SHIVERING IS A UNIVERSAL thermogenic mechanism in all endothermic homeotherms (16). In adult birds, it appears to be the only means of thermoregulatory heat production during cold exposure (9). The mechanisms of shivering thermogenesis in birds have been studied extensively using electromyographic and calorimetric methods (10, 13, 25, 26, 30). A major shortcoming in these studies is that the experiments are performed in metabolic chambers or other special setups to which the animals are transferred for the measurements, and where they cannot carry out their normal daily activity patterns. Furthermore, the electrodes for electromyography are usually affixed shortly before each experiment, which incurs variance between experiments.

Several aspects of shivering cannot be studied by such measurements and have therefore remained poorly known or hypothetical. More data are needed to shed light on the following issues. The first issue is the interaction between locomotor activity and shivering. Although some data exist on the effects of treadmill exercise on shivering in birds (e.g., Ref. 19), the interaction between voluntary motor activity and shivering has not been studied in birds during their voluntary daily activities. In addition to the neural aspects of this interaction, this issue also has implications regarding the hypothesis that activity-induced thermogenesis can substitute for shivering.

The second issue is the continuity of shivering. In short-term experiments, shivering has been shown to be continuous below the thermoneutral zone. This would imply that, in winter, birds living at high latitudes have to shiver always when they are not flying (30). However, it is not known whether this actually happens in a freely moving bird. This relates to the fact that there is very little information on the daily pattern of shivering in birds or mammals in general (see, however, Ref. 6).

The third issue is the relationship of muscle electrical activity to actual heat production. Previous studies have shown that appropriate indexes of electromyogram (EMG) amplitude correlate well with heat production in short-term measurements (10), but it is not known how much this relationship changes during the daily light-dark (LD) cycle or how it is influenced by nonthermal stimuli such as fasting or feeding. Such experiments necessitate chronic electrodes so that segments of EMG at different conditions can be reliably compared. Conclusions about the presence or absence of nonshivering thermogenesis are often based on changes in the ratio of electrical activity to heat production. These conclusions are valid only if the normal shifts in this ratio are known and accounted for.

The fourth issue is diurnal variation in the parameters of muscle electrical activity. Parameters of the electrical activity of muscle obtained by signal analysis of EMGs can be used to study motor unit function during shivering. Although a number of studies on the various frequency and amplitude characteristics of the electromyographic activity of shivering birds have been made (10, 26, 31), none of these are based on continuous measurements in semi-free birds.

To shed light on the issues listed above, this study reports the interactions of shivering (pectoral muscle electrical activity), oxygen consumption, body temperature, and activity observed in pigeons living in their home cages. By transforming the cages into metabolic chambers and utilizing a very flexible recording system
for shivering, long-term recordings from birds that performed a variety of normal daily activities was accomplished and most of the problems of acute experiments were avoided.

MATERIALS AND METHODS

Animals. Adult, male pigeons (Columba livia) were obtained from a supplier of local animals in Tallahassee, Florida. The body weight of the birds before the experiment ranged from 325 to 425 g. For at least 2 mo before any experimental work, the birds were housed with other pigeons in an indoor avairy maintained on a 12:12-h LD cycle, with the ambient temperature (Ta) ranging between 19 and 22°C. Food and water were available ad libitum in the avairy. The food was a commercial high-carbohydrate pelleted food (Purina Nutriblend Gold) with a caloric value of 18.4 kJ/g, as determined by bomb calorimetry. The composition of the food is described by the manufacturer as ~60% carbohydrate, 14% protein, 7% fat, 6.5% ash, and 3% added minerals.

Apparatus. A metabolic chamber where the birds lived individually during the experiment was housed inside an environmental chamber that provided precisely controlled levels of Ta (~0.1°C) and a daily photoperiod when an overhead incandescent lamp was lighted (illumination ~40 lx of 2,250 K light measured at the approximate height of the pigeon's head). The chambers were completely darkened during the daily dark phase (D). The airtight metabolic chambers were made of clear, acrylic plastic (53 cm by 27 cm by 28 cm; total capacity 40 dm³) and had a plastic grid floor and underlying paper to catch droppings from the bird. The lid of the chamber was removable to allow chamber maintenance. When ad libitum feeding conditions were in effect, the pigeons could obtain food and water during the light phase (L) by pecking on response keys mounted on a wall of the metabolic chamber (details in Ref. 22). A low perch running the width of the chamber was mounted on the floor, ~20 cm from the wall on which the keys were mounted. A small, infrared-sensitive videocamera provided a lengthwise perspective of the chamber, which made it possible to record behavioral events in selected parts of L and D. When the pigeon was on the perch facing the feeder wall, the video image showed a full frontal image.

Oxygen consumption (V̇O₂, ml/min) was measured by open-circuit respirometry. Ambient air was brought to a dew point and sent to a paramagnetic O₂ analyzer (Servomex 1155). This was done on a schedule such that a measurement of the O₂ content (1 part per million resolution) of the samples from the chamber and the supply air was obtained every 2.5 min. The difference between the supply air and the chamber air concentrations was corrected to standard temperature and pressure (0°C, 760 mmHg) and stored in a computer. Instantaneous values of V̇O₂ were calculated by isolating each sample point using dynamic equations similar to those of Bartholomew et al. (1).

Body temperature (Tb) was measured by means of precalibrated thermosensitive radiotransmitters (model T, mass 5 g; Barrows, San Jose, CA) implanted in the pigeon's abdominal cavity under halothane anesthesia. The transmitter pulse rate (~500 Hz at 37°C) was processed by software to provide mean Tb measurements with high resolution (0.01°C) in every 2.5-min period of the day. Signals from the transmitter were picked up by three orthogonal antennas located under the cage in each chamber, and a three-channel receiver combined the signals and sent the pulse rate to the computer once each second. Any outlying pulse rates in each 2.5-min period were removed by software before the average Tb for each 2.5-min period was stored (usually 2 or fewer outliers per 149 measures obtained in each 2.5-min period). Data obtained during each 24-h period were saved to disk at the end of each photophase.

Electromyography. To record EMGs related to shivering thermogenesis, three gold-plated hook electrodes were chronically implanted into the pectoral muscle of the pigeons under halothane anesthesia. Three electrodes were positioned in a triangular configuration 10–14 mm away from the keel and ~30 mm caudally from the cranial tip of the sternum at a depth of ~10 mm. The electrode shafts measured 5 mm in length and 0.25 mm in diameter. The electrodes were bent back to an angle of 35 degrees, leaving 2.5 mm for each arm, and ultraflexible, multistrand, Teflon-coated steel wires (Cooner Wire, no. AS632; 15 strands, each 0.025 mm in diameter; total outer diameter 0.30 mm) were connected to them. The distance between the insertion points was 4 mm. The wires were threaded subcutaneously to the back of the bird and connected to a miniature plug in a flexible harness. A flexible cable from the harness was connected to a plug in the lid of the chamber. The cable allowed the bird to move freely in the chamber. Remote television observation showed that the cable did not affect feeding or sleeping behavior of the bird and that the general activity of the bird did not change.

At least 1 wk was allowed for recovery after the operation. The EMG signal was led to a Grass P511 amplifier that had a gain of 5,000 and a high-pass frequency of 50 Hz and a low-pass frequency of 580 Hz (-3 dB points), both with roll-off of 40 dB/decade. Postmortem examination showed that there was no scar formation around the electrodes during a period of several weeks.

Three different sampling techniques (10) were used for analysis of EMG. 1) Root mean square (RMS) EMG was collected continuously (up to 8 wk) for each 2.5-min period together with Tₖ and V̇O₂. 2) Mean rectified value (MRV) of EMG was collected at a high time resolution (sampling rate 28 Hz) for 24 h on specific days. 3) Samples (1–5 min) of raw EMG were recorded on an instrumental tape recorder for offline signal analysis.

To obtain the 2.5-min RMS values of EMG, the amplifier output was fed to a circuit (Analog Devices AD 536A) that provides an analog output of the signal's RMS using a 120-ms time window inside the square root operator. The analog RMS output was fed to a circuit (Analogue Devices AD 536A) that provides an analog output of the signal's RMS using a 120-ms time window inside the square root operator. The analog RMS value from the circuit was further smoothed by feeding it through a resistor-capacitor (RC) circuit with a time constant of 120 ms and then sampled by a 16-bit data-acquisition board to provide 20 averages per second. Thus the RMS for each bin was the average of 2,980 individual readings (149 s × 20 Hz) collected during the 2.5 min. The last second of each bin (150 s) was used to calculate the RMS EMG value and other variables, which were then written to disk every 24 h.

To study the "on-off" characteristics of shivering EMG with high time resolution, the internal (120 ms) time constant of the RMS circuit was inactivated, which makes the circuit a full-wave rectifier. The rectified EMG was then smoothed with an RC circuit using a 7.5-ms time constant and sampled at 28 Hz using an A/D board and a personal computer. This combination of smoothing ("integration") and sampling rate allows detection of short breaks in EMG for 24 h with reasonable data file sizes. The data thus produced represent MRV of shivering EMG instead of RMS. This does not hamper the analysis because RMS and MRV are both valid measures of EMG amplitude (see Ref. 10). For each 2.5-min bin, 4,096
data points were collected, and the remaining 4 s were used to write the data on disk and close the file. The data were stored on a hard disk as 16-bit integers, which produced 4,718,592 bytes per 24 h, which was the typical duration of these recordings. The data were then read into a software package (DaDISP, DSP Development) for further analysis.

For signal analysis, representative samples (4-8 min) of EMG were stored on magnetic tape using an instrumentation tape recorder (EMI SE 3000, EMI Technology). The recorder was used in analogic mode in which our tests showed its frequency response to be flat between 40 and 1,300 Hz. The EMG samples thus obtained were used for spectral analyses with a DATA 6000 signal analyzer (Data Precision, Analogic). Amplitude spectra were obtained both from raw and "demodulated" EMG (15). To obtain demodulated EMGs, the signals from the tape were rectified (RMS circuit with a time constant of zero) and then filtered using a low-pass RC circuit with a time constant of 7.5 ms. This procedure produces an analog signal that is proportional to the short-term variations and oscillations in EMG intensity, such as produced by motor unit synchronization (7). Except for being done offline, the procedure is essentially the same as was used to get the "fast-response" MRV EMG described earlier. Analysis of demodulated EMG has proven to be an efficient method when searching for rhythmic patterns in the short-term fluctuations of EMG intensity (e.g., tremor; see Ref. 15).

For raw EMG spectra, the sampling rate was 2 kHz and sample length was 512 data points. From these data, the fast Fourier transform algorithm produces spectra that have a frequency range from 0 to 500 Hz divided in 256 frequency bins. To obtain a representative spectrum for each sample of EMG on the tape, 64 individual spectra calculated from consecutive segments of the signal were averaged. For spectra of demodulated EMG, the sampling rate was 200 Hz and sample length was 512 points. The spectra produced had a frequency range from 0 to 100 Hz divided in 256 bins. For each sample of EMG, 16 individual spectra were averaged, and the average spectra were then smoothed using a five-point convolution.

Behavioral activity/video scoring. To facilitate the subsequent correlation of behavioral events and shivering, raw EMG was also recorded on the audio channel of the videotape whenever video recordings were made. Behavioral categories included easily identified species-typical behaviors (preening, body-scratching by foot, drinking, wing-stretching, defecation (cloacal dropping), walking, standing still while alert, behavioral resting, behavioral sleep), as well as behaviors related to the prevailing experimental conditions (exploratory searching for food or water in the vicinity of the feeder/waterer, pecking the response keys to obtain food or water, prominent movements of the food-filled crop during the dark phase after particularly large food loads). Representative instances of these behaviors were selected for analysis with respect to their relationship to pectoral EMG activity.

Feeding and Tₐ conditions. Water was available at all experimental sessions. Data were obtained in several feeding conditions (ad libitum food; days 1–7 of fasting) and at three levels of Tₐ (21°C, 11°C, 1°C) while the 12:12-h LD cycle was maintained. All changes of temperature lasted between 1 and 5 days and no acclimation effects were found.

RESULTS

Interaction between shivering and voluntary muscular activity. The EMG signal from the pectoral muscle was virtually artifact-free. None of the following behavioral activities induced spurious EMG in the pectoral muscle: preening, walking, scratching, stretching, pecking, drinking, vocalization, defecation. Examples of the EMG signal during some of these behaviors at 21°C are shown in Fig. 1, A and B.

On the other hand, ongoing shivering induced by lower levels of Tₐ was not directly inhibited by any of the above activities (Fig. 2, A and B). The intensity of shivering was often initially modulated by a sudden burst of activity such as drinking, but returned to normal levels within a few seconds. In particular,
activities that go on for a long time, such as preening, had practically no influence on shivering after the initial effect.

That shivering in the pectoral muscle is virtually continuous in cold even during L where activity is high is evident from Fig. 3, which shows the distribution of MRV EMG values collected at a rate of 28 samples/s for L and D at two different temperatures. EMG intensities were above 5 µV (the basal EMG level caused by cross-talk from ECG activity) 98.3% of the time at a $T_a$ of 1°C even during L (as compared with 99.7% in D), when there is much activity due to feeding, preening, walking, etc. Modulation by these behavioral activities obviously causes the greater variation of EMG levels in L seen in Fig. 3. The distribution of EMG values is close to normal in both cases at 1°C, but the coefficient of variation of MRV EMG was significantly higher in L than in D.

Although behavioral activities do not inhibit shivering directly, the inevitable heat production associated with movements may decrease the need for shivering. To illustrate this, the shivering levels in L and D at various $T_a$ values, calculated from 8.3-h periods around the midpoints of L and D, are shown in Table 1. Note that there was significant shivering even at 21°C, probably because the effective air circulation required for fast-response $V_O^2$ measurements increased heat loss. None of the differences between paired L and D shivering levels are significantly different. In L, however, the birds are maintaining a $T_b$ that is ~2°C higher than in D and have a higher $V_O^2$. This may result from the inevitable increase in basal metabolic rate (BMR) in L, but also if activity-induced heat is retained in the body or if the heat produced by a unit of electrical activity is not constant.

Shivering, $T_b$, and $V_O^2$. An example of the data that was used as the basis for these analyses is shown in Fig. 4. Calculation of instantaneous $V_O^2$ values permitted the use of the 2.5-min bins to correlate $V_O^2$ to EMG. That the shivering-induced increases in $V_O^2$ were traced by high fidelity by our measuring system was shown by cross-correlation analyses, which confirmed that there was no lag between changes in EMG and $V_O^2$ at this temporal resolution. To obtain a plot of $V_O^2$ vs. EMG, all the bins from L or D of a day, excluding 2 h at the beginning and end to avoid the shifts in variables occurring at L-D transitions (i.e., leaving 8 h for analysis), were used. The plot thus obtained always showed a distinct group of minimum ("floor") values that were correlated to shivering-linked EMG during minimal behavioral activity, and scattered points that could be attributed to activity-induced $V_O^2$. Typically, this activity-induced "hump" of points was located at low EMG values in D but was more widespread in L. To obtain a specific plot of $V_O^2$ vs. shivering EMG, points with muscular activity other than shivering have to be excluded from the analysis. These points were filtered from the raw data as follows. The data were first sorted according to EMG values. For each 5- or 10-µV interval, the data were then sorted according to $V_O^2$. Data points with $V_O^2$ values within 15% of the minimum of the bin were used for the final plot. If a 5-µV bin contained 10 or more data points it was used; otherwise, a bin width of 10 µV was used. Intervals with fewer than 10 data points were not used. The procedure is illustrated in Fig. 5, which shows an example of the data for one plot.

Fig. 2. Two examples of effects of various types of behavior on shivering in pectoral muscle of pigeon. A: light phase (L). B: dark phase (D). Details as in Fig. 1. (Note, in this experiment, P43 was fed 22 g at hour 9 of L of each day; it typically ate the food within a few minutes.) Sleep pertains to behavioral sleep.
before the filtering procedure. That this method selects data points with minimal behavioral activity was confirmed when two independent observers rated activity from videotape during each VO2 measure in the plot. The activity scores for the accepted bins were close to zero, while those for the rejected bins were dramatically higher (see inset in Fig. 5). Because the birds are less active in D, the number of useful data points was higher for D than L.

Data plotted by this method showed that the relationship of VO2 to shivering was not constant (Fig. 6). The slopes of these plots were consistently higher during L than during D in all the conditions tested (0.001 < P < 0.05, paired t-test, 8 tests in 3 pigeons; in one case at 11°C P = 0.12). In addition, the slope was further lowered by fasting (4–6 days, 15–20% body mass loss, Fig. 7). In all cases, the regression slopes were significantly different from zero, indicating a linear increase in VO2 with increasing EMG. The y-intercepts of the plots (activity-free VO2 at zero shivering) were significantly higher in L than in D, which indicates a nocturnal shift to a lower BMR.

Signal analysis of EMGs. Extensive spectral analyses of raw and demodulated EMGs were undertaken to study 1) whether there is a change in the recruitment of motor units or their firing pattern during shivering in response to L, D, fasting, or Ta and 2) whether such changes can explain the shifts observed in the VO2-EMG relations in these conditions.

Overall, the spectra of raw EMG were very similar in all conditions (Fig. 8). There was, however, a clear downward shift in the median frequency of the spectra with the lowering of Tb. This is especially clear in fasting birds, which show a pronounced hypothermia during D. There was a shift of ~40 Hz in median frequency per 5°C drop in Tb.

The spectra of demodulated EMG differed markedly between the experimental conditions (Fig. 9). There was a distinct peak in the spectra at 8–10 Hz at 21°C, especially in fasting birds. This is an indication of a partial motor unit synchronization in these conditions. At 1°C, however, this peak was absent. Similarly to median frequency in the spectra of raw EMG, the peak shifted to lower frequencies in fasting birds during D. Another peak observed in all the spectra at very low frequencies is obviously caused by the breathing-induced synchronization of motor units (11, 27). It did not change with ambient conditions.

**DISCUSSION**

The pectoral muscle of the pigeon is an excellent model for studying the role of shivering thermogenesis in maintaining homeothermy. The muscle is electrically silent when there is no shivering even if the bird is moving around in the cage and performing its daily activities (Fig. 1). A similar observation has been made earlier for the effects of walking (5). Furthermore, excluding flying, which was not possible in our experimental conditions, none of the daily activities of a bird directly inhibit (or enhance) ongoing shivering in the pectoral muscle (Fig. 2). Distinguishing electrical activity due to shivering from other types of muscular contraction (postural, voluntary movement) is much more complicated in leg or neck muscles, which are directly involved in the maintenance of posture. This

---

**Table 1. Shivering intensities in successive periods of L and D based on long-term measurements of EMG from the pectoral muscle at various ambient temperatures and ambient conditions**

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>21°C</td>
<td>12.81 ± 7.78</td>
<td>8.89 ± 4.59</td>
</tr>
<tr>
<td>21°C fasting</td>
<td>14.85 ± 5.35</td>
<td>15.40 ± 4.01</td>
</tr>
<tr>
<td>11°C</td>
<td>40.72 ± 2.67</td>
<td>44.75 ± 2.06</td>
</tr>
<tr>
<td>1°C</td>
<td>138.52 ± 24.55</td>
<td>138.12 ± 24.56</td>
</tr>
</tbody>
</table>

Values are means ± SE in microvolts [root mean square electromyogram (EMG) values] calculated from representative 8.3-h sections (200 2.5-min bins) in each condition; n = 3 pigeons. All nonfasting data are from birds fed ad libitum. Fasting data are from the fifth day of fasting, when body mass was ~85% of the ad libitum value. None of the differences between paired light phase (L) and dark phase (D) measurements are significantly different from each other.
also makes birds in general a suitable model for such studies, as none of the major muscles in mammals shows this independence.

A similar independence of shivering and motor activity has been shown in pigeons performing treadmill exercise. Shivering in the pectoral muscle can be induced by spinal cooling during exercise (20). In contrast to the effects of spontaneous walking, a rapid partial suppression of shivering occurs in cold-exposed pigeons when they are subjected to treadmill exercise and shivering remains at a lower level for the duration of the exercise (19). This modulation can either be a direct neural interaction originating from the organization of the motoneuronal system (18) or an adjustment to increased muscular heat production. In this study, the
effects of activity, if any, on shivering in freely moving pigeons were much smaller and always transient, which suggests that startle reactions and direct neural inhibition are involved in treadmill experiments. Motor activity may decrease the need for shivering indirectly by increasing internal heat production. This is probably one reason why shivering was not higher during L, although the birds maintained a higher $T_b$, which together with the coincident increase of thermal conductance (12) would necessitate more intensive thermogenesis. Data in the literature on the intensity of thermogenic muscle activity during the daily LD cycle are very limited. In one previous study (6), pectoral muscle EMG in the pigeon was lower during D. This may indicate that the conditions did not allow the birds to utilize the heat produced from the normal daily activity and forced them to resort to shivering to elevate their $T_b$ to the preferred level during L. Thus our observations lend support to the hypothesis that even moderate motor activity can reduce the need for thermoregulatory thermogenesis. However, the increase in BMR occurring at the D-L transition and seen as shifts in the y-intercepts in Fig. 6 (magnitude about 15%) may be a more important source of nonthermoregulatory heat. The quantitative role of each of these mechanisms cannot be assessed without further experiments.

On the other hand, the observation that actual thermogenesis at the same level of muscle electrical activity is higher during L (Figs. 5 and 6; see below) suggests that even if there is a need for enhanced thermoregulatory thermogenesis (shivering) during L, this does not necessarily result in higher electrical activity of the muscle. Finally, it should be noted that the mean L and D values of shivering used in this way tell nothing of the short-term variability of thermogenesis, which is intricately connected to the various phases (e.g., the transitions between L and D) of the
The complicated relation of daily activity and shivering is illustrated by the fact that the coefficient of variation in shivering intensity is much greater at 1°C during L than during D (Fig. 3), although the amplitudes distribute normally in both cases. Despite the greater variation, shivering remains virtually continuous even during L. It is clear that only fatigue-resistant muscle fibers can be recruited for such a long-term activity.

The existence of thermogenic mechanisms other than shivering in birds has been suggested on several occasions (e.g., Ref. 2). As the absence of brown adipose tissue in birds is now confirmed (24), these hypotheses are based on observations of differential changes in $\dot{V}O_2$ and electromyographic indexes of shivering. The changes in the $\dot{V}O_2$-to-EMG ratio induced by the LD cycle and fasting observed in this study show that conversion of muscle electrical activity to values of heat production has to be done with caution even in the same individual. This is a novel finding and has not been reported before.

At least the following factors might account for the observed shifts in the $\dot{V}O_2$-to-EMG ratio. 1) The propagation of motor unit action potentials is slower at lower tissue temperatures. Body temperature in normally fed pigeons is ~2°C lower in D than in L and during fasting this difference may reach 8°C. The increased duration of individual action potentials at low $T_b$ will increase RMS EMGs even if the levels of motor unit activation and $\dot{V}O_2$ do not change. That muscle fiber conduction velocity changes with temperature is indicated by the shifts toward lower frequencies in the EMG spectra (Fig. 8, Refs. 14, 17). 2) The contribution of peripheral muscles to thermogenesis may decrease in D. Sleep-and fasting-induced hypothermia represent states of altered metabolism, which may change the distribution of blood flow to peripheral muscles. Measuring EMG from one muscle and $\dot{V}O_2$ from the whole animal will thus result in changes of the $\dot{V}O_2$-to-EMG ratio. Such changes are known to occur with changes in vigilance and other physiological variables of the animal (8, 23, 32). 3) The recruitment order and firing pattern of muscle fibers for shivering may be influenced by the vigilance or the feeding condition of the animal, which will alter EMG amplitudes. Evidence for such shifts was obtained from spectral analyses of the demodulated EMGs in the present study. Thus differences in the $\dot{V}O_2$-to-EMG ratio observed at different experimental conditions should not be interpreted as adaptive changes in thermogenesis or as the presence of nonshivering thermogenesis before more direct explanations can be ruled out.

Spectral analyses indicate that the basic frequency characteristics of muscle electrical activity related to shivering are independent of $T_a$, feeding state, and phase of the LD cycle. However, demodulated EMG is more sensitive for detection of changes in the firing patterns of motor units. Demodulated EMG has been successfully used to detect interspecific differences in motor unit synchronization of shivering mammals (7). The present results suggest that by combining long-term measurements with EMG demodulation, physiologically relevant changes can be observed within the same species subjected to various thermal challenges.
One important consequence of motor unit synchronization is increased tremor, which is thermally maladaptive because it increases convective heat loss (13). In this light, the decreased synchronization seen in the 8- to 10-Hz range at 1°C seems logical. Further experiments are needed, however, to elucidate the adaptive significance and the physiological basis of such changes in motor unit firing patterns.

Perspectives

Long-term electromyographic recordings of muscle activity constitute a normal routine in sleep studies (for studies in the pigeon, see Refs. 21, 28, 29), but they are mostly used to detect postural activity, which is intended to help classification of sleep states. Typically, EMG electrodes for sleep studies are placed in neck muscles, which do not contribute significantly to shivering thermogenesis because of their small mass. Continuous electromyographic recording of voluntary motor activity has also been accomplished in freely moving rats (3).

Methodological studies (4) show that variation in the anatomic positioning of bipolar wire electrodes has a much greater effect on the obtained EMG than the choice of electrode material or the dimensions of the electrode. For example, doubling or halving the tip length induces a maximal change of 8% in electrode impedance. EMGs recorded with chronic electrodes, such as used in this study, thus avoid a major obstacle in obtaining repeatable EMGs. Long-term recordings of EMGs are thus technically and physiologically feasible, but have not been implemented in studies of shivering. Such measurements are needed to dissect total thermogenesis into its various facilitative (shivering, nonshivering thermogenesis) and obligatory (BMR, diet-induced thermogenesis, activity) components. Combined with recent evidence of nonshivering thermogenesis in avian skeletal muscle (e.g., Ref. 2), they provide a means for an integrative approach to avian homeothermy.

There are several reasons why the avian pectoral muscle is an ideal model for studying shivering thermogenesis. In addition to its large mass, which makes it the major thermogenic organ, its thermogenic functions are largely independent of motor or postural activity. A simplifying factor is the lack of brown adipose tissue thermogenesis in birds (24). Also, because shivering (at least in the pigeon) is continuous on a long-term basis, a representative estimate of shivering intensity and its variation can be obtained from EMGs of reasonable duration. On the other hand, the state-dependent relation of actual thermogenesis to muscle electrical activity shows that complicating factors exist. Long-term recordings of thermogenesis and other thermoregulatory variables in quasinatural conditions constitute an efficient tool for analyzing these interactions. With the advent of modern implantable telemetric transmitters and data loggers, such experiments are becoming more and more feasible and should be encouraged.

We thank Patrick Basco and Raquel Reistenberg for performing the behavioral scoring of videotapes, Don Donaldson for help with the computer programs, Paul Hendrick for electrode manufacture, and Seppo Saarela for helpful comments on the manuscript.

This work was supported by grants from the Academy of Finland to E. Hohtola and from the National Science Foundation of the United States (IBN-9222369) to M. E. Rashotte.

Present address of E. Hohtola and address for reprint requests: Univ. of Oulu, Dept. of Biology, PO Box 333 FIN-90570, Oulu, Finland.

Received 1 October 1996; accepted in final form 10 July 1998.

REFERENCES


