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ORIGINAL PAPER

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Twitching and quivering of the tentacles during snail olfactory orientation

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Abstract In *Helix aspersa* the posterior tentacles house a sensitive olfactory organ. We studied two types of tentacular movements, twitch and quiver. A twitch is a brief retraction (mean duration, 4.1 s); a quiver is a rapid lateral movement (350 ms) unaccompanied by retraction. We videotaped the tentacles while snails explored an open field. When an attractive odor source, linalool, was present at one side of the arena, the snails consistently moved towards it. By contrast, if only the carrier substance was present the snails moved in random directions. Twitching was 50 times more frequent during linalool trials than during control trials, while quivering was 1.4 times more frequent. Twitching increased steadily and dramatically as snails approached the linalool source and, in the temporal dimension, the maximum rate of twitching occurred when the snails arrived at the odor source. Quivers occurred at a fairly constant rate. Twitching is interpreted as a mechanism to remove odor molecules trapped in the liquid covering of the olfactory epithelium, thus resulting in better temporal resolution for olfactory perception. Quivering may be a mechanism to increase access of odor molecules to receptors by decreasing the boundary layer at the surface of the tentacle.

Key words Olfaction · Gastropod mollusc · *Helix aspersa* · Boundary layer

Introduction

In a lecture emphasizing the importance of interruptions for olfactory perception, Dethier (1987) reviewed the roles played by "sniffs, flicks and pulses." Included in these phenomena are the patterned movements of the olfactory organ seen in many animals, for example, the rapid vibrations of the antennules in crustacea (Snow 1973; Schmitt and Ache 1979) and tongue flicking in reptiles (Cooper 1994). These behaviors are thought to enhance olfactory performance by altering fluid dynamics in such a way as to reduce the boundary layer at the surface of the olfactory organ, thus improving access of odor molecules to the receptors (Moore et al. 1991). In this paper we examine whether snails might exhibit comparable behaviors.

The principal olfactory organ of terrestrial snails is located at the tip of the posterior (superior) tentacles. Snails that lack one posterior tentacle are unable to locate olfactory sources diffusing in still air, while snails lacking both posterior tentacles are unable to orient even when there is a directional wind (Chase and Croll 1981). The olfactory organ consists of a specialized patch of epithelium (about 1 mm^2) with its associated neural and secretory structures (Chase and Tolloczko 1985, 1993).

The tentacle movements described in this paper occur in a context that includes larger-scale movements of the tentacles. Snails orient to an olfactory source using both tropotaxis and anemotaxis (Chase and Croll 1981; Chase 1982). They sample the environment by moving their heads, and thus their tentacles, from side to side in tandem movements that are smooth but neither periodic nor stereotyped. Other movements, which are the subject of this paper, are superimposed on these larger movements and they are performed unilaterally. One can distinguish twitches, which are brief retractions, from quivers, which are rapid lateral movements without retraction. The purpose of this study was to determine whether the occurrence of twitches and quivers is correlated with olfactory orientation, and thus whether these behaviors might be added to Dethier's compendium of "sniffs, flicks, and pulses" in the service of olfactory perception.

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Materials and methods

We used adult specimens of *Helix aspersa* (curled shell lips) obtained from California. The animals were stored in estivation for 6 weeks, then activated with water but starved for 2–4 days prior to use. On days when observations were to be made, the snails were first showered with tepid water to initiate activity. An active snail was placed on a small piece of glass (5 cm square). When it had recovered from this displacement and once again showed searching movements, the glass and the snail were transferred to the experimental arena, at which point the snail continued to search, undisturbed by the transfer. One snail at a time was observed in the arena.

The experimental arena consisted of a printed grid (26-cm square) overlaid with a piece of non-glare glass (Fig. 1). A strip of absorbent paper was placed on the glass at one edge of the grid so that the center of the paper was situated at a distance of 12.2 cm from the center of the grid. A snail, transported on the carrier glass, was placed in the center of the grid. Immediately thereafter, 15 drops of an odor solution were evenly distributed on the paper. The arena was designed to be free of any directional cues that might influence a snail's spatial movements, apart from the introduced odor. The initial orientation of the snail was systematically varied in four directions. At the end of a trial the glass covering the grid was thoroughly cleaned using a commercial ammonia spray to remove mucus trails. A fan was operated for at least 5 min between trials to dissipate experimental odors. Air currents during the trials were minimized by conducting the experiments in a small room and by limiting the investigator's movements. Ambient air currents were visualized by videotaping the dispersion of a smoke plume from a source of titanium tetrachloride (Schal 1982) under conditions approximating those during experimentation. The distribution of smoke was variable (turbulent) at discrete times but the pattern of dispersal was effectively averaged over time, as observed by the incremental deposition of titanium oxide crystals. After several seconds the distribution of crystals approximated a Gaussian gradient centered around the application spot. The maximum velocity was approximately 0.05 m s^{-1}.

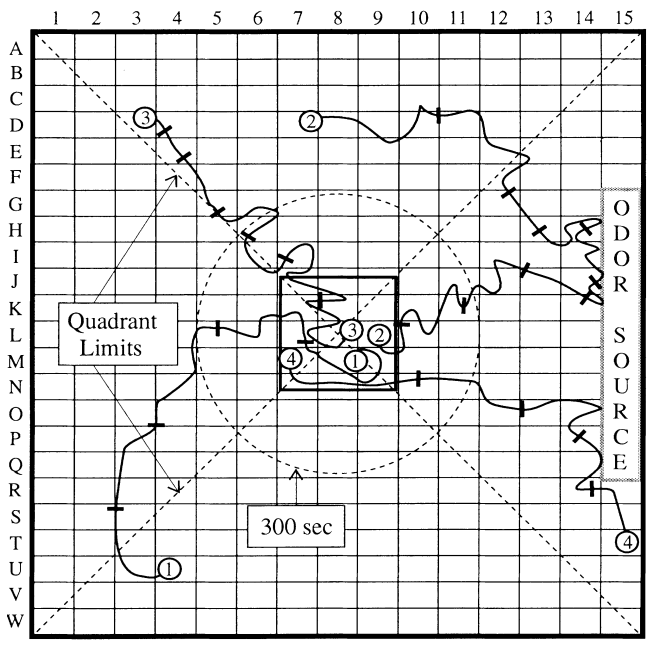

Fig. 1 The experimental grid (26-cm square) with the tracks of four representative snails. The *short lines* intersecting the tracks are 1-min time marks. The *long diagonal lines* define the quadrants used for the analysis of residency times (Fig. 3). The *central square* locates the starting position, and the *dotted circle* indicates the boundary for aborting trials when there was insufficient locomotion

The snail's movements were recorded using a video camera and a video cassette recorder (VCR). The camera was mounted on a carriage and positioned directly over the snail's head. It was fitted with a macro adapter ring for recordings at a focal distance of 13 cm. Neon lights were also mounted on the carriage. As the animal locomoted, the camera was moved so that the head and tentacles remained constantly in view. A snail was judged to be in a given grid sector when the anterior most portion of its foot was in the sector. Time was given by the VCR clock, with a resolution of 33 ms (30 frames s^{-1}). Measurements of an animal's speed of locomotion were obtained from plots of itineraries with time markers, as shown in Fig. 1. The plots were then digitized, and the path lengths were measured using SigmaScan software.

Data collection began immediately after the paper was loaded with the odor solution. Recording continued for 600 s or until the snail exited the arena, whichever came first. Trials were aborted if the snail failed to move for 200 consecutive seconds or if it failed to travel at least 6 cm within 300 s (Fig. 1).

For an attractive odor, we used a 1% dilution of linalool in propylene glycol. Linalool is a terpene oil commonly found in edible plants, and it is a natural attractant for *H. aspersa* (Linhart and Thompson 1995). To enhance the attractiveness of linalool, some snails were conditioned by exposing them overnight to a 0.5-g slice of carrot root that had been loaded with a drop of linalool. By establishing an association between the odor (linalool) and the food (carrot), this procedure promotes attraction to the conditioned odor (Croll and Chase 1977; Teyke 1995). The initial pool of 63 snails that were tested with linalool comprised 34 naive snails and 29 conditioned snails. In separate trials, pure propylene glycol was used as a control stimulus (45 snails).

Behaviors exhibited by the left and right tentacles were combined to yield a single score for each trial. This procedure was justified by the absence of any significant difference in the frequencies of either twitches or quivers exhibited by the two tentacles (χ^2 test; twitches: $P = 0.6$, $n = 182$; quivers: $P = 0.949$, $n = 125$). Similarly, when rates were compared for the tentacle nearest the odor source at the time of the behavior versus the tentacle farthest from the source, there were no significant differences (twitches: $P = 0.919$, $n = 47$; quivers: $P = 0.805$, $n = 75$). The data are expressed as means ± standard errors, except in Table 1 where standard deviations are used.

Results

We wanted to compare snails that were orienting toward an odor source and snails that were searching in the absence of any apparent target. To validate our assumption that a local source of linalool odor would elicit oriented locomotion, and propylene glycol would not, we first analyzed the end points of the snails' excursions. These positions were determined either when a snail departed from the grid or at the 600-s timed limit to a trial. The data are reported in Fig. 2 as a distribution of end points relative to the four grid quadrants (Fig. 1). The end points were significantly biased toward the odor source in linalool trials (χ^2, $P < 0.001$, compared to chance), but unbiased in propylene glycol trials ($P > 0.50$ for both the source quadrant and the quadrant opposite to the source). The percentage of snails that ended their trials within the quadrant that contained the odor source was significantly greater in linalool trials than in propylene glycol trials (χ^2, $P < 0.02$). After these trials, subsets of the initial groups were selected for further analysis. The linalool group comprised

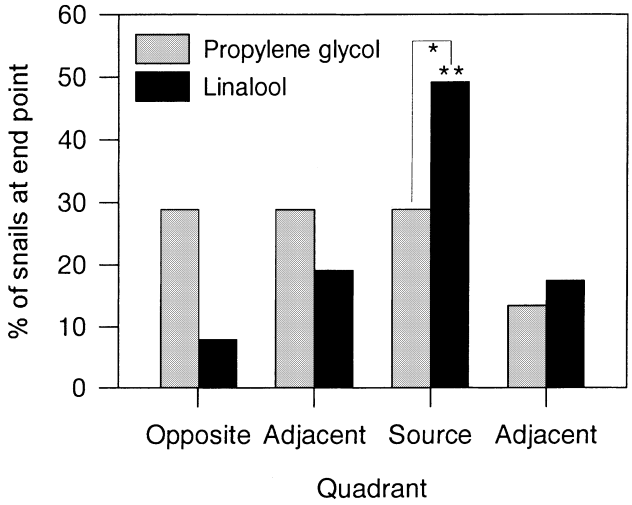

Fig. 2 The end points of trials determined either when a snail reached the arena's spatial limit (Fig. 1) or when the trial's temporal limit (600 s) expired. The source quadrant was loaded with either pure propylene glycol or 1% linalool in propylene glycol. The locations of other quadrants relative to the source are indicated. $n = 63$ for linalool trials; $n = 45$ for propylene glycol trials. χ^2 tests; $*P < 0.02$ (propylene glycol versus linalool); $**P < 0.001$ (linalool versus chance)

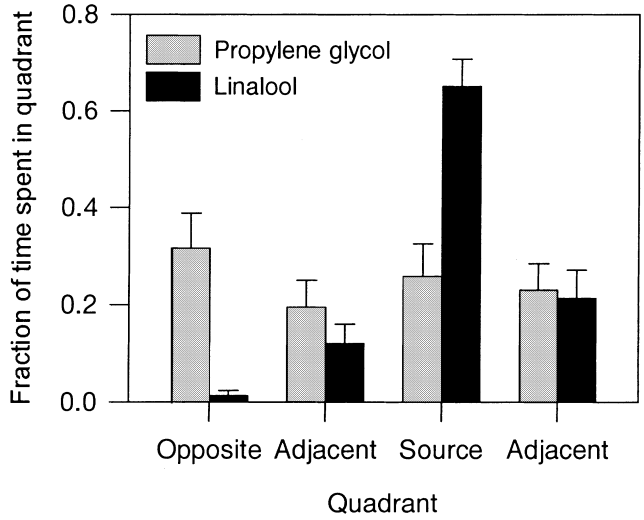

Fig. 3 The time spent in each grid quadrant expressed as a fraction of the total trial duration. The distribution of residency times was random in propylene glycol trials (ANOVA; $P > 0.05$) but significantly biased in linalool trials ($P < 0.001$). $n = 25$ for both groups, as in all subsequent figures

25 snails, all of which reached the odor source within the 600-s time limit but which were otherwise randomly selected from the larger pool; 12 snails were naive and 13 snails had been conditioned by pairing linalool with carrot. The propylene glycol group also comprised 25 snails; they were randomly selected from the larger pool.

We next calculated the amount of time individual animals spent in each of the four grid quadrants. Figure 3 shows that linalool caused the animals to spend a disproportionate amount of their time in the target quadrant (ANOVA; $P < 0.001$). In the absence of linalool, the distribution of times did not depart significantly from chance ($P > 0.4$). Thus, the data shown in Figs. 2 and 3, together with the knowledge that linalool is a natural attractant in the field (Linhart and Thompson 1995), demonstrate that the animals were orienting positively to linalool but insignificantly, if at all, to propylene glycol.

Examples of a twitch and a quiver are illustrated in the video image sequences of Fig. 4. Both types of events appeared to be spontaneous; they were not occasioned by any obvious change in illumination or any observable mechanical stimulus. A twitch was defined as a retraction of the posterior tentacle sufficient to cause a disappearance of the eyespot (Fig. 4a). Table 1 lists the several motor components of individual twitches that were identified by a frame-by-frame analysis of 40 twitches (resolution 33 ms). An initial fast phase of retraction, lasting 0.4 ± 0.1 s (mean ± SD), was clearly distinguished from a second, slower phase lasting 0.7 ± 0.4 s. A slight bending of the tentacle is usually evident at the end of the first phase such that the tip lies either lateral or ventral to the tentacle's longitudinal axis

Table 1 Component analysis of twitch duration, based on the observation of 40 twitches in 20 snails. Time zero is the moment the eye spot first disappears (due to inversion). Early retraction is separated from late retraction by a brief deceleration. Extension is complete when the eye spot reappears. Means ± SD are shown

Component	Duration (s)
Early retraction	0.4 ± 0.1
Late retraction	0.7 ± 0.4
Total retraction	1.1 ± 0.4
Internal pause	1.7 ± 1.6
Extension	1.3 ± 0.5
Total	4.1 ± 2.1

(Fig. 4, at 0.33 s). After a highly variable period of internal pause (1.7 ± 1.6 s), the tentacle is once again extended (1.3 ± 0.5 s). A quiver was defined as a rapid sideways movement of the tentacle involving mainly the tip, with no retraction. Quivers are variable in duration (350 ± 100 ms) and often consist of two or more consecutive movements. They are rapid, subtle movements (Fig. 4b) that can nevertheless be reliably detected on videotape, as we confirmed by repeated observations of selected records. Their brief duration precludes a quantitative analysis of their components from videotaped records.

The frequency of both twitching and quivering increased during linalool trials as compared to propylene glycol trials. Twitching increased from 0.1 to 5.0 min^{-1} ($P < 0.001$). Quivering increased substantially less than twitching, from 3.5 to 4.8 min^{-1}, but the difference was significant ($P < 0.05$). To determine whether there was any spatial or temporal patterning of these behaviors, a further analysis was performed. The propylene glycol

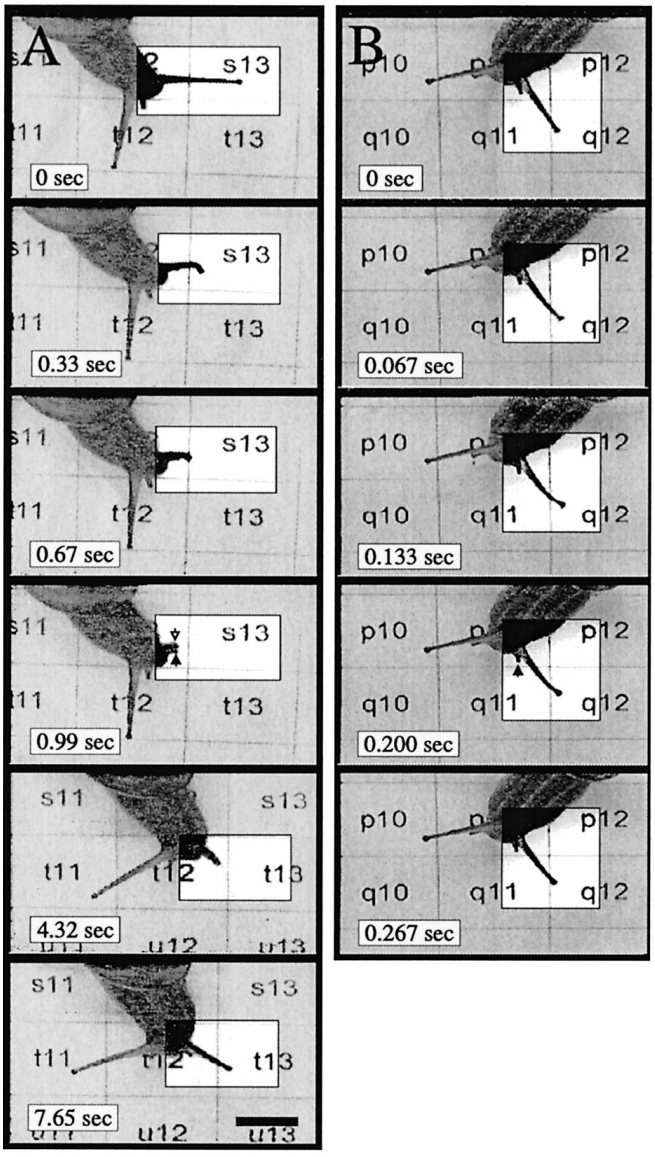

Fig. 4A, B Video frame sequences of a twitch (**A**) and a quiver (**B**). *Filled arrowheads* point to the anterior tentacle; *open arrowhead* points to the posterior tentacle. *Scale bar* (bottom of **A**) = 1 cm

records gave no indication of either a spatial or temporal pattern for either type of behavior (data not shown).

A spatial dissection of twitching and quivering in the presence of a linalool source is presented in Fig. 5. The frequency of quivering shows no clear pattern. Twitching, on the other hand, increased dramatically as the snails approached the linalool source. From an initial mean rate of 0.2 twitches min^{-1} at the start box, the rate increases to 8.7 twitches min^{-1} at the source. Figure 5 also shows the mean time spent in each column. As the snails approached the source (columns 11 and 12) residency times decreased due mainly to better orientation toward the odor source. Residency times increased when they arrived at the source (columns 13 and 14) because some animals slowed their rate of locomotion while others moved parallel to the odor source (i.e., within a

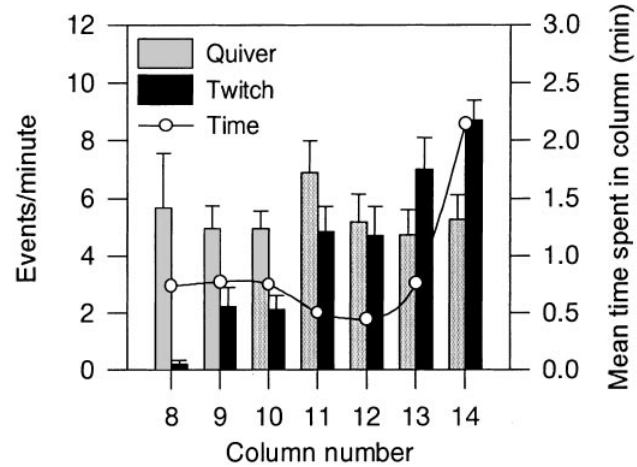

Fig. 5 The frequencies of twitching and quivering as a function of location during orientation to linalool (*y*-axis at left). The trials began at column 8; the odor source was at column 15 (columns refer to markings in Fig. 1). Also shown is the mean time spent in each column (*y*-axis at right). The frequency of twitching increased dramatically as the source was approached and as the animals decelerated. In contrast, the frequency of quivering was fairly constant

column). Early on (columns 8–11) the rate of twitching is not related to residency times, but near the source (columns 12–14) the increase in twitching is strongly correlated with the increase in residency times.

Another way to describe the influence of linalool is to analyze the timing of twitches and quivers relative to the total time elapsed during travel to the source. In Fig. 6 the frequencies are normalized as fractions of the time to reach the source. The graph shows that, on average, quivering continues at a relatively constant rate throughout a trial, although there is a slight decline once

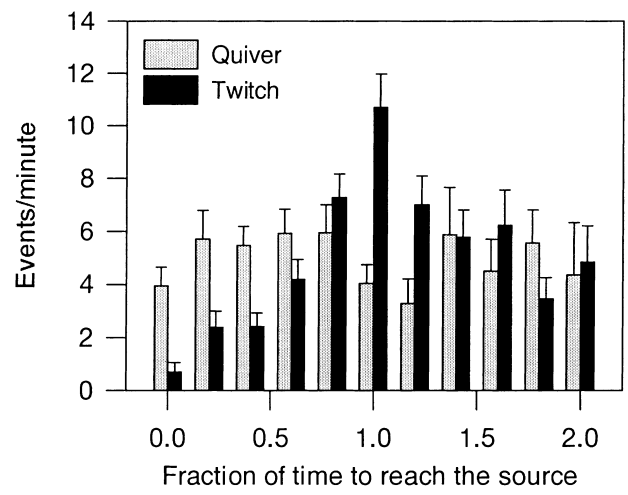

Fig. 6 The frequencies of twitching and quivering as a function of time during orientation to linalool. The time to reach the source is normalized to 1.0 (range of actual times 50–415 s). Twitching is more sensitive to time than is quivering. Fractional values > 1.0 typically represent time spent at, or close to, the odor source (see Fig. 5)

the source is reached. By contrast, the frequency of twitching increases steadily as the snail approaches the source, from a low of 0.7 events min^{-1} at the start to a peak of 10.7 min^{-1} by the time the snail reaches the source. (Rates differ from those given in Fig. 5 due to different methods of calculation). Thereafter, there is some decline in twitching frequency but the rates remain higher than during the early approach to the source. These continued high rates of twitching occur while the animals remain close to the source; 50% of the snails were in either column 13 or column 14 at fractional time 1.8.

Discussion

Twitches and quivers are distinct phenomena with independent rates of occurrence and different stimulus contingencies. We view them as two independent mechanisms that have evolved to facilitate olfactory orientation. Each type of behavior will be discussed separately.

Quivers occur at a more or less constant rate regardless of the animal's position with respect to the source. The slight decrease in quiver frequency near the source, evident in Figs. 5 and 6, might be attributed to competitive interference from the increasingly frequent twitches. Given that twitches last on average 4.1 s, and that quivers and twitches are physically incompatible acts, the time available for quivering is substantially reduced by frequent twitches. Thus, when the snails are at the source and twitching at the rate of 8.7 min^{-1} (Fig. 5), they are engaged in twitching 60% of the time. Alternatively, the decline in quiver frequency might signify lessened demands on signal detection since the stimulus concentration is high near the source.

Although quivering was significantly more frequent during linalool trials than during propylene glycol trials, the increase was only 37%. This, plus the fact that there was no obvious modulation of the behavior in the course of orientation to the odor source, raises the question whether quivering is related to olfactory perception. The movements of the tentacles during quivering resemble the flicking movements of the antennules in crustacea and, while the fluid dynamics of the situations differ in detail, the ultimate effect of tentacle quivering may be the same as for antennule flicking, namely to increase access of the odor molecules to the chemosensory organ. During the intervals between quivers, the tentacle surface is surrounded by a boundary layer where molecular diffusion primarily determines the rate at which molecules reach the receptors. Quivering will induce turbulence and entrain odor particles into the air space near the tentacle surface. Because turbulent diffusion is more efficient than molecular diffusion, sampling itself becomes more efficient. In addition, because the receptors will be adapting, in the intervals between quivers, to a relatively constant molecular environment, quivering causes the snail to sample the environment at discrete times, or digitally. Digital sampling also occurs in crustacea, but its functional significance is uncertain (Moore et al. 1991).

For a stationary tentacle in air moving at 0.05 m s^{-1} (the approximate maximum observed in our experiments) the Reynold's number is approximately 3.4. We estimated the effect of quivering by calculating the change in the displacement thickness, which is a measure of the loss of mass flow due to the boundary layer (Schlichting 1995). If the quiver velocity is taken as 0.007 m s^{-1} (from Fig. 4), and directed opposite to the air current, the displacement thickness will be reduced by $\pm 6\%$ during a quiver. The magnitude of the quiver effect will increase as air velocity decreases below 0.05 m s^{-1}, as may well occur when the snail is on the ground or even under litter.

Conceivably, quivering might be unrelated to perception but a consequence of the animal's greater speed of locomotion in the presence of attractive odor. We tested this idea by calculating the correlation between the average speed of a snail during a trial and its quiver rate. Whereas there was a significant correlation during propylene glycol trials ($r = 0.496$; $P = 0.012$; $n = 25$), there was no significant correlation during linalool trials ($r = 0.246$; $P = 0.235$; $n = 25$). Also, the mean of the average speeds was only slightly greater during linalool trials than during propylene glycol trials (18.6 versus 17.6 cm s^{-1}; $P = 0.642$; t-test). Since the measure of average speed may obscure moment-to-moment variations (the snails typically slowed down as they reached the linalool source, shown in Fig. 5), we also examined the correlation between quivering and speed based on fractional units of the total time to reach the source, as in Fig. 6. When five animals from each of the two odor conditions were analyzed in this way, there was again no significant correlation between speed and quiver rate ($r = 0.198$; $P = 0.067$; $n = 86$ time bins). Collectively, these data indicate that the increase in quiver rates during linalool trials is not likely due to an increase in speed alone, but the functional interpretation of quivering is uncertain, and direct experimental tests of the fluid dynamical considerations may be required to settle the issue (Moore et al. 1991).

The motor pathway for quivering is probably the same as for tentacle bending. Bending occurs during withdrawal of the tentacle (Fig. 4) as well as during orientation to learned food odors (Peschel et al. 1996). About two dozen motoneurons in the cerebral ganglion, including the giant neuron C3, send axons into the internal and external peritentacular nerves to innervate the tentacle's tegumental muscle (Peschel et al. 1996; Prescott et al. in press). These neurons spike even under "spontaneous" conditions due to a large excitatory synaptic input. When chemical or mechanical stimuli are applied to the tentacle the spike rates increase and bursts of activity are recorded in the nerves (Chase and Hall 1996; Peschel et al. 1996; S. Prescott, unpublished observations). These bursts could produce the quality of movement that characterizes quivering.

Twitches were affected even more than quivers by the olfactory environment. The overall frequency of twitches increased dramatically in the presence of linalool (Fig. 5). Also, unlike quivers, the frequency of twitches steadily increased during a trial as the snail approached the odor source (Figs. 5, 6). We hypothesize that the significance of twitching lies in its potential for temporarily removing chemical stimuli from the olfactory epithelium. We will first discuss the mechanisms for stimulus removal, then we will offer functional interpretations.

There are several related mechanisms that might remove odor molecules from the snail's olfactory organ, all of which are consequences of the tentacle's retraction by inversion. First, and most obviously, is the simple removal of the tentacle tip from the olfactory airspace into the internal environment of the snail. However, this action alone could not be sufficient because the olfactory epithelium is covered with a thin layer of aqueous fluid (Chase and Tolloczko 1985) and odor molecules will remain trapped in this fluid. Retraction of the tentacle may cause some molecules to diffuse into the hemolymph. Also, detailed observations of tentacle retraction by Wondrak (1977), largely confirmed by us, suggest another mechanism. Retraction per se is preceded by an invagination of the tip. Next, as the tip begins to retract, the external face of the olfactory epithelium is pulled against the interior surface of the tentacle wall. This movement should result in a wiping action that would clean the surface of the olfactory organ. Finally, re-extension of the tentacle after a twitch is effected entirely by hydrostatic pressure. It is likely that re-extension is accompanied by an extrusion of liquid to the surface of the olfactory organ that will dilute the concentration of "old" odor molecules still trapped on the surface. It should be possible to test the hypothesis of stimulus removal by loading the aqueous covering of the olfactory organ with a visible or radioactive marker, then measuring its concentration before and after a twitch.

Chemicals might be removed from the olfactory organ because they are irritating. In an earlier study, we delivered pure chemical compounds at known concentrations to single tentacles of the snail *Achatina fulica* (Chase 1982). It was observed that twitching occurred with all compounds, including both attractive and non-attractive stimuli, and the frequency of twitching increased as the concentration of the odor increased. Similarly, our electrophysiological study of the motoneuron C3 (Chase and Hall 1996), mentioned above, revealed that the cell is sensitive to stimulation of the tentacle by a variety of odors. Since C3 is the principal motoneuron responsible for tentacle withdrawal in *H. aspersa* (Cottrell et al. 1983; Prescott et al. in press), the electrophysiological and behavioral results are consistent in indicating that the mechanism linking olfactory stimulation with tentacle retraction is non-selective for odor quality. The results suggest that any chemical may be irritating at sufficiently high concentration.

We prefer an interpretation of twitching that is related to our functional interpretation of quivering. As already mentioned, fluid dynamics create a boundary layer at the surface of the tentacle that traps "old" odor molecules while denying "new" ones access to the receptors. A second trap for odor molecules is the liquid on the surface of the snail's olfactory epithelium. We propose that by (partially) removing "old" odor molecules trapped in the aqueous covering, twitches renew the immediate environment of the receptors. This permits "new" airborne molecules to dominate the olfactory response. The net result is to increase the temporal resolution of the snail's olfactory system.

It may be possible to test the hypothesis that twitching improves olfactory performance. The tentacle retractor nerve is entirely responsible for carrying the central motor signal for the initial, fast component of tentacle withdrawal (S. Prescott, unpublished observations). Therefore, lesions of this nerve should allow one to study olfactory orientation in animals that have an intact olfactory sensor but an impaired ability to twitch. We expect them to perform more poorly than intact animals in locating a linalool source.

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