, Mozell (1958) found that the response to amyl acetate was consistently shorter in rise time than that to heptane. Moulton (1963) found evidence for spatial patterning while recording with chronically implanted electrodes in the rabbit.

Both Walsh (1956) and Basavaraju (1961) found some evidence for specificity in the responses of rabbit olfactory bulb neurons but Leveteau and MacLeod (1966) found little indication of specificity when recording from single glomeruli in this animal.

In 1963, Gesteland et al. demonstrated that single olfactory receptors in the frog have a highly individual, wide selectivity. The receptors were categorized into eight extensively overlapping groups.

Döving (1965; 1966a, b) demonstrated that the responses of bulbar neurons in the frog showed a high degree of correlation dependent on the similarity of the stimuli. Higashino et al. (1969) also found a high correlation between the responses to pepperminty and to camphoraceous odors.

Another approach to the problem of olfactory quality coding comes from the work of the German comparative zoologists. They have found that the olfactory sense cells of insects fall into two broad classes. Some receptors respond only to substances which play a significant role in the life of the animal. Schneider et al. (1964) observed that some of the sensory cells of the tricodial hairs of the male Asiatic silkmoth respond vigorously only to the sexual lure substance of the female but give a small inhibitory response to fruity odors. The second class of receptors respond to a broad spectrum of odorants. Some of the cells of the tricodial hairs of the silkmoth respond in this manner. Lacher (1964) investigated a similar receptor in the placodial sensillum of the honeybee. The general odor receptors of both animals respond with facilitation to some odors and with inhibition to others. They form no discriminable classes in their response patterns; each receptor responds to its own unique set of stimuli.

The purpose of this study was to investigate further the neural mechanisms which account for the ability of animals to discriminate one odor from another. The approach used in these experiments is a familiar one. At a particular neuroanatomical level, the electrical activity of a sequential sample of single neurons is recorded. The responses of each neuron to the members of a stimulus battery represent the basic information in the study. From the response patterns of these single neurons, a matrix of odorant patterns across neurons can be constructed. Previous investigations have concentrated primarily at one anatomical level. This study permits the comparison of response
patterns at the receptor and at the olfactory bulb levels and, consequently, the observation of any transformations that may occur from the most peripheral level to that of the second-order neurons.

The tortoise, *Gopherus polyphemus*, is a particularly appropriate animal for an experiment of this type. Single receptor activity (Shibuya and Shibuya, 1963), as well as olfactory nerve responses (Tucker, 1963), can be recorded and the olfactory bulbs are readily accessible.

**METHOD**

Each tortoise was anesthetized with 5 cc of 50% urethane per kg body weight. One polyethylene cannula was inserted into the lower trachea to ease the animal’s breathing and a second cannula was passed through the upper trachea into the animal’s mouth. The second cannula permitted air or odor to be drawn through the animal’s nose by the normal route. The animal was then placed in an ear-bar type head holder. A small Teflon plate was slipped under the mouth cannula to prevent blockage by the tongue and the mouth was clamped closed.

**Mucosa**

The skin and the cartilage overlying one nasal passage was cut away. The dorsal mucosa was removed by means of a scalpel and fine forceps. The septal mucosa was then directly accessible. The surgical intervention was ringed with odorless stopcock grease and a thin glass plate with a small central hole was impressed upon the ring. The presence of the stopcock grease and the polyethylene mouth tubing had no discernible effect on the preparation. This was inferred from the low baseline firing rate of the receptors and the absence of response to cleaned air being drawn through the nose. The indium-filled, Pt-black-tipped micropipette was driven through the hole by means of a heavy microdrive and the hole was sealed with stopcock grease. The electrode was advanced through the mucosa at the rate of 1 μm/min until a unit was encountered. The stimulus series was then begun.

**Olfactory Bulb**

A trephine hole was introduced into the anterior dorsal surface of the skull. The dura was cut away and the pia removed by means of fine forceps. The micropipette, of the same type used in recording from the mucosa, was advanced until it touched the surface of the bulb. Pt-Ir stimulating electrodes were placed across the olfactory nerve leading to that bulb. The trephine hole was filled with 3% agar Ringer to prevent respiratory pulsations. The micropipette was advanced in 1-μm steps. The olfactory nerve was stimulated once every 5 sec and the compound potential of the bulb was recorded. When a unit was observed superimposed on the second wave of the compound potential, the microelectrode advance was halted and the stimulus series was begun.

**Stimulation**

Cleaned air and odorous stimuli of determinate concentration were generated by the olfactometer shown in Fig. 1. An airstream from a rotary compressor (a) was dried...
and cleaned by filtration through indicating silica gel (b) and activated charcoal (c). The stream was then saturated with water vapor by bubbling through distilled water (d). The flow rate of the airstream was controlled by means of a needle valve (e) and monitored at the rotameter (f). The air continuously flowed past the animal's nose (g) which had been fitted into a small glass chamber. The odorants were stored in saturator bottles at room temperature (21°C). Saturated vapor, drawn from a bottle, was injected into the airstream from a pump-driven syringe (h). The tip of the needle was inserted into a Teflon sleeve (i) in the air line. By varying the size of the syringes and the pump drive rate, log dilutions to $-8.0$ were obtained. The duration of the pump drive was controlled by a timing system (j). The stimulus was delivered to the animal's mucosa by the action of a negative pressure pump (k). The flow rate was controlled by means of a needle valve (l) and monitored by a rotameter (m). This stream was normally drawn through the room side of a three-way stopcock (n). The cannula (o) which passed into the mouth of the animal was attached to the other arm of the stopcock. Nasal flow rate was established by switching the stopcock from room to animal. The flow rate was maintained at 120 cc/min unilateral. This value was calculated under the assumption that there was approximate equality between the flow rates in the two nasal cavities.

**Figure 1.** Diagram of the olfactometer and the stimulus delivery system.
Stimuli were delivered to the preparation by the following method. Once the flow through the nose had been established, the needle of a vapor-laden syringe was inserted into the port in the Teflon sleeve and the syringe was then driven automatically for 1 sec. The syringe was immediately withdrawn and cleaned air was drawn through the nose for 1 min. After an additional interval of 2 min, the next stimulus was delivered.

The stimuli were chosen on the basis of two criteria. The first was membership in one of Amoore's (1962) qualitative classes. The second was related to the magnitude of the integrated olfactory nerve response relative to amyl acetate. Response-concentration functions, based on integrated olfactory nerve responses, had previously been generated for 63 odorants. In order for an odorant to be included in the battery, its response level had to reach equivalence with the amyl acetate response at $-2.5 \log$ concentration. Two concentrations of each stimulus were used: the high concentration produced a response equivalent to amyl acetate response at $-2.5 \log$ concentration and the low produced one equivalent to that at $-3.5 \log$ concentration.

The stimuli used in this experiment, with their equivalent concentrations, are shown in Table I.

### Recording

Indium-filled, Pt-black-tipped micropipettes were used throughout the experiment. The neural activity was led through a simple cathode follower to a Grass P6 preamplifier (Grass Instrument Co., Quincy, Mass.). The audio-monitored spike activity was displayed on a Tektronix 502 oscilloscope (Tektronix, Inc., Beaverton, Ore.) and photographed with a Grass camera.

### RESULTS

#### Mucosa

The neural activity of 40 single units in the olfactory mucosa was recorded. The units and the tip of the recording electrode could be kept in proximity for periods ranging from 30 min to 6 hr. The majority of the units were held for approximately 1 hr and 30 min.

Of the 40 units tested with the higher concentration of the 27 odorants in the stimulus array, 19 (48%) responded to one or more of the odorants. The base line firing rate of these cells was quite low, averaging 0.05 impulses/sec. Two units were completely silent and the rate of the remaining units varied from 1 impulse/1.4 sec to 1 impulse/1.7 min. Silent units and units with very low spontaneous rates could be identified because the mechanical stimulus generated by the advance of the electrode produced a single impulse discernable in the oscilloscope trace. The type of response obtainable from this preparation, illustrated in Fig. 2, was always excitatory with a maximum frequency of 16 impulses/sec. The responses exhibited several different forms. Some were high frequency or low frequency bursts (phasic); others began with a high impulse frequency and then declined over a period of several seconds (phasic-
TABLE I
STIMULI USED AND THEIR EQUIVALENT CONCENTRATIONS

| Class       | Odorant                      | Log concentration |
|-------------|------------------------------|-------------------|
|             |                              | Low   | High  |
| Camphoraceous | tert-Butyl methyl ether      | -4.0  | -2.75 |
|             | Cyclohexanol                 | -1.5  | -0.75 |
|             | Gineole                      | -3.5  | -2.0  |
|             | p-Dichlorobenzene            | -3.0  | -1.0  |
|             | tert-Amyl alcohol            | -2.5  | -1.25 |
| Pungent     | Propionaldehyde              | -2.5  | -1.75 |
| Ethereal    | Carbon tetrachloride         | -2.5  | -1.0  |
|             | Acetone                      | -1.5  | -1.0  |
|             | Methyl formate               | -1.75 | -1.0  |
| Floral      | Anisole                      | -2.75 | -1.0  |
|             | Acetophenone                 | -2.5  | -0.5  |
|             | Phenetole                    | -2.25 | -1.5  |
| Putrid      | Trimethylamine               | -3.25 | -2.0  |
|             | Methylamine                  | -4.0  | -3.25 |
| Almond      | o-Tolualdehyde               | -2.0  | -1.0  |
|             | Benzaaldehyde                | -2.5  | -1.25 |
| Aromatic    | Chlorobenzene                | -3.0  | -1.25 |
| Lemon       | Limonene                     | -1.75 | -0.75 |
| Unclassified| Amyl acetate                 | -3.5  | -2.5  |
|             | Isoamyl acetate              | -3.25 | -1.25 |
|             | Butyl acetate                | -4.0  | -2.75 |
|             | 2-Nonanone                   | -1.5  | -1.0  |
|             | 2-Butanone                   | -3.5  | -2.0  |
|             | Hexanol                      | -4.0  | -1.5  |
|             | Heptane                      | -2.0  | -0.75 |
|             | Citral                       | -2.25 | -1.0  |
|             | Benzylamine                  | -2.75 | -2.25 |

tonic); a few were steady trains of impulses which, in the most extreme case, lasted for 27 sec (tonic). Of the 11 units which were tested with the lower concentration, all showed a decrease in the number of odorants to which they responded. This decrease was, on the average, 65%.

The responses of the 19 units are displayed in Fig. 3. These are the responses to the higher of the two test concentrations. A blank indicates that, although tested with the odorant, the unit did not respond. Each odorant excites a unique sequence of receptor units; the pattern for one odorant is duplicated by no other. Even chemically related substances, such as amyl acetate and butyl acetate, show little overlap. Of the seven units which responded to amyl acetate, only two responded to butyl acetate. This occurred despite the observation that the response-concentration functions for these two substances, measured by the output of the olfactory nerve bundle, are very similar. No sig-
significant pattern similarity was found between odorants that were qualitatively similar.

When the receptors were stimulated by the lower of the two concentrations, a matrix similar to the one obtained at the higher concentration was produced. The number of odorants to which each unit responded, however, was reduced by 29–100%.

In regard to specificity, the sample of receptor units cannot be characterized easily. The number of odorants to which each unit responded is shown in Fig. 4. The most limited units responded to one odorant and the most general, to 15. The remainder fell between these two values, with half the units responding to four or fewer odorants.

The unique pattern for a particular odorant results from the differential sensitivity of the units in the sample. The individual units responded to differing numbers of odorants. For a particular neuron, the magnitude of the response to one odorant was found to be different from the magnitude of response
to another. This is exemplified in Fig. 5, which shows the response magnitudes of Unit 14 to the seven odorants to which it was sensitive.

For the odorants for which response-concentration data was available, the dynamic range varied from 0.5 log concentration units to 2 log concentration units. The response-concentration functions from Unit 14 for four odorants is shown in Fig. 6. Although the thresholds for amyl acetate and butyl acetate are considerably lower than for the other two odorants, the peak output for isoamyl acetate and propionaldehyde is much higher. Butyl and amyl acetate also show a marked decline in response magnitude subsequent to their peaks.

Several response-concentration functions exhibited an inflection in their course. This can be seen in the isoamyl acetate curve at -2.25 log concentration in Fig. 6. A similar inflection is evident at -2.25 log concentration in the amyl acetate curve shown in Fig. 7. Because each unit could be held for only a limited amount of time, each point on the curves represents a single stimulation.
Figure 4. Number of odorants to which each receptor unit was sensitive.

Figure 5. Differential sensitivity of receptor Unit 14.

Olfactory Bulb

Recordings were obtained from 18 single units in the olfactory bulb. These units could be held for approximately 1.5 hr, which permitted testing with the higher but not the lower of the two concentrations.
All of the 18 units responded to at least one member of the test battery at the higher concentration. They showed a spontaneous firing rate of 0-2.5 impulses/sec with an average rate of 1 impulse/sec. The maximum frequency observed during a response was 39 impulses/sec. The responses of several units are shown in Fig. 8.

Olfactory bulb neurons can be categorized into two types. There are neurons that respond exclusively with facilitation and those that respond with
facilitation to some odorants and with inhibition to others. The units of both classes are neither highly specific nor nonspecific but rather show a continuous gradation in the number of odorants to which they respond (Fig. 9).

**Figure 8.** Oscilloscope photographs of olfactory bulb unit responses. (A), response of Unit 3 to p-dichlorobenzene at $-1.0$ log concentration; (B), response of Unit 4 to heptane at $-0.75$ log concentration.

**Figure 9.** Number of odorants to which each olfactory bulb unit was sensitive.

The matrix of responses is presented in Fig. 10. Each odorant produced a unique pattern of facilitory and inhibitory responses across the units. Furthermore, the odorants to which a unit was sensitive produced responses of differ-
ent magnitudes. As at the mucosal level, qualitatively or chemically similar odorants did not generate similar patterns across units.

**FIGURE 10.** Matrix of olfactory bulb responses by units and odorants.

**DISCUSSION**

Several contrasts exist between receptor level activity and activity at the bulbar level. The spontaneous firing rate and the maximum frequency of firing during a response are considerably higher for the bulbar neurons. Both facilitory and inhibitory responses are observable at the bulbar level; the receptors respond only with an increase in frequency. The neurons of the bulb also have a higher probability of responding. Only 45% of the mucosal units responded to at least one stimulus but all of the bulbar units responded to at least one. This may be a consequence of the 26,000:1 convergence that occurs as olfactory nerve fibers enter each glomerulus.

The inhibition observed at the bulbar level may play a significant role in the coding of odor quality. The role of inhibition in quality coding has been
well established in the visual (Hartline, 1938; Barlow, 1953; Kuffler, 1953; Hubel and Wiesel, 1959), auditory (Galambos and Davis, 1944; Katsuki et al., 1958), and somesthetic (Poggio and Mountcastle, 1963) systems. Inhibitory responses from olfactory bulb neurons in the rabbit had previously been observed by Mancia et al. (1962).

Döving's work has given strong support to the notion that inhibition is of significance in the coding of odor quality. In 1964, he reported that the greater proportion of responses from frog bulbar neurons was inhibitory. These responses, and the less frequent facilitory ones, were used by Döving (1966 a) to generate chi-square matrices which measured the degree of similarity between pairs of substances belonging to the homologous series of normal aliphatic alcohols, acetates, and ketones. Döving (1966 b) applied the same similarity analysis to the responses of units to odorants drawn from five of Amoore's (1962) stereochemical groups and established that a high degree of similarity exists among the members of each of three classes.

The possibility exists that some receptors are more easily narcotized than others (Mullins, 1955) and that this type of high sensitivity may contribute to inhibition in the chemical senses. In order to lessen this possible effect, the higher of the two concentrations was selected by the following method. The magnitude of the response to amyl acetate at \(-2.5\) log concentration was taken as a standard. The response to this concentration lies in the middle of the response-concentration function for this substance rather than at its maximum. The concentration values for the other stimuli were chosen on the basis of equal response magnitude relative to the amyl acetate standard. Furthermore, the concentrations of those odorants which produced inhibition in some neurons at the bulbar level yielded only facilitory responses at the receptor level.

The patterning of single unit responses at the level of the mucosa and the bulb in this preparation has been observed in other experiments. In vertebrates, it has been seen by Leveleau and McLeod (1966) when they recorded from single glomeruli in the rabbit bulb and by Mathews¹ in records obtained from single neurons in the bulb of the rat. Two receptors in insects provide patterning effects that closely resemble those found in this preparation. These are the “general” sensory cells of the silkmoth (Schneider et al., 1964) and the placodial sensillum of the honeybee (Lacher, 1964). The two response types, facilitation and facilitation/inhibition found at the level of the bulb in this study, are present in the work on the honeybee. In the study on the silkmoth, there is a third, “purely” inhibitory, type of unit.

Inflections in response-concentration functions have been observed by Mozell (1958) when recording from bulbar neurons in the rabbit and by

¹ Mathews, D. F. 1966. Response patterns of single units in the olfactory bulb of the rat to air and odor. Ph.D. Thesis, Brown University, Providence, R.I.
Moulton (1960) in his behavioral study of the rat's ability to detect aliphatic acetates. Recording from rat olfactory nerve bundles, Mathews observed similar anomalies in the response-concentration functions for several odorants.

The inflections appearing in some of the response-concentration functions for single receptors suggest that one receptor may possess more than one type of site for a particular odorant. According to Moulton (1960), were the initial portion of the curve merely to level off an explanation might be structured in terms of absorption of the odor molecules on the receptor (Beidler, 1954) or penetration of the receptor membrane by the odorant (Davies, 1953). As he points out, however, neither of these account for the decrease in the function after the first peak has been reached; Mullins's (1955) proposal that some receptors are more easily narcotized than others does offer an explanation for this decrement in the function.

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