Respiration of a monotreme, the echidna, *Tachyglossus aculeatus*

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BENTLEY, P. J., CLYDE F. HERREID II, AND KNUT SCHMIDT-NIELSEN. Respiration of a monotreme, the echidna, *Tachyglossus aculeatus*. Am. J. Physiol. 212(5): 957-961. 1967.—The minute volume, tidal volume, and respiratory frequency were measured in three echidnas breathing air and various air-CO₂ mixtures. Increased concentration of CO₂ in the inspired air caused large increases in minute and tidal volume but little change in respiratory rate. However, normal variation in minute volume of echidnas breathing air was principally the result of change in respiratory rate. The end-tidal (alveolar) CO₂ concentration was 5-6% whereas the O₂ was 14.5%, both values being similar to those of typical placental mammals. Burrowing echidnas voluntarily tolerate CO₂ concentrations of about 5%. The sensitivity of these animals to CO₂ was compared to other homeotherms and found to be low, but definite conclusions cannot be drawn until results on more species are available.

CO₂ sensitivity; minute volume; tidal volume; alveolar gases

MONOTREMES ARE EGG-LAYING MAMMALS that probably evolved sometime in the mesozoic era before the marsupial and placental mammals. There are two contemporary genera, *Ornithorhyncus* (the platypus) and *Tachyglossus* (the echidna), both confined to the Australian region. These animals are rather specialized with regard to the habitats where they live. The platypus is semiaquatic and catches its food principally under water on the beds of rivers and streams, whereas the echidna is terrestrial and lives on termites, which it obtains by burrowing into their nests. The echidna can burrow rapidly into the soil, presumably to avoid enemies and possibly, in deserts, to avoid the heat.

Our knowledge of the respiratory physiology of mammals and the essential role of carbon dioxide in its regulation stems largely from the classical studies of Haldane and Priestley (6) on man. Subsequent information includes measurements of respiratory parameters such as tidal volume, minute volume, and alveolar carbon dioxide and oxygen concentrations in a variety of placental mammals. Particular attention has been paid to diving placental such as the seal and duck (2).

Respiration in the echidna is of interest as there is little information about respiration in nonplacental mammals, and furthermore the echidna has a body temperature of only 31°C with an oxygen consumption of only half that expected in a placental mammal of the same size (12). In addition, both the echidna and the platypus have a manner of life where respiratory specializations associated with diving would not be surprising.

We have measured various respiratory characteristics of the echidna, including minute volume and tidal volume, as well as alveolar CO₂ and O₂ concentration and the respiratory responses to different concentrations of CO₂ in the inspired air.

METHODS

Animals. Three echidnas, *Tachyglossus aculeatus*, (2 females, 1 male) were obtained from Australia and maintained in the laboratory on a milk and egg diet with vitamin and mineral supplements (12) for nearly 2 years. They were kept in large wooden boxes containing crushed corncobs (San-I-Cel) at a depth of about 50 cm.

Experimental methods. The echidnas were tied to a restraining board after taping their wrists and ankles to prevent chafing. A cut-out section at one end of the board allowed free movement of the head and snout. A moderate amount of movement was possible on the board and the animals adapted themselves remarkably well to the situation. Periods of inactivity lasting 60-90 min were regularly observed when animals often slept. It was during such “quiet” periods that the experiments were performed. A period of activity followed such periods of quiet but usually after 15-30 min another prolonged period of rest occurred.

Separation of inspired and expired air was made with a simple water valve system so adjusted as to minimize...
TABLE 1. Respiration in resting echidnas

<table>
<thead>
<tr>
<th>Tidal volume, ml/breath</th>
<th>Tani V, 4.4 kg</th>
<th>Red V, 2.9 kg</th>
<th>Blue V, 3.0 kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>27.8±1.2</td>
<td>24.3±1.0</td>
<td>24.9±0.7</td>
<td></td>
</tr>
<tr>
<td>Minute volume, ml/min</td>
<td>337±14.2</td>
<td>382±9.8</td>
<td>704±17.8</td>
</tr>
<tr>
<td>Frequency, breaths/min</td>
<td>12.9±0.5</td>
<td>14.4±0.5</td>
<td>25.2±1.8</td>
</tr>
<tr>
<td>End-tidal CO2, %</td>
<td>5.49±0.28</td>
<td>5.68±0.14</td>
<td>4.63±0.16</td>
</tr>
<tr>
<td>End-tidal O2, %</td>
<td>14.56±0.38</td>
<td>14.77±0.27</td>
<td>14.28±0.24</td>
</tr>
<tr>
<td>Expired air CO2, %</td>
<td>2.98±0.10</td>
<td>4.07±0.18</td>
<td>2.37±0.12</td>
</tr>
<tr>
<td>Expired air O2, %</td>
<td>17.4±0.13</td>
<td>16.25±0.31</td>
<td>17.74±0.05</td>
</tr>
<tr>
<td>Alveolar ventilation, ml/breath</td>
<td>293.1</td>
<td>288.6</td>
<td>560.4</td>
</tr>
<tr>
<td>RQ, expired air</td>
<td>0.84</td>
<td>0.88</td>
<td>0.80</td>
</tr>
</tbody>
</table>

Results are given as means ± SE (range). Mean values for gas analyses are based on 5 samples; frequencies and volumes are based on 25 determinations. Calculations of dead space, alveolar ventilation, and RQ were made from mean determinations and consequently no variability values are given.

The animals were allowed to breathe air until constant base-line values were obtained. The gas mixture was then administered. After 6 min, volumes of expired air were measured at 1- or 2-min intervals until a plateau was observed. This usually took another 4-8 min. Atmospheric air was then given to the echidnas until respiration returned to the original base-line levels. The experiment was then repeated with a different gas mixture. The experiments were designed so that in each echidna five measurements of respiration were made while it breathed each gas mixture. The order for testing the gas mixtures was randomized within groups using all five mixtures. These measurements were done on three different days with several days elapsing between experiments on each animal.

Analyses. The volumes of air breathed by the animals were determined by measuring their displacement of water in a simple manometer system. The values were corrected to BTPS. Compositions of the gas mixtures, tidal and expired air were analyzed with a Scholander 0.5-cc gas analyzer (13).

Respiratory dead space was estimated from concentrations of CO2 in the end-tidal and expired air and corrected for the instrument dead space (4).

RESULTS

Flower and Lydekker in 1891 (5) noted that echidnas in captivity rapidly burrowed down into the soil of the

FIG. 1. A: relationship of respiratory minute volume to respiratory rate in the resting echidna breathing room air. B: relationship of respiratory minute volume to the tidal volume in three echidnas under same conditions as in A. Each animal is represented by a different symbol.
RESPIRATION OF ECHIDNA

Fig. 2. Respiratory parameters of three echidnas breathing various concentrations of CO₂. Each point on the graphs represents
pen where they were kept. Our echidnas were kept in large boxes containing crushed corncob, and we observed that they also burrowed deeply into this litter staying “submerged” at depths of 30-60 cm for pro-
longed periods. We attached long thin polyethylene tubes to the spines on the head and measured the CO₂ con-
centration of the air in the region of their faces while they were buried. The highest CO₂ concentration we
recorded was 6.93 % (O₂ 13.89 %); 1 hr later it was
6.19 %. Ten minutes later the animal changed position and a concentration of 4.87 % was recorded. In another
instance an animal stayed submerged at a depth of 60 cm
for 9 hr. The initially recorded CO₂ was 5.54 %, and the
final concentration after 2 hr was 5.11 %. Thus, it ap-
ppears that these animals regularly withstand CO₂ con-
centrations in excess of 5 % while burrowing, suggesting
the possibility of some respiratory adaptations.

Respiration in the resting echidna. A large number of
measurements of respiratory rate, tidal volume, and
minute volume were made in three echidnas while they
were resting quietly on the restraining board (Table
1). The male had a greater minute volume than the two
females, but the tidal volume was similar, the difference
being due to a greater respiratory rate.

The extraction of oxygen from the inspired air was
similar to that in other mammals as indicated by the
cnd-tidal O₂ concentrations (Table 1). The concentra-
tions of O₂ and CO₂ in the expired air indicate a respira-
tory quotient of about 0.85. As the dead space of the
mask was about 8 ml compared to about 4 ml in the
animal, the concentrations in the expired air in a free-
breathing animal would probably differ slightly from the
figures in Table 1.

Relationship of minute volume to respiratory rate and tidal
volume during normal breathing. In mammals alterations in
the normal minute volume are caused by a combination
of changes in tidal volume and respiratory rate. When
the echidna was in a resting condition differences in
minute volume were mainly due to changes in the res-
piratory rate (Fig. 1A). The tidal volume was relatively
constant over a wide range in minute volume (Fig. 1B).
Thus when the minute volume was 300 ml, the respira-
tory rate was 12/min and the tidal volume about 25 ml.
When the minute volume doubled, the respiratory rate
also doubled, while the tidal volume remained essentially
the same. The male echidna had a consistently higher
minute volume than the two females. This was entirely
due to a greater respiratory rate.

Effects of inspired CO₂ on respiration. The effects of in-
creased CO₂ in the inspired air were examined. Concentra-
tions ranging from 0.8 to 9.9 % were administered and
the respiratory rate, tidal volume, and minute volume
were measured. As seen in Fig. 2A the minute volume
increased as much as 4 times. This change, unlike the
variations seen in normal breathing, was due to increased
tidal volume (Fig. 2C). The respiratory rate was not
increased and in many cases was even decreased (Fig.
2B).

The greatest rate of increase in minute volume was
observed with CO₂ concentrations in excess of 5 %. The
highest values of tidal and minute volume were recorded
in each echidna when breathing 9.9 % CO₂. The tidal
volumes were 137, 82, and 115 ml whereas the minute
volumes were 1.9, 1.3, and 2.4 liters. This represents a
two-fold increase in both tidal volume and minute volume
from the normal resting levels.

DISCUSSION

The parameters of respiration in the echidna are com-
parable with those of placental mammals. The alveolar
FIG. 3. Changes in respiratory minute volume (as percent increase over resting level) of different species breathing various concentrations of CO$_2$. The results have been calculated from the following sources: seal (11), man (4), dog (1), duck (3).

(or end-tidal) CO$_2$ concentration in man is 5.95%, dog 5.68%, seal 6.3% (6, 7, 11), and echidna 5.49%. The corresponding O$_2$ concentrations are: man 14.6%, dog 13.6%, seal 11.6%, and echidna 14.4%. It is difficult to compare such parameters as tidal and minute volume in different mammals owing to the variability in their size and O$_2$ consumption. The values observed in the echidna, however, are, not peculiar in any way and are within the wide limits of variation seen in the placental mammals (7).

The echidna has an O$_2$ consumption about one-half that expected in a placental mammal of the same size and also has the relatively low body temperature of about 31°C (12). Despite these differences it is notable that the extraction of O$_2$ from the inspired air is comparable with placental mammals.

Alterations in respiratory minute volume in placentalts may be brought about by changes in respiratory rate and tidal volume. In the normal resting echidna there are variations in minute volume, and these are related almost exclusively to alterations in the respiratory rate. In contrast to this, examination of the classic results of Haldane and Priestley (6) reveals that variations in the resting minute volume of man were brought about principally by changes in tidal volume rather than respiratory rate (see also 8). However, when the respiratory minute volume of the echidna is increased by high concentrations of inspired CO$_2$, the change is brought about by increased tidal volume while respiratory rate is unchanged or in some cases is even decreased. The experiments of Haldane and Priestley (6) indicate that the response of man breathing CO$_2$ mixtures is similar.

It has been widely suggested that the mechanisms controlling respiration in diving animals are relatively insensitive to CO$_2$ (2), and even burrowing animals such as the pig and armadillo exhibit "diving" responses such as bradycardia (9). If we examine the effects of breathing CO$_2$ mixtures in relation to the percent increase in minute volume (Fig. 3) the echidna is less sensitive than man, dog, or seal and the duck is the least sensitive. It is rather surprising to note that the seal appears to be as sensitive as man or dog in its response to inhaled CO$_2$. If one further examines the results of Robin et al. (11) and compares increases in normal alveolar CO$_2$ with percent increase in minute volume, the seal can only be judged slightly less sensitive than man. Thus for an increase of 10 mm Hg PA$_{CO_2}$ man increases minute from about 12 to 31 liters/min whereas in the seal the increase is from about 4 to 8 liters/min. We hesitate to draw any definite conclusions about sensitivity to CO$_2$ in relation to diving and burrowing, as results are only available on a few species and the differences could be dictated by other factors. Thus the echidna is the smallest mammal on which this kind of information is available, and it also has a low rate of oxygen consumption. Further measurements on a wider range of mammals are needed. However, it is noteworthy that the echidna voluntarily stays for extended periods of time in situations where the CO$_2$ concentration may be as high as 6.9%. When "submerged" it seems to prefer concentrations less than about 5%; it was above this level that the greatest experimental increases in minute volume were observed.

Parer and Metcalfe (10) recently measured the CO$_2$ and O$_2$ tensions in the arterial blood of the echidna and they concluded that the alveolar CO$_2$ is regulated at a far higher level than the usual mammalian one of about 40 mm Hg. They suggested that this is an adaptation to the burrowing habits of the animals. Our measurements of alveolar CO$_2$ (and O$_2$) concentrations do not support their results, the concentrations being typical of those in most other mammals. There is some indication that the echidnas used by Parer and Metcalfe were not in a steady state because their figures indicate an RQ of 0.69. The apparent discrepancy between measurements of blood and alveolar air may be resolved by further study.

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REFERENCES