HEART AND RESPIRATORY RATES IN THE SMALLEST MAMMAL, THE ETRUSCAN SHREW SUNCUS ETRUSCUS (INSECTIVORA : SORICIDAE)

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K.D. JÜRGENS, R. FONS**, T. PETERS*, S. SENDER**

** Zentrum Physiologie, Medizinische Hochschule, D-30623 Hannover, Germany*

*** Laboratoire Arago, Université P. et M.-Curie (Paris 6), NRSR URA 2156, 66651 Banyuls-sur-Mer cedex, France*

HEART RATE
RESPIRATORY RATE
OXYGEN TRANSPORT
ELECTROCARDIOGRAM
SHREW
TORPOR

ABSTRACT. – Heart and respiratory rates in resting and in stressed Etruscan shrews (*Suncus etruscus*) as well as in animals rewarming from torpor have been measured in order to investigate the adaptation of the ventilatory and circulatory oxygen transport system of the smallest mammal (average body weight below 2 g) to its outstanding weight-specific oxygen consumption rate (270 $mlO_2/(kg\ min)$ at T_a = 22 °C). We found a mean respiratory rate of 661 and a maximal one of 894 min^{-1}. Mean resting heart rate was 835 and the maximal one 1,511 min^{-1}, which is the highest heart rate ever reported for an endotherm. It turned out that compared with larger mammals the respiratory rate of *S. etruscus* is increased in proportion to its outstandingly high metabolic rate, whereas the heart rate is increased much less, so that additionally adaptations of stroke volume and blood properties are required to assure a sufficient circulatory oxygen transport. During rewarming both rates increased with body temperature according to a Q_{10} of 2.2.

FRÉQUENCE CARDIAQUE
FRÉQUENCE RESPIRATOIRE
TRANSPORT D'OXYGÈNE
ÉLECTROCARDIOGRAMME
MUSARAIGNE
TORPEUR

RÉSUMÉ. – Les fréquences cardiaque et respiratoire de la Musaraigne étrusque (*Suncus etruscus*) ont été mesurées sur des individus au repos, en état de stress ainsi que sur des animaux se réchauffant après un état de torpeur, dans le but d'étudier l'adaptation du système d'apport d'oxygène sur les plans respiratoire et circulatoire chez le plus petit Mammifère (poids moyen inférieur à 2 g) à son taux hors du commun de consommation d'oxygène par rapport à son poids (270 $mlO_2/(kg\ min)$ à T_a = 22 °C). Nous avons trouvé un rythme respiratoire moyen de 661 et un rythme maximal de 894 min^{-1}. Au repos, la fréquence moyenne des battements cardiaques est de 835 et la fréquence maximale est de 1 511 min^{-1}, ce qui représente la plus haute fréquence cardiaque jamais enregistrée chez un endotherme. Il s'est avéré que, comparativement à des Mammifères de taille plus importante, la fréquence respiratoire de *S. etruscus* augmente proportionellement au taux du métabolisme alors que l'augmentation du rythme cardiaque est beaucoup moins importante, de sorte que des adaptations supplémentaires du volume de flux sanguin déplacé par battement et des propriétés du sang s'avèrent nécessaires pour assurer un transport circulatoire d'oxygène suffisant. Pendant le réchauffement, les deux rythmes (cardiaque et respiratoire) augmentent avec la température du corps selon une proportion de Q_{10} égale à 2.2.

INTRODUCTION

The Etruscan shrew, *Suncus etruscus* (Savi, 1822), is the smallest mammal. The mean adult body weight (BW) of wild animals is 1.8 g. This species is especially interesting from a physiological point of view, since it has the highest body weight-specific energy consumption rate of all mammals. At an ambient temperature (T_a) of 22 °C a resting shrew consumes about 270 ml O_2 per kg and minute (Fons *et al.* 1976), which is nearly 70 times as much as resting humans do consume. Consequently there must be an adaptation to this outstandingly high oxygen demand at all levels of the oxygen transport system of this species. In our present study we investigated the convective oxygen transport systems, i.e. transport from the air into the lung by the ventilatory system and from the lung into the tissues by the circulatory system. Since these transport rates primarily depend on the frequencies of the respiratory system and of the heart, respectively, we have measured these parameters. The adaptive properties of the convective parts of the oxygen transport cascade are discussed.

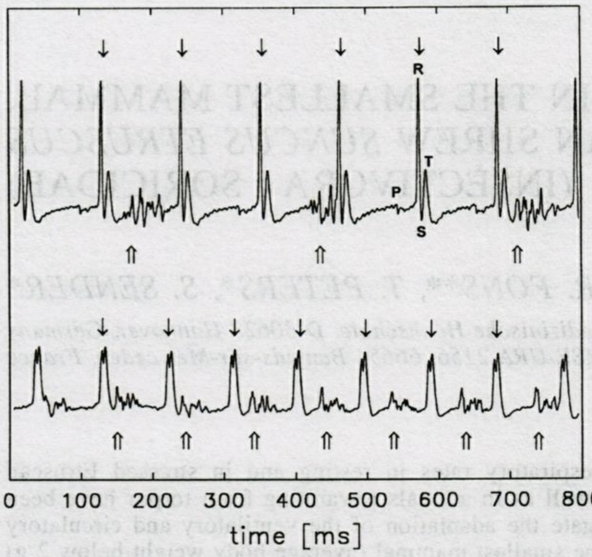

Fig. 1. – Recordings of electrocardiograms of *S. etruscus*. In the upper trace characteristic peaks of the cardiac cycle are marked. Heart rates were determined from R-peak intervals (single arrows), respiratory rates from the electric phenomena associated with breathing muscle activity (double arrows).

MATERIALS AND METHODS

The animals investigated were caught around Banyuls-sur-Mer in summer and kept in a terrarium until measurements were carried out. They were fed with mealworms and crickets and had access to water ad libitum. The investigations were done with seven individuals, 3 males and 4 females, with an average body mass of 2.4 g. Torpor was induced by starving the animal for one night and exposing it to a cold environment of 4 ºC the next morning. As soon as an animal had entered a complete torpid state it was transferred to a room with Ta = 22 ºC, where it spontaneously rewarmed.

We obtained the heart rate and the respiratory rate of the Etruscan shrew in the following way : an animal was confined in a small plastic box, in which it stood on stainless steel electrodes with its forelegs and hindlegs, respectively. We then recorded the electrical potential difference between these electrodes, i.e. we measured the electrocardiogram (ECG). Different ECGs differed in shape because the animals contacted the electrodes with their extremities in different ways.

Figure 1 shows two typical ECG recordings. In the upper trace the characteristic ECG peaks, the P-wave, the RS-complex and the T-wave are indicated. Typical for shrews in the absence of the Q-wave and the ST-segment. From the number of T-peaks (single arrows) per time the heart rate (HR) was calculated.

In the electrical recordings also a second rhythmic phenomenon is to be seen, as is indicated in the upper and the lower trace of Fig. 1 by the double arrows. This rhythm is different in phase and frequency from the heart signal and was identified as the electrical activity of the respiratory muscles during inhaling. Therefore, this signal was used to determine the breathing rate (BR). In animals rewarming from torpor shivering and movements produced considerable electrical activity in the body temperature range 20 to 30 ºC, so that readings of the breathing frequency were not possible in this range.

In order to prove that this second signal really is caused by the respiratory system, we independently recorded the movements of the thoracic wall of several shrews. This was done using a LASER autofocus system (Rodenstock RM600), designed to measure distance changes in the micrometer range. Figure 2 shows an example of such a recording that exhibits the breathing excursions.

RESULTS AND DISCUSSION

Ventilation

At T_a = 22 ºC in the resting state we found a mean respiratory rate (BR_{rest}) of 660-670 breaths per minute. As can be seen from table 1A, the results from the electrical recording and the LASER measurements are nearly identical. This rate is somewhat lower than the value of 800/min reported by Morrison *et al.* (Morrison *et al.* 1959) for the 3 g weighing shrew species *Sorex cinereus*. The breathing frequency of the four times larger species *Crocidura russula* (Nagel 1991) is only one fourth (160/min) of the rate found in *Suncus etruscus*. When the animals were physically irritated by touching their snout with a stick, which simulated the attack of an enemy, the rates increa-

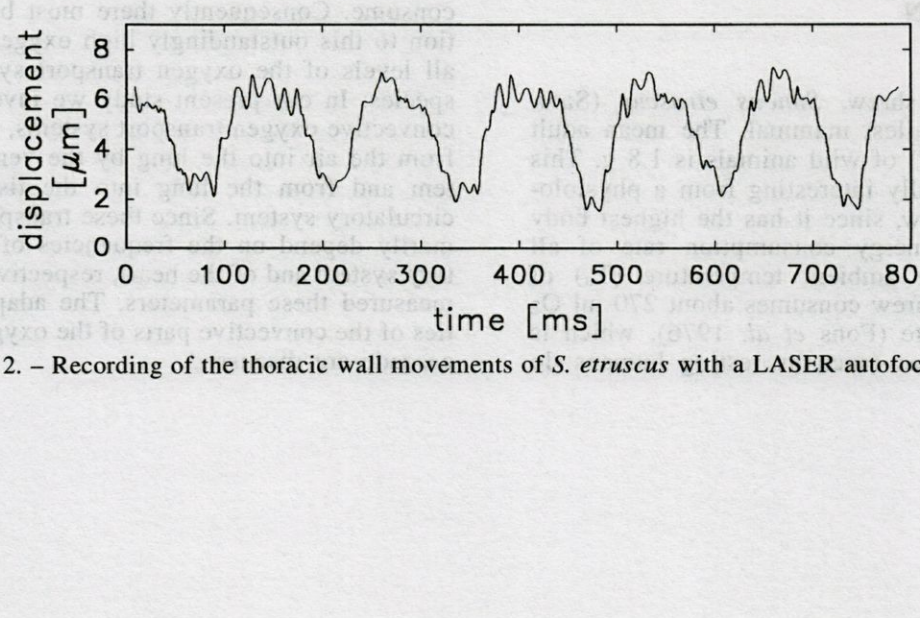

Fig. 2. – Recording of the thoracic wall movements of *S. etruscus* with a LASER autofocus system.

sed. The highest respiratory rate (BR_{max}) recorded amounted to about 900 breaths per minute, which is a little lower than the rate of 1,080/min reported by Morrison *et al*. for *Sorex cinereus*. For *C. russula* a maximal respiratory rate of about 500/min is obtained from the literature (Nagel 1991).

What do these frequency data mean for the ventilatory gas transport rate in the smallest mammal? Table I shows a comparison of the weight specific ventilatory oxygen transport rates between *Suncus etruscus* and man. The resting shrew at T_a = 22 °C consumes 67 times as much oxygen per unit body weight ($\dot{V}O_2/BW$) as humans do. The respiratory frequency of *S. etruscus* is also 67 times as high as that of man. As is shown in table 1B, the other factors contributing to the respiratory oxygen transport rate, the relative tidal volume (TV/BW) (Stahl) and the fraction of oxygen extracted from the air per breath, are almost the same in the shrew and in man. The higher weight-specific ventilatory oxygen transport rate at rest can obviously entirely be achieved by a higher breathing frequency.

Circulation

Table IC shows the heart rates measured in *S. etruscus*. The resting heart rate at T_a = 22 °C (HR_{rest}) is 835 beats per minute, which is higher than found in other small shrews like *Sorex minutus* (748/min) (Vornanen 1992) or *Sorex cinereus* (600/min). Upon physical irritation mean maximal values (HR_{max}) of nearly 1,100 beats per minute were obtained, which is also higher than the mean maximal rates found in other shrews upon injection of isoproterenol or exposure to cold (5,7). The highest single value we recorded was 1,511 per minute. This is the highest heart frequency ever reported for a mammal or for a bird. Under this condition the P-wave of a cardiac cycle immediately follows the T-wave of the preceeding one, which indicates that the utmost heart rate has been reached.

What do these rates mean for the circulatory oxygen transport in *S. etruscus* ? A comparison of the resting heart rates of Etruscan shrew and man (Table ID) shows that they differ by a factor of 12. Since the relative oxygen transport rate is 67 times higher in the shrew, there must be other differences between the small and the large mammal. As we have shown in an earlier study, *Suncus etruscus* has a very large relative heart weight, which is three times as high as that of man (Bartels *et al.* 1979). It can be concluded from allometric relations that consequently the relative stroke volume (SV/BW) is about three times higher in the shrew as well (Holt *et al.* 1968). Additionally, we have shown that the amount of oxygen extracted from the blood perfusing the tissue ($avDO_2$) is also larger in the shrew than in man (1). Because of a higher oxygen capacity and a lower oxygen affinity, 1.8 times as much oxygen is released from the shrew's blood compared to man at the same oxygen partial pressure difference of 60 Torr. So, if we multiply these three factors (Table 1D) we nearly get the factor of 67 that is required to achieve the appropriate blood oxygen transport rate.

From our results it is concluded that at 22 °C ambient temperature the ventilatory oxygen transport rate of resting Etruscan shrews is adapted to its oxygen consumption rate by its high respiratory rate alone. In contrast, the adaptation of the

Table I. – A, Resting and maximal breathing rates of *Suncus etruscus*, * obtained from electrical recordings, + obtained from thoracic wall movements. B, Weight specific ventilatory oxygen transport rate in Etruscan shrew and man : $\dot{V}O$-2 = BR x.TV/BW x air oxygen extraction. The last column shows the factor by which the parameters of shrew and man differ. C, Resting and maximal heart rates of *Suncus etruscus*. D, Weight specific blood oxygen transport rate : $\dot{V}O_2/BW$ = HR x.SV/BW x $avDO_2$. The last column shows the factor by which the parameters of shrew and man differ.

A

S. etruscus (n=7) T_a = 22°C	BR_{rest} [min^{-1}]	BR_{max} [min^{-1}]
Mean ± SD	661 ± 93* 668 ± 140+	758 ± 109
highest single value	-----	894

B

T_a = 22°C	*S. etruscus*	man	factor
$\dot{V}O_{2rest}$/BW [mlO_2/(kg min)]	268	4	67
BR_{rest} [min^{-1}]	661	10	66
TV_{rest}/BW [ml air/kg]	7.7	7.5	1
oxygen extraction [ml O_2/ ml air]	0.053	0.053	1

C

S. etruscus (n=7) T_a = 22°C	HR_{rest} [min^{-1}]	HR_{max} [min^{-1}]
Mean ± SD	835 ± 107	1093 ± 235
highest single value	-----	1511

D

T_a = 22°C	*S. etruscus*	man	factor
VO_{2rest} / BW [mlO_2/(kg min)]	268	4	67
HR_{rest} [min^{-1}]	835	70	12
SV_{rest}/BW [ml blood/kg]	3.4	1.1	3
$avDO_{2rest}$ [mlO_2/ml blood]	0.093	0.050	1.8

convective oxygen transport in the circulation requires more changes. The higher heart rate contributes a factor of 12, the remainingh factor of 5.6 is achieved by the adaptation of heart size and blood properties.

The greater potential of the ventilation in the smallest mammal must be regarded not only under the aspect of oxygen transport but also the aspect of acid base regulation at heavy exercise, when hyperventilation is required to compensate a lactic acidosis.

Heart and respiratory rate in animals rewarming from torpor

Etruscan shrews can enter a torpid state, if they need to reduce their energy expenditure because of a lack of food or large heat loss at low ambient temperatures. We found that body temperature on average dropped down to 12 °C in the torpid state. Active rewarming takes place at a rate of about 1° C/min, which requires a large convective oxygen transport capacity also at low body temperatures in order to supply the heat producing tissues, brown adipose tissue and skeletal muscle, with a sufficient amount of oxygen. We, therefore, have measured how respiratory and heart frequency change with body temperature during the rewarming phase of the shrew. At 12 °C body temperature the mean respiratory rate amounts to 145 breaths per minute and the mean heart rate to 170 beats per minute. With increasing body temperature respiratory rate (Fig. 3 top) and heart rate (Fig. 3 bottom) increase nearly exponentially. For both of these relationships a Q_{10} of 2.2 is calculated, a value in the range known for the change of metabolic rate with body temperature in mammals. This leads to the assumption that although the rewarming mechanism is an active process induced by the thermoregulatory system, the circulatory and the ventilatory oxygen transport system can follow the rewarming stimulus only in such a way as the metabolic rates of the participating muscles do increase with muscle temperature.

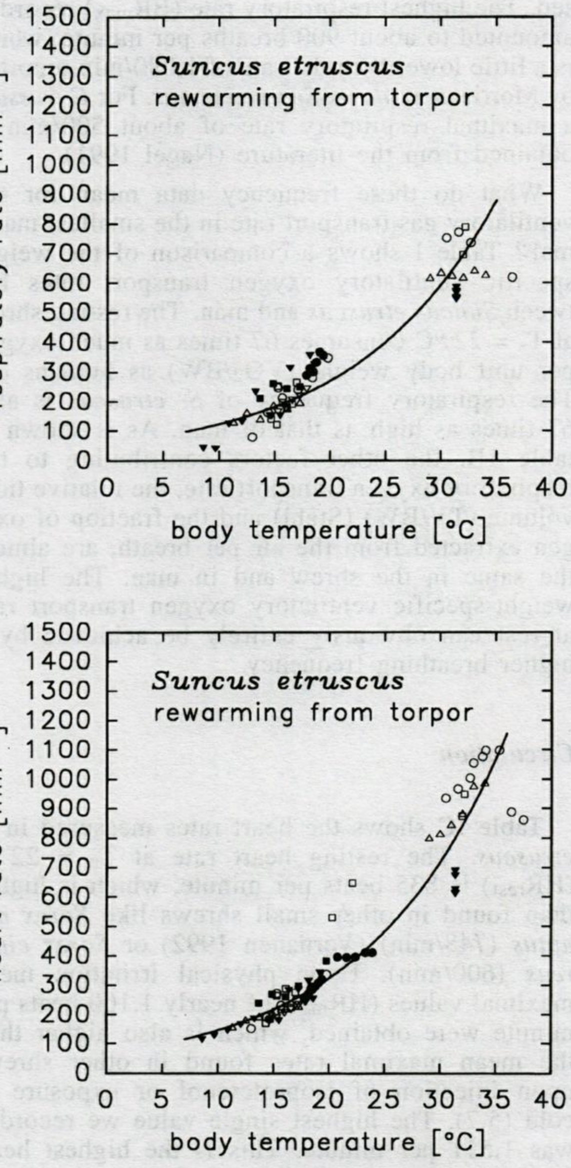

Fig. 3. – Top, Respiratory rates of *Suncus etruscus* rewarming from torpor, obtained from ECG recordings. Different symbols indicate different individuals. The solid line is the best fit of an exponential function (Q_{10} = 2.19). Bottom, heart rates of *Suncus etruscus* rewarming from torpor. Different symbols indicate different individuals. The solid line is the best fit of an exponential function (Q_{10} = 2.21).

CONCLUSION

In the smallest mammal, the Etruscan shrew *Suncus etruscus,* resting as well as the maximal respiratory rates are among the highest found in small mammals. The high breathing rate at rest assures an adequate ventilatory oxygen transport without the need for a larger relative tidal volume than found in other mammals including man (Stahl 1967). Resting and maximal heart rates are even higher than in any other mammal. Nevertheless, for a sufficient circulatory oxygen transport rate at rest *S. etruscus* requires a 3 times larger relative stroke volume and a nearly 2 times larger $avDO_2$ than found in humans. In the torpid state body temperature of *S. etruscus* can drop to 12 °C. During rewarming heart and respiratory rates increase with an apparent Q_{10} of 2.2, a value holding also for the temperature dependence of metabolic rates in mammals.

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