

LUMINESCENT FLASH AVOIDANCE IN THE NOCTURNAL CRAB *PORTUNUS XANTUSII*

I. THE EFFECTS OF LUMINESCENCE AND MECHANICAL STIMULATION ON HEART RATE

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Summary

In crabs, the ratio of the heart rate before to that after sensory stimulation (the response ratio) provides a reliable indicator of the effects of sensory stimulation on cardiac activity. The nocturnally active crab *Portunus xantusii* (Stimpson) exhibits rapid decreases in heart rate in response to the luminescent flashes produced by the sea pansy *Renilla kollikeri* (Pfeffer) and to mechanical stimulation. Crabs move away from luminescent and mechanical stimuli and this behavior is well correlated with the cardiac responses. Therefore, cardiac response ratios can be used as a reliable bioassay to determine the components of sensory stimuli that are important in eliciting behavioral responses. The similar cardiac responses to both luminescent and mechanical stimuli suggest that a single command pathway may be responsible for triggering startle behavior in response to a wide variety of rapid, brief and intense sensory stimuli. Heart rate also varied depending on the body size of the crab and the ambient temperature. Small crabs had faster heart rates than larger crabs, and the relationship between heart rate and body size is described by the equation: $f_H = 794.3x^{-0.59222}$, where f_H is heart rate in beats per minute and x is carapace length in millimeters. Heart rate increased with increasing temperature over a range of 10–22°C, but no further increases occurred at higher temperatures. The Q_{10} for the range 10–20°C was 1.8.

Introduction

Bioluminescence is a widespread phenomenon among coastal marine organisms and serves a number of important functions (Morin, 1983). A distinctive type of luminescent signal, which is produced by a phylogenetically diverse and numerically abundant assemblage of coastal organisms, consists of one or more brief flashes that are only produced in response to mechanical stimulation. In general, the intensity and duration of the flashes are directly proportional to stimulus

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intensity. Morin (1983) suggested that the probable function of this type of luminescence is to deter visually orienting predators, and called these signals 'contact flash predator deterrents'. Empirical support for this hypothesis has been established for luminescent species in both planktonic and benthic ecosystems. The luminescence produced by dinoflagellates decreases the feeding efficiency and changes the feeding behavior of herbivorous copepods (Esaías and Curl, 1972; White, 1979; Buskey *et al.* 1983). The luminescence produced by a Caribbean brittle-star elicited avoidance behavior in a number of nocturnally active predators, while non-predators were relatively unaffected by the light flashes (Grober, 1988*b,c*). Three species of portunid crabs from Caribbean reefs exhibited increased avoidance and decreased predatory behavior in response to luminescent brittle-stars compared to their behavior in response to non-luminescent controls (Grober, 1988*a*).

Portunus xantusii (Brachyura:Portunidae) is a common, nocturnally active crab found on sand bottom habitats along the coast of Southern California (Schmitt, 1921). This and other crab species make up a significant proportion of the nocturnal predators in this habitat (Morin *et al.* 1985). Two other common and often abundant members of the sand bottom community are the luminescent sea pansy *Renilla kollikeri* and the sea pen *Stylatula elongata* (Gabb). Although it is not known whether *P. xantusii* is a predator on either of these animals, Morin (1976) suggests that luminescence in the Pennatulacea (sea pens and sea pansies) probably functions to deter nocturnally active crab and fish predators.

The behavioral responses of *P. xantusii* to *Renilla* and *Stylatula* luminescence have not been studied in the field, but my preliminary laboratory observations had shown that these crabs, similar to tropical portunids (Grober, 1988*a,b*), exhibit burrowing or swimming behavior in response to luminescence. The purpose of this study was to see whether temperate portunids respond to luminescent flashes in a similar manner to tropical species, and to describe the physiological correlates of these responses.

Many previous studies have used the activity of the heart and gill bailers (scaphognathites) to assess the effects of a wide range of variables on the physiology of decapod crustaceans (for review, see Wilkens, 1981). Heart and scaphognathite beating rates in decapods are known to be affected by body size (Maynard, 1960; Ahsanullah and Newell, 1971; DeFur and Mangum, 1979), ambient temperature (Ahsanullah and Newell, 1971; Florey and Kriebel, 1974; Morris and Taylor, 1984) and O₂ availability (Uglow, 1973; Florey and Kriebel, 1974; DeFur and Mangum, 1979; Morris and Taylor, 1984). In addition, crabs, lobsters and crayfish produce cardiac responses (bradycardia or cardiac arrest) to a variety of optical and tactile stimuli (Larimer, 1964; Larimer and Tindel, 1966; Uglow, 1973; Florey and Kriebel, 1974; Wilkens *et al.* 1974; Cumberlidge and Uglow, 1977).

Mislin (1966) was the first to suggest an 'optocardial reflex' based on his observations on two crayfish and one crab species, which showed that optical stimulation caused cardiac arrest. Florey and Kriebel (1974) have since suggested

that heart rate should be an excellent bioassay of sensory perception in decapods. This study correlates the behavioral and cardiac responses of crabs to luminescent flashes and demonstrates the utility of a cardiac bioassay for probing the characteristics of sensory stimuli that elicit behavioral responses from crabs. I also show that portunid crabs from temperate (this study) and tropical habitats (Grober, 1988a) respond to luminescent flashes with similar avoidance behavior.

Materials and methods

Animals and preparations

Specimens of *Portunus xantusii* (15–37 mm carapace length, both sexes) were obtained from Marinus Inc. and Pacific Biomarine (Los Angeles, CA, USA). The animals were maintained at UCLA in aquaria kept at 15°C in a recirculating seawater system. All animals were fed biweekly on mussels and fish.

Heart activity was measured by implanting an impedance electrode on either side of the heart in accordance with the impedance technique described by Dyer and Uglow (1977). Using 30 gauge syringe tips, holes for the impedance electrodes were made in the carapace. The impedance leads were held in place with a small rubber band stretched lengthwise across the carapace dorsally and attached to the lateral spines. Dental wax was used to seal the leads in the carapace. The output from the impedance leads was sent to the analog-to-digital converter of an Acorn computer data acquisition and analysis system (Lighton, 1985). This system is capable of sampling four data channels simultaneously, and provides extensive software for data manipulation and analysis. Morris and Taylor (1984) have also used the Acorn computer and impedance techniques to analyze heart rate in an intertidal prawn.

Effects of sensory stimuli

After insertion of the electrodes, crabs were placed in an octagonal Plexiglas aquarium (each wall length 30 cm) in 10 cm of sea water kept at $15 \pm 1^\circ\text{C}$ by a recirculating cooler (Lauda K-2 RD). Crabs were allowed at least 24 h to recover from the electrode implant and maintained on a 12 h: 12 h light: dark cycle. Since *Portunus xantusii* is normally nocturnally active (Morin *et al.* 1985), experiments were only conducted during the regular dark periods of a controlled diel cycle.

Each crab ($N=5$) was presented with three different types of stimuli. Luminescent, mechanical and control stimuli were each presented five times in a random order, with the exception that the same stimulus was not given twice in succession.

Luminescent stimuli

Luminescence was produced by mechanically stimulating colonies of *Renilla kollikeri*. *Renilla* colonies were positioned 2 cm from the crab and then mechanically stimulated with a long plastic probe. Two or three quick prods with the probe elicited a wave of luminescence, which lasted 4–8 s, across the colony.

Variation between luminescent stimuli was unavoidable due to slight variation in the strength of the mechanical prods and variation in the responsiveness of the individual *Renilla*. However, it is likely that this variation was well within the range of signals that *Portunus xantusii* would receive under field conditions. This range of signals is also consistent with the luminescence that is naturally elicited from *Renilla* by free-ranging crabs (M. S. Grober, personal observation).

Mechanical stimuli

Direct mechanical stimulation of the crab was done to determine the cardiac responses of these animals to a different sensory stimulus. Mechanical stimuli to the crabs were produced by firmly prodding one cheliped of a subject with the plastic probe. The mechanical stimuli were also somewhat variable, although great care was taken to produce stimuli of similar strength and duration. A stimulus duration of approximately 5 s was chosen to match the duration of the luminescent stimuli.

Control stimuli

To establish that the luminescence was responsible for any observed effects on heart rate, a single manipulation was conducted to control for the potential effects of *Renilla* chemicals and also to ensure that the prods used to elicit luminescence from the *Renilla* did not mechanically stimulate the crabs. *Renilla* colonies were first anesthetized in 0.36 mol l^{-1} magnesium chloride (isotonic to sea water), which inhibited the production of luminescence for the duration of the trial (20–30 min). After anesthetization, the *Renilla* were then placed in the seawater aquarium and stimulated in the same manner as described above for the luminescent stimuli but without the ensuing production of light.

To avoid habituation, crabs were given at least 10 min between stimuli. The test aquarium was illuminated from below with an infrared light source and the crab could be observed with the aid of an infrared-sensitive night vision scope (Varo Inc., Detect-IR-Scope 5500C). Crustaceans have poor vision in these far red wavelengths (Goldsmith and Fernandez, 1968; see also Grober, 1988b). This viewing procedure allowed exact placement of the stimuli and for pre- and post-stimulus observations of the crabs, but did not affect crab behavior.

For all three types of stimuli, heart rate was recorded for 10–15 s before and after the presentation of the stimulus. A number of previous studies have shown that heart rate can vary widely both between and within individuals and with the experimental conditions (McMahon and Wilkens, 1972; Florey and Kriebel, 1974; Cumberlidge and Uglow, 1977; McDonald *et al.* 1977). To control for this variation, the ratio of the heart rate 10 s immediately prior to the stimulus to the heart rate during the first 10 s after the stimulus (the response ratio) was used. This method assessed the effects of the stimuli on heart rate and also allowed comparisons among the stimulus types. This technique also controlled for variation in basal heart rate due to slight changes in ambient temperature or minor differences in crab size. Since changes in heart rate in response to sensory

stimulation are usually rapid and brief (Larimer and Tindel, 1966; Florey and Kriebel, 1974; Cumberlidge and Uglow, 1977), the 10 s comparison time for the response ratio provided a valid bioassay of cardiac responsiveness to sensory stimulation. The duration of the arrhythmia associated with sensory stimulation was also determined and measured as the time from the beginning of cardiac arrhythmia to the resumption of pre-stimulus cardiac activity levels.

Response ratios were analyzed using a repeated measures ANOVA (Tabachnick and Fidell, 1983). The five trials of each stimulus on a given crab were treated as the repeated measure. This analysis provided an estimate of variation within trials. If this variation was not significant, then all trials within stimulus types were treated as individual samples for analysis of the main effects (stimulus type). Comparisons among the response ratios for the three stimulus types were made using the least significant difference (LSD) method and an experimentwise error rate of 0.05 (Sokal and Rohlf, 1981).

Using the infrared scope, all crab behavior was observed before and for 30 s following presentation of the stimulus. Behavior was then divided into three categories (see also Grober, 1988*a,b*): (1) movement of the body or chelipeds towards the stimulus, (2) movement of the body or chelipeds away from the stimulus, and (3) no response. Using a χ^2 analysis, the frequency of each behavioral category was compared among stimulus types, with the control stimuli serving as the expected values. This analysis assumed that the repeated trials on individual crabs were independent events.

Effects of body size and temperature

To develop an accurate cardiac bioassay of crab behavior, it was important to determine the effects of other physical and biological variables on heart rates, so that these factors could be controlled when testing the effects of sensory stimuli. For this reason, the effects of body size and temperature on heart rate were also investigated. 19 crabs were used in both of the following sets of experiments. Crabs of different sizes were kept at $15 \pm 1^\circ\text{C}$ and heart rate was sampled every 0.05 s for 1 min. Mean heart rate was determined for each record and plotted as a function of the carapace length of the crab. Heart rates of these same crabs were also sampled at 2–3°C intervals for temperatures ranging from 10 to 25°C. Water temperature was monitored with a thermocouple probe connected to a separate data input channel of the computer. The thermocouple was previously calibrated against a mercury thermometer for temperatures between 0 and 100°C. Mean heart rate and temperature were determined from 1-min recordings with samples taken at 0.05-s intervals.

Results

Most crabs maintained a steady heart beat (Fig. 1A) with a mean heart rate in an undisturbed crab (28 mm carapace length) at 15°C of $108.5 \pm 9.8 \text{ beats min}^{-1}$ ($\bar{x} \pm \text{s.d.}$). Crabs exhibited increases in heart rate (up to a maximum of 185 beats

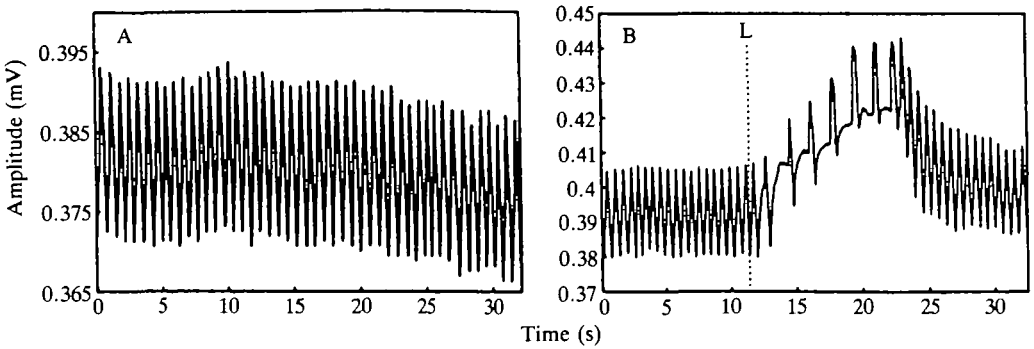


Fig. 1. Electrocardiograms of the crab *Portunus xantusii* showing (A) undisturbed cardiac activity in a dark-adapted crab and (B) the effects of *Renilla* luminescence on crab heart rate. L is the time mark for the luminescent flash. Flashes were produced 2 cm from the eyes of the crab. Flash duration was approximately 5 s. All recordings were conducted at $15 \pm 1^\circ\text{C}$.

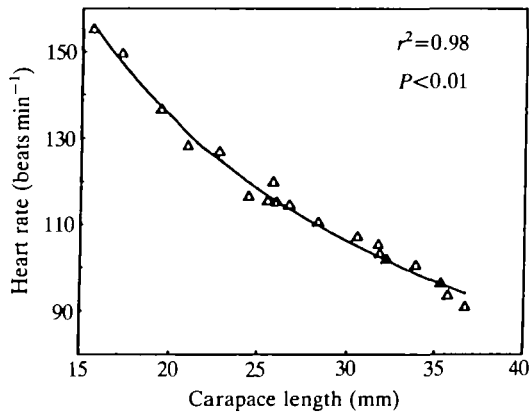


Fig. 2. Heart rate plotted as a function of carapace length for 19 individual *Portunus xantusii*. All recordings were made on dark-adapted crabs at $15 \pm 1^\circ\text{C}$.

min^{-1}) during the first few minutes following insertion of the electrodes and took from 6–18 h to return to a consistent and stable rate.

Effects of body size and temperature

Heart rate varied inversely with body size (Fig. 2). A regression of the heart rate versus body size provided the following equation:

$$f_H = 794.3x^{-0.59222}$$

where f_H is the heart rate in beats min^{-1} and x is the carapace length in mm.

Heart rate increased with increasing temperature within the range 10 – 22°C (Fig. 3). There was no further increase in heart rate between 22 and 26°C . **A**

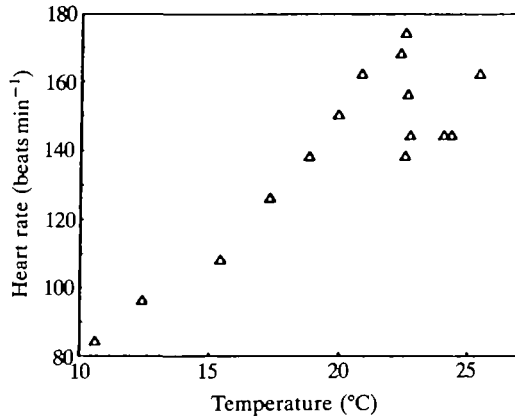


Fig. 3. Heart rate plotted as a function of ambient temperature for an individual crab with a carapace length of 29 mm.

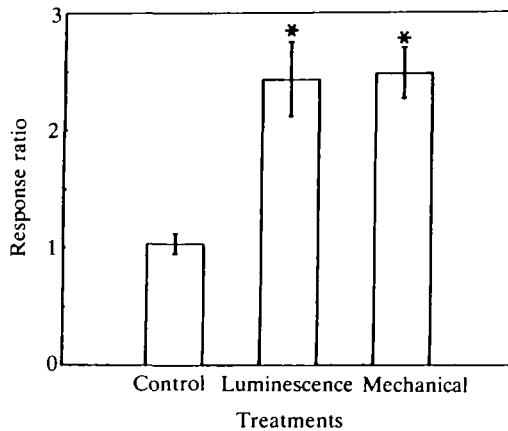


Fig. 4. Response ratios (ratio of heart rate 10s before to that 10s after stimulus) to visual and mechanical sensory stimuli and to control stimuli for five individual *Portunus xantusii*. $N=25$ for all three bars within a treatment (five crabs were observed over five trials with each treatment). * $P<0.01$, Repeated-measures ANOVA. See text for details.

logarithmic plot of heart rate *versus* temperature provided a Q_{10} of 1.8 between 10 and 20°C ($N=19$).

Effects of sensory stimuli on heart rate and behavior

Both luminescent flashes and mechanical prods produced significant increases in the response ratio compared to the control (Fig. 4). This increase in the response ratio is the result of a rapid decrease in heart rate following a stimulus (see Fig. 1B). The period of decreased heart rate for both luminescent and mechanical

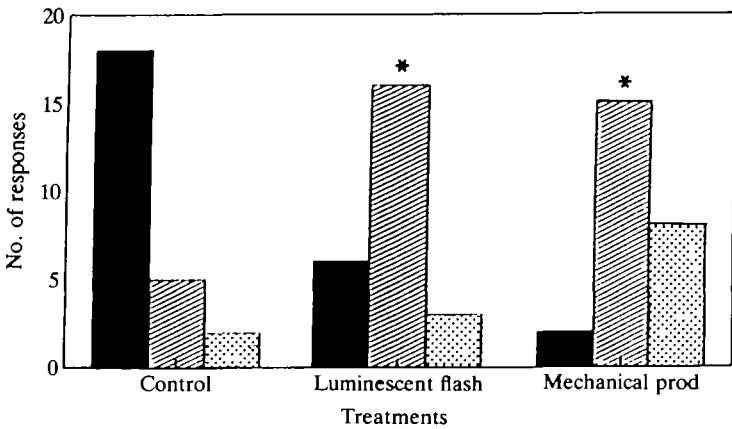


Fig. 5. Number of responses of *Portunus xantusii* for each behavioral category after presentation of the two sensory stimuli and the control stimulus. $N=25$ for the three bars combined within a treatment. Five crabs were observed over five trials with each treatment. * $P<0.001$, χ^2 goodness-of-fit test, with the results from the control stimuli used as the expected values. Black bars, no response; cross-hatched bars, movement away from the stimulus; stippled bars, movement towards the stimulus.

stimuli ranged from 7 to 28 s, with an average of 13.7 ± 9.6 s ($\bar{x} \pm s.d.$, $N=50$). There was no significant difference between the response ratios for the luminescent and mechanical stimuli ($P<0.05$, LSD).

There were significant differences between the control group and the two stimulus groups in the frequencies of the three behavioral responses (Fig. 5). In 70% of the trials, the control group showed no response. In contrast, the majority of the trials for both the luminescent and mechanical stimuli resulted in movement away from the stimulus. Crabs showed higher frequencies of no responses and lower frequencies of moving towards the stimulus in response to luminescent stimuli than to mechanical stimuli (Fig. 5).

Discussion

Relationship between heart rate and body size

The relationship between heart rate and body size in *Portunus xantusii* is similar to that established for *Carcinus maenas*, another species of portunid crab (Ahsanullah and Newell, 1971). Although the slopes of the regression lines for these two species are very close, the y -intercept in *P. xantusii* (794.3) was substantially higher than for *C. maenas* (347.1). There are at least two possible explanations for the higher heart rates exhibited by *Portunus xantusii*. First, *P. xantusii* is a temperate to sub-tropical species and the California populations exist at the northern extreme of its range. This species may therefore be adapted to warmer temperatures and would be expected to have a higher heart rate. Metabolic rate is proportional to temperature in poikilotherms and higher

metabolic rates would necessitate higher delivery and removal rates for blood gases and metabolites. The absence of individual acclimation of heart rate within a range of temperatures (5–25°C for 14–21 days) in *C. maenas* (Ahsanullah and Newell, 1971) suggests that geographic variation in the Q_{10} of crabs represents an evolutionary response at either the population or the species level. Second, in a comparison of heart rates between three species of portunid crabs, Uglow (1973) found that the intertidal species (*C. maenas*) had a significantly lower heart rate than two subtidal species. This difference is probably due to: (1) the higher concentration of dissolved oxygen in air *versus* water, and (2) the greater density of water causing a greater resistance working against the ventilatory apparatus. The end result of these considerations is that obligate water breathers spend much greater amounts of energy to extract oxygen from the environment. The higher energetic cost of ventilation would require higher rates of tissue perfusion, and thus higher heart rates. Since *P. xantusii* is exclusively subtidal, their higher heart rates compared to *C. maenas* may at least partly result from the same phenomenon.

The relationship of heart rate to temperature in *Portunus xantusii* yields a Q_{10} of 1.8 between 10 and 20°C, and this is similar to values for *C. maenas* ($Q_{10}=1.7$ between 10 and 20°C, Ahsanullah and Newell, 1971) and values for two species of *Cancer* (*C. magister* and *C. productus*; $Q_{10}=2$ between 4 and 19°C, Florey and Kriebel, 1974). Both species of *Cancer* and *P. xantusii* show a plateau at 22°C, beyond which there is no predictable change in heart rate with increasing temperature.

Responses to sensory stimulation

The results from the present study demonstrate that portunid crabs from temperate environments produce behavioral responses to luminescent flashes that are very similar to the responses of tropical portunids to brittle-star luminescence (Grober, 1988a,b). These responses include movement of the body or cheliped away from the point of luminescence. In addition, *Portunus xantusii* exhibits predictable and repeatable decreases in heart rate in response to *Renilla* luminescence and mechanical stimulation, and the responses to both types of stimuli are very similar (Figs 4 and 5).

The physiological importance of prolonged decreases in ventilation and circulation was discussed by Burnett and Bridges (1981). They suggested that spontaneous bradycardia and apnoea functioned to optimize the expenditure of energy during periods of non-activity by utilizing oxygen stores built up during periods of ventilation. While this interpretation is useful from an energetic standpoint, it does not explain why heart and scaphognathite rates change in response to sensory stimulation. The only functional interpretation proposed for this response is that the decreases in heart and scaphognathite activity produce concomitant decreases in electrical output and water movement around the animal (McMahon and Wilkens, 1972). This rapid decrease in physiological activity of the prey may help disguise it from predators that utilize electrical or mechanical cues

for catching prey (Wilkins *et al.* 1974), and for this reason it has been described as a component of the 'death-feigning behavior' in decapod crustaceans (McMahon and Wilkins, 1972) which was originally proposed by Horridge (1965). Although death-feigning may be a plausible explanation for some species, it is unlikely to be the primary explanation for bradycardia in portunids, since this physiological response is also highly correlated with active movements away from the stimulus (Figs 4 and 5). Such movements would certainly be more likely to reveal the position of a crab, *via* electrical and other sensory stimuli, than would small changes in cardiac or ventilatory activities. There is not enough information available to develop a satisfactory interpretation of sensory-induced changes in heart rate. Nonetheless, because it correlates with the production of avoidance behavior, this physiological response provides a robust bioassay that can be used to determine the specific characteristics of sensory stimuli that can elicit avoidance or startle behavior from portunid crabs (Grober, 1990).

The cardiac responses of portunid crabs to luminescent stimuli may represent an example of the well-documented responses of many animal species to rapid and intense sensory stimuli (startle response; for a review, see Eaton, 1984). Further support for this suggestion comes from two related areas. First, in most cases of sensory stimulation, both the heart and the scaphognathites of decapod crustaceans exhibit a coordinated and rapid decrease in beating (Larimer, 1964; McMahon and Wilkins, 1972; Cumberlidge and Uglow, 1977). Wilkins *et al.* (1974) went on to demonstrate that this coordinated response is the result of a command system of interneurons, located in the circumesophageal connectives, which innervate both the heart and gill bailers. In addition, stimulation of this command system also elicits leg movements (Wilkins *et al.* 1974), which are a common behavioral response of portunids to luminescent flashes (Fig. 5, and Grober, 1988a). Second, a wide variety of sensory stimuli elicit similar decreases in heart and/or scaphognathite rates (Larimer, 1964; Larimer and Tindel, 1966; Uglow, 1973; Florey and Kriebel, 1974; Wilkins *et al.* 1974; Cumberlidge and Uglow, 1977; present study). The generality of this response apparently results from multisensory convergence onto the same command system. This command system may be the primary neural pathway that enables the central pattern generators for ventilation and circulation to be overridden by sensory input (Wilkins *et al.* 1974).

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