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Dual Effects of Dopamine on the Adult Heart of the Isopod Crustacean *Ligia exotica*

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ABSTRACT—In the adult heart of the isopod crustacean *Ligia exotica,* the cardiac ganglion acts as the primary pacemaker with the myocardium having a latent pacemaker property. We show several lines of evidence that dopamine modulates the heartbeat of adult *L. exotica* affecting both pacemaker sites in the heart. Dopamine caused positive chronotropic (frequency increase) and inotropic (amplitude increase) effects on the heartbeat in a concentration dependent manner. The time courses of these effects were considerably different and the inotropic effect appeared later and lasted longer than the chronotropic effect. Dopamine rapidly increased the frequency of the bursting activity in the cardiac ganglion neurons and each impulse burst of the cardiac ganglion was always followed by a heartbeat. Moreover, dopamine slowly increased the amplitude and duration of the action potential plateau (plateau potential) of the myocardium. When the myocardial pacemaker activity was induced by application of tetrodotoxin, which suppresses cardiac ganglion activity, dopamine slowly increased the amplitude and duration of the myocardial plateau potential while decreasing its frequency. These results suggest that dopamine modulates the heartbeat in adult *L. exotica* producing a dual effect on the two pacemaker sites in the heart, the cardiac ganglion and myocardium.

Key words: heart modulation, dopamine, crustacea, *Ligia exotica*

INTRODUCTION

Investigations on decapods and stomatopods suggest that generally the crustacean heart is neurogenic (e.g. Alexandrowicz, 1932, 1934; reviewed by Maynard, 1960). In these animals, the myocardium has no inherent automaticity and the cardiac ganglion acts as a dominant pacemaker; bursting activity of the cardiac ganglion produces periodic bursts of excitatory junctional potentials (EJPs) on the myocardium and causes its periodic contraction, the neurogenic heartbeats (e.g. Irisawa *et al*., 1962; Anderson and Cooke, 1971; reviewed by McMahon *et al*., 1997).

Recently, however, some phylogenic diversity in cardiac pacemaker mechanism of crustaceans has been reported. In the brachiopod *Triops longicaudatus*, there are no neurons in the heart and the heart is myogenic with the heartbeat arising from the endogenous pacemaker activity of the myocardium (Yamagishi *et al*., 1997). In the isopod *Ligia exotica*, the cardiac pacemaker is transferred from the myocardium to the cardiac ganglion during juvenile development and thereafter the cardiac ganglion functions as the primary pacemaker with the myocardium having a latent pacemaker property (Yamagishi and Hirose, 1997).

Moreover, some diversity is found in the mechanisms of neural and neurohormonal modulation of the heartbeat among crustaceans. In the neurogenic heart of decapods, the pacemaker activity of the cardiac ganglion is subject to modulation via acceleratory and inhibitory neurons in the central nervous system (reviewed by McMahon *et al*., 1997). The heart is also modulated neurohormonally by several amines and peptides released from the pericardial organ (reviewed by Cooke and Sullivan, 1982). The amines, however, appear to affect the cardiac ganglion but not directly the myocardium (reviewed by Wilkens, 1999). In contrast, the branchiopod myogenic heart appears to have no neural innervation from the central nervous system (Yamagishi *et al*, 2000), and several amines modulate the heartbeat affecting directly the myocardium (Yamagishi, 2003). In the heart of the isopod *L. exotica*, acceleratory and inhibitory neurons in the central nervous system innervate both the cardiac

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ganglion and myocardium and modulate their pacemaker activities (Yamagishi and Ebara, 1985; Sakurai and Yamagishi, 1998a, b; Sakurai *et al*., 1999a, b). However, neurohormonal modulation of the *Ligia* heart has not been investigated yet.

We, therefore, examined the effects of several biogenic amines on the heart of adult *L. exotica*. We found that dopamine, which is one of the identified neurohormonal amines released from the decapod pericardial organ (Sullivan *et al*, 1977), modulates the heartbeat affecting two pacemaker sites in the heart, the cardiac ganglion and myocardium. Some of the results presented here have been published previously in abstract form (Yamagishi, 1999).

MATERIALS AND METHODS

Adult males and females of the littoral isopod crustacean *Ligia exotica,* 25 to 38 mm in body length, were collected on the Pacific coasts at Hitachinaka and Kominato, Japan. They were maintained in the laboratory at room temperature. More than 80 specimens were used for the experiments.

Anatomy of the heart and the method of dissection were as described previously (Yamagishi and Ebara, 1985). Contraction of the heart (mechanogram of the heartbeat) was recorded in semi-isolated heart preparations (Yamagishi and Hirose, 1997). Briefly, the heart was kept intact in the pericardial cavity and isolated together with the dorsal carapace. The preparation was pinned dorsal side up in the experimental chamber and part of the dorsal carapace was removed over the middle region of the heart. The suspensory ligament, which was left attached to the heart, was tied using fine thread and was connected to a mechano-electric transducer (Nihon Kohden, TB-651T). Mechanograms of the heartbeat were also recorded in completely isolated heart preparations. No detectable differences in the heart responses to dopamine were found between the two types of preparations.

In some cases, motor activity of the cardiac ganglion was recorded simultaneously with the mechanogram of the heartbeat in semi-isolated heart preparations. In these cases, impulse bursts were extracellularly recorded from an anterior nerve branch of the cardiac ganglion by sucking the distal cut end of the nerve into a suction electrode (Yamagishi and Ebara, 1985).

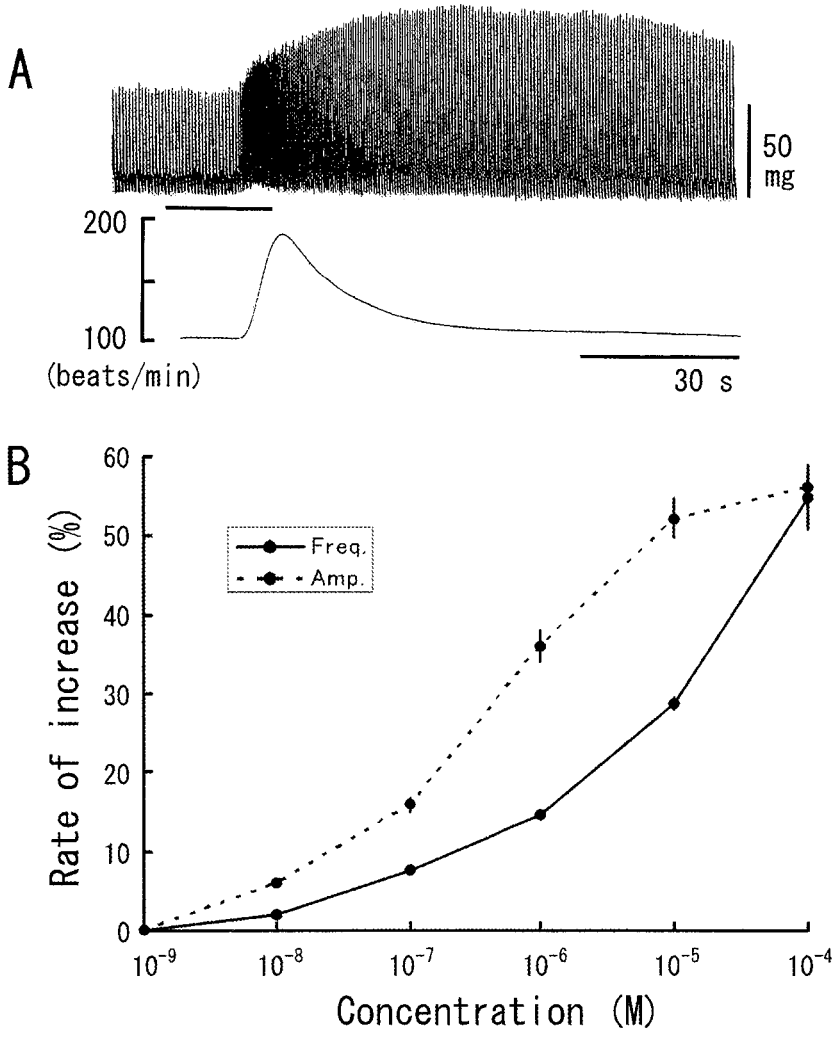

Fig. 1. Effects of dopamine on the heartbeat. (A) Mechanogram (upper trace) and frequency (lower trace) of the heartbeat. Dopamine (10^{-4} M) was applied during the period (20 s) indicated by the horizontal bar under the mechanogram. (B) Relationships between rate of increase (%) in the frequency (solid line) and amplitude (dotted line) of the heartbeat and dopamine concentration (M). Each plot shows the mean value (Mean ±SEM) obtained from 13 preparations.

The membrane potential of the myocardial cells and cardiac ganglion neurons was recorded using a conventional glass microelectrode filled with 3 M KCl (electric resistance, 10 to 30 MΩ). Activity of the myocardial cells was recorded from the ventral myocardium of the heart in semi-isolated heart preparations pinned ventral side up in the experimental chamber. To record activity of the cardiac ganglion neurons located on the inner surface of the dorsal heart wall, the heart was opened by a longitudinal incision of the ventral heart wall, isolated completely and pinned inner side up in the experimental chamber. Intracellular activity was recorded by inserting a microelectrode into one of the six neurons composing the cardiac ganglion (Yamagishi and Ebara, 1985). Data were recorded using a magnetic tape recorder (Sony Precision Technology, PC204AX) and a chart recorder (Graphtech, WR7700).

In all the experiments, the preparation was continuously perfused with aerated physiological saline having the following composition (in mM): NaCl 586, KCl 14, $CaCl_2$ 25, $MgCl_2$ 4.5, Tris-HCl 5 (pH 7.4) (Yamagishi and Ebara, 1985). Dopamine (dopamine hydrochloride, Wako) was added at various concentrations to the saline just before use and was applied to the heart by changing the perfusing saline. In some cases, 10^{-6} M tetrodotoxin (TTX, Wako) was added to the saline. All the experiments were performed at a temperature of 20 to 23°C

RESULTS

We first examined the effects of dopamine on the heartbeat. The beat frequency of the semi-isolated heart preparations used was in the range from 96 to 186 beats/min. In the case shown in Fig. 1A, application of 10^{-4} M dopamine for 20 s caused a 77.5% increase in the frequency (from 102 to 181 beats/min) and a 88.2% increase in the amplitude (from 56.7 to 106.7 mg). However, these positive chronotropic (frequency increase) and inotropic (amplitude increase) effects were different in time course. The frequency increased rapidly to the peak and then decreased to the control level. In contrast, the amplitude increased slowly and peaked more than 30 s after the frequency peak, and then decreased slowly to the control level. Thus, the peaks of the chronotropic and inotropic effects appeared separately when dopamine was applied for a short period of several tens of seconds. When dopamine was applied continuously, the frequency and amplitude of the heartbeat increased to a steady level with the frequency increase preceding the amplitude increase (data not shown).

To obtain dose-response relationships, dopamine was applied at various concentrations for 20 s (n=13). Both the frequency and amplitude of the heartbeat increased in a concentration dependent manner (Fig. 1B). The threshold concentration of dopamine to produce the acceleratory effect on either the frequency or amplitude of the heartbeat was between 10^{-9} and 10^{-8} M. The curve of the amplitude

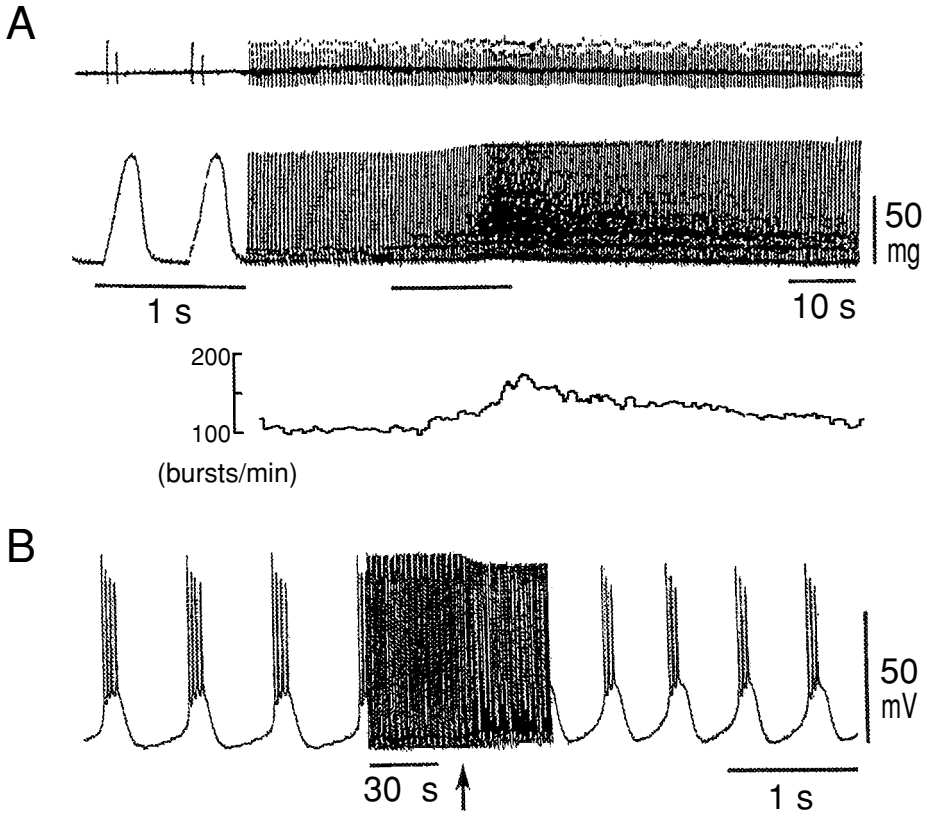

Fig. 2. Effects of dopamine on the cardiac ganglion activity. (A) Impulse activity in an anterior nerve branch of the cardiac ganglion (top trace), mechanogram of the heartbeat recorded simultaneously (middle trace) and frequency of the ganglionic impulse burst (bottom trace). Dopamine (10^{-5} M) was applied during the period (20 s) indicated by the horizontal bar under the record. Note the different time scale for the left portion of the trace. (B) Pacemaker bursting activity recoded intracellularly from a cardiac ganglion neuron. Dopamine (10^{-4} M) was continuously applied from the time indicated by the arrow under the record. Note the different time scale for the central portion of the trace.

increase appears to saturate at 10^{-5} M, while that of the frequency increase appears not to saturate even at 10^{-4} M.

We next examined the effects of dopamine on the cardiac ganglion activity by recoding impulse bursts from a nerve branch of the cardiac ganglion (n=7). Fig. 2A shows a representative example of simultaneous recording of the cardiac ganglion activity and the heartbeat. Each heartbeat appeared following an impulse burst of the cardiac ganglion. Application of 10^{-5} M dopamine for 20 s caused a 61.5% increase (from 104 to 168 /min) in the frequency of the ganglionic impulse burst and every impulse burst was followed immediately by a heartbeat.

We further examined the effects of dopamine on the pacemaker bursting activity of the cardiac ganglion neurons by inserting a microelectrode into one of the six neurons comprising the cardiac ganglion (n=16). The bursting frequency of the cardiac ganglion usually declines in an opened heart preparation compared to a semi-isolated one (Yamagishi and Ebara, 1985); the bursting frequency of the cardiac ganglion neuron in the preparations used was in the range of 43 to 89 bursts /min. In the case shown in Fig. 2, continuous application of 10^{-4} M dopamine caused a 67.7% increase (from 65 to 107 / min) in the bursting frequency of the cardiac ganglion neuron. Dopamine thus accelerated the pacemaker bursting activity of the cardiac ganglion neurons while the number of spike potentials in a burst was unchanged or often decreased.

In the heart of adult *L. exotica*, the myocardial action potential composed of a plateau potential and spike potentials superimposing on it (Yamagishi, 1996) is evoked synaptically by the cardiac ganglion activity and causes the heartbeat (Yamagishi and Hirose, 1997). We therefore examined the effects of dopamine on the membrane potential of the myocardial cells (n=9). Fig. 3A shows a representative example. Application of 10^{-5} M dopamine for 20 s caused a 20.5% increase (from 151 to 182 /min) in the frequency of the myocardial action potential. Moreover, dopamine changed the contour of the myocardial action potential; the duration and amplitude of the plateau potential increased slowly, peaked more than 30 s later than the fre-

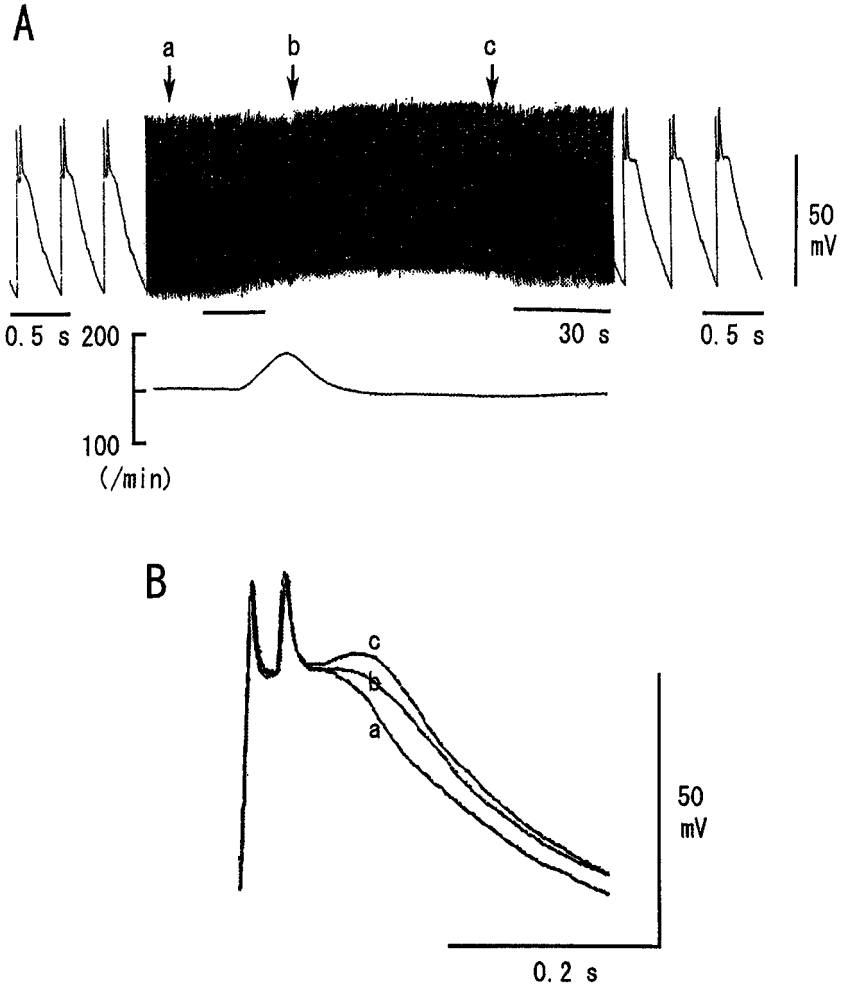

Fig. 3. Effects of dopamine on the myocardial activity. (A) Electrical activity recorded intracellularly from a myocardial cell (upper trace) and frequency of the myocardial action potential (lower trace). Dopamine (10^{-5} M) was applied during the periods (20 s) indicated by the horizontal bar under the record. Note the different time scale for the central portion of the trace. (B) Three action potentials obtained at the times indicated by the arrows (a, b and c) in A are superimposed.

quency peak, and then decreased slowly to the control level (Fig. 3B). The time course of the change in the plateau potential was similar to that of the positive inotropic effect of dopamine on the heartbeat (cf. Fig. 1A).

The heartbeat of adult *L. exotica* is changed from neurogenic to myogenic by application of TTX that suppresses the cardiac ganglion activity; myocardial plateau potentials appeared spontaneously lacking TTX-sensitive spike potentials, each of which is followed by a myogenic heartbeat (Yamagishi and Hirose, 1997). We therefore examined the effects of dopamine on the pacemaker activity of the myocardium induced by TTX application (n=6). Fig. 4 shows a representative example. In the neurogenic heart perfused with normal saline, application of 10^{-5} M dopamine for 20 s caused a 25.8% increase (from 177 to 230 /min) in the frequency of the myocardial action potential (Fig. 4A). Dopamine caused also a slow increase in the duration and amplitude of the action potential plateau (data not shown). In contrast, in the myogenic heart perfused with saline containing 10^{-6} M TTX, application of 10^{-5} M dopamine for 20 s caused a slow 25.8% decrease (from 163 to 121 /min) in the frequency of the myocardial plateau potential while increasing its amplitude and duration (Fig. 4B).

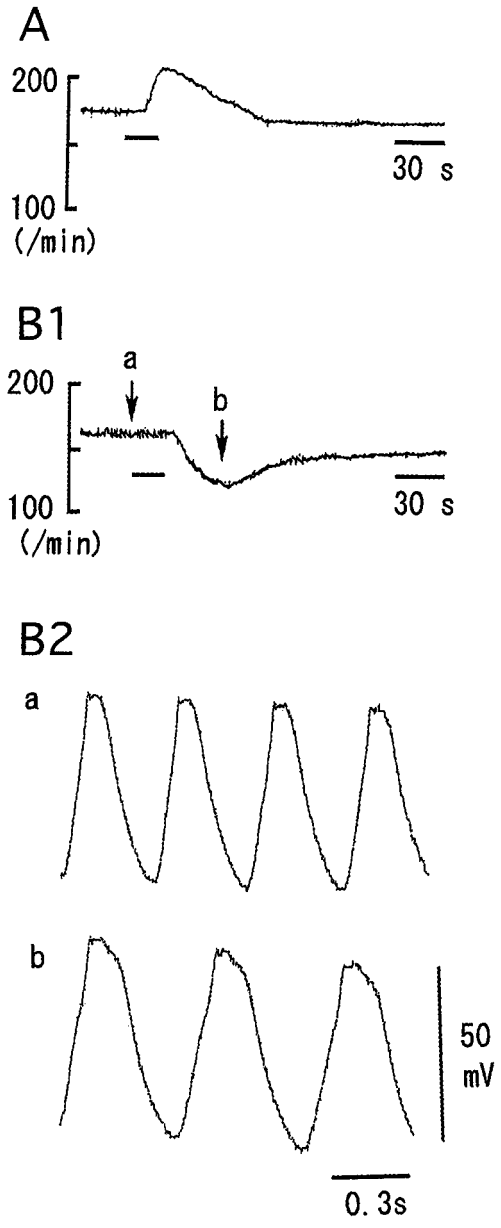

Fig. 4. Effects of dopamine on the myocardial activity in normal and TTX-containing saline. Frequency of the myocardial action potential recorded intracellularly for the same preparation in normal saline (A) and in saline containing 10^{-6} M TTX (B1). Dopamine (10^{-5} M) was applied during the 20s period indicated by the horizontal bar under the record. (B2) Myocardial plateau potentials recorded at the times indicated by the arrows (a and b) in B1.

DISCUSSION

Dopamine produced positive chronotropic and inotropic effects on the heartbeat of adult *L. exotica* with different time courses; the frequency of the heartbeat increased rapidly and the amplitude slowly. Therefore, the peaks of the chronotropic and inotropic effects appeared separately when dopamine was applied for a short period (Fig. 1A). Moreover, some differences were found in dose-response curves of dopamine between the chronotropic and inotropic effects (Fig. 1B). These observations suggested dual effects of dopamine on the *Ligia heart*.

In the heart of adult *L. exotica*, the cardiac ganglion functions as the primary pacemaker with the myocardium having a latent pacemaker property (Yamagishi and Hirose, 1997). Dopamine increased rapidly the frequency of the bursting activity of the cardiac ganglion neurons and every impulse burst of the cardiac ganglion was followed by a heartbeat (Fig. 2). These results show clearly that dopamine causes a positive chronotropic effect on the heartbeat by accelerating the pacemaker activity of the cardiac ganglion neurons. All six neurons comprising the *Ligia* cardiac ganglion have pacemaker and motor functions and produce synchronously impulse bursts via electrical connections among them (Yamagishi and Ebara, 1985). All the neurons in the cardiac ganglion appear to be homogeneous and we could not determine dopamine sensitivity of individual neurons.

Dopamine increased the amplitude and duration of the plateau potential of the myocardium (Fig. 3) and the time course of the plateau potential change was similar to that of the inotropic effect on the heartbeat (Fig. 1A). This effect of dopamine was confirmed in pacemaker activity of the myocardium induced by perfusion of TTX-containing saline; dopamine increased the amplitude and duration of the myocardial plateau potential (Fig. 4). Magnitude of contraction of crustacean skeletal and cardiac muscle depends on the absolute value of the potential change (Orkand, 1962: Atwood and Dorai Raj, 1964; Brown, 1964; Holley and Delaleu, 1972). In the *Ligia* heart, reinforcement of the action potential plateau (plateau potential) of the myocardium induced by stimulation of the cardioacceleratory nerve

results in an increase in the amplitude of the heartbeat (Sakurai and Yamagishi, 1998b). These facts lead to the conclusion that dopamine produces an inotropic effect on the heartbeat by reinforcing the myocardial plateau potential.

Dopamine produces usually acceleratory effects on the heart in insects (e.g. S.-Rózsa and V.-Szöke, 1972; reviewed by Miller, 1985) and molluscs (e.g. S.-Rózsa and Nagy, 1967). However, dopamine is not consistently acceleratory in molluscs (reviewed by Jones, 1983). Similarly, some differences in the effect of dopamine on the heart have been reported in crustaceans. Dopamine produces acceleratory effects on the heart of several decapods (Florey and Rathmayer, 1978; Wilkens *et al*., 1985; Yazawa and Kuwasawa, 1994), of the stomatopod *Squilla oratoria* (Ando *et al*., 1995) and of the isopod *Ligia exotica* (Yamagishi *et al*., present study), but produces inhibitory effects on the heart of the decapod *Cancer magister* (Airriess and McMahon, 1992) and of the isopod *Bathynomus doederleini* (Tanaka *et al*., 1992).

On the other hand, targets of dopamine modulation appear to be different among crustacean hearts with different pacemaker mechanisms. In the neurogenic heart of decapods, impulse bursts generated in the cardiac ganglion produce bursts of EJPs on the myocardium and cause periodic contraction of the myocardium (reviewed by Maynard, 1960; McMahon *et al*., 1997); dopamine causes positive chronotropic and inotropic effects by affecting the cardiac ganglion (Miller *et al*., 1984; Berlind, 1998). In the heart of the isopod *L. exotica*, both the cardiac ganglion and myocardium have pacemaker properties and, in the heart of adults, impulse bursts generated in the cardiac ganglion induce synaptically action potentials in the myocardium and causes its periodic contraction (Yamagishi and Hirose, 1997). The results of the present study show that dopamine causes a positive chronotropic effect by affecting the cardiac ganglion and a positive inotropic effect by affecting the myocardium. In the branchiopod *T. longicaudatus*, the heart is myogenic (Yamagishi *et al*., 1997) and dopamine causes positive chronotropic and inotropic effects by affecting the myocardium (Yamagishi, 2003).

Dopamine is one of the neurohormones released from the decapod pericardial organ (Sullivan *et al*., 1977; reviewed by Cooke and Sullivan, 1982). The presence of the pericardial organ-like structure is reported in some isopods (Delaleu, 1970), but no biochemical and physiological investigations on it have been performed. Investigations on the presence and secretion of dopamine in the nervous system of *L. exotica* are required.

The cardiac pacemaker of *L. exotica* is transferred from the myocardium to the cardiac ganglion during juvenile development and the heartbeat changes from myogenic to neurogenic (Yamagishi and Hirose, 1997). In the present study, dopamine decreased the frequency of myocardial pacemaker activity induced by perfusion with TTX-containing saline. This fact suggests that the chronotropic effect of dopamine on the heartbeat changes from negative to positive during development. Investigations on developmental changes in dopamine modulation of the heartbeat are now in progress.

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