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Negative Relationship between Odor-Induced Spike Activity and Spontaneous Oscillations in the Primary Olfactory System of the Terrestrial Slug *Limax marginatus*

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ABSTRACT—Although primary olfactory systems in various animals display spontaneous oscillatory activity, its functional significance in olfactory processing has not been elucidated. The tentacular ganglion, the primary olfactory system of the terrestrial slug *Limax marginatus*, also displays spontaneous oscillatory activity at 1–2 Hz. In the present study, we examined the relationship between odor-evoked spike activity and spontaneous field potential oscillations in the tentacular nerve, representing the pathway from the primary olfactory system to the olfactory center. Neural activity was recorded from the tentacular nerve before, during and after application of various odors (garlic, carrot, and rat chow) to the sensory epithelium and the changes in firing rate and spontaneous oscillations were analyzed. We detected the baseline amplitude of the oscillations and baseline spike activity before stimulation. Odor stimulations for 20 s or 60 s evoked a transient increase in the firing rate followed by a decrease in the amplitude of spontaneous oscillations. The decrease in the amplitude was larger in the first 8 s of stimulation and subsequently showed recovery during stimulation. The amplitude of the recovered oscillations often fluctuated. Odor-evoked spikes appeared when the amplitude of the recovered oscillations was transiently small. These results suggest that the large oscillations could inhibit spike activity whereas the first transient increase in spike activity was followed by the decrease in the oscillation amplitude. Our results indicate that there is a significant negative correlation between spontaneous oscillations and odor-evoked spike activity, suggesting that the spontaneous oscillations contribute to the olfactory processing in slugs.

Key words: intrinsic activity, mollusk, olfactory processing, tentacular ganglion

INTRODUCTION

Odor-induced oscillatory activity in the olfactory bulb was first described in hedgehog by Adrian (1942). Since then, the functional significance of the induced oscillations for olfaction has been studied in vertebrates (Adrian, 1942, 1950; Ottoson, 1959; Boeijinga and Lopes da Silva, 1989; Freeman, 1994; Chapman *et al*., 1998; Dorries and Kauer, 2000; Nikonov *et al*., 2002; Brody and Hopfield, 2003) and invertebrates (Laurent, 1997; Christensen *et al*., 1998; Vickers *et al*., 2001). On the other hand, the olfactory system also displays spontaneous oscillatory activity. Spontaneous oscillatory activity in the olfactory bulb was first reported in the frog by Gerard and Young (1937). Adrian (1950) described the following features of spontaneous oscillations in the mammalian olfactory bulb. *(1)* The spontaneous (intrinsic) oscillations vary according to the level of anesthesia and are completely inhibited by deep anesthesia. *(2)* In light anesthesia, the amplitude of spontaneous activity gradually increases when the olfactory epithelium is unstimulated. *(3)* Large spontaneous activity is simultaneously

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recorded in the presence of irregular spike activity in mitral cells. *(4)* Strong olfactory stimuli can abolish spontaneous oscillations and it may take from 1 to more than 60 sec for the spontaneous oscillations to reappear. *(5)* The presence of irregular firing of the mitral pathway hinders the transmission of weak olfactory signals. Therefore, in the olfactory bulb of an unanesthetized animal, the olfactory signals can compete with the intrinsic activity, suggesting that the intrinsic oscillatory activity contributes to the olfactory processing. However, there are no studies that have confirmed the importance of spontaneous oscillations on olfactory processing.

The tentacles are the sense organs of slugs. Each tentacle houses one tentacular ganglion, the primary olfactory system, at the tip. The tentacular ganglion and its digit-like extensions contain primary and secondary olfactory neurons (Chase, 1986). The tentacular nerve is the neural pathway from the tentacular ganglion to the procerebral (PC) lobe, the olfactory center, and contains fibers of the primary and secondary olfactory neurons (Chase, 1986; Ito *et al.*, 1999, 2000). Spontaneous oscillations of about 1.5 Hz can be recorded from the surface of the tentacular ganglion in *Limax marginatus* (Inokuma *et al.*, 2002) and from the cut-end of the tentacular nerve (Ito *et al.*, 2001). Odor stimulation decreases the amplitude of spontaneous oscillations in the tentacular nerve (Ito *et al.*, 2001). This phenomenon is reminiscent of the behavior of spontaneous activity described by Adrian (1950).

The aim of the present study was to define the relationship between the spike activity of olfactory projection neurons and spontaneous oscillations in slugs. We simultaneously recorded odor-induced spike activity and spontaneous oscillations from the tentacular nerve in the terrestrial slug *L. marginatus*. We found a negative relationship between odor-evoked spike activity and spontaneous activity. For example, high-amplitude spontaneous oscillations were accompanied by a decrease in odor-evoked spike activity whereas odor-evoked spike activity was associated with a decrease in the amplitude of spontaneous oscillations. Our findings suggest that the intrinsic oscillatory activity contrib-

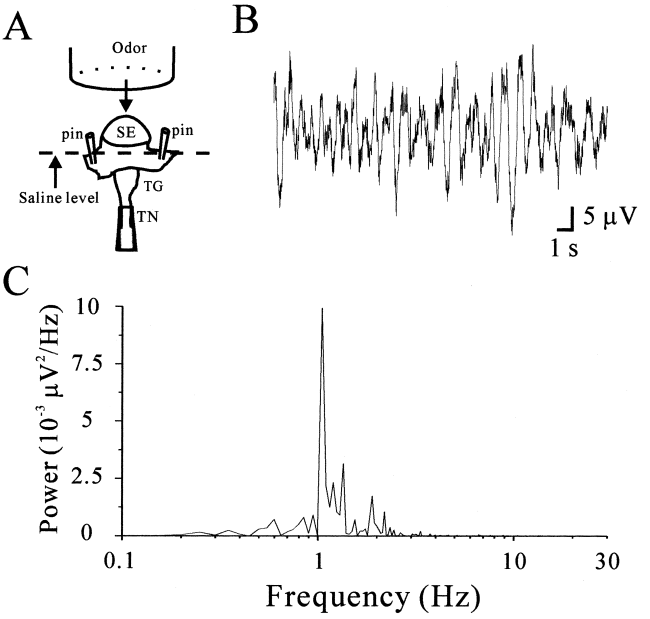


Fig. 1. Spontaneous activity in the tentacular nerve. A. Schematic drawing of the experimental set-up. The preparation was pinned to sylgard bottom. Saline level was adjusted just below the sensory epithelium. Odor was applied through the tube placed above. B. Local field potentials of spontaneous activity recorded from the tentacular nerve. The signal was digitally filtered with a band pass filter (0.1–30 Hz). C. Corresponding power spectrum of the spontaneous oscillation shown in B. Note the main oscillatory component at 1 Hz. SE, sensory epithelium; TG, tentacular ganglion; TN, tentacular nerve.

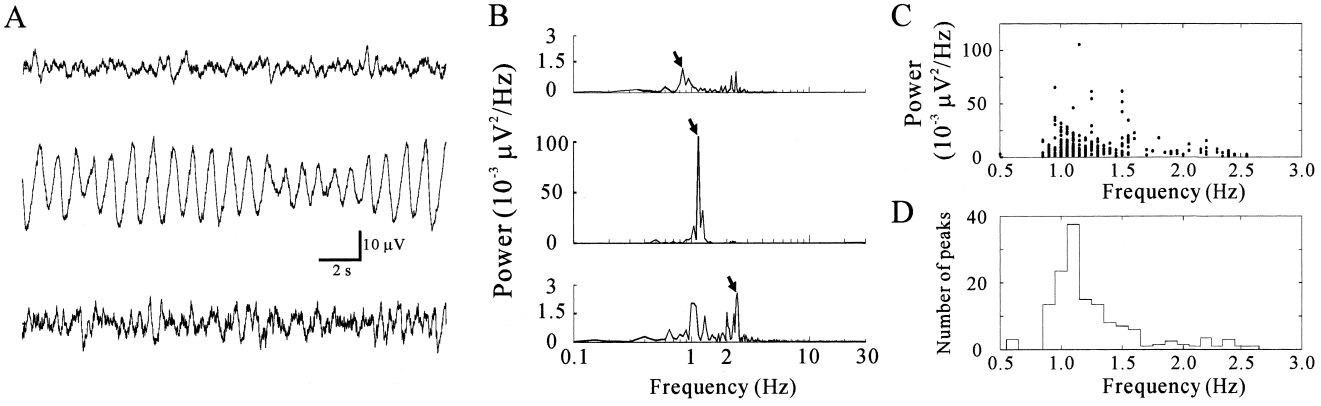


Fig. 2. Relationship between the amplitude and frequency of spontaneous oscillations. A. Examples of spontaneous oscillations recorded from three preparations. B. Corresponding power spectra of the spontaneous oscillations shown in A. Arrows indicate the highest peaks in each power spectrum. Note that the highest amplitude of the oscillations was observed when the frequency was around 1 Hz. The amplitude and frequency of spontaneous oscillations differed from one preparation to another, and they often changed over time even in the same preparation. C. Relationship between amplitude and frequency of the maximum peaks in the power spectra. Recordings from 16 inferior tentacles were divided into 20 s epochs, and then the power spectrum for each epoch was calculated. The amplitude of the maximum peak in each power spectrum was plotted against frequency. Note that high peaks were distributed around the 0.9–1.6 Hz frequency range. D. Histogram of the number of maximum peaks in the frequency domain. Note that most peaks are distributed around the 0.9–1.6 Hz frequency range.

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utes to olfactory processing in slugs in a manner different from that reported in mammalian olfactory bulbs (Adrian, 1950).

MATERIALS AND METHODS

Animals

The terrestrial slugs *L. marginatus,* maintained in our laboratory on a 12:12 light:dark cycle at 19°C and fed on a paste of rat chow, were obtained either from our laboratory colony or collected in the open field.

Electrophysiological recording

Dissections were performed as described previously (Hatakeyama *et al*., 2001; Fujie *et al*., 2002). Briefly, the inferior tentacles were dissected out in a dish filled with a dissection solution that contained (in mM) 35 NaCl, 2 .KCl, 4.9 $CaCl_2$, 28 $MgCl_2$, 5 glucose, and 5 HEPES (pH 7.6). The chamber was filled with *Limax* saline (see Kimura *et al*., 1998 for composition). The local field potential (LFP) of the tentacular nerve was recorded from the cut-end using a glass suction electrode filled with *Limax* saline. Neural activity was led to a high-impedance probe (JB-101J, Nihon Kohden, Tokyo, Japan) and an AC amplifier with a 0.5 Hz to 1 kHz bandpass filter (Bioelectric Amplifier MEG-1200, Nihon Koden). Signals were digitized at 2000 Hz and stored in a computer.

Odor application

Before odor stimulation, the level of saline solution in the chamber was lowered so that the sensory epithelium could be exposed to deodorized and humidified air, which was applied at a flow rate of 10 ml/min for 3 min (Fig. 1A). Odor was applied for 20 or 60 s by switching the air flow pathway from a glass tube containing a filter paper soaked with 1 ml of distilled water to a glass tube containing a filter paper soaked with 1 ml of an odor solution as described

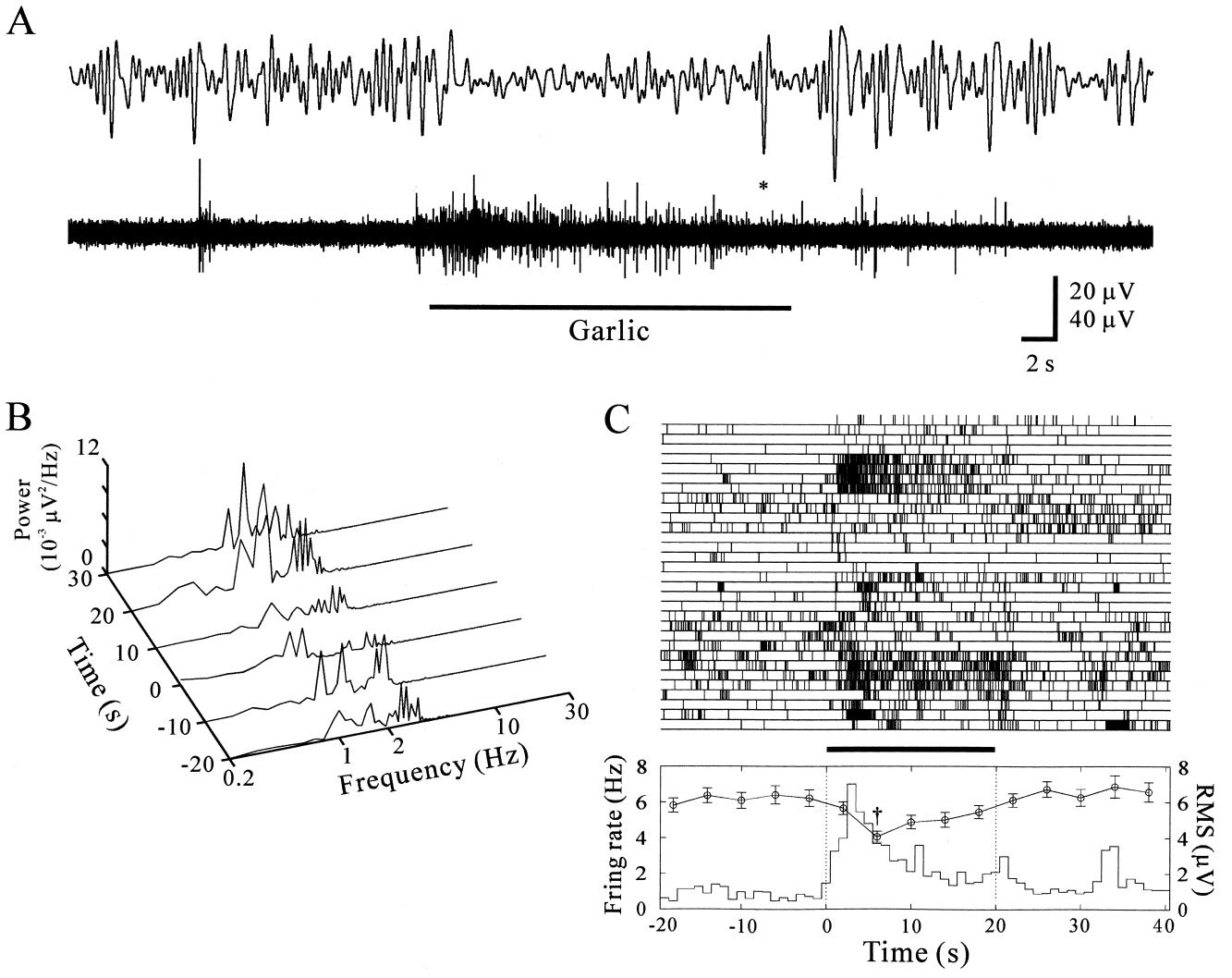


Fig. 3. Neural response to garlic odor recorded from the tentacular nerve. A. LFP signal (0.1–30 Hz, top) and spike activity (150–1000 Hz, bottom) in response to garlic odor stimulation (20 s). An asterisk points to recovery of the amplitude accompanied by suppression of spikes. B. Power spectral array of the garlic odor response shown in A. Peaks around 1–3 Hz decreased during odor stimulation (0–20 s). C. Raster plots and peri-stimulus time histogram of garlic odor responses in tentacular nerve. The mean firing rate (white bars) was determined from the spike number in each bin (1 s), and then averaged over the trials. The mean RMS values (open circles) in the 0.6–2.4 Hz (4 s epochs) were plotted together. Significance was determined between each epoch and the first epoch. Data are expressed as mean ± SEM for the mean RMS values. $^{\dagger}P<0.01$.

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previously (Ito *et al.*, 2001). Garlic paste, undiluted carrot juice, and 33% rat chow solution were used for odor solutions. For short-term odor application (20 s), we recorded 32 trials from 8 inferior tentacles for the garlic odor, 36 trials from 9 inferior tentacles for the carrot odor, and 32 trials from 8 inferior tentacles for the rat chow odor. One to five trials per odor were tested in one preparation. For prolonged odor application (60 s), we recorded 16 trials from 5 inferior tentacles for the garlic odor, 18 trials from 4 inferior tentacles for the carrot odor, and 17 trials from 5 inferior tentacles for the rat chow odor

Data analysis

Signal analysis was performed off-line with a custom-made program developed with MATLAB (ver. 6.5.0.180913a; The MathWorks, Natick, MA, USA). Spectral analysis was performed on 0.1–30 Hz band filtered signals of LFP oscillations and 150–1000 Hz band filtered signals of spike activity. The power spectra of the LFP oscillation were computed using the fast Fourier transform on a standard rectangular window. We used the root-mean-square (RMS) value to estimate the time dependent changes in the amplitude of the oscillations as described previously (Ito *et al.*, 2001). The recording was divided into 4-sec epochs. The raw data were first digitally filtered with the frequency band (0.6–2.4 Hz), and then the RMS value of voltage of the filtered signal was calculated for each epoch. The mean (± SEM) value of RMS voltage for each epoch was compared to that of the first epoch by Mann-Whitney U test. *P* values less than 0.05 were considered to represent significant differences.

To examine the relationship between the amplitudes and the frequencies of the main peaks in the power spectra, the recordings of spontaneous activity were divided into 20-sec epochs, and the amplitude and frequency of the highest peak in each epoch were calculated.

RESULTS

Spontaneous oscillations

Fig. 1 shows an example of the spontaneous oscillations recorded from the tentacular nerve. Robust periodic

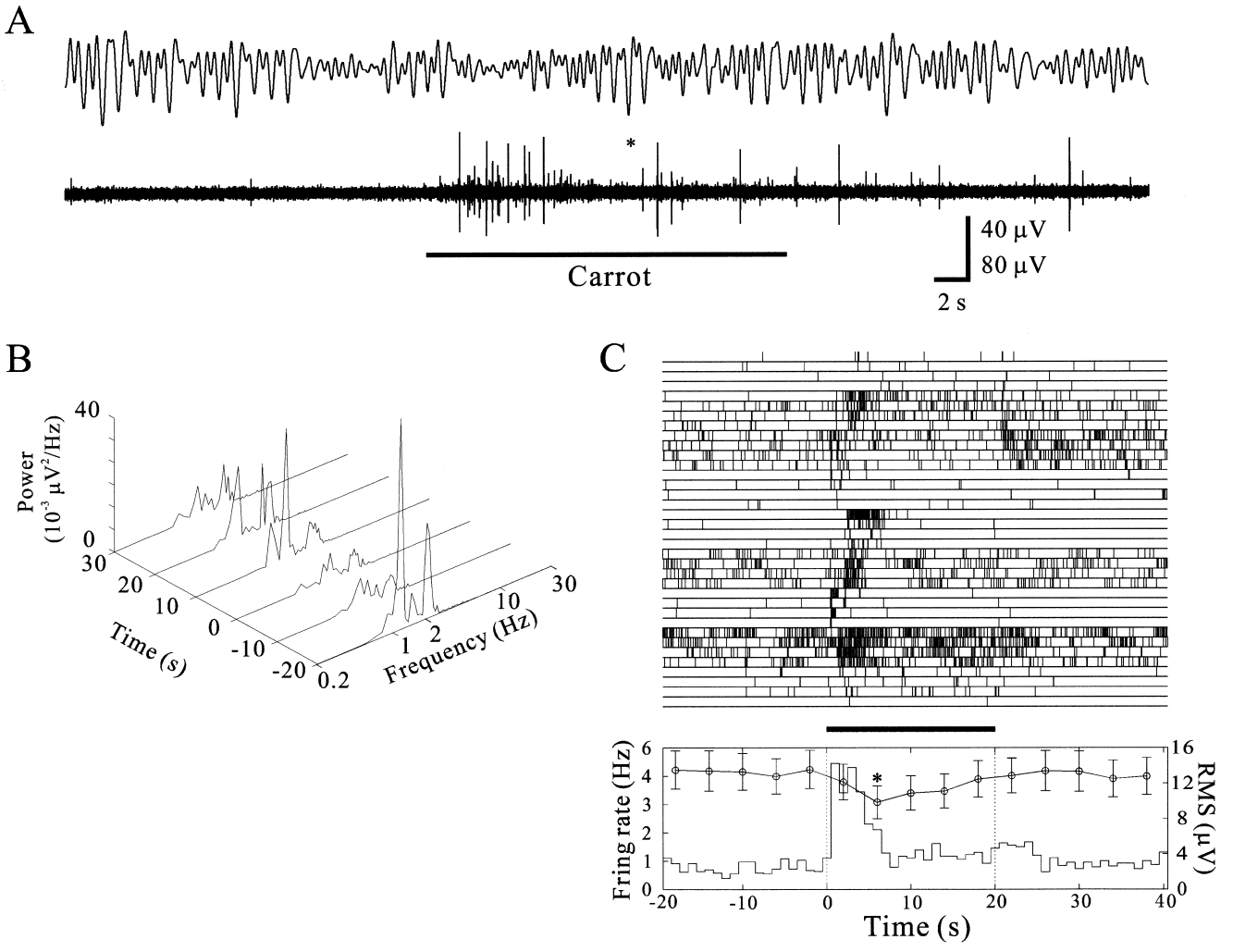


Fig. 4. Neural response to carrot odor recorded from the tentacular nerve. A. LFP signal (0.1–30 Hz, top) and spike activity (150–1000 Hz, bottom) in response to the carrot odor stimulation (20 s). An asterisk points to recovery of the amplitude accompanied with suppression of spikes. B. Power spectral array of carrot odor response shown in A. Peaks around 1–3 Hz decreased during the first half of odor stimulation (0–10 s). C. Raster plots and peri-stimulus time histogram of carrot odor responses in tentacular nerve. The mean firing rate (white bars) was determined from the spike number in each bin (1 s), and then averaged over the trials. The mean RMS values (open circles) in the 0.6–2.4 Hz (4 s epochs) were plotted together. Significance was determined between each epoch and the first epoch. Data are expressed as mean ± SEM for the mean RMS values. $^{*}P<0.05$.

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spontaneous oscillations at 1–2 Hz were continuously recorded from each preparation (Fig. 1B). The corresponding power spectrum of the wave showed that the frequency of the oscillations was about 1 Hz, and that the power was distributed around 1 Hz (Fig. 1C). Other preparations also showed robust oscillations, although the amplitude and frequency of the oscillations differed from one preparation to another (Fig. 2A). The power spectra showed that the large peaks were distributed in the 1–2 Hz (Fig. 2B). To examine the relationship between the amplitude and frequency of spontaneous oscillations in different preparations, the power of the highest peak in each epoch was plotted against the frequency (Fig. 2C). The plots showed that the power was highest at frequency range of 0.9–1.6 Hz. The histogram of the number of maximum peaks showed that the frequency of the maximum peaks was about 1.05 Hz in most cases (Fig. 2D).

Odor-induced spikes and changes in amplitude of spontaneous oscillations

We examined the changes in spike activity and spontaneous oscillations in the tentacular nerve in response to various odor stimuli. Common features were noted in neural responses to garlic, carrot, and rat chow odors in the tentacular nerves. For example, 20-s odor stimulation reduced the amplitude of spontaneous oscillations and increased the mean firing rate (Figs. 3A, 4A and 5A). Odor-induced reductions in spontaneous oscillations were largest during 4–8 s of odor application for all the odors tested. Furthermore, a short recovery of the amplitude accompanied by suppression of spikes was observed in the last 12 s of stimulation (asterisks in Figs. 3A, 4A and 5A). The power spectral

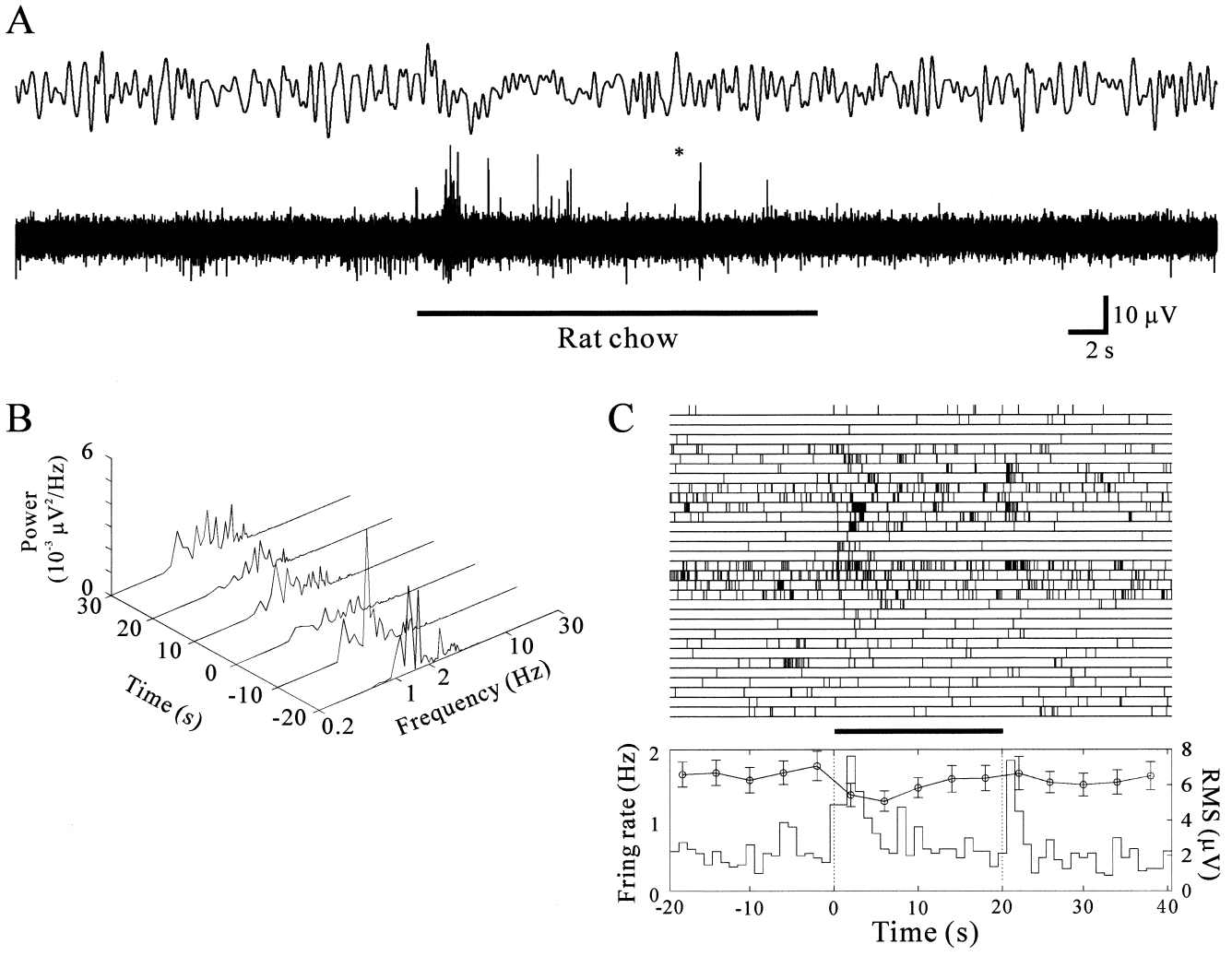


Fig. 5. Neural response to rat chow odor recorded from the tentacular nerve. A. LFP signal (0.1–30 Hz, top) and spike activity (150–1000 Hz, bottom) in response to rat chow odor stimulation (20 s). An asterisk points to recovery of the amplitude accompanied by suppression of spikes. B. Power spectral array of rat odor response shown in A. Peaks around 1–3 Hz decreased during odor stimulation (0–20 s). C. Raster plots and peri-stimulus time histogram of rat chow odor responses in tentacular nerve. The mean firing rate (white bars) was determined from the spike number in each bin (1 s), and then averaged over the trials. The mean RMS values (open circles) in the 0.6–2.4 Hz (4 s epochs) were plotted together. Significance was determined between each epoch and the first epoch. Data are expressed as mean ± SEM for the mean RMS values.

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arrays showed a decrease in the oscillatory activity in the 0.6–2.4 Hz in response to odor application, and recovery of oscillations after stimulation (Figs. 3B, 4B and 5B). The raster plots and histograms of tentacular nerve spikes showed that the firing rates increased in response to odor stimulation (Figs. 3C, 4C and 5C). The large transient increase of the firing rate was followed by a decrease of RMS voltage value in the 0.6–2.4 Hz band (Garlic, $P<0.01$; Carrot, $P<0.05$) (Figs. 3C and 4C, bottom). However, the odor of rat chow, which is the daily food for slugs, failed to significantly decrease RMS in the 0.6–2.4 Hz band (Fig. 5C).

Changes in amplitude of spontaneous oscillations are dependent on baseline amplitude

Although the three tested odors reduced the amplitude of spontaneous oscillations, some test trials failed to do so (garlic, 4 of 32 trials were failures; carrot, 5 of 36 trials; rat chow, 5 of 32 trials). To test the possibility that the amplitude change might depend on the pre-stimulus oscillatory activity, we plotted the RMS values of the decrease (left) and increase (right) responses of all trials. Fig. 6 shows that the response was an increase only when the RMS value of the baseline activity was small. On the other hand, when the RMS value of the baseline activity was very large (>35 μV), the response showed a slight decrease.

Neural response to prolonged odor application

Careful analysis of the short odor stimulation tests showed that the amplitude of spontaneous oscillations correlated with the firing rate during the second half of odor application (10–20 s). During this period, the amplitude of spontaneous oscillations appeared to return to the basal level whereas the firing rate decreased. However, the period of odor stimulation (20 s) was too short to allow proper analysis of the correlation between LFP amplitude and firing rate. We therefore examined the effects of prolonged odor application (60 s) on the amplitude and firing rate and their correlation. Similar to the short tests, odor-induced decreases in spontaneous oscillations were largest in 4–8 s of odor application for all odors tested in the study (Fig. 7). The amplitude started to show recovery by 24–28 s from the odor onset and reached a plateau level, which was slightly below the basal level (Fig. 7). The time of recovery of oscillation amplitude, determined by the position of the last epoch showing a significant decrease, showed the following order: no significant change in amplitude for rat chow odor, 16–20 s for garlic odor and 44–48 s for carrot. The order of decrease in the firing rate from the initial peak was also the same: rat chow, garlic, and carrot. For the response to rat chow odor, the decrease in the firing rate was the fastest and returned to the basal level 7 s after the stimulus onset. For the response to garlic odor, the firing rate continued to decrease from the initial peak at the stimulus onset but remained at a level higher than the baseline (pre-stimulation). For the response to carrot odor, the firing rate decreased from the initial peak at 2 to 8 s after the stimulus onset but then remained at a level higher than the baseline.

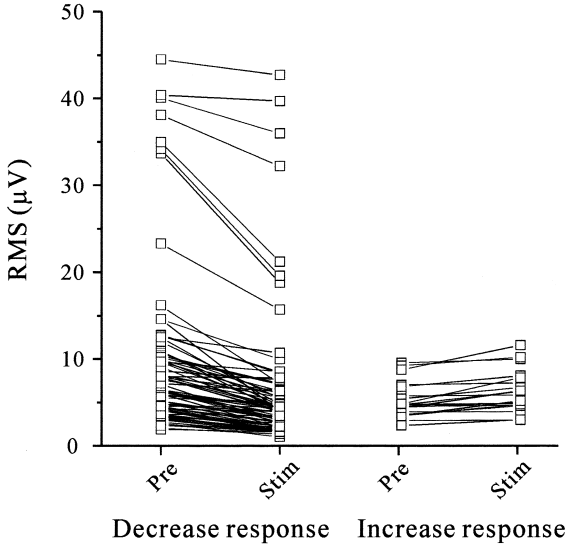


Fig. 6. The amplitude of spontaneous oscillations in tentacular nerve changes in a pre-stimulus-amplitude-dependent manner. The RMS values of pre-stimulus activity (the first epoch) and those of during-stimulus activity (the 7th epoch) were plotted. The decrease (left) and increase (right) responses are plotted separately. Trials of three odors are grouped together. Note that the increase responses were induced only when the pre-stimulus amplitude was small. Pre; pre-stimulus; Stim, during stimulus.

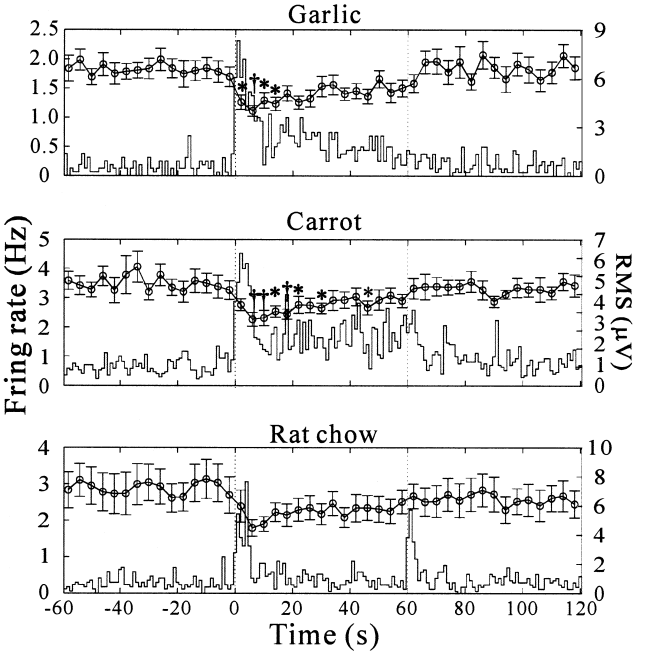


Fig. 7. Neural responses to prolonged odor stimulation recorded from the tentacular nerve. The peri-stimulus time histograms for garlic, carrot, and rat chow odors are shown. The mean firing rate (white bars) was determined from the spike number in each bin (1 s), and then averaged over the trials. The mean RMS values (open circles) in the 0.6–2.4 Hz (4 s epoch) were plotted together. Data are expressed as mean ± SEM for the mean RMS values. $^{*}P<0.05$; $^{\dagger}P<0.01$.

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Thus, our results suggest that the amplitude of spontaneous oscillations correlated with the firing rate, so that a faster recovery of the amplitude was associated with a faster return of the firing rate to the basal level.

Relationship between odor-evoked spike activity and amplitude of spontaneous oscillations

The initial transient increase in the firing rate in response to the odor stimulus was often followed by the largest decrease in the amplitude of spontaneous oscillations (carrot 20/33; garlic 19/35; rat chow 21/37) (Figs. 3–5, 7). We analyzed the statistical significance using G-test of independence (log likelihood ratio test). To perform this, all trails including the short and long stimulations of the three kinds of odor stimulations were collected. The responses were classified into 4 types (Odor-evoked spike activity with (1) and without (2) the following LFP decrease; no odor-evoked spike activity with (3) and without (4) the following LFP decrease). There was a significant difference (P<0.05, G=7.03) in frequencies between the odor-evoked spikes with and without the following LFP decrease. This finding suggests that the initial transient decrease in the amplitude of spontaneous oscillations is correlated to the increase in odor-evoked spike activity. The amplitude of the oscillations then recovered as described above. It is possible to consider this recovery of oscillatory activity as re-established oscillations in response to odor stimulation. The same relationship between the amplitude and spike rate seemed to be present after the initial decrease in the amplitude. For example, a transient increase of the amplitude was noted between the spike trains during carrot odor stimulation (Fig. 4). To confirm this, we calculated the instantaneous RMS value of spontaneous oscillations at each spike time using a short time window (1.667 s) centered on each spike time in prolonged odor stimulation tests and compared the mean RMS values before stimulation. The first 8 s stimulation period was omitted to examine the relationship between the amplitude of the re-established oscillation and the spike activity. The means of instantaneous RMS values during stimulation were significantly lower than the mean RMS values before stimulation for garlic, carrot, and rat chow odors (Fig. 8A). The smaller instantaneous RMS values than the mean RMS values during stimulation meant that the spikes appeared when the LFP amplitude transiently decreased. Further, we calculated the correlations between the instantaneous RMS values and the firing rates before, during, and after stimulation (Fig. 8B). There were significant negative correlations before (r=–0.167, P<0.0001), during (r=–0.170, P<0.0001), and after (r=–0.148, P<0.0001) stimulation. These results showed that spike activity was related to the

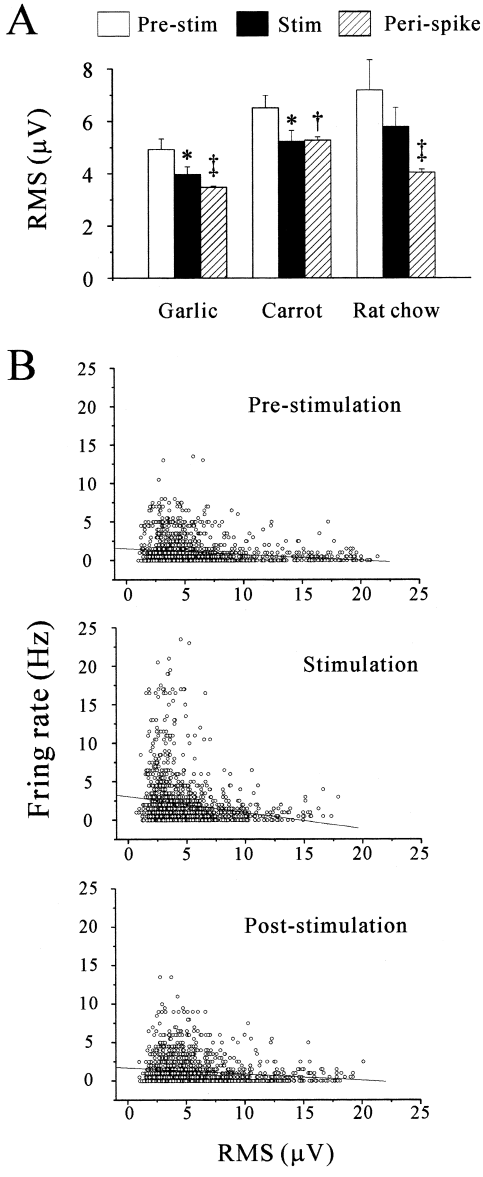


Fig. 8. Relationship between spike activity and amplitude of LFP oscillations in the tentacular nerve. A. Comparisons between the mean RMS values and the means of the instantaneous RMS values (hatched bar). The mean RMS values during stimulation (black bar) and the instantaneous RMS values were compared to the mean RMS values before stimulation (white bar) using Mann-Whitney U test. The mean of the instantaneous RMS values of the LFP oscillations at odor-evoked spike time was significantly smaller than the mean RMS value before stimulation. Data are expressed as mean ± SEM. $^{*}P$<0.05; $^{\dagger}P$<0.01; $^{\ddagger}P$<0.001. B. Correlations between the instantaneous RMS values and the firing rates. The instantaneous RMS values and firing rates before, during, and after stimulation were calculated using the 2 s time window. The firing rate was calculated using the spike number in the time window and the period of the time window (2 s). Ninety time windows were obtained from one trial including before (30 time windows), during (30 time windows), and after (30 time windows) stimulation and analyzed. We collected 1500 time windows from the carrot (510 time windows from 17 trials), garlic (480 time windows from 16 trials), and rat (510 time windows from 16 trials) odor trials and plotted together. The Pearson's product-moment correlation coefficients before, during, and after stimulation were calculated using 1500 time windows, and they were –0.167, –0.170, and –0.148, respectively. There were significant negative correlations (P<0.0001) before, during, and after stimulation.

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amplitude of spontaneous oscillations.

DISCUSSION

In the present study, we found that various natural food odors (garlic, carrot, and rat chow) increased tentacular nerve spike activity and at the same time decreased the amplitude of spontaneous oscillations at 0.6–2.4 Hz in the tentacular nerve in *L. marginatus*. Odor-evoked spikes only appeared when the amplitude of the spontaneous oscillation was small. These results suggest that there is a negative relationship between odor-evoked spike activity and spontaneous oscillations in the primary olfactory processing of slugs.

Two types of oscillations in the primary olfactory system in *L. marginatus*

In the present study, we found that the amplitude of spontaneous oscillations recorded in the tentacular nerve significantly decreased in response to odor stimulation. However, in some tests, odor application failed to reduce the amplitude when the baseline amplitude (before stimulation) was small. In addition, when the baseline amplitude was very large, odor application produced only a slight decrease in the amplitude of spontaneous oscillations. Such characteristics indicate that the change in amplitude of spontaneous oscillations was sensitive and insensitive to odors depending on the baseline amplitude. Indeed, an odor-insensitive oscillatory activity has been observed in the tentacular ganglion that exhibits two types of oscillatory states ("fast oscillations" and "slow oscillations") (Inokuma *et al*., 2002). The fast oscillations were normal spontaneous oscillations at about 1.5 Hz and showed no changes in response to an odor stimulus, whereas the slow oscillations were serotonin-induced (0.5 Hz) and their amplitude decreased upon odor stimulation. Although we recorded from the tentacular nerve rather than the tentacular ganglion, the spontaneous signals recorded simultaneously from the tentacular ganglion and nerve were almost the same except that the polarity of the signals was opposite to each other (Ito *et al*., 2003b). Our results were consistent with those of the previous study (Inokuma *et al*., 2002). However, our results defined a new property of the fast oscillations: odor-induced decrease in the amplitude of the fast oscillations that was dependent on the baseline amplitude.

Functional roles of spontaneous oscillations for olfactory processing in slug and hedgehog

We found common issues in the roles of spontaneous oscillations in olfactory processing between slug and hedgehog. Our results showed that odor-induced spike activity decreased the amplitude of spontaneous oscillations. Adrian (1950) found that an olfactory stimulus could decrease or abolish the spontaneous oscillations in the hedgehog olfactory bulb. Furthermore, we found only a slight decrease occurred when the baseline activity was very large (Fig. 6). Adrian (1950) also reported that weak odors failed to decrease the intrinsic oscillations in anesthetic-containing media that induced large spontaneous oscillations in hedgehog. However, one difference was evident in the manner in which transmission of olfactory signals to the central olfactory system was reduced. We found that the presence of high-amplitude spontaneous oscillations was correlated with low firing rate during odor stimulation. Adrian (1950) showed that irregular spikes in mitral cells were noted even in the presence of high-amplitude spontaneous activity, resulting in the decrease in the signal to noise ratio of olfactory signals. Therefore, our data suggest that the intrinsic oscillatory activity in the *Limax* primary olfactory system contributes to the olfactory processing in a slightly different manner compared with the hedgehog olfactory bulb. The highly interconnected GABAergic and putatively cholinergic networks in the digits, cell masses, tentacular ganglion, and tentacular nerve in the primary olfactory system were characterized physiologically (Ito *et al*., 2003a) and histologically (Ito *et al*., 2003b). These regions display the single coherent oscillations spontaneously. When the sensory epithelium is unstimulated, the large spontaneous oscillations may reduce the spontaneous firing of the projection neurons with neurites to the PC lobe in the primary olfactory system. However, when the sensory epithelium is stimulated, the decrease in the LFP oscillations would release the projection neurons from the suppression of firing. This would result in a signal-to-noise ratio improvement.

In conclusion, our results indicated that odors can evoke spike activity in the tentacular nerve, representing the conduit between peripheral and central olfactory organs, and at the same time they decrease the amplitude of the LFP oscillations in *L. marginatus*. Our data suggest that the intrinsic oscillatory activity contributes to the olfactory processing by a negative relationship between spontaneous activity and odor-evoked spike activity.

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