and passed through a pulse shaping and counting unit. Acontinuous record of cell firing rate was obtained on a Servoscribe pen recorder. The spike activity was also monitored on Telequipment oscilloscopes.

Results. The ability of HA-966 to antagonize amino-acid excitation was confirmed by applying the drug with an outward current of 40–60 nA to cells in the cuneate nucleus which were excited by pulses of glutamate lasting about 5 sec. HA-966 reduced glutamate excitation on 35 cells of 48 tested (73%) (Figure 1). Difficulty was experienced in demonstrating the specificity of this antagonism since no substances consistently excite cuneate neurones other than amino-acids and some chelating agents[11]. However, a few cells (6) were found which were excited by acetylcholine[11,12], and on all these cells HA-966 proved able to reduce glutamate excitation by at least 50% without affecting acetylcholine excitation to any detectable extent (Figure 1).

Monosynaptically evoked spikes were induced in 40 of 112 neurones studied in the cuneate nucleus. All but 3 of these units were encountered 600–800 μm below the surface of the cuneate nucleus. The iontophoresis of HA-966 resulted in a blockade of this monosynaptically induced activity in 28 of the 40 cells (70%). Glutamate excitation was reduced by at least 50% in all these cells at the time of synaptic blockade (Figure 2). 11 cells, including that illustrated in Figure 2, showed polysynaptically induced spikes following the monosynaptic spike. The later spikes were unaffected by HA-966, indicating that this antagonist was not having any direct local anaesthetic effect on the cell membrane, and was not producing a generalized nonspecific blockade of all synaptically induced activity. Atropine was applied to 6 cells and in none of these did any apparent change of synaptically evoked activity result.

Discussion. The efficacy and specificity of the antagonism of aminoacid excitation by HA-966[13–15] has been confirmed.

The possibility must be considered that by stimulating the cerebral cortex activity was being induced in the cuneate nucleus over pathways other than the PT. This is unlikely since it has been shown that cortically-induced excitation of cells in the dorsal column nuclei is abolished by sectioning the PT[16,17]. The PT, however, is known to send collaterals to these nuclei, capable of monosynaptically activating neurones there[18].

All the short latency spikes seen in the present study were encountered relatively deeply in the cuneate nucleus. A PT origin for these spikes is therefore supported by anatomical studies showing that PT axons terminate preferentially in the deeper layers of the dorsal column nuclei[19,20].

The antagonism by HA-966 of synaptically induced spikes therefore suggests that the neurotransmitter released by axons of the PT might be an excitatory amino-acid, though HA-966 cannot differentiate between several amino-acids such as glutamate, aspartate and DL-homocysteate[13,15]. Glutamate is a particularly strong candidate since it is present in high concentrations in the dorsal column nuclei[21], it is present in synaptosomes in the cerebral cortex[22] and it can be 'released' at the cortical surface by stimulation of some, but not all, afferent pathways[23]. It has also been shown that some cortical neurones excited by the PT are extremely sensitive to the microiontophoresis of glutamate[10]. These findings suggest that glutamate may be the pyramidal tract neurotransmitter.

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Locomotory Energetics in a Marsupial (*Antechinomys spenceri*) and a Rodent (*Notomys alexis*)

R. V. Baudinette, Karen A. Nagle and R. A. D. Scott[1]

School of Biological Sciences, The Flinders University of South Australia, Bedford Park 5042 (South Australia),
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Summary. Steady state oxygen consumption was compared in a rodent *Notomys alexis* and a marsupial *Antechinomys spenceri*. The marsupial was found to diverge from predicted eutherian energetic patterns. *N. alexis* appears to use energy storage as a significant part of the step cycle before becoming bipedal. Aerobic scope and heat storage during running are similar in both species.

Marsupials generally have standard rates of oxygen consumption about 30% below the predicted eutherian values, body temperatures 2–3 degrees lower[2] and resting heart rates about half that given for eutherian species[3]. We report here on a comparison in energy expenditure during locomotion between a marsupial and a rodent of similar body form and weight.

Materials and methods. Rates of oxygen consumption, body temperature, stride length and frequency were measured in 2 individuals of the carnivorous dasyurid marsupial *Antechinomys spenceri* (28.2 g and 31.6 g) and 5 specimens of the murid rodent *Notomys alexis* (mean body weight 27.4 g). Both inhabit the Australian desert, occurring sympatrically over part of their range. They

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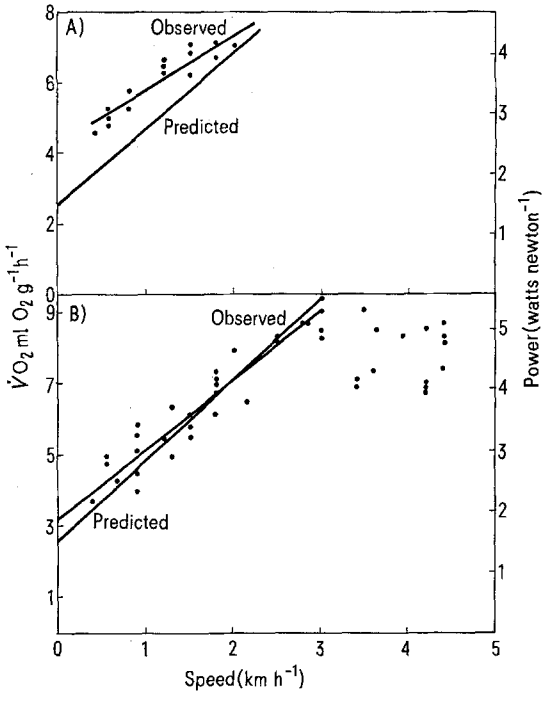

Fig. 1. Steady state oxygen consumption as a function of speed in *Antechinomys spenceri* (A) and *Notomys alexis* (B). Slopes of the relationship between rate of oxygen usage and running velocity were determined by the method of least squares. The predicted lines are from TAYLOR et al.[5].

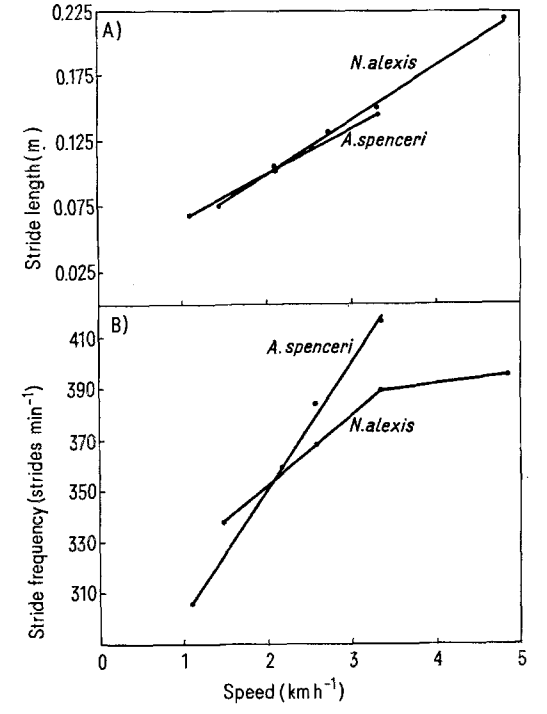

Fig. 2. Stride length (A) and stride frequency (B) in *Notomys alexis* and *Antechinomys spenceri* as a function of running speed. Data points represent mean values from at least 4 running experiments.

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The measured gradients and y-intercepts for the relationship between oxygen consumption and speed in *N. alexis* and *A. spenceri* together with the predicted eutherian values[5].

Speed range (km h^{-1})	Measured gradient	Predicted gradient	Measured y-intercept	Predicted y-intercept
N. alexis				
0.5–3.0	1.96	2.25	3.21	2.62
A. spenceri				
0.5–2.0	1.47	2.17	4.32	2.57

have long hind limbs and a long tufted tail similar to the Northern hemisphere desert rodents of the genera *Jaculus* and *Dipodomys*. Previous work on locomotion, and anatomical details of *A. spenceri* and a related species of *Notomys* has been recorded elsewhere[4].

The animals were trained to run inside a perspex chamber (0.51 × 0.31 × 0.11 m) resting on a motor-driven treadmill. Air was metered through the chamber at a rate of 61 min^{-1} and differences in fractional oxygen content of chamber and room air were recorded continuously with a Servomex model OA 184 paramagnetic oxygen analyser. Only steady state oxygen consumption was considered, this being taken as less than 5% variation during a 15 min test period. The chamber was tested for leaks by bleeding in Nitrogen gas and checking for the appropriate dilution. Heat production was calculated from measurements of oxygen consumption using 20.112 KJ as an energetic equivalent. Heat storage terms were calculated from rectal temperature changes (taken with a thermocouple accurate to ± 0.1 °C) using a tissue specific heat of 3.47 KJ (kg °C)$^{-1}$. Stride length and frequency were measured from film exposed at 128 frames per sec. These recordings were made separately from oxygen consumption tests.

Results. Oxygen consumption initially increased linearly with speed in both species (Figure 1). Comparisons with the predicted eutherian gradients and y-intercepts from TAYLOR et al.[5] are shown in the Table. At low speeds, oxygen consumption in *N. alexis* is statistically indistinguishable from predicted eutherian values, but the gradient of the relationship between oxygen consumption and speed for *A. spenceri* is lower ($p < 0.05$).

In an earlier study, MARLOW[4] recorded a maximum running speed in *A. spenceri* of 13.96 km h^{-1}. We could not induce our animals to run at speeds greater than 3.3 km h^{-1} on the treadmill, and above 2 km h^{-1} steady oxygen consumption could not be measured since the animals performed only sprints of short duration. 2 individuals of *N. alexis* ran at speeds up to 11 km h^{-1} for short periods of time, but steady state oxygen demand could not be measured at speeds greater than 4.4 km h^{-1}. At less than 1 km h^{-1}, both groups of animals tended to move intermittently and stride length and frequency measurements are meaningless. Oxygen consumption at these speeds however met our criteria of steady state and are reported. At no time were the *Antechinomys* observed to move bipedally, but *N. alexis* individuals were observed to hop for short periods at speeds around 11 km h^{-1}.

The length of stride in both species increased with increasing speed over the range in which we could induce the animals to run but patterns of stride frequency differed (Figure 2). *A. spenceri* showed a linear relationship over the speed range but the rodent maintained the number of strides per min relatively constant at speeds above 3.3 km per h, thereafter increasing speed primarily by increasing

the length of stride. It is significant that oxygen consumption levels and stride frequencies are relatively constant in *Notomys* at speeds above 3 km per h, the speed at which the gait changes from a walk to a quadrupedal bound. Similar patterns have been obtained during bipedal locomotion in the red kangaroo, this being attributed to storage of energy in elastic elements[6]. Our data also suggest a possible large storage component but in contrast to the kangaroo, occurring during quadrupedal locomotion. The observation that oxygen consumption stabilizes during quadrupedal running has also been made in *Notomys cervinus*[7]. Although our results are qualitatively similar at low and intermediate speeds, we do not find prolonged steady state oxygen consumption levels at higher speeds in the smaller *N. alexis* and find no evidence of a further change in the rate of oxygen consumption as reported in this work.

Given the differences in resting metabolic parameters between eutherians and marsupials, are there differences in aerobic capacity or heat storage between the rodent and the marsupial? If we assume that the plateau of oxygen consumption at high speds represents the maximal oxygen uptake rate (*max* $\dot{V}O_2$), the ratio *max* $\dot{V}O_2$ to standard $\dot{V}O_2$ for *Notomys* is approximately 5.3. We cannot suggest that *Antechinomys* was running at maximal rates of oxygen uptake as the animals are known to run at greater speeds than those at which we could induce in our experiments, however, the ratio of *max* $\dot{V}O_2$ to standard $\dot{V}O_2$ at the highest measured oxygen consumption levels is 7.0 for the lighter animal and 7.1 for the heavier. It appears therefore that the scope for aerobic metabolism is not lower in the marsupial species. The mean resting body temperature for *N. alexis* was 37.8 °C and for *A. spenceri* 36.4 °C. Both groups of animals were run at 2 km h^{-1} for 10 min, a speed which produced oxygen consumption rates of close to 7 ml O_2 g^{-1} h^{-1} in both species. Mean heat storage in *N. alexis* was 0.0399 MJoule (kg h^{-1}) and in *A. spenceri* 0.0405 MJoule (kg h^{-1}). This represents mean values of 28.3 and 29.3% respectively of the total heat production at these speeds; values insignificantly different at the 5% level of confidence. It appears therefore that the lower resting body temperatures in the marsupial confers no advantage in actual heat stored.

Conclusions. We conclude that the apparent specialization of long hind limbs in *N. alexis* results in no marked differences from predicted eutherian locomotory patterns at low running speeds. However, energy demands for locomotion plateau at higher speeds and its appears that elastic storage may become significant. A similar limb specialization occurs in *Antechinomys* but we could not induce steady state running at speeds above 2 km h^{-1}. This difference in maximum voluntary steady state speed, together with the observation that at low speeds the marsupial expends more energy in locomotion than the rodent, provides, even within the limitations of a treadmill experiment, an interesting comparison.

Slow Current Changes Underlying Square Shaped Potential Waves in Warmed *Aplysia* Neurones

M. Gola

Département de Biophysique des Neuromembranes, C.N.R.S., Institut de Neurophysiologie et Psychophysiologie, 31, Chemin Joseph-Aiguier, F-13274 Marseille Cedex 2 (France), 28 November 1975.

Summary. On warming, the regularly firing L_{11} neurone of *Aplysia* turns into a bursting-type neurone. The bursts of spikes are produced by slow square waves which can also be obtained at room temperature by adding TTX or Co^{++}. Experiments with slow ramp voltage clamp show that warming induces a negative slope (or negative resistance) on the current-voltage characteristic and very slow current variations (τ = 10 to 50 sec) in response to potential changes. The square waves are explained by these two phenomena.

Chalazonitis[1] and Arvanitaki[2] reported that a regularly firing *Aplysia* neurone, denoted 'Gen'[3] or L_{11}[4] generates bursts of spikes when temperature is raised above 25 °C. High frequency bursts are due to slow cyclic potential changes such as in the 'Br' or R_{15} bursting neurones of *Aplysia*[5]. Moreover, voltage clamp experiments indicated that steady current-voltage relations in bursting neurones have a negative slope usually called negative resistance (NR)[6–8], and undoubtedly slow potential waves are due to the instability caused by the NR[9–12]. The present work provides additional evidence for a relationship between steady NR and slow potential changes; also it shows that a slow regenerating mechanism is needed.

Materials and methods. The experiments were performed on the firing cell – 'Gen' or L_{11} – of the parietovisceral ganglion of *Aplysia fasciata*. The ganglion was isolated and pinned in a plexiglass chamber continuously perfused with artificial sea water. Two independent glass microelectrodes filled with 2.5 *M* KCl were inserted in the cell for respectively recording and current injection. The electrical circuit for current or voltage clamping has been already described[13]. To determine i-V relations, a symmetrical triangular ramp pulse was applied to the control amplifier input. The slopes of the positive or negative potential ramps were (±) 0.8 to 3 mV/sec and the potential investigated ranged from −70 mV to 0 mV. The i-V relations obtained with the slow depolarizing ramps can be considered as the steady i-V characteristics of the membrane[11].

Slow permanent records were made on a Philips pen recorder. The temperature was controlled with a thermo-

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