rat spans both the prenatal and postnatal periods of development, in the present study, stress was effective only during prenatal differentiation. This is not too surprising since it is known that newborn rats pass through a stress-nonresponsive period for the first 10 days after birth (*11*). Paradoxically, while the newborn rat lacks the normal adrenal response to environmental stress, its adrenals show an increased sensitivity to ACTH (*11*). We are currently testing the possibility that by stressing the mother, enough ACTH or adrenal steroids can be transferred to the pup through the milk to influence the process of sexual differentiation which, in the rat, continues to about 10 days of age.

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Olfactory Bulb Units: Activity Correlated with Inhalation Cycles and Odor Quality

Abstract. *Single olfactory bulb units were studied in two macrosmatic species of rodents under conditions intended to preserve the cyclical stimulation which normally accompanies nasal breathing. Patterns of unit activity related to the inhalation cycle were observed in all animals, often in the absence of specific stimuli, and could not be explained in simple mechanical terms. Distinctive changes in these patterns occurred in response to certain odors, and were generally independent of changes in the overall firing frequency. These findings indicate that a change in the overall firing frequency of unit discharges is neither a necessary nor sufficient measure of responsiveness to odors in the rodent olfactory bulb, and that stimulus-specific temporal distributions of unit firing may be involved in olfacto-endocrine activities.*

Among mammals from mouse to monkey, olfacto-endocrine factors figure prominently in the control of critical activity patterns upon which individual and species survival depend. In many species of rodents, carnivores, and primates, scented glandular secretions (pheromones), produced under the combined influence of interoceptive and exteroceptive stimuli, influence in turn the endocrine cycles and the reproductive, territorial, or social behavior of conspecific animals (*1*). Pheromones appear to exert their effects in at least two ways. First, they are distinctive cues or signals and, as such, trigger specific responses from other members of the species. Anyone who has tried to take an estrous bitch for a walk around the block will testify to the potent attractant effects of certain hormone-dependent scents. Second, pheromones normally present within the immediate environment may exert long-term effects. That is, they contribute to the stable background necessary to maintain essential consummatory activities. It is a notorious fact that the absence of familiar odors, or the presence of unfamiliar ones, may interfere with normal patterns of such varied activities as eating, sleeping, copulation, and maternal behavior. Furthermore, specific mammalian pheromones, produced under endocrine control, have been implicated in the regulation and maintenance of normal reproductive cycles (*2*).

In most mammals, pheromones and other airborne stimuli are continuously swept in wave-like fashion across the primary olfactory receptors deep within the nasal cavity. Under what we call resting conditions, when the normal respiratory rhythm provides a basis for repetitive and periodic sampling of the olfactory background, the normal sampling epoch coincides with the nasal inhalation phase of each respiratory cycle. Whenever a distinctive change in the quality of the inhaled air is detected during regular nasal breathing, most mammals react by sniffing, a sign of active olfactory exploration which tends to take precedence over any routine consummatory activities. Sniffing involves increase in the mean frequency of nasal inhalations and in the overall rate of odor sampling. These changes are accompanied by corresponding decreases in the duration of each sampling epoch. Thus, under both resting and active conditions, olfactory stimulation remains an essentially periodic process. This periodic patterning of nasal air flow may itself play a role in the processing of olfactory information.

In an attempt to elucidate the mechanisms whereby animal scents exert their effects upon behavioral and endocrine activities in rodents, we have been studying the responses of single olfactory bulb units to various odors in two macrosmatic species: the Syrian golden hamster (*Mesocricetus auratus*) and the prairie deermouse (*Peromyscus maniculatus bairdii*). For reasons already noted, precautions have been taken to preserve the periodicity of odor stimulation which occurs under natural conditions. We report two findings consistently obtained in each of more than 100 animals of both species and sexes, tested under various conditions and at ages ranging from two weeks to six months. These are (i) a general tendency for olfactory bull units to exhibit a definite temporal pattern of firing with respect to particular phases of the nasal inhalation cycle and (ii) the occurrence of stimulus-specific changes in this pattern in the presence of various odors. Such changes often occurred without a corresponding alteration in the overall frequency of unit firing. We conclude that stimulus-specific differences in the

distribution of unit activity during the inhalation cycle may contribute to the processing of olfacto-endocrine information in the rodent olfactory bulb.

Each animal was anesthetized by inhalation with a mixture of methoxyflurane, nitrous oxide, and oxygen, and double tracheal intubation was performed. One polyethylene cannula was inserted caudally, toward the bronchi; a second was inserted rostrally, through the larynx. Anesthesia was continued via a t-tube connected to the caudal cannula, the animal's head was secured in a stereotaxic instrument, and a craniotomy was performed over the olfactory bulbs. In about one-third of the animals studied, recordings were made with anesthesia maintained in this way. The remaining animals were treated with local anesthesia (subcutaneous lidocaine around the skin incisions and at points of stereotaxic restraint), and the inhalation anesthesia was discontinued. Paralysis was produced with subcutaneous injections of gallamine triethiodide (Flaxedil), and positive-pressure pulmonary ventilation was induced via the caudal cannula by a respirator that periodically delivered a mixture of nitrous oxide and oxygen (70:30) at rates and tidal volumes that could be varied over a wide range.

In all animals, artificial nasal inhalation was induced by connecting the rostral tracheal cannula to the same respirator, which had been modified to supply negative pressure pulses and thus simulate nasal inhalation. Artificial nasal inhalation rates were varied, in different cases, from 40 to 240 per minute. For animals paralyzed with Flaxedil, nasal inhalation rate and phase corresponded exactly with pulmonary insufflation rate and phase. Comparable inhalation rates were also used with animals not treated with Flaxedil, but since the latter were spontaneously respiring, corespondence between nasal and pulmonary air flow was not enforced. Comparisons between results obtained with paralyzed and spontaneously respiring animals were planned in order to test for centrifugal influences on bulb activity from caudal brain regions controlling spontaneous respiration. The need for such comparisons is obviated by the fact that our main findings were essentially equivalent in both groups.

Odor stimuli used in this experiment included pure chemicals (for instance, amyl acetate, cineole, phenethyl alcohol, and octane) and chemically undefined substances of animal origin. Among the latter were scents of live animals of different species, age, sex endocrine status, and relationship to the subject (for example, pups, parents, or siblings), bedding from the subject's home cage, soiled bedding from the cage of an unfamiliar animal, and unused bedding. The system of stimulus delivery (*3*) allowed us to add the odor stimuli at measured rates into a clean air stream which played continually on the external nares of the experimental animal. The overall rate of flow of the clean air stream was sufficient to preclude nasal inhalation of external room air and to mask changes in rate due to onset or termination of the stimulus. Stimulation trials generally lasted 30 seconds and were separated by intervals several minutes in duration. For any given olfactory bulb unit, several stimuli were presented in a counterbalanced order. In most cases, each stimulus was presented several times.

Conventional electrophysiological techniques (*4*) were used to record extracellularly from single olfactory bulb units. The latter were easily isolated and could generally be held for several hours. Most of the units sampled in this study were located in or near the mitral cell layer. They exhibited moderate rates of spontaneous activity under background (clean air) conditions, and were found to be odor-sensitive in that they tended to show changes in firing rate in response to stimuli. Comparing the overall frequency of unit activity for appropriate time periods before, during, and after stimulation, we found that the response of rodent olfactory bulb units could be classified with respect to three characteristics: (i) duration (phasic changes at the onset or termination of stimulation, or tonic changes lasting throughout the period of stimulus presentation), (ii) direction (excitatory or inhibitory), and (iii) degree (minimal, moderate, or marked). For any given unit, some odors might produce one kind of overall effect, others might produce different effects, and still others might produce no change. Many units were found to exhibit similar overall responses to dissimilar odors and dissimilar overall responses to similar odors. In other words, we found, in agreement with others (*5*), that changes in the overall frequency of activity of olfactory bulb units do not necessarily correspond simply or systematically with variations in quality of odor.

Figure 1 (top) illustrates the time course of changes in frequency of discharges in response to three different scents by a representative unit in the olfactory bulb of an adult male deermouse. These three frequency response histograms (FRH) exemplify our frequent failure to find stimulus-specific changes in the overall frequency of unit activity. In all three histograms, onset of the stimulus was accompanied by a moderate phasic inhibition; and in the first and third histograms, termination of the stimulus was followed by a brief burst of activity. The overall level of activity during the latter two-thirds of stimulus presentation (the final 20 seconds) in all three cases tended to fall within the upper range of normal pre- and poststimulus activity levels.

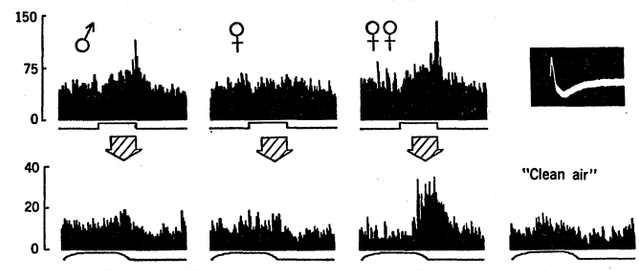

Fig. 1. (Upper half) Frequency response histograms (FRH). Time base is 100 seconds. Each histogram shows the overall frequency of action potentials of a single neural cell in the olfactory bulb of an adult male deermouse. Stimuli were the scents of three other deermice, a male (♂), an anestrous female (♀), and an estrous female (♀♀), and were presented from second 30 to 60 (indentation in baseline). Each histogram is based upon two counterbalanced presentations of the stimulus series. The vertical height at each time point indicates the total number of action potenials detected. Inlay at right shows 30 superimposed unit action potentials (sweep length, 5 msec). (Lower half) Inhalation cycle histograms (ICH). Time base is 272 msec. Each ICH is a summation of all the inhalation cycles during second 40 to 60 of the histogram above (144 cycles). The baseline shows nasal air flow during a single inhalation cycle. Each ICH shows that activity of the olfactory unit varies with time during the inhalation cycle. At the right is the ICH for the filtered air stream (*"Clean air"*). For further details, see text.

Bearing in mind that stimulus-related changes in the overall frequency of unit activity are quite similar in the three histograms and that the firing frequencies during the final 20 seconds of stimulation failed to differentiate among the three stimuli, let us consider a somewhat different mode of analysis.

Beneath each FRH in Fig. 1 is an inhalation cycle histogram (ICH) which depicts unit activity within the inhalation cycles which occurred during second 40 to 60. The ICH baseline represents nasal air flow during a single inhalation cycle. Each ICH is constructed by summing, for each point during the cycle, the discharge frequencies recorded in many successive inhalations. In the present case, the respirator had been set to produce about 220 inhalations per minute. Thus, each cycle lasted 272 msec, and 72 successive cycles occurred during the 20-second sampling periods. Each stimulus was presented twice, so that each ICH is based on 144 inhalation cycles. The lower right ICH shows the pattern of firing during 144 inhalations under background (clean air) conditions.

Even in the absence of any known odors in the clean air stream, a slight degree of patterning with respect to the inhalation cycle is evident. This finding was quite common in our series and agrees with the report of Walsh (*6*), who attributed the effect to mechanical stimulation of the nasal epithelium. While this interpretation cannot be ruled out, the presence of various contaminants in the filtered air remains a plausible alternative possibility. In any event, the background patterning is clearly not due to mechanical pulsations arising in the vicinity of the electrode tip as a result of the pulmonary insufflation cycle. This could be shown by the fact that patterning appeared even when pulmonary insufflation and nasal inhalation were not correlated (animals not paralyzed with Flaxedil). Furthermore, the patterning effect disappeared immediately if the nasal air flow was interrupted.

While we cannot exclude the possibility that patterning in the presence of filtered air is at least partly due to mechanical stimulation of the nasal mucosa, we can show that the shape of the ICH is, indeed, subject to drastic alteration as a function of odor quality. A simple mechanical interpretation cannot account for this finding. In Fig. 1, for example, the stimulus containing the scent of the estrous female (♀♀) produced a virtual reversal in the normal (clean air) pattern of activity during the inhalation cycle, whereas the other two stimuli produced much more modest changes. The effect of the estrous female's scent upon patterning was considerably greater, and its distinctiveness from the other two stimuli was more pronounced, than might have been expected by simply comparing the corresponding FRH's.

Although we cannot prove that patterning of olfactory bulb unit activity during the inhalation cycle is actually involved in the sensory processing of odor stimuli, we have observed many instances in which stimulus-specific changes in the pattern are considerably more pronounced than any corresponding alterations in the overall activity. This general finding holds for all of the odors with which we have worked, but it is often most impressive in the case of ethologically relevant scents. A striking example is illustrated in Fig. 2. Here, as in Fig. 1 (bottom), the abscissa represents the length of an inhalation cycle, and each tracing begins with the initiation of nasal air flow. In this case, however, the unit recorded was from the olfactory bulb of a female hamster pup 21 days of age, and the duration of the inhalation cycle was 1.5 seconds.

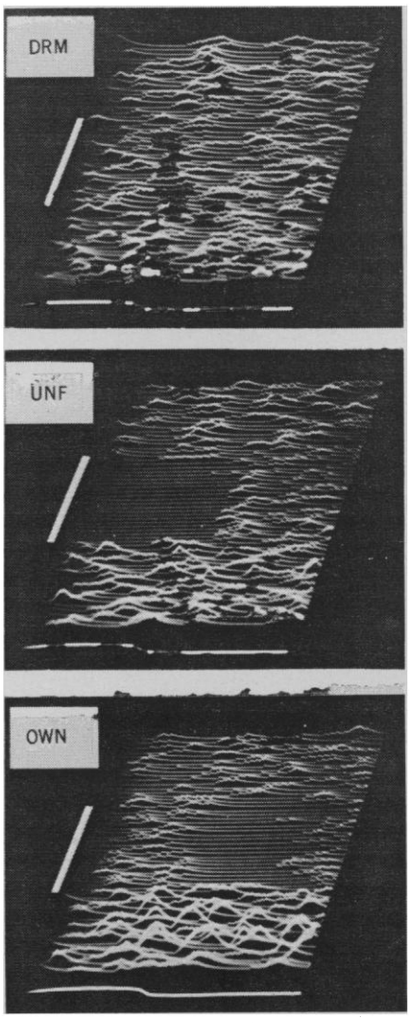

Fig. 2. Cycle-by-cycle displays of discharge frequency for a single unit in the olfactory bulb of a female hamster pup 3 weeks of age. Each horizontal tracing corresponds to a single inhalation cycle (1.5 seconds), and successive tracings are displaced upward and to the right. In each display, the 30 seconds (20 inhalation cycles) of stimulus presentation are indicated by an oblique bar at left. The inlay is 30 superimposed unit discharges (sweep length, 5 msec). For further details, see text.

The methods of photographic and electronic display (*7*) in Fig. 2 are intended to convey the impression of a three-dimensional surface made up of successive inhalation cycles. On each surface, successive tracings are displaced upward and to the right by a fixed amount so that the order of cycles is from front to back. The data for a single unit were fed through a Schmitt trigger to a capacitative circuit that converted the frequency of discharges into an analog voltage signal. An increase in voltage (discharge frequency) appears as an increase in height and in brightness within each trace. Thus, these variations in height and brightness reflect frequency of unit discharges at corresponding phases of the inhalation cycle. This method of display has the advantage of showing both the exact time-course of changes and cycle-to-cycle variability.

The solid oblique bar to the left of each tracing spans the inhalation cycles during which odors were presented. The stimuli were bedding from the pup's own litter (*OWN*); from an unfamiliar hamster litter of the same age (*UNF*); and from an adult male deermouse (*DRM*). From the tracings before and after presentation of the odors in each of the three displays, it is apparent that this particular unit had a moderate amount of background activity, but showed little patterning during the inhalation cycle. The deermouse scent had little effect on background activity. Both hamster scents profoundly inhibited unit activity, but did so during different phases of the inhalation cycle.

We find that the activity pattern of a given unit during the inhalation cycle is to a large extent independent of the length of the cycle. That is, if other conditions remain constant, the general shape of the ICH for a given unit remains unchanged over a wide range of

inhalation rates. The activity maxima and minima thus do not simply reflect some fixed latency from onset of nasal flow to onset of excitation or inhibition. Also, although the sharpness of the peaks and troughs in the ICH are related to the concentration of an effective odor, the timing of the peaks and troughs generally is not. In addition, the activity patterns during the inhalation cycle remain stable and reproducible for several hours. (In contrast, the overall firing frequency can spontaneously undergo as much as two- to threefold changes over these extended periods.) These three types of invariance would be expected if the observed activity patterns during the inhalation cycle were involved in specifying and monitoring the olfactory environment under both resting and active conditions.

Our results suggest that changes in the overall firing frequency of units in the olfactory bulb provide neither a necessary nor a sufficient indication of unit responsiveness to specific odor stimuli. The effect of stimuli upon unit activity within the inhalation cycle must also be considered. The use of periodic inhalation cycles in electrophysiological studies preserves a characteristic feature of normal olfactory stimulation. The regular and periodic patterning of nasal air flow may itself play a role in the processing of neural information about odor quality. Although the neural structures responsible for stimulus-specific modulation of activity of olfactory bulb units have not been identified, the many recurrent pathways of the bulb itself (*8*) and the centrifugal inputs from at least three separate (and more caudal) regions of the limbic forebrain (*9*) are likely candidates.

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3. Compressed breathing air from a standard air cylinder was passed through a calibrated reducing valve, dried with $CaSO_4$, filtered through charcoal, heated to 25°C by passage through coils in a water bath, and rehumidified. The total flow was then divided into two main streams. The first was used to provide the background (clean air) flow. It was passed through a calibrated flowmeter and valve to a mixing chamber and nose cone that was fitted loosely around the snout of the experimental animal. The other stream was divided by parallel valves and flowmeters into equal substreams. Some of the substreams were passed through a group of large jars containing stimulus objects or animals. One of these jars remained empty. The jars rested on a heated platform that maintained their interior temperature constant at about 25°C. The other substreams passed through t-connectors whose stems were fitted to syringes containing pure chemical vapors. The vapors were injected into the latter substreams by an infusion pump. All substreams then were passed to a distribution valve system. Odor-bearing substreams were normally ported to a remote waste receptacle containing activated charcoal. A stimulus delivery line led from the distribution valve system to the mixing chamber and nose cone, and under background conditions received the substream from the empty jar. Stimuli were presented by a manual switch that simultaneously removed the substream of the empty jar from the stimulus delivery line and replaced it with a preselected, odor-bearing substream. Thus, except for a brief switching transient, there was no net change in air flow to the mixing chamber and nose cone during stimulus presentation. To terminate a stimulus presentation, the manual switch was reversed, so that the substream of the empty jar was returned to the stimulus delivery line. The concentration of an odor arriving at the nose cone could be controlled by varying the ratio of air flow in the stimulus delivery line to that in the main clean air stream. The concentration of pure chemical odors could be controlled further by varying the rate of the infusion pump.
4. Glass capillary microelectrodes were drawn to a tip diameter of less than 1 μ and were filled with 2*M* NaCl saturated with fast green FCF. Iontophoretic injection of the dye after a recording session aided in locating the recording site [R. C. Thomas and V. J. Wilson, *Nature* **206**, 211 (1965)]. Amplified unit potentials were displayed on a cathode-ray oscilloscope and recorded on magnetic tape along with other relevant data. Histograms were constructed by analyzing the tape recording with the aid of a spike discriminator and small digital computer.
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Theta Rhythm: A Temporal Correlate of Memory Storage Processes in the Rat

Abstract. *We examined the amount of theta rhythm (4 to 9 hertz) in cortical electroencephalograms of rats for 30 minutes after training in one-trial tasks. Some animals received electroconvulsive shock after training. The amount of theta in the electroencephalogram after training was positively correlated with the degree of subsequent retention of a footshock, whether animals had received electroconvulsive shock or not.*

Numerous studies have attempted to find electroencephalogram (EEG) correlates of learning (*1*). In a summary of research published prior to 1961, Morrell noted that a hypersynchronous cortical EEG wave form in the range of theta rhythms (4 to 9 hz) was associated with the early stages of conditioning in carnivores and concluded that such waves might be correlated with the "inscribing of an experience into neural structure" (*2*).

Although they are most prominent in the hippocampus (*3*), theta waves are readily recorded from many regions of the brain, including cortex, when rodents and carnivores are alert or aroused, and during the early stages of conditioning (*4*). Thus, the hypersynchronous cortical correlate of conditioning appears to be a cortical theta rhythm.

Adey and his associates (*5*) have proposed a critical role for theta rhythms during memory consolidation. They suggest that long-term changes in the pattern of theta rhythms might reflect the consolidation of specific information over extended periods of conditioning. However, it may be that theta rhythms merely reflect the activation of brain processes which are related to, or possibly involved in, memory storage (*6*). In this view, a simple relationship might exist between the amount of theta during the period after