

# Timing of Odor Stimulation Does Not Alter Patterning of Olfactory Bulb Unit Activity in Freely Breathing Rats

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## SUMMARY AND CONCLUSIONS

1. The effect of the timing between nasal airflow and ongoing tracheal respiration on single-unit activity in the olfactory bulb (OB) of the rat was examined. Nasal and tracheal breathing were dissociated with the use of a double tracheal cannulation technique that allowed independent control of nasal airflow and control of the synchronization of nasal airflow and tracheal breathing.

2. When amyl acetate-saturated air was presented to the nose, OB units showed a distinct reorganization of activity known as respiratory patterning. Of 43 cells examined, 29 fired maximally after inspiration, and 14 fired maximally after expiration. In all 43 cells the patterning of OB activity was synchronized with the time course of the nasal stimulation. This synchronization was independent of the point in the ongoing respiratory cycle (tracheal breathing) at which the odor stimulation was applied.

3. Patterning of OB single-unit activity was also observed when odor was applied as a series of "inspirations" without intervening expirations. Patterning was observed to follow the time course of the odor stimulation even when this was considerably longer and slower than normal breathing. No patterning of activity was observed during continuous odor stimulation or in the absence of odor stimulation.

4. It is concluded that respiratory patterning of OB single-unit activity in the rat is not directly dependent on centrifugal inputs synchronized to respiration. Rather, the observed pattern of neural activity reflects the phasic stimulation of the olfactory receptors with each inspiration and the dynamics of the circuitry intrinsic to the bulb itself.

## INTRODUCTION

A general question in sensory processing concerns whether neural responses are strictly stimulus driven or determined in part by the internal state of the brain. This question is particularly relevant in the olfactory bulb (OB), where neural activity of freely breathing mammals is stimulus driven in a striking manner. In the presence of odor, neural activity increases and becomes strongly synchronized with respiration. In the absence of odor, spontaneous activity is not correlated with respiration. At first blush, this phenomenon might seem to be the obvious consequence of the periodic arrival of odorant at the olfactory receptors with each inspiration and the ensuing washout of odor molecules with expiration. However, the modulation of activity does not appear to be a simple superposition of stimulus-driven activity on spontaneous activity. Units firing with inspiration are strongly inhibited during expiration, and units firing with expiration are strongly inhibited during inspiration (Chaput and Holley 1980, 1985).

The origin of this *partitioning* of activity is not understood. There are two possible mechanisms (which are not

mutually exclusive): 1) the partitioning is driven primarily by the phasic nature of the input and reflects the dynamics of the circuitry intrinsic to the OB (i.e., inhibitory feedback loops); and 2) partitioning involves a phasic modulation of OB activity by centrifugal inputs to the bulb that are synchronized to respiration. Chaput and Holley (1980) noted that the suppression of activity between inspirations is not likely to be due to mitral cell self-inhibition via granule cells, because the observed interruption of activity is longer than the inhibition from mitral-granule-mitral interaction. They suggested an inhibitory process with a longer time constant, perhaps acting at the glomerular level, as a more likely mechanism.

Previous results do not clearly resolve whether centrifugal inputs to the bulb are essential to respiratory synchronization. Some studies have attempted to distinguish between intrinsic and extrinsic sources for respiratory patterning by sectioning centrifugal pathways to the OB (Chaput 1983; Onoda and Mori 1980; Pager 1980; Potter and Chorover 1976) and by examining OB activity in the absence of odors (Ravel et al. 1987; Ravel and Pager 1990). Ravel et al. (1987) found that respiratory patterning of OB activity persisted when nasal airflow was interrupted. This result is in contrast to those of Macrides and Chorover (1972) and Onoda and Mori (1980), who reported that respiratory patterning disappeared immediately when nasal airflow was interrupted. Macrides and Chorover (1972) also observed respiratory patterning of OB activity when "clean air" was used as a stimulus and attributed this effect to the mechanical stimulation of olfactory receptors that had been suggested by Walsh (1956). Chaput (1983) explored the effect of olfactory peduncle sectioning on single-unit responses in OB and found instances where respiratory patterning was diminished by this manipulation (Fig. 5 of Chaput 1983) and instances where patterning was enhanced (Fig. 6 of Chaput 1983). Pager (1980) reported respiratory patterning of OB activity that persisted in tracheotomized animals and disappeared after peduncle sectioning. Experiments involving sectioning raise the concern that all centrifugal inputs might not have been eliminated and that such procedures might have affected the general physiology of the OB in a global manner (i.e., by removal of tonic inputs or non-specific effects of surgery such as damage to blood supply).

In the experiments described here, we have examined the role of centrifugal inputs to the respiratory patterning of OB activity by uncoupling periodic stimulation of the nasal epithelium from respiration while disturbing the circuitry itself as little as possible. This was achieved by controlling the relative timing between odor stimulation and ongoing tracheal breathing. This method seeks to avoid some of the

confounding variables that may have affected the results of the previous studies described above. Specifically, we investigated whether the odor-driven patterning of OB neural activity was affected by the timing between odorant delivery to the nasal mucosa and ongoing free tracheal breathing. If the patterning of OB activity were dependent on centrifugal input synchronized to respiration, one would expect the patterning of activity to change when odorant arrives at the nasal mucosa at different phases of the ongoing respiratory cycle.

## METHODS

Recordings of single- and multiunit activity were made from 43 cells in the OB of 8 male Sprague-Dawley albino rats (250–400 g). Rats were anesthetized with urethane (1.5 g/kg) and treated with atropine (0.04 mg/kg). A tracheal tube fitted with a thermocouple (Iron/Constantan 0.003"; Omega) was inserted caudally into the trachea to measure free breathing, while a second flexible polyethylene tube was inserted rostrally through the larynx to the postnasal cavity to allow air to be pushed and pulled past the nasal epithelium. A small tube (1 cm in length) fitted with a thermocouple at one end was inserted into the external naris to provide a measure of airflow through the nose. The nasal thermocouple was located ~0.5 cm from the tip of the nose. The time constant of the thermocouples was ~250 ms. The animal was placed in a stereotaxic holder with an odor port placed in front of the nose. An exhaust located a short distance in front of the animal continuously drew odorized air away from the setup (Fig. 1). This double cannulation technique was adapted from Macrides and Chorover (1972) and Onoda and Mori (1980).

Odor stimulation consisted of filtered air saturated with amyl acetate (Aldrich) at a flow rate of 250–300 ml/min. Compressed room air was regulated (20 psi) and filtered through anhydrous calcium sulfate (drierite) to absorb water, activated charcoal to absorb organic contaminants, a molecular sieve to absorb inorganic contaminants, and finally a 0.1- $\mu$ m filter (Balston Microfibre Filter, grade BQ, rated at 99.99% efficiency) to remove particulate matter. The air was metered through calibrated flow meters and introduced through a glass tube (6 in long, 1 in wide) filled with glass wool to provide increased surface area for evaporation. The glass wool in one tube was saturated with amyl acetate, while another was saturated with distilled water. A three-way Teflon valve switched the odorized air to the odor port in front of the rat's nose. When the odor was not presented, it was continuously exhausted so as to minimize any changes in pressure within the saturator tube. While the animal breathed freely through its tracheal tube, air was cyclically drawn in and out of the nasal cavity through the tube inserted into the postnasal cavity by alternately applying 0.2-s pulses (250–300 ml/min flow rate) of vacuum (inspiration) and positive pressure (expiration) of filtered, warmed humidified air from the saturator tube containing distilled water. Consequently, the duration and timing of nasal inspiration/expiration were fixed. The output of the tracheal thermocouple was passed through a window discriminator to allow the nasal airflow cycle to be triggered by each tracheal inspiration. The relative timing between the tracheal inspiration/expiration cycle and nasal inspiration/expiration cycle was adjusted by introducing a delay between the output of the window discriminator and the onset of the nasal airflow cycle with the use of a Master-8 programmable pulse generator that controlled two Teflon valves (General Valve, series 1) supplying positive and negative pressure pulses.

An incision was made in the scalp, and the skull was exposed. A small hole was made over the right OB and the dura removed. Glass (borosilicate) saline-filled microelectrodes (tip diameter, 2–5  $\mu$ m) were lowered into the bulb. A silver-chloride wire in-

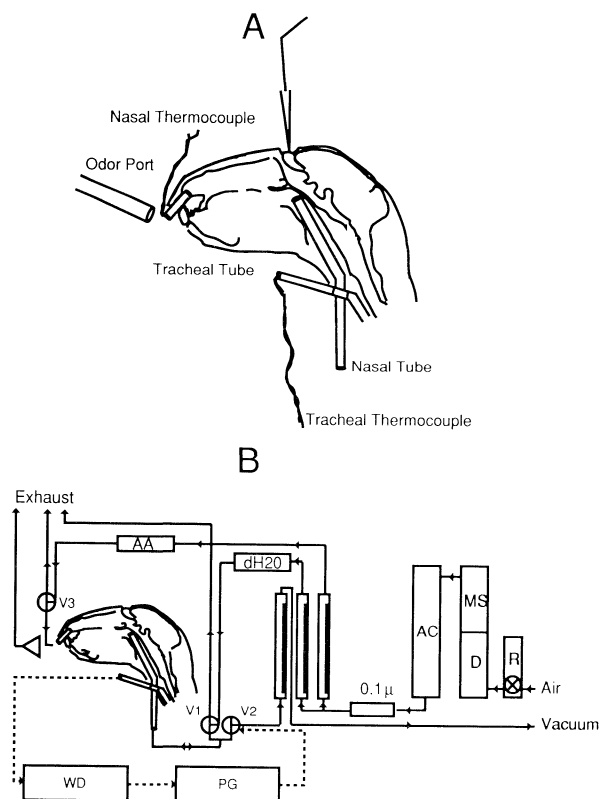


FIG. 1. *A*: cross section of a rat head showing the double tracheal cannulation preparation. One tube is inserted caudally into the trachea to allow free breathing. Another is inserted rostrally to the back of the nasal cavity so that air can be pushed and pulled past the nasal epithelium. A 3rd small tube is inserted into the external naris. An odor port supplies odor-saturated air to the nose. Tracheal and nasal tubes are fitted with thermocouples to monitor airflow. An electrode inserted into the olfactory bulb is also shown (adapted from Onoda and Mori 1980). *B*: schematic diagram of the olfactometer. Compressed air is regulated (R), desiccated (D), and passed through a molecular sieve (MS), activated carbon (AC), a 0.1- $\mu$ m borosilicate filter, and metered by calibrated flow meters (250–300 ml/min). The odor line sends air through a glass tube filled with glass wool and saturated with amyl acetate. Teflon valve V3 controls the application of odor. Artificial respiration through the nose is achieved by alternatively applying 0.2-s pulses of vacuum (inspiration) and positive pressure (expiration) with valves V2 and V1, respectively. Positive-pressure air was passed through a saturator tube containing distilled water and passed under the heating pad on which the animal rested. The cyclic nasal airflow was triggered and synchronized to tracheal breathing by sending the output of the tracheal thermocouple through a window discriminator (WD) that triggered a programmable pulse generator (PG) and controlled valves V1–3. Arrows show the direction of airflow. Solid lines represent tubing. Dashed lines represent signal wires.

serted under the skin at the caudal end of the wound was used as an indifferent electrode. Neural signals were amplified by an A/C differential amplifier (Bak Electronics) and filtered between 200 and 2,000 Hz. Spike trains were digitized and stored on a Macintosh IIx for subsequent analysis. When unit activity was driven by odor, a series of trials were performed in which the onset of nasal stimulation (inspiration/expiration) was delayed incrementally by 100 ms. For each delay setting, activity was recorded over 10–20 respiratory cycles.

Spike activity was analyzed by partitioning the records into individual respiratory cycles. Each respiratory cycle was divided into 25 equally spaced time bins. The nasal and tracheal thermocouple signals and concurrent neural activity were assigned to corresponding time bins. This method normalized respirations of slightly different duration so that unit activity could be averaged

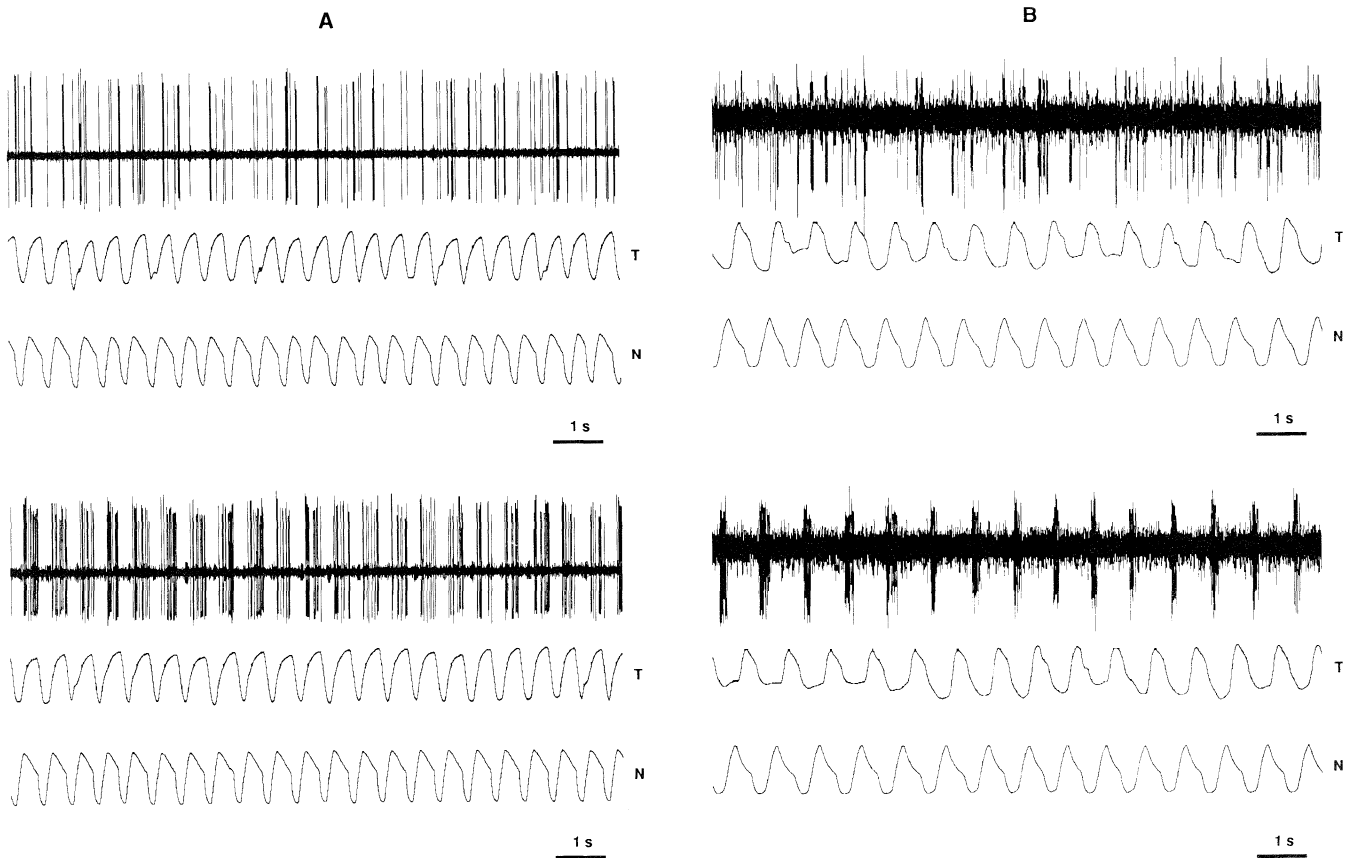


FIG. 2. *A, top panel:* little or no respiratory patterning is observed in response to room air. *Top trace:* olfactory bulb (OB) unit in an anesthetized rat with room air being pumped in and out of the nose. *Middle trace:* output of the thermocouple in the tracheal tube (T). *Bottom trace:* output of the thermocouple in the nostril (N). Upward deflections of thermocouples denote heated out-going air. Downward deflection denotes cooler in-going air. *A, bottom panel:* respiratory patterning appears when odor is presented. *Top trace:* OB unit with amyl acetate-saturated air presented to the front of the nose (see METHODS). *Middle and bottom traces:* same as above. Note the synchronization of activity with respiration: bursts of spikes followed by periods of strong inhibition. *B:* response of another cell in the absence (*top panel*) and presence of odor (*bottom panel*). This cell fires during a different phase of the respiratory cycle.

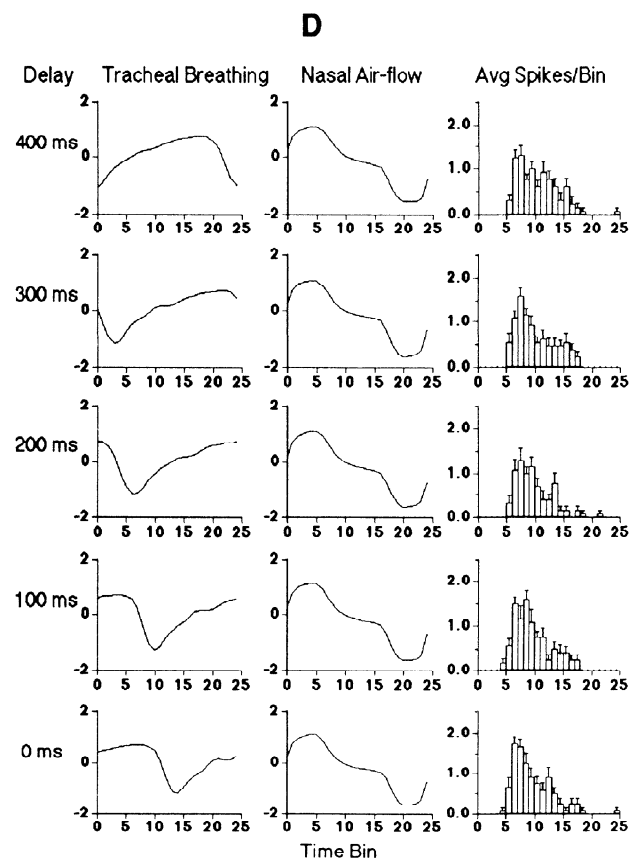
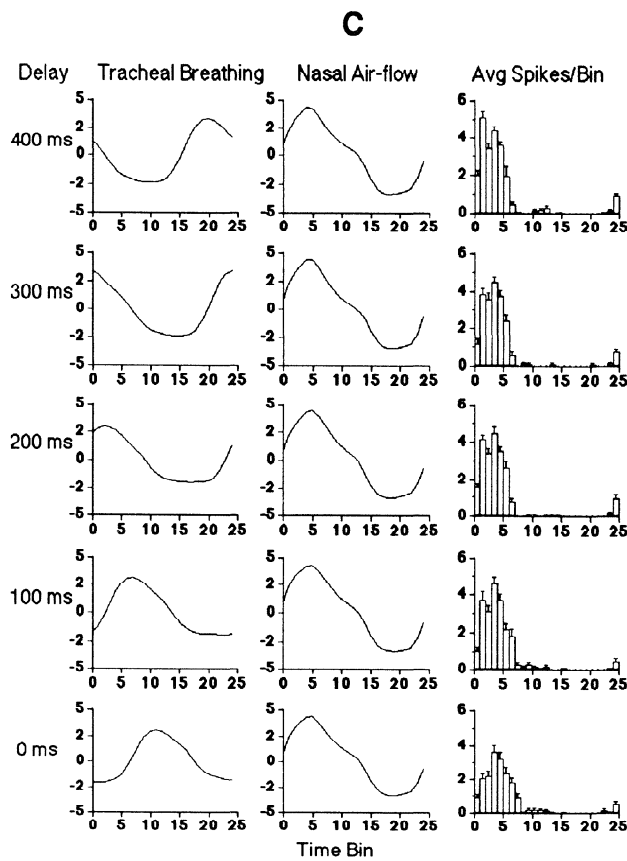
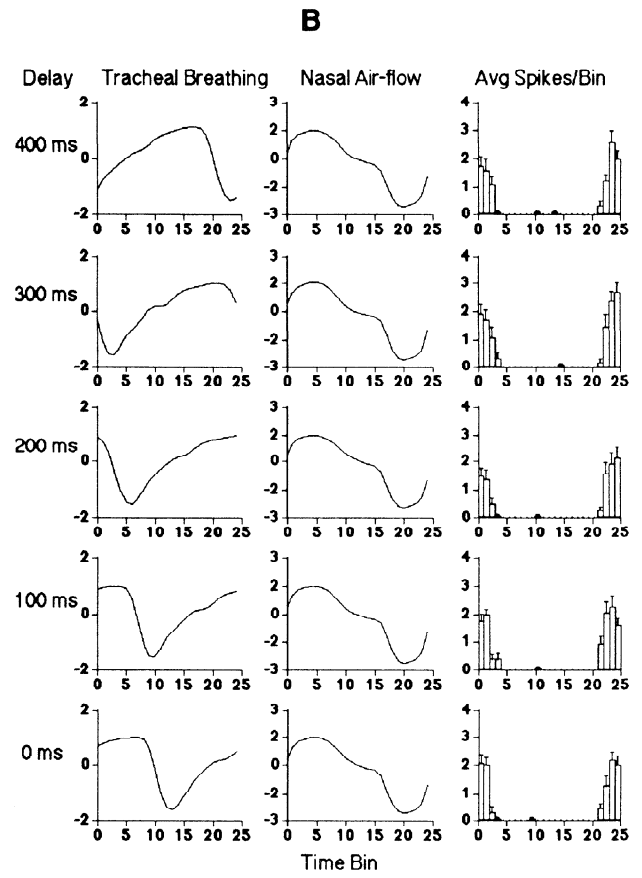
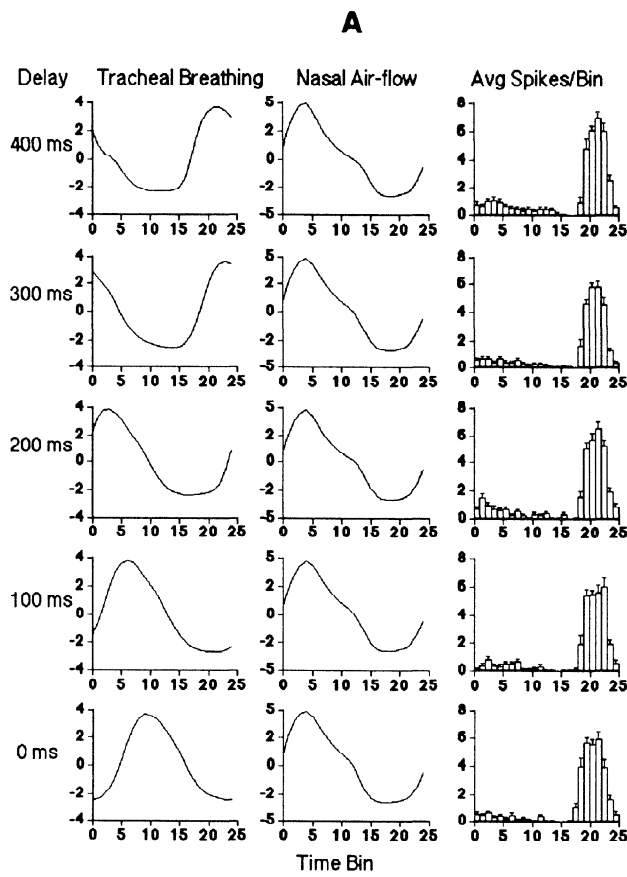
over sequential respirations and compared across stimulus presentations. This method of analysis was adapted from Chaput and Holley (1980) and Onoda and Mori (1980).

## RESULTS

As previously observed, strong patterning of OB single-unit spikes is produced by olfactory stimulation. This partitioning is shown in Fig. 2. The *top half* of Fig. 2*A* shows a single-unit recording from the OB of an animal with filtered air cyclically flowing in and out of the nasal cavity in synchrony with ongoing tracheal breathing. The *middle trace* shows the output of a thermocouple placed in the tracheal breathing tube, whereas the *bottom trace* shows the output of a thermocouple placed in a tube inserted into the external naris. Upward deflections of the thermocouple traces show the passage of heated air over the wire (exhalation), whereas downward deflections show the inward flow of cooler air (inspiration). The neural activity does not appear to be driven by the ongoing respiratory rhythm. The *bottom half* of Fig. 2*A* shows the response of the same unit when amyl acetate-saturated air was delivered to the nose. The relative timing between ongoing tracheal breathing and cyclic airflow applied to the nose was the same in the

*top and bottom* of Fig. 2. In the presence of odor, the unit activity was clearly synchronized with the nasal airflow. The activity of this particular cell seems to be suppressed during inspiration. Of the 43 cells included in this study, 29 cells showed excitation after inspiration and suppression after expiration. Fourteen cells showed suppression after inspiration and excitation after expiration. However, firing was sometimes synchronized to intermediate phases of the nasal stimulation as shown in Fig. 3 (discussed below).

If centrifugal inputs to the OB generated the observed patterning of activity, then the timing or amount of activity should be affected by the temporal relationship between odor stimulation and ongoing breathing. To analyze the effect of the relative timing between nasal airflow and tracheal breathing, records such as those shown in Fig. 2*B* were divided into individual respiratory cycles. Each cycle was divided into 25 equally spaced time bins. The number of spikes occurring in each time bin was averaged over the number of respiratory cycles. The data for four cells are shown in Fig. 3. Within each group of graphs, each row was produced by applying this analysis to a single record such as the one shown in Fig. 2*B*. The records for each row were obtained by setting a time delay between ongoing respiration and the imposed nasal airflow (0, 100, 200, 300, and



400 ms, respectively). The three columns in each group of graphs show the average free tracheal breathing, average nasal airflow, and average number of spikes per corresponding time bin. The abscissas for all graphs are the 25 time bins into which each respiratory cycle is divided. The time bins cannot be assigned time units because they are used to normalize respiratory cycles of slightly different durations. The ordinates for the tracheal and nasal breathing plots are in arbitrary units and are scaled to appear similar. The graphs are aligned on the rising phase of the nasal airflow. As a result, the free tracheal breathing waveform shifts as the delay is varied. Note that the spike histograms do not shift as the delay between tracheal and nasal airflow is varied. The patterning of spikes is synchronized with the nasal airflow and is not affected by the timing of nasal stimulation with respect to tracheal breathing. Similar results were observed in all 43 cells from which we recorded. The data from the four cells shown in Fig. 3 also illustrate that peak firing may occur at different phases of the nasal stimulation.

Because of variability in the recordings, small nonsystematic changes were observed from one trial to another (between delay conditions). To assess the amount of random variation between trials, a few cells (9) were recorded without changing the relative timing between odor stimulation and ongoing breathing over 10–20 trials. In general, the small changes observed when timing was not changed were of the same magnitude as those observed when the relative timing between stimulation and breathing was manipulated (Fig. 4).

In the course of these experiments, several additional observations were made concerning the patterning phenomenon. While air was pulled continuously through the nose, a long odor pulse (10 s) was presented. In response to this type of stimulation, OB units often showed an initial burst of firing followed by a period of habituation or inhibition over which activity decreased but did not show patterning correlated with ongoing tracheal respiration (Fig. 5). Many units showed a burst of activity immediately after the termination of such an odor pulse (Fig. 5), which lasted several seconds (10–15 s).

With the double tracheal cannulation technique, pulses of air could be drawn into the nose without an intervening positive pressure pulse (inspiration without expiration). Drawing pulses of odorized air through the nasal cavity in this way elicited a pattern of activity similar to that observed when an expiration phase was present (Fig. 6), suggesting that the silent phase of patterned OB activity is not merely the consequence of odorant being washed out of the nasal epithelium.

Lastly, by applying long odor pulses, it is possible to re-

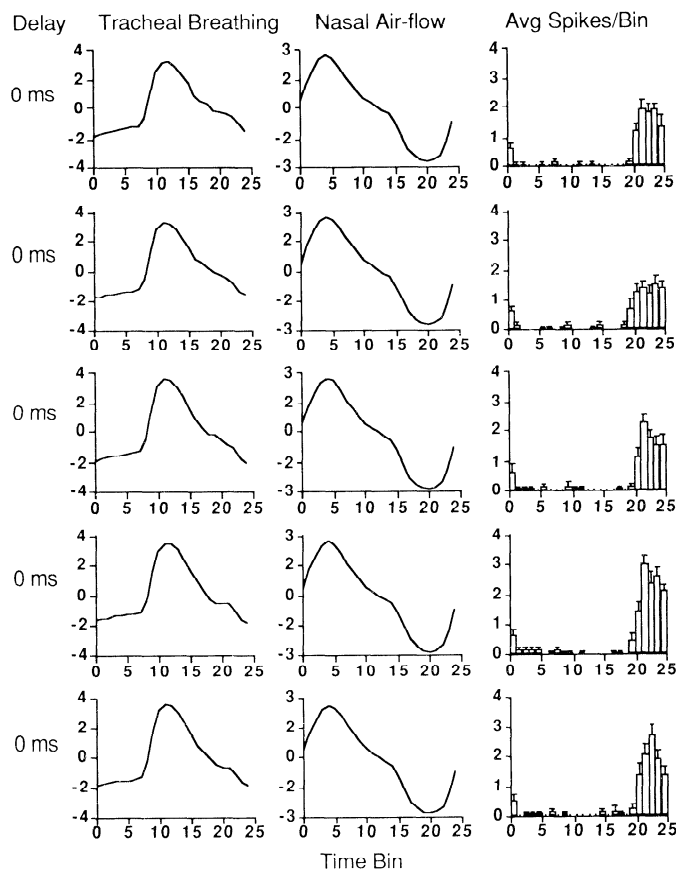


FIG. 4. Control condition illustrates the degree of variation observed between trials. Recordings were made under the same conditions as in Fig. 3 but without changing the delay between tracheal breathing and the onset of nasal stimulation. Data are plotted in the same format as Fig. 3; however, here each row is simply a repetition of the previous trial.

produce a pattern of activity that closely resembles respiratory patterning, but on a longer time scale. Figure 7 shows the response of an OB unit as air is continuously drawn through the nose. The *bottom trace* shows the odor valve alternately being turned on and off for 2 s. The cell begins firing with the first odor pulse and continues while the odor valve is closed. With the second exposure to odorant, the cell's activity is strongly inhibited. When the odor valve is closed, the activity appears to "rebound" with a vigorous burst of firing only to be suppressed by the next odor pulse. Note that, although the cell initially fired in response to odor, the dominant response is reversed. Over successive presentations the unit fires when the odor valve is closed and is suppressed when the valve is open. Consequently, it may be important to observe the responses of cells to the types of repeated stimulation generated by free breathing or sniffing in addition to responses to single pulses of odor to

FIG. 3. Relative timing of stimulation does not effect olfactory bulb (OB) unit activity. Four examples of odor-induced respiratory synchronization of OB unit activity. Data for each of the 4 cells show tracheal airflow (*left column*), nasal airflow (*middle column*), and number of spikes per time bin (*right column*). All quantities were averaged across 10–20 respiratory cycles. From *bottom to top*, the delay between ongoing tracheal breathing and triggered nasal airflow was changed from 0 to 400 ms. To facilitate comparison of spike data across delay conditions, the onset of nasal airflow was used as the time origin. This is why tracheal breathing appears to shift in time rather than the nasal airflow. Spike activity is time locked to nasal stimulation and does not appear to be affected by the relative timing of tracheal breathing. The 4 cells show the predominant types of responses. Note the spike histogram peak occurring at different phases of the respiratory cycle for each cell.

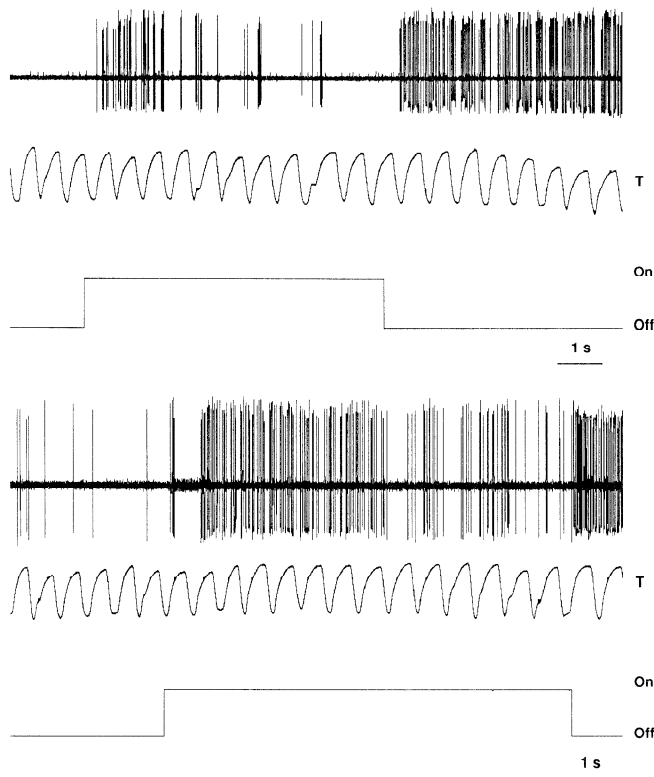


FIG. 5. Long odor pulses produce excitation followed by inhibition. These 2 records show the response of olfactory bulb units to a long ( $\sim 10$  s) odor pulse (*bottom trace*) produced by applying a continuous vacuum (inspiration) to the nasal cavity while the odor valve was switched on for several seconds. *Top panel*: unit responds with an initial burst of activity that rapidly diminishes as the stimulation continues and then exhibits a strong rebound when the stimulation is terminated. *Bottom panel*: cell has a more complex response showing a burst, followed by a pause, followed by a strong response that wanes over time, and finally a vigorous rebound after the stimulus is terminated. Tracheal breathing is shown by the *middle trace*.

better understand the coding of odor information by OB units.

## DISCUSSION

The observation that OB temporal firing patterns are highly correlated with respiration cycles (Adrian 1950; Chaput and Holley 1980, 1985) might at first seem to be the obvious consequence of the periodic arrival of odorant at the nasal epithelium with each inspiration. However, the increase in firing with inspiration and complete suppression of firing (below spontaneous rates) during the periods between inspirations suggest a more complex phenomenon. This phenomenon has already been studied in a variety of preparations yielding diverse and sometimes conflicting results.

Although previous studies have employed methods that dissociate tracheal respiration from nasal airflow, few have directly examined the effect of the relative timing between breathing and odor stimulation. For example, Doving (1987) used a preparation in which nasal airflow and respiration were independent and found that the maximum response to odor stimulation was achieved at a nasal airflow rate that most closely matched the rate estimated from sniffing behavior of the unrestrained rat. However, only the

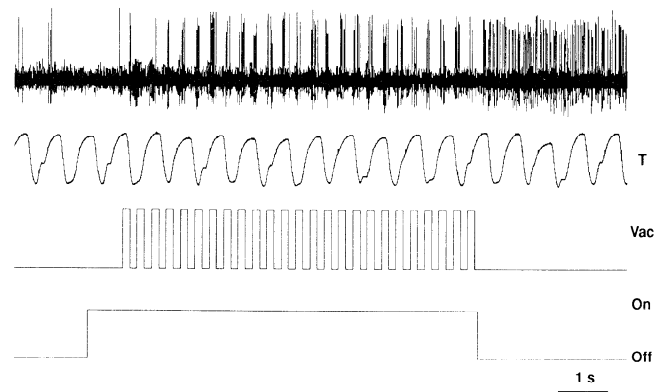


FIG. 6. Expiration is not necessary to produce patterning of activity. Patterning can be observed in the absence of the expiration phase of simulated respiration suggesting that "washout" of odor is not essential to the phenomenon. Here only vacuum (inspiration) pulses (0.2 s) were applied after the odor valve (*bottom trace*) was switched on. Also note the rebound of unpatterned activity at the end of the odor and vacuum pulses. Tracheal breathing is shown by the *2nd trace* from the top.

effect of nasal *flow rate* was tested, not the *timing* of nasal airflow with respect to ongoing respiration. Macrides and Chorover (1972) used double tracheal cannulation to allow independent control of nasal airflow. They observed no differences in the patterning of OB unit activity between two different preparations; one group of paralyzed rats with nasal airflow adjusted to correspond in frequency and phase to ventilator-driven respiration and a second group of non-paralyzed rats in which nasal airflow and voluntary tracheal respiration were not synchronized. Their findings were consistent with the results reported here.

One approach used in studies of patterning has involved blocking or bypassing nasal airflow. Macrides and Chorover (1972) reported that patterning disappeared when the nasal airflow was interrupted in both of their experimental preparations described above. Similarly, Onoda and Mori (1980), with the use of a free breathing double tracheal cannulation preparation, found that the patterning of unit activity in the OB disappeared when nasal airflow was bypassed. However, Ravel et al. (1987) found that 30 of 80

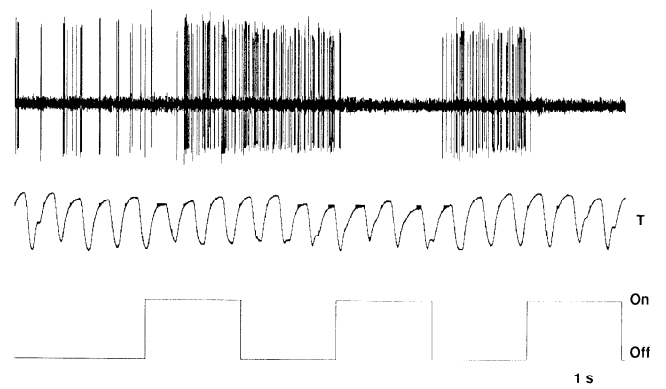


FIG. 7. Development of patterning in 1 unit with the use of a series of odor pulses with 2-s duration. Continuous vacuum pulled air through the nose. *Bottom trace*: odor valve being switched on and off. First pulse of odor through the nose elicits a long burst of activity that continued after the valve was closed. Subsequent pulses of odor suppress firing. Consequently, firing only occurs during the interval between "inspirations" when the odor valve is closed. Tracheal breathing is shown in the *middle trace*.

OB units they encountered displayed respiratory patterning under tracheal breathing conditions when nasal airflow was blocked. They interpreted these results to suggest involvement of centrifugal inputs in the patterning of OB unit activity and postulated that such input could arise from the monosynaptic projection from the preoptic magnocellular nucleus (PMN). Ravel and Pager (1990) found a similar distribution of respiration correlated and noncorrelated OB unit activity but also noted that mean firing rates of OB units were increased when air was allowed to flow through the nose. One limitation of all these comparisons is that, during nasal breathing, the olfactory receptors are stimulated, increasing the input to OB, whereas, in the absence of nasal airflow, the input to the bulb is less. One might expect the dynamics of the bulb to be different under these two conditions. The experimental protocol used here maintained the same *magnitude* of olfactory stimulus and only varied the timing of the stimulus with respect to free tracheal breathing.

A more direct test of the role of OB inputs in respiratory patterning has been to cut centrifugal projections. Potter and Chorover (1976) recorded from mitral cells in intact and isolated OB in hamsters [severing projections from either the anterior olfactory nucleus (AON) alone or AON and lateral olfactory tract (LOT)] and found units in the isolated OB to be hyperactive and hyperresponsive. Mitral cells of isolated bulbs were found to be less synchronized with ongoing respiration than those in intact OB and exhibited faster habituation, and slower recovery from habituation. They concluded that the circuitry underlying respiratory synchronization is intrinsic to the bulb but subject to centrifugal modulation, which sharpens its temporal response properties. Onoda and Mori (1980) characterized several different classes of OB respiratory patterned responses. To examine the possible influence of centrifugal input on these responses, they unilaterally sectioned the LOT and found that respiration-synchronized firing patterns persisted. However, a number of centrifugal inputs are not eliminated by ipsilateral LOT cuts including projections from the AON and contralateral projections. Chaput (1983) explored the role of centrifugal inputs in the patterning of OB unit activity by sectioning the olfactory peduncle in rabbits. This resulted in several changes in OB activity. In peduncle sectioned rabbits he found some units that showed little or no respiratory patterning and other units that showed patterning marked by increased firing during inspiration. In general, he reported that OB single-unit responses to odor stimulation were increased throughout the respiratory cycle. On the basis of these observations, he suggested that centrifugal fibers modulate the *degree* of respiratory patterning, which is itself established by neural circuits intrinsic to the OB. However, a loss of respiratory patterning due to peduncle sectioning may not necessarily imply the loss of phasic (respiratory synchronized) centrifugal modulation. These results might also be ascribed to a loss of a tonic centrifugal input essential to the dynamics of

the bulbar circuitry. The experiments described here differ from these previous studies in that all centrifugal inputs to the bulb were left intact.

In summary, our results demonstrate that respiratory patterning is unaffected by the timing of stimulation relative to ongoing breathing. This suggests that patterning is primarily a consequence of periodic excitation of olfactory receptors acting on the circuitry intrinsic to the OB. Some form of centrifugal modulation may still account for the results reported for the isolated OB preparations discussed above. These findings are consistent with the conclusions of Potter and Chorover (1976), Onoda and Mori (1980), and Chaput (1983). The mechanism responsible for patterning remains unclear. Possible mechanisms for responses such as those seen in Fig. 7 might be depolarization-induced inactivation (cells becoming too depolarized to spike) or a recurrent inhibition of longer duration than the mitral-granule-mitral feedback loop in which inhibitory units have a higher threshold than the excitatory units. A mechanism for units that are driven during inspiration and inhibited during expiration might be some form of long-lasting inhibition. The double tracheal cannulation preparation may be used to address some of these questions by systematically varying the frequency, intensity, and duration of odor pulses in a freely breathing animal.

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