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# Bioelectric field potentials of the ventilatory muscles in the crayfish

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**Abstract**

This study investigated the pattern of the electrical field potentials recorded near the prebranchial chamber of the native crayfish *Astacus leptodactylus*. Inside the prebranchial chamber, the electrical waves had maximal amplitude and showed 2–4 peaks per cycle. Potentials with the same frequency but smaller amplitude and simpler shape were also recorded outside the chamber, near the edge of the carapace, and at some distance towards the caudal direction. Correlation of these electrical potentials with movements of the scaphognathite in intact *Procambarus cubensis* with a transparent external wall of the prebranchial chamber has shown a high coincidence both in rate and phase of the two processes. The electrical activity picked up by an electrode located in the prebranchial chamber or near it represents the cumulative electrical field generated by the muscles moving the scaphognathite, and may be termed as the electroscaphognathitegram (ESG). The correlation of the mechanoscaphognatitegram determined optically from the magnified image of the scaphognathite and the ESG allowed us to suggest that the ascending phase of single electrical wave corresponds to the activation of the muscles responsible for downward movement of the scaphognathite, whereas its descending phase reflects its upwards movement.


*Keywords:* Crayfish; Decapods; Bioelectric field potentials; Scaphognathite; Ventilatory muscles

## 1. Introduction

Oxygen uptake in decapod crustaceans occurs across the gills that are situated in two (one on each side) narrow branchial chambers. For renewal of the water near gills, these animals use a very efficient pumping system consisting of two specialized appendages, scaphognathites (SG), one on each side, at the anterior ends of the branchial chambers. The SG, a strongly modified second maxilla, is a blade like structure which moves from a fully levated (dorsal) to a fully depressed (ventral) position, drawing water across the gills by its rhythmic movements. The neuronal circuitry of the ventilatory pattern generator is known to a lesser degree than that of the generators of the heart and stomatogastric rhythms. Only in the crab has the circuitry been investigated in some detail; it was shown that the generator is situated in the fused thoracic ganglion and consists of several non-spiking interneurons and approximately 30 motor neurons (Mendelson, 1971; Simmers and Bush, 1980; DiCaprio, 1989). In the crayfish, it is located in the suboesophageal ganglion but its neuronal architecture is not known.

Many different techniques have been used for recording the activity of the SGs in various deca-

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pods. Most of them, however, are highly invasive, and require the animal to be immobilized and partially damaged (McMahon and Wilkens, 1972; Pilkington and Simmers, 1973; Naynert, 1975; Young, 1975; Berlind, 1977; McMahon and Wilkens, 1977). Thus, the investigation of normal ventilatory activity that is known to depend strongly on the behavioral situation of the crayfish (Shuranova and Burmistrov, 2001) has not been possible. Until today, studies of the SG-activity in minimally restrained small crustaceans have only been possible by using the impedance technique of activity measure. It was introduced by Dyer and Uglow (1977), in their work with tiny (0.3–0.4 g) *Crangon crangon* and later became popular among physiologists dealing with heart and ventilation activity in various decapods (Dyer and Uglow, 1978; McMahon and Wilkens, 1983; Schapker et al., 2002). The technique is based on using the impedance pneumograph that produces a small oscillating current (2 μA; 25 kHz) between the electrodes. As noted by authors, 'Anything which causes an impedance change between the electrodes produces a proportional voltage change …' (Dyer and Uglow, 1977, p.119).

For a number of years we have studied the ventilatory activity of free moving crayfish *P. cubensis* using another non-invasive technique that is based on recording the bioelectric field potentials produced by the SG-moving muscles (Shuranova et al., 1993; Burmistrov and Shuranova, 1996; Shuranova and Burmistrov, 2001). The aim of this paper is to substantiate this novel field potential technique.

## 2. Methods

The experiments were carried out on the freshwater crayfish *Astacus leptodactylus* and *P. cubensis*. The native crayfish, *A. leptodactylus*, were obtained from a local market (Moscow, Russia). The range in the body length, from rostrum to telson, was 8–12 cm. The crayfish *P. cubensis* were taken from a population raised in the laboratory; their body lengths ranged from 4 to 6 cm, and their weight varied from 2.5 to 4 g.

There were four experimental sessions carried out on the animals fastened with narrow rubber bands to the bottom of a tank, which was covered with a layer of synthetic material and filled with water (0.8 l in experiments with *Astacus*, 0.4 l in experiments with *Procambarus*). Although the crayfish were not harmed, the conditions were highly unnatural and stressful. The experimental recording periods lasted two to 3 h. After an experiment, crayfish were returned to their home tank and appeared to resume their normal behavior. The first session was carried out on large intact crayfish *Astacus* ($n=8$), and sessions 2 though 4 were conducted on *P. cubensis*.

The first session was aimed at studying electrical potentials recorded at different points near the prebranchial chamber and inside it. The potentials were registered by one or two recording electrodes (enameled copper, 0.1 mm in diameter, exposed end was 1–2 mm); they were fixed on the carapace with plasticene. One or two reference electrodes were placed on an adjacent part of the carapace or in the water of the chamber. The potentials were amplified with a standard biological amplifier 'Medicor' (Hungary) with a time constant of 0.3–0.5 s. The polarity of the recordings was chosen in such a way that an upward deflection corresponded to negativity of the external electrical signal. A data recorder SDR-41 (Japan) was used to record and store the slow potentials. Some signals were also sent directly (via the interface PCL-718) to a computer.

During the 2nd through 4th sessions intact, specially selected *P. cubensis* whose external wall of the prebranchial chamber was transparent enough to visually observe the rhythmic SG-movements were used. At the 2nd session ($n=5$), both the electrical potentials at the anterior opening of the prebranchial chamber, and movements of the SGs and other appendages located near the mouth opening were recorded. Videorecording of the SG-movements was carried out by the Video Camera Recorder CR-2000S (Germany) or Panasonic VHS-C Movie Camera (NV-VX30EN, Japan), magnified 15 times.

In the 3rd session, the crayfish *P. cubensis* ($n=7$) was fastened on its side in a glass vessel with the bottom covered with a layer of transparent material (Sylgard). An emitter of infra-red light (AL107B; power 10 mW, λ 0.9–1.2 mm) was situated under the vessel. Above the crayfish, at the area of the prebranchial chamber, a small photo-transistor was placed (working area $1.2\times1.2$ $mm^2$, $S_{1\ int}$ not less than 0.8 mA/lx). Optical signals and electrical activity near the prebranchial chamber were recorded in complete darkness.

In the 4th session ($n=8$), displacements of the magnified SG-image were recorded on the screen

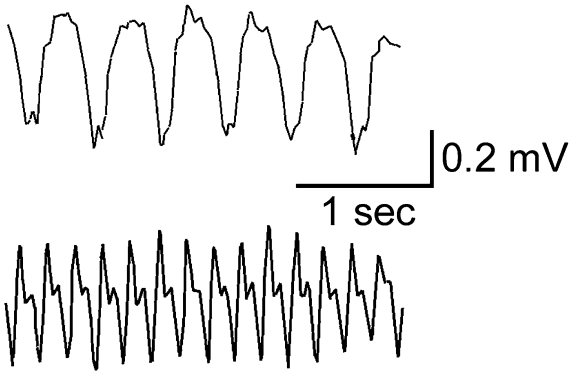


Fig. 1. Two 3-s fragments of the electrical potentials (negativity upwards) which were recorded near the anterior opening of the prebranchial chamber in *A. leptodactylus* (top), and *P. cubensis* (bottom) are shown. The crayfish were held in place with rubber bands while immersed in water.

of the monitor which allowed the placement of a photo-transistor near the bottom or the top of the image in the prebranchial chamber. One channel of the amplifier monitored signals from the photo-transistor and the second channel monitored the electrical potentials at the anterior opening of the prebranchial chamber. Both signals were captured directly on a computer and were stored for later analysis.

## 3. Results

In restrained as well as in the freely moving crayfish, an electrode whose bare tip was bent slightly under the carapace near the anterior opening of the prebranchial chamber detected a sequence of the electrical waves appearing with the rate of several cycles per second. This electrical activity was highly regular, and the duration of a single wave was a reliable index of the average rate. It should be noted that in the experiments on the immobilized crayfish lying in an unnatural posture, the SGs were working probably close to the upper limit of their capabilities because of the stressful state of the animal (Shuranova and Burmistrov, 2001). Under these conditions, the rate of the potentials measured in *Astacus* was lower than in *Procambarus* (Fig. 1). In different experiments on *Astacus*, the rate varied from 1.5 to 3 Hz whereas in experiments on *Procambarus* it varied from 3 to 5 Hz. The mean rate for *Astacus* was $2 \pm 0.08/\mathrm{s}$ ($n=8$) and for *Procambarus* it was $4.9 \pm 0.1/\mathrm{s}$ ($n=20$).

The parameters of single waves remained almost constant during the 2-h experiments; sometimes a gradually developing decrease in amplitude and a slight rise in the duration of the waves was observed. The shape of the wave depended on its duration. The shortest wave (approx. 0.2 s) had the simplest (almost sinusoidal) shape, with only one maximum. The longer waves sometimes had a plateau with a second peak. The position of the second peak in subsequent waves was variable.

The first question to be addressed concerned the distance from which one can record an electrical signal related to the SG-activity, and how the location of the electrode at the 'near-SG' space affects recording. To compare signals from different sites in the 'near-scaphognathite' space, we moved an electrode as shown schematically at the center of Fig. 2: Point 1 corresponds to an electrode position near the anterior opening; Point 2, the electrode was slightly introduced inside the chamber; Point 3, the electrode outside the chamber at the projection of the middle part of the SG-plate; Point 4, the electrode near the base of the second antenna; and Points 5–7, the electrode near the 1st, 2nd and 4th thoracic legs.

Waves with maximal amplitude were recorded when the recording electrode was positioned near the anterior opening (point 1) and when it was

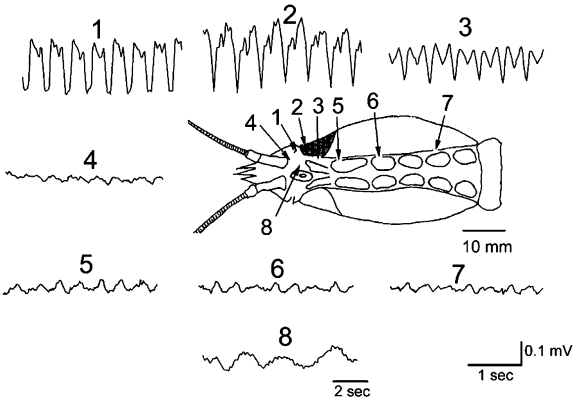


Fig. 2. Examples of electrical potentials at various points of the 'near-SG' space of *Astacus*. The schematic drawing of the anterior part of the crayfish (ventral side up) shows the sites where electrical potentials were recorded. They are designated by the following: 1, near the anterior opening; 2, inside the prebranchial chamber; 3, outside, near the projection of the middle point of the SG-plate; 4, near the base of the second antenna; 5, 6, 7—near the base of the 1st, 2nd and 4th thoracic legs; 8, near the mouth opening). Calibrations: 0.1 mV, 1 s (for fragments 1–7), 2 s (for a fragment 8).

introduced into the prebranchial chamber (point 2). At point 3, the amplitude was smaller, and the shape of the potential wave different. At points 5–7, the amplitude was further reduced, and the shape was relatively simple. However, it was possible to see that potentials probably related to the activity of the SG-muscles when an electrode was moved rather far from the prebranchial chamber in a caudal direction (up to the base of the 4th walking leg). In contrast, if an electrode was moved rostrally, the potential waves decreased very rapidly in their amplitudes, and at the base of the second antenna (point 4), they were barely detectable. When an electrode was taken away from the carapace toward the mouth opening, at a distance of 3–5 mm, the above described potential waves were almost absent; instead, it was possible to record the slower potential waves which were probably associated with the activity of the muscles of the 3rd maxilliped (point 8).

For a more detailed study of the electrical field potentials, we recorded simultaneously with two electrodes located at different sites inside and outside the prebranchial chamber (Fig. 3). Comparisons were made of the potentials picked up within the anterior opening and those located outside the chamber (A). In different trials, one or both electrodes were positioned with one electrode at the posterior end of the chamber and the other electrode outside near the base of the 1st thoracic leg (B). The results indicated that the configuration of the potential waves inside the prebranchial chamber was more complex than that outside it. The internally recorded potentials consisted of two to four components whereas externally recorded potentials had a flattened shape, mostly with only one maximum. Both, the internally and externally recorded potentials, were strongly synchronous with each other.

On the contrary, if one electrode was shifted relative to the other electrode, the potentials recorded showed an obvious change in their correlation. When one electrode was near the anterior, and the other—near the posterior end of the SG, the potentials recorded by them differed in their phases by almost 180°. This effect was seen both in a short fragment of a record (Fig. 4, top), and in the cross-correlation function counted for 10 s (Fig. 4, bottom).

These experiments also investigated the degree to which this electrical activity depended on the potentials produced by nearby appendages. In the

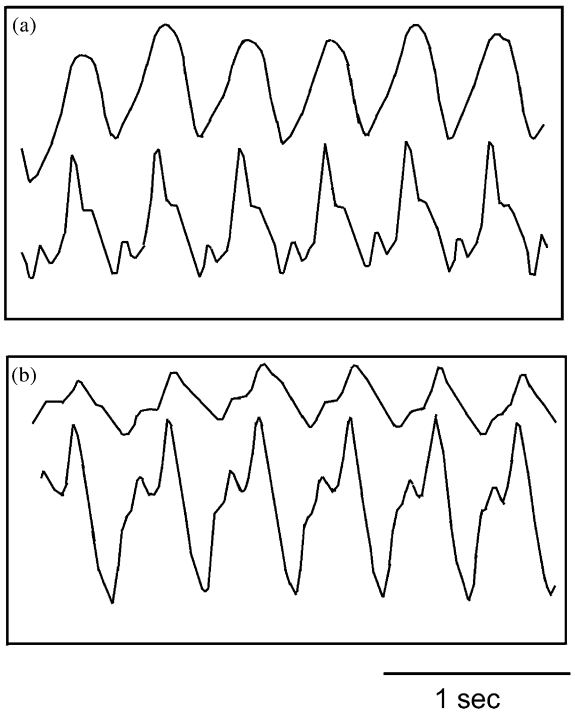


Fig. 3. Three-second fragments of electrical activity were recorded for the same experimental setting on *Astacus* by two electrodes, one placed inside the prebranchial chamber (lower record), and the other outside the chamber (upper record) but close to the first electrode [(a) the electrodes are near the anterior tip of the SG-plate, (b) near its posterior tip].

area surrounding the mouth opening, where the above-described rhythmical activity was recorded, there were no consistently active appendages, except of the SG. In animals that were immobilized and lying ventral side up, or on their side, occasional rhythmical movements of the exopodites of the 1st and 2nd maxillipeds located not far from the recording electrode were observed. They were, however, only sporadically active and functioned at higher frequencies than the SGs. Moreover, comparison of the electrical activity in both situations (moving or motionless exopodites) did not reveal any differences in the recorded field potentials, suggesting that the muscles of the exopodites did not contribute to the potentials.

It seems that the electrogram recorded by an electrode located in the water, near the prebranchial chamber, or inside it represents the summed electrical activity of the SG-moving muscles. This was already supposed earlier (Shuranova et al., 1993) and was supported by these results. By analogy with the electrocardiogram (ECG), it was named

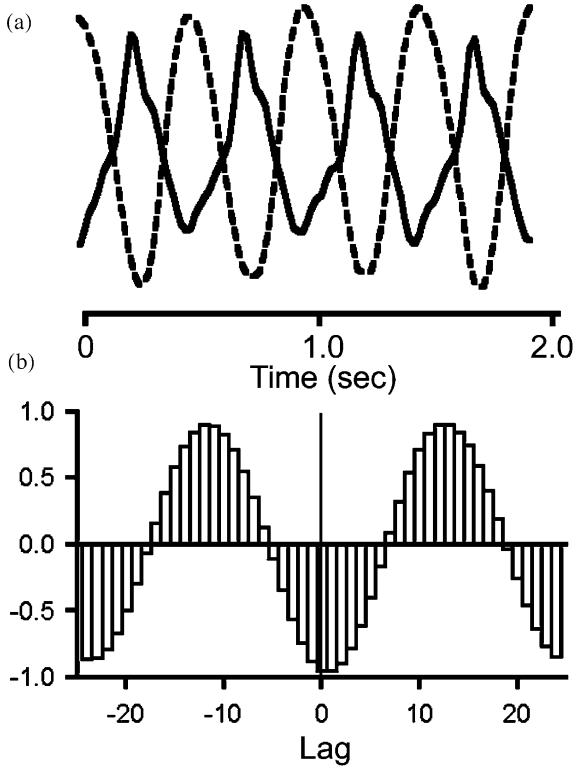


Fig. 4. A 2-s fragment of electrical potentials recorded in *Astacus* by two electrodes is shown. One is in the anterior opening (solid line) while the other is near the base of the 1st thoracic leg (dashed line) (a). A cross-correlation function for the same conditions (10-s record) is also shown (b).

the scaphognathitegram (SGG), or the electroscaphognathitegram (ESG).

In the 2nd through 4th experimental sessions with *P. cubensis*, the natural movements of the SG were correlated with the ESG. As was mentioned in the Methods, in some individuals it was possible to observe the SG-movements through the carapace. The SG-movements were counted with a 6 times slower replay of the video tapes. The recordings indicated a similarity between the rates of the SG-movements and the ESG waves. It was also shown by direct observation that when SG-movements slowed down or stopped for several seconds in response to an external perturbation, the same changes were measured in the electrical activity.

In the following session, another technique was utilized to record movements of the SG. With a phototransistor located above the area of the prebranchial chamber, rhythmic oscillations, with the rate of several cycles per second, were recorded when a crayfish was illuminated by an infrared emitter placed under the vessel (Fig. 5a). Comparison of these oscillations with the electrical potentials recorded near the anterior opening showed good coincidence between both processes (Fig. 5b,c). It should be noted that both recording

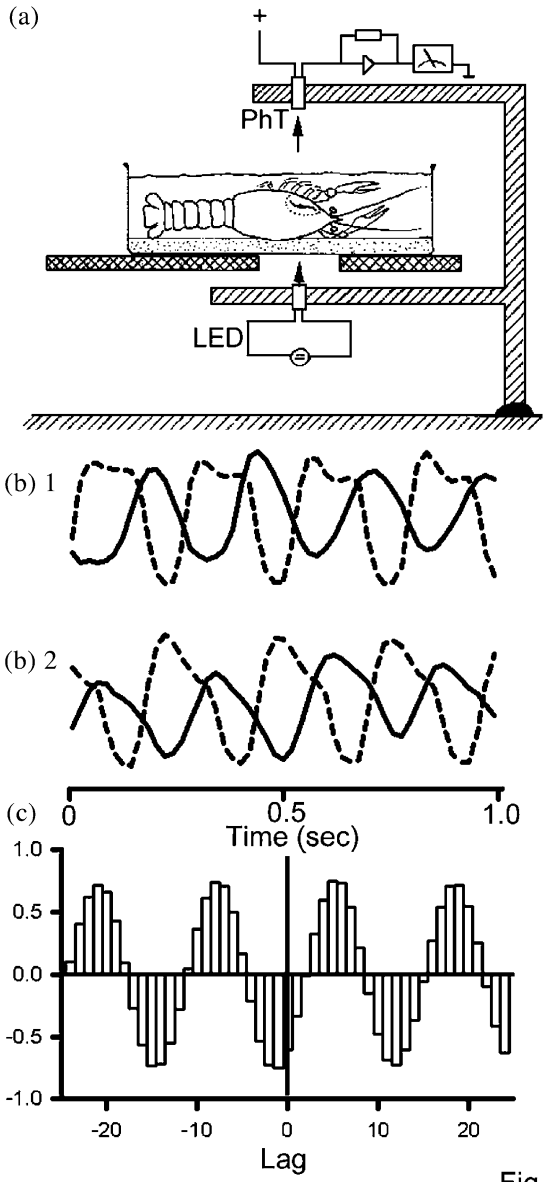


Fig. 5. Schematic drawing of the experimental conditions used for optical recording of the SG's movements of *P. cubensis*. [(a) LED—light-emitting diode, PhT—photo-transistor]. Two 1-s fragments from a 10-s simultaneous recording of the electrical potentials (dashed line) and movements of the scaphognathite (solid line) are shown (b1 and b2). A cross-correlation function of both records counted for a 10-s period is also shown (c).

techniques not only detected the same frequency, but that they also both had a strong coincidence of phase between the electrical and mechanical waves. This optically recorded activity may be determined, by analogy with the electroscaphognathitegram, as mechanoscaphognathitegram (MSG). However, this technique did not illuminate the precise temporal relations between the electrical and mechanical waves, because it was impossible to correlate the parameters of the MSG waves with the location of the SG inside the prebranchial chamber.

In the last session, the displacements of SG, in a magnified image on the TV screen, were recorded. The same phototransistor as in the previous session was used but the image was taken at several points within the prebranchial chamber. Contrary to the previous session, which used the 'natural' dimensions of the SG and prebranchial chamber, in this series of experiments the images of the structures were magnified 15 times or even to a greater magnification when the video camera 'recorded' the SG through the binocular microscope. This allowed us to locate the sensor on the upper or the lower border of the prebranchial chamber (or between them). We also chose which particular part of the SG image would appear under the sensor,-anterior or posterior tips, or middle point (hinge) (Fig. 6a). We used mostly the latter location and in different trials placed the phototransistor near the upper or the lower border of the prebranchial chamber. From such images, the length of the SG was approximately 1/10 of the body length, the length of the prebranchial chamber was close to this value, and its height was approximately $\frac{1}{2}$ of its length. So, for a 4–6 cm *P. cubensis* these values were approximately 3 and 5 mm, respectively.

The examples of the recordings obtained in these experiments are presented in Fig. 6b. In Fig. 6b1 the sensor was in the upper position, and in Fig. 6b2 it was near the lower border of the prebranchial chamber. The position of the SG could be determined precisely in relation to its position in the chamber. Therefore, it could be determined precisely at what moment the SG began to move downwards or upwards. This allowed correlation of the direction of the SG movement with the phase of the electrical wave. In fact, it was possible to extrapolate the time when the SG reached the 'sensorless' border of the prebranchial chamber, as seen in Fig. 6c. The main point deduced from these experiments was that the downward movement of the SG, (i.e. activity of depressors), coincided with the onset of the negativity of the electrical wave. The upwards movement (i.e. the activity of levators) was seen at the end of the rising phase of the electrical wave, or on its falling phase.

## 4. Discussion

The most unexpected finding of this study was that a infrared light from an emitter situated under a crayfish lying on its side could pass through the animal's body and be detected by a sensitive phototransducer. The shadowing of the light beam by the SG moving up- and downwards was recorded as oscillatory activity synchronous with electrical potential waves recorded at the exhalent channel of the prebranchial chamber. Not only was the rate of both processes the same, but there was strict coincidence of phase relations between their maxima (Fig. 5b,c). This seems to imply that these potentials represented the activity of the SG-moving muscles. It is clear, however, that this technique has its limitations. Since the size of the phototransistor was close to the size of the SG itself, acuity was low. It was also impossible to determine the strict position of the detector relative to the prebranchial chamber.

Observations of SG movements performed with the naked eye, a low-power microscope, or a TV screen indicated that the SG movements were rather complex. The SG-plate ('bailer') moved not only up and down but also constantly twisted along its long and short axes. This observation corresponds to the literary data. 'The motion of the blade-like paddle can be resolved into two components: it sweeps dorsoventrally across the pumping chamber and at the same time it pivots anteroposteriourly about the fulcrum of the protopodite' (Pasztor, 1968). More strictly, there are four components in this motion: pronation of the posterior tip, depression of the bailer, its levation, and supination of the posterior tip (Naynert, 1975; Young, 1975). An analysis of bailer movements in the crab submerged upside down in a small tank of water and recorded by cinematographic camera (16 f.p.s.) after unilateral removal of its chelae, maxillipeds, and the floor of the prebranchial chamber (Pilkington and Simmers, 1973) showed that the amplitude of excursion of the middle point of the SG is greater than that of either tip, and

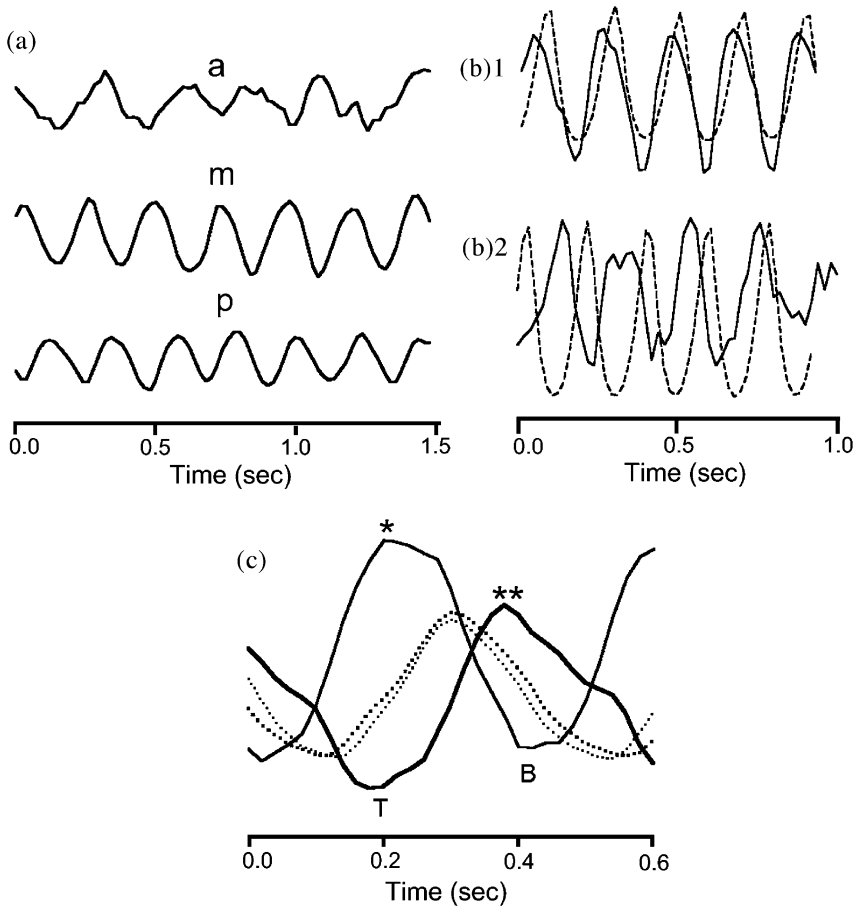


Fig. 6. (a) Movements of the scaphognathite recorded at different times of the same experiment by a photo-transistor placed on the anterior (*a*), middle (*m*), and posterior (*p*) parts of the magnified scaphognathite image as observed on a monitor are shown. With the use of the magnified image we could locate the placement of the sensor and correlate the placement with the electrical wave forms. (b) Comparison of the movements of the scaphognathite (solid line) and electrical activity (dashed line) recorded simultaneously in *P. cubensis* (b1, the photo-transistor is near the top of the prebranchial chamber and b2, near the bottom of the chamber). (c) Two short (0.6 s) fragments taken from subsequent files and superimposed on each other. Within each of the 10-s files, a moment was chosen when the electrical waves (dashed line) in both records had a similar time course. This allowed a comparison of the time course in the mechanical events, recorded by the detector in the upper position (thick line) and in the lower position (thin line). Note the moments when the SG was near the top (T) or bottom (B) of the prebranchial chamber, respectively; '*', '**' – time moments when the SG will reach the top or the bottom of the prebranchial chamber may be predicted even if the phototransistor is only at one border of the prebranchial chamber.

that the movements of the two tips are approximately 180° out of phase. The movements of different points of the SG were recorded in the crab by a movement monitor whose sensitive element consisted of a narrow strip of photoresistive material (Young, 1975; 'the dorsal carapace and hepatopancreas were removed to allow access to the SG through the epimeral wall'). The anterior and posterior tips spent a large fraction of the cycle in the extreme levated and depressed positions, flipping rapidly between these extremes. The middle point ('hinge') showed a slightly more even, somewhat sinusoidal movement. The movements of the posterior and anterior tips of the SG are out of phase (Young, 1975, Fig 12).

In the last session of our experiments, we recorded the displacements of three different points of the magnified image of the SG obtained in the intact crayfish lying in the water on its side (Fig. 6a). The middle point of the SG appeared to be the most regular with respect to shape and amplitude of its movements. In addition, maxima of

three curves characteristic for the detector's position on the SG image correlated with similar moments in the ESG wave were not coincident: the posterior and anterior tips reached their peak values with a phase shift of approximately 180° (Fig. 6c). It is interesting to note that the data obtained on the intact crayfish are close to those obtained in acute experiments on the crabs (compare Fig. 6c in this paper with Fig. 1 in Pilkington and Simmers, 1973, and with Fig 12b in Young, 1975).

The above-described rhythmical sequence of electrical potentials, termed the ESG, are suggested to reflect the summed electrical field generated by the SG-moving muscles for several reasons. There is strong correlation not only in frequency but also in time course of electrical and mechanical events. Also, no other rhythmically active muscles exist in the region where the ESG potentials can be detected. The amplitude and the shape of electrical waves depend on the position of an electrode relative to the SG. A phase shift was observed between the waves recorded by the anteriorly and posteriorly located electrodes. This is probably related to the well-established fact that the posterior tip of the SG-plate begins to move earlier than the anterior tip. We suggest that the muscles driving the posterior tip are activated prior to the muscles moving the anterior tip. The results of this work give only the first indication on the existence of the electrical field produced by the activity of the ventilatory muscles in the crayfish. Further investigation is needed to illuminate the configuration and parameters of this field.

In the crayfish, 11 muscles located in coxopodite and basipodite (Pasztor, 1968; Pilkington and Simmers, 1973) move the SG. Based on the anatomical and functional features, Young (1975) divided 10 muscles found in the crab into four groups designated as L1, L2 (levators) and D1, D2 (depressors). The electrical activity of these muscles as well as that of the associated motor axons was studied in acute experiments on the crayfish (Pasztor, 1968; Moody-Corbett and Pasztor, 1980) and crab (Young, 1975). Regularly spaced bursts of nerve impulses evoke EPSPs in the muscle fibers. Most of the muscle fibers are innervated by one motor axon, though there are some innervated by 2–4 motor neurons. The contraction sequence of different ventilatory muscles in the crayfish has been described by Pasztor (1968) and in the crab by Young (1975). In crab, the majority of the cycle (approx. 60%) corresponds to the activity of depressors. The activation of levators begins at the very end of depressors' activity with some overlap between them. Various muscles belonging to the same group (i.e. depressors or levators) work together. The unified actions of the muscles may be the reason why the slow extracellular bioelectric waves can be monitored inside the narrow prebranchial chamber and outside it, near the border of the carapace. The high-resistance fresh water seems to act as a low-pass filter, which summates and flattens the potentials of many muscle fibers transforming them into slow electrical waves whose duration corresponds to the duration of a single ventilatory cycle.

Under the conditions of the above-described experiments on *P. cubensis,* upon correlation of the ESG and MSG, a mostly high-frequency (up to 4–5 Hz) ESG was obtained. The shape of single waves was very simple (almost sinusoidal), and their amplitude was stable. This may be attributed to the stressful state of the animal (Shuranova and Burmistrov, 2001) and/or significant overlap of the activity of different ventilatory muscles. The correlation of both the ESG and MSG showed that the first phase of the electrical wave represents the activity of depressors, whereas the end of this phase and a part of the second phase are caused by the activity of their antagonists.

In normally behaving crayfish, the rate of ventilation is usually much smaller, and many different shapes of single waves are observed (see, e.g. Fig. 4 in Shuranova and Burmistrov, 2001). Often, two clearly discernible peaks can be observed, though three or four peaks are also possible. The peaks may represent the activity of the four above mentioned muscle groups. It is clear, however, that the problem of interpretation of the electrical signals produced by several sources and propagated in the conducting medium is extremely complicated. One may refer to numerous studies in the genesis of different rhythms in the human electroencephalogram. The situation with the electric field produced by the ventilatory muscles is simpler, but it seems to need special investigations in chronic experiments in the crayfish.

In decapod crustaceans, the ventilatory pattern is under the strong control of the higher nervous centers (Larimer, 1964; Wilkens et al., 1974; Wilkens, 1976; Taylor, 1982; McMahon and Wilkens, 1983). The influence exerted on the ventilatory pattern generator has been evaluated mostly

using changes in mean rate of ventilation. The impedance technique, which is simple and non-invasive, seems to be well adapted for this task. At the same time, despite year-long use of this technique, there are no data about the parameters of single components comprising the impedancegram and its correlation with the activity of the ventilatory muscles. The authors who introduced this technique noted that it was used 'to obtain qualitative data on the movements of the scaphognathite' (Dyer and Uglow, 1978, p. 195). The contribution of different SG muscles to the impedance changes has not been determined. In addition, the technique is based on applying an electrical current to the two leads, which may have an effect to the animal.

We suggest that the above-described technique of the ESG recording has some advantages over the impedance technique. It allows one to observe not only mean changes in the rate of ventilation but also to detect immediate changes in the activity of the motor generator of the ventilatory rhythm reflected in the changes of the shape and/or amplitude of single ESG-waves. The ESG is an integral index of the electrical fields of the ventilatory muscles, whereas the impedancegram reflects the SG-movements. Non-invasive recording of the electrical waves caused by neural input from the central pattern generator may be helpful in studying nervous control of various behavioral manifestations in intact free moving decapods.

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