J. exp. Biol. **145**, 339–351 (1989)
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BASIC FUNCTIONAL PROPERTIES OF THE CARDIAC MUSCLE OF THE COMMON SHREW (*SOREX ARANEUS*) AND SOME OTHER SMALL MAMMALS

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Accepted 27 April 1989

Summary

The resting heartbeat frequency of all the studied wild small mammals (body mass 3–20 g) was lower than that predicted by the allometric equation for a typical mammal. The heart rate of the laboratory mouse was a little higher than the expected value.

The ventricular mass of the small wild mammals was higher than predicted for their size, but that of the laboratory mouse was below the expected value. Thus, adequate cardiac output in the wild small mammals is achieved by compensating the low heartbeat frequency with greater stroke volume. The shrew species are notable exceptions, which, despite having a metabolic rate 2–3 times higher than the mammalian average, neither have exceptionally high heart rates nor larger hearts than other wild small mammals.

The adaptation of the shrew heart to high metabolic rate may reside in the shape of heart. The ventricular myocardium of shrews is characteristically long and narrow with a tapered apex, whereas other small mammals have rounder hearts.

The duration of the ventricular action potential was short and inversely proportional to the resting heart rate of the mammalian species. Caffeine ($5\,mmol\,l^{-1}$) strongly decreased the isometric contractile force of right ventricular strips in all the studied mammals. These findings suggest that in the small mammals intracellular stores are the main source of activating Ca^{2+}, whereas transsarcolemmal Ca^{2+} movement may only serve the triggering function.

Introduction

Most studies of contractile regulation of mammalian cardiac muscle have been made on a small number of species of laboratory animals. Even within this small group of five or six species, prominent species-specific differences appear in the regulation of cardiac contractility. In particular, rat heart tissue is known to be exceptional among cardiac tissues of the common laboratory mammals, and changes from the 'common' mammalian type to the 'exceptional' type during the first 2 or 3 weeks of postnatal life (Langer, 1978; Vornanen, 1984*a*,*b*, 1985). During

Key words: heart rate, heart mass, action potential, shrew, small mammal, caffeine.

this early life period, heart rate rises from about 270 beats min^{-1} to over 500 beats min^{-1} (M. Vornanen, in preparation). Thus, the peculiar contractile properties of the adult rat heart could be related to the relatively high heartbeat frequency.

In this paper the connection between heart rate and contractile properties of cardiac tissues has been investigated in small wild mammals. Heart rate is inversely proportional to the size of the animal. Therefore, the small mammals are suitable for a study of the connection between high heart rate (metabolic rate) and basic contractile and electrophysiological properties of cardiac tissue. Shrew species are especially interesting in this respect, since their metabolic rate is 2–3 times higher than that of other mammals of the same size (Morrison *et al.* 1959; Vogel, 1976; Nagel, 1985*a*).

Materials and methods

Animals

The species investigated were six small wild mammals and two laboratory rodents (Table 1). The wild animals were caught near the university campus in small fall traps, which were inspected at 4- to 8-h intervals. In the laboratory the animals were kept individually in small terraria with a substratum of moss, and were fed with appropriate food for each species until used in the experiments.

Measurement of heart rate

Heart rate of resting, unrestrained animals was measured by recording the electrocardiogram *via* the paws (Vetterlein *et al.* 1984; Nagel, 1985*b*). One animal at a time was placed in a small plastic cage (10 cm × 10 cm × 8 cm), the floor of which consisted of nine separate copper plates. Each metal plate was connected through shielded lead to a switchboard. When the animal was resting on the floor so that its hind and front paws were on separate plates, the switchboard was used to connect these plates to the oscilloscope. The number of QRS-peaks per time interval was calculated from the oscilloscope screen.

Table 1. *Species used in the experiments*

Order	Family	Species
Insectivora	Soricidae	*Sorex araneus*
		Sorex minutus
		Neomys fodiens
Rodentia	Arvicolidae	*Clethrionymus glareolus*
	Muridae	*Rattus norvegicus* (Wistar strain)
		Mus musculus (MRI strain)
		Micromys minutus
	Zapodidae	*Sicista betulina*

Intracellular recording

Animals were killed by a blow on the head and the heart was quickly excised and transferred to cold (<2°C) physiological saline of the following composition ($mmol\,l^{-1}$): NaCl, 127·9; KCl, 4·0; $MgSO_4$, 1·5; NaH_2PO_4, 0·4; $NaHCO_3$, 12·0; $CaCl_2$, 2·5; glucose, 10·0; pH 7·4. The solution was pregassed with 95 % O_2/5 % CO_2 and oxygenation was continued throughout the experiment. The right ventricular wall was separated from the rest of the heart and carefully stretched on the bottom of a Petri dish, the floor of which was covered with silicone. Physiological saline was added so that it just covered the muscle. The preparation was paced to contract at 0·2 Hz using field electrodes connected to a Grass SD9 stimulator. Membrane potentials were recorded with conventional glass microelectrodes filled with $3\,mol\,l^{-1}$ KCl (50–70 MΩ). Ag–AgCl was used as the reference electrode. Resting potentials were directly read from the digital meter of the electrode amplifier (WPI Ks-700) and action potentials were photographed from the screen of an oscilloscope using a Polaroid camera. These experiments were carried out at room temperature (20°C).

Tension recording

To investigate the effects of caffeine on the mechanical performance of the myocardium, small ventricular strips (diameter <0·8 mm) were excised from the right ventricular wall and obliquely suspended in a 10-ml tissue bath. The chamber was filled with physiological solution, which was continuously gassed with 95 % O_2/5 % CO_2 and the temperature of the solution was kept at 30°C. Muscles were paced to contract at 0·2 Hz by square wave pulses of 5 ms duration and about 1·5 times the threshold voltage from the stimulator. Isometric contractile tension was measured at the optimum length of the muscle (L_{max}) by a force transducer (Grass FT.03) using a Grass 7D polygraph. Signals were also displayed on the screen of the oscilloscope. When a steady tension development by the muscle had been achieved, caffeine was added as a concentrated solution to give the final concentration of $5\,mmol\,l^{-1}$.

Heart mass

After atria and connective tissue had been trimmed away, the heart mass was determined by weighing the ventricular myocardium.

Statistics

Mean values among groups of species were compared by one-way analysis of variance and significant differences ($P < 0·05$) between two species were tested after analysis of variance by Scheffe's test.

Results

Heart rate

Typical recordings of the electrocardiogram (ECG) and action potential are

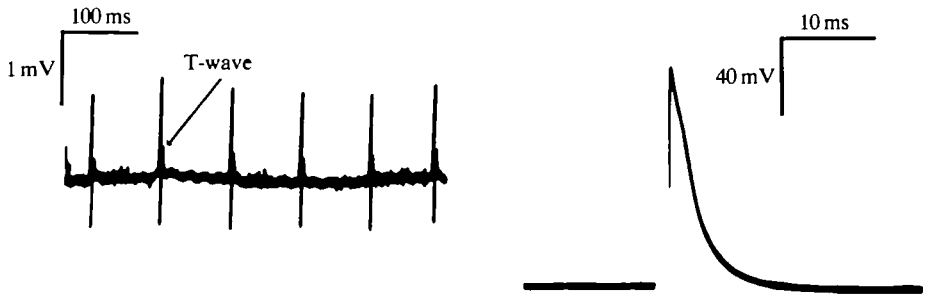

Fig. 1. Original oscilloscope tracings showing electrocardiogram (heart rate, 684 min^{-1}) and ventricular action potential of the common shrew, *Sorex araneus*. The arrow indicates the T-wave in the ECG recording.

shown in Fig. 1 for the common shrew *Sorex araneus*. The resting heart rates (f_H) of all the small wild mammals was below the values predicted by the equation, $f_H = 241 M_b^{-0.25}$ (Stahl, 1967) where M_b is body mass (Fig. 2). The heart rates of *Micromys minutus*, *Clethrionymus glareolus* and *Sicista betulina* deviated most from the expected values. Also, the heart rate of the common shrew (*Sorex araneus*) was clearly lower than the predicted value for such a small mammal. The heartbeat frequency of shrew heart was, however, a little higher than that of the other small wild mammals. By contrast, the heart rate of the white laboratory

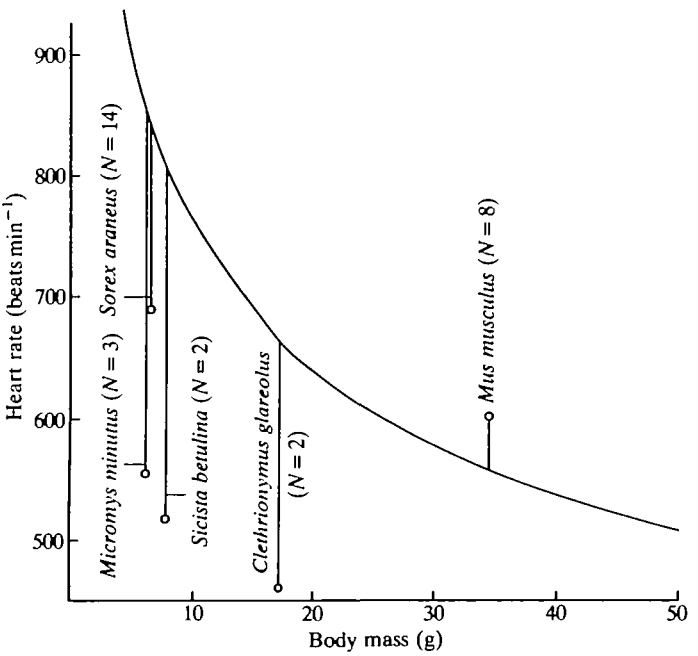

Fig. 2. Deviation of the measured resting heart rates of some small mammals from the values predicted by an allometric equation for a typical mammal (Stahl, 1967).

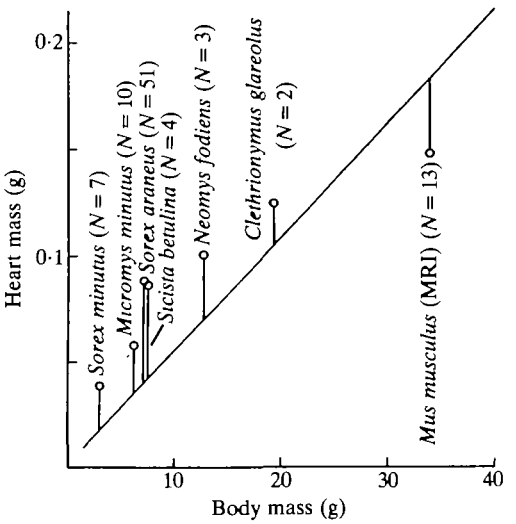

Fig. 3. Deviation of the measured heart masses of some small mammals from the values predicted by the allometric equation for a typical mammal (Stahl, 1967).

mouse conformed rather closely to the general mammalian trend, as was also the case for the white rat (data not shown). This means that the heart rate of a 35 g laboratory mouse is higher than that of wild rodents weighing 6–8 g.

Heart size

In general, the mammalian heart constitutes about 0·59 % of the whole body mass (M_b), as expressed by the equation $M_h = 0{\cdot}0059 M_b^{0{\cdot}98}$ (Stahl, 1967). Comparison of the measured values of the heart mass of the small mammals with the predicted values (Fig. 3), shows that the ventricular myocardium of the small wild mammals is larger than the mammalian average. The deviation is largest (132 %) for the smallest shrew species (*Sorex minutus*), and smallest (40 %) for the biggest shrew (*Neomys fodiens*). By contrast, the ventricular mass of the laboratory mouse is somewhat lower (−20 %) than the expected value (Table 2).

Heart shape

The shape of the ventricular muscle is important in several respects to the function of the heart. According to Laplace's law, the greater the radius of curvature of the heart, the more work is needed to obtain the same blood pressure, i.e. elongated hearts are more efficient than rounder hearts. The hearts of the shrew species were found to be long and slender with a tapered apex, whereas the hearts of rodent species were clearly rounder (Fig. 4). A further comparison of heart shape was made by calculating the ratio between the length and breadth of the ventricular myocardium, and this index showed that the shrew ventricles differ from those of other small mammals and of the laboratory mouse (Fig. 5).

Table 2. *Comparison of heart mass and heart rate with the expected values from allometric equations in seven small mammals*

Species	Body mass (g)	Heart mass (mg)	Expected heart mass (mg)	% of predicted value	Relative heart mass (%)	Heart rate (min^{-1})	Expected heart rate (min^{-1})	% of predicted value	BMR (ml O_2 g^{-1} h^{-1})
Sorex araneus	7·59 (57)	78·4	43·0	182	1·03	690 (14)	817	84	7·43[1]
Sorex minutus	2·90 (6)	38·3	16·7	229	1·32	–	–	–	8·60[2]
Neomys fodiens	12·79 (5)	100·6	71·7	140	0·79	–	–	–	3·22[1]
Micromys minutus	6·27 (12)	57·4	35·7	161	0·92	554 (3)	856	65	2·86[3]
Sicista betulina	7·58 (4)	86·0	42·9	201	1·14	543 (2)	817	67	3·20[4]
Clethrionymus glareolus	19·50 (2)	125·5	108·4	116	0·64	461 (2)	669	69	1·52[5]
Mus musculus (MRI)	34·00 (13)	147·0	186·9	79	0·43	604 (8)	561	108	1·62[5]

Expected values for heart mass and heart rate according to the equations, $M_h = 0{\cdot}0059 M_b^{0.98}$ and $f_H = 241 M_b^{-0.25}$, respectively (Stahl, 1967).
BMR, basal metabolic rate.
Data from: (1) Nagel (1985*a*); (2) Sparti & Genoud (1989); (3) Grodzinski *et al.* (1988); (4) Johansen & Krog (1959); (5) Morrison (1948).
Values in parentheses are number of animals, studied.

Table 3. *Resting potentials and characteristics of action potentials in ventricular muscle of four mammalian species*

	Action potential amplitude (mV)	Resting potential (mV)	Action potential duration at different repolarization levels				
			10 %	25 %	50 %	75 %	90 %
Rattus norvegicus (20)	102·4 ± 1·5	72·8 ± 1·0	8·5 ± 0·6	19·3 ± 1·4	29·6 ± 1·8	44·6 ± 2·1	73·9 ± 3·7
Mus musculus (20)	102·7 ± 1·0	71·5 ± 0·3	2·8 ± 0·5*	5·8 ± 0·5*,†	11·4 ± 0·7*,†	21·9 ± 1·3*,†	62·9 ± 4·1*,‡
Micromys minutus (11)	109·1 ± 2·1	72·3 ± 0·5	2·2 ± 0·2*	4·0 ± 0·3*	8·2 ± 0·4*	16·4 ± 1·2*,†	39·2 ± 3·7*,†
Sorex araneus (20)	102·0 ± 2·0	73·8 ± 1·4	1·3 ± 0·1*	2·4 ± 0·2*	3·8 ± 0·2*	6·3 ± 0·4*	10·4 ± 0·8*

* Significantly ($P < 0{\cdot}05$) different from rat; † significantly different from common shrew (*Sorex araneus*); ‡ significantly different from harvest mouse (*Micromys minutus*).
Values are means ± S.D. The number of experiments is given in parentheses.

Fig. 4. Ventricular myocardii of the small mammals: *Sorex minutus*, *Sorex araneus*, *Micromys minutus* and *Mus musculus* (MRI strain) (from left to right). Scale bar, 10 mm.

Action potentials

The short duration of the plateau phase of the action potential of the rat heart is an exceptional feature among the studied laboratory mammals. Heart rate must be limited by action potential duration (or *vice versa*). So it is not surprising that the duration of the ventricular action potential in small, wild mammals is short (Fig. 1) and inversely related to heartbeat frequency (Fig. 6, Tables 2 and 3). Thus the action potential characteristics of the adult rat heart are by no means peculiar, but are common to mammals with high cardiac frequency. The short action potential duration of the excised shrew heart is not a consequence of the experimental conditions, because *in vivo* the action potential duration is also very short. This is evident from the ECG recording, in which the QRS-complex (ventricular depolarization) is immediately followed by the T-wave (ventricular repolarization) (Fig. 1).

Effect of caffeine

Caffeine ($5\,mmol\,l^{-1}$) caused a large reduction of developed tension in the

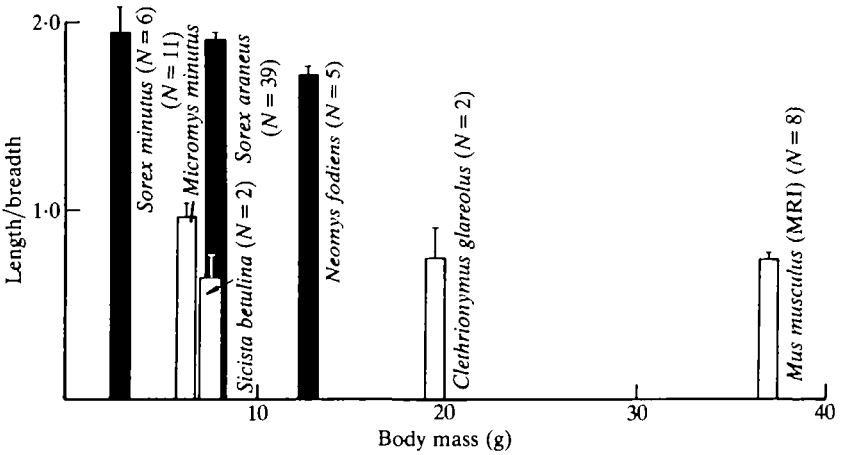

Fig. 5. Histogram of the length/breadth index describing the ventricular shape of the hearts of some small mammals. The index is the ratio between maximal length and maximal breadth of the ventricular myocardium. The solid bars are for the shrew species. The cardiac indices of the shrew species differ significantly ($P<0{\cdot}05$) from those of all other species.

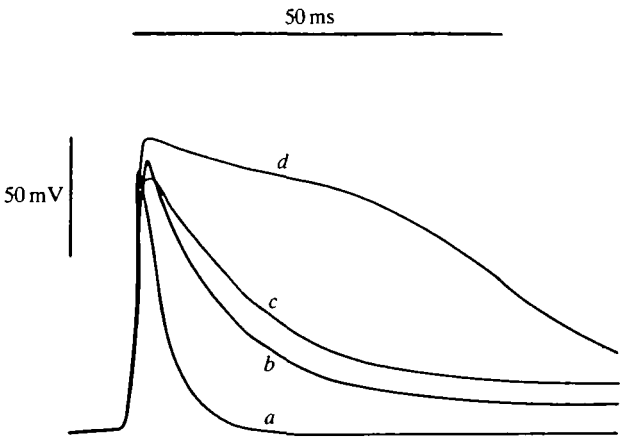

Fig. 6. Superimposed oscilloscope tracings of the ventricular action potentials of *Sorex araneus* (*a*), *Micromys minutus* (*b*), *Mus musculus* (MRI strain) (*c*) and *Rattus norvegicus* (Wistar strain) (*d*). Redrawn from tracings.

ventricular strips of all the studied species (Fig. 7). The decline of developed tension was rapid and was followed by a slight recovery in some species.

Discussion

The specific metabolic rate of mammals increases with decreasing body mass,

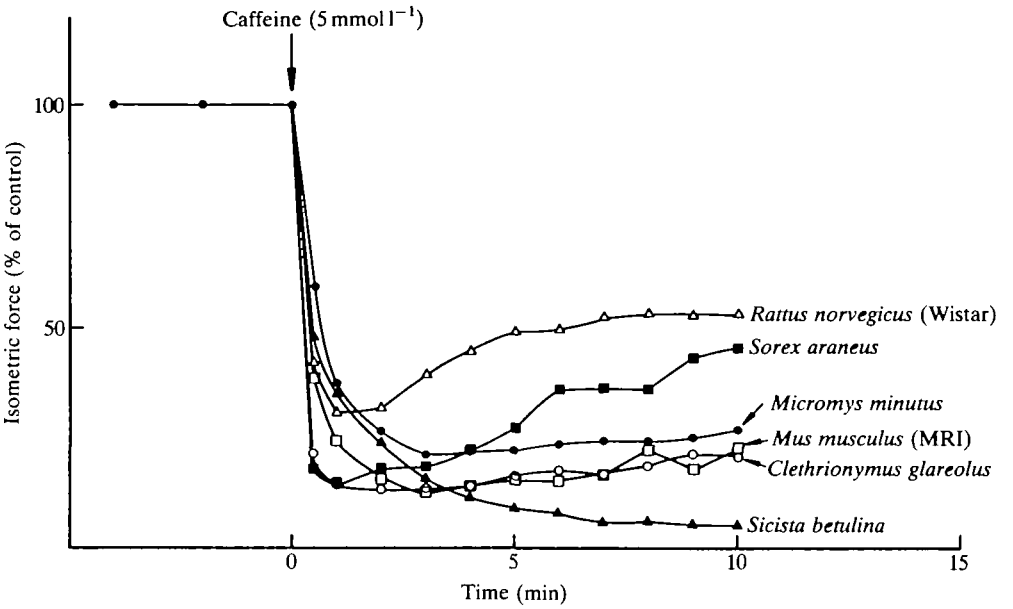

Fig. 7. Effect of caffeine (5 mmol l^{-1}) on the contractile force of right ventricular strips from the small mammals. The results are the means of 2–4 preparations from 1–3 animals.

i.e. energy metabolism is higher in a small individual than in a large one. Moreover, metabolic rate per unit body mass of the red-toothed shrews (subfamily Soricinae) is 2–3 times higher than that predicted for a typical mammal of their size (Morrison *et al.* 1959; Vogel, 1976; Nagel, 1985*a*). The circulatory system, including cardiac muscle, has somehow to cope with the demands of this high metabolic rate. This study demonstrates that the working myocardium is adapted to fulfil the circulatory demands imposed by high metabolic rate.

The volume of blood circulating through the body in a given time (cardiac output) is determined by the stroke volume (heart size) and heart rate. These two variables were measured in a number of small mammals.

The size of mammalian heart is independent of body size, constituting about 0·59 % of the body mass (Stahl, 1967). The present results clearly show that the size of the ventricular myocardium of small wild mammals is greater than is to be expected from this general mammalian trend, as documented earlier for a number of shrew species (Pucek, 1965; Bartels *et al.* 1979; Nagel, 1985*a*). By contrast, the heart mass of the laboratory mouse is somewhat lower than predicted by the allometric equation. Shrew species, despite having a metabolic rate 2–3 times higher, do not have significantly larger hearts than other equally small mammals.

In most mammals at rest, the heartbeat frequency (f_H) increases when body size decreases according to the equation: $f_H = 241 M_b^{-0.25}$ (Stahl, 1967). All the studied wild mammals markedly deviate from this prediction in the direction of lower frequencies. A notable feature is that the heartbeat frequency of a 35-g laboratory

mouse is higher than that of wild rodents weighing 6–8 g. Even the common shrew, with a threefold higher metabolic rate than would be expected for its size, has a lower heartbeat frequency than that calculated according to the general mammalian trend. Our value for the heart rate of the common shrew (690 beats min^{-1}) is in agreement with the determinations of Nagel (1985*a*), who recorded 627 beats min^{-1}. The heart rate of the common shrew is, however, higher than that of the birch mouse (*Sicista betulina*) and harvest mouse (*Micromys minutus*), which are about the same size. The reason for the unexpectedly low heart rates is not immediately clear. One possibility is that the heartbeat frequency of active animals is considerably higher than the measured resting values, especially for the very active shrew species. Maximal heart rates were not measured in the present study, but earlier studies with restrained animals suggest that maximal heart rates are also unexpectedly low in these mammals (Morrison *et al.* 1959). Another possibility is that cellular restrictions appear which would hinder the unlimited increase of heartbeat frequency with decreasing body size. A cardiac cycle involves a rather complex sequence of electrical and mechanical events to trigger contraction and to restore relaxation, which requires a certain minimum time. Therefore, it seems likely that the general mammalian relationship between heart rate and body size, as expressed by Stahl's equation, does not hold true for the small wild mammals. Possibly the upper limit of heart rate, which allows a complete contraction–relaxation cycle to occur, is achieved in these small mammals.

In the small wild rodents, sufficient cardiac output is maintained by compensating for the restricted heart rate with large stroke volume, i.e. heart size. In the shrews, this holds only partially, for the increased heart size is not enough to compensate for the low heart rate, considering their high metabolic rate. It appears that the shape of the heart provides adaptation of cardiac function to the high metabolic rate in shrews. Shrew hearts are characteristically long and narrow with a tapered apex, while other small mammals have more typical rounder hearts. According to Laplace's law, a chamber with small end-diastolic volume, i.e. with a small internal radius in cross-section, requires less myocardial tension to develop an equal intraventricular pressure than one in which the radius is larger. Thus, an elongated ventricle would generate equal blood pressure using less energy, or a higher blood pressure using the same amount of energy, than a rounder heart. Adaptation of haematological factors may also reduce the cardiac output needed to support the high metabolic rate (Wołk, 1974; Bartels *et al.* 1979).

One peculiar feature of the cardiac muscle of adult rats compared with that of other laboratory mammals is its short action potential duration (Mitchell *et al.* 1984; Langer, 1978). The action potential duration is limited by the heartbeat frequency: with a heart rate of 700 beats min^{-1} (shrew) one complete cycle can only occupy 86 ms; and with 360 beats min^{-1} (rat), 167 ms. Therefore, it is not unexpected to find that the duration of the action potential plateau is inversely proportional to the heartbeat frequency (10 and 74 ms for shrew and rat, respectively). In the light of this data, the short duration of the rat cardiac action

potential is by no means exceptional, but conforms to the general inverse relationship between metabolic rate (heart rate) and action potential duration. A common physiological mechanism for short action potential duration and high metabolic rate seems to be the thyroid state (Binah *et al.* 1987; Tomasi, 1984).

All muscles were paced at 5 s intervals so that, under the experimental conditions, frequency was not a limiting factor for action potential duration. Therefore, the differences in the configurations of action potentials are caused by species-dependent, inherent membrane currents and cellular mechanisms which regulate action potential duration. The plateau duration of the cardiac action potential is mainly determined by an inward Ca^{2+} current. Inactivation of the Ca^{2+} current is regulated by membrane voltage, and also by intracellular Ca^{2+} level near the inner mouth of the Ca^{2+} channel (Brown *et al.* 1981; Fischmeister *et al.* 1981; Mitchell *et al.* 1983; Kokubun & Irisawa, 1984). A Ca^{2+}-dependent component of inactivation of the Ca^{2+} current seems to be one factor that regulates the duration of the cardiac action potential in the rat heart (Josephson *et al.* 1984*a*). Recently, a transient (early) outward current, carried by potassium ions, has been described in rat and mouse ventricular myocytes (Josephson *et al.* 1984*b*; Benndorf & Nilius, 1988). Whether these two current systems are also responsible for the rapid repolarization of the cardiac action potential in the small wild mammals remains to be shown by voltage-clamp experiments.

Caffeine is known to improve contractility of mammalian cardiac muscle, with a few exceptions such as rat heart and Purkinje fibres of the dog heart (Hess & Wier, 1984). Caffeine exerts multiple actions on the cardiac cell. It improves Ca^{2+} influx through sarcolemmal Ca^{2+} channels, but impairs the function of the sarcoplasmic reticulum (SR) by emptying its Ca^{2+} content (Goto *et al.* 1975; Blinks *et al.* 1972; Blayney *et al.* 1978; Hess & Wier, 1984). Owing to these antagonistic effects on cellular Ca^{2+} regulation, the effect of caffeine is a balance between increased sarcolemmal Ca^{2+} entry and diminished Ca^{2+} release from the SR. Therefore, in tissues where Ca^{2+} stores in the SR are the main source of contractile Ca^{2+}, attenuation of twitch tension would be the result, whereas in tissues where sarcolemmal Ca^{2+} influx dominates, the final effect would be improvement of contractility. In all the six species studied caffeine (5 mmol l^{-1}) caused a rapid and dramatic decline of developed tension. This was followed by a slight recovery in some species. These findings suggest that in all these small mammals the SR is the main source of activating Ca^{2+}. The partial recovery is probably due to caffeine's effect on contractile proteins (Fabiato & Fabiato, 1976).

The present results suggest that Ca^{2+} entry through the sarcolemma during the action potential does not significantly contribute to cardiac contraction in small mammals, as may be the case in larger laboratory mammals with lower heart rates. Although the action potential duration in these small mammals is sufficient for maximal activation of the sarcolemmal Ca^{2+} channel, requiring 2–3 ms (Isenberg & Klöckner, 1982; Mitchell *et al.* 1983), the time for diffusion of Ca^{2+} from sarcolemmal sites to the contractile proteins may be too short at the high heart rates encountered in these small mammals. A high heartbeat frequency requires

that the diffusion distance is as short as possible for the activating Ca^{2+}. Therefore, the regulation of intracellular Ca^{2+} concentration may be accomplished primarily by the SR, which closely surrounds the myofibrils. Ca^{2+} influx during the short plateau phase of the action potential could function as a trigger for a large release from the SR and for the replenishment of SR Ca^{2+} stores. Thus, although sarcolemmal excitation triggers contraction, regulation of cardiac contractility may take place at the level of myofibrils by the surrounding SR. In this regard, the contractile regulation of the cardiac muscle of the small mammals resembles that of skeletal muscle.

This study was financially supported by the Reseach Council for the Natural Sciences of the Academy of Finland.

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