The aim of this study was to use whole body calorimetry to directly measure the change in body heat content ($\Delta H_b$) during steady-state exercise and compare these values with those estimated using thermometry. The thermometry models tested were the traditional two-compartment model of “core” and “shell” temperatures, and a three-compartment model of “core,” “muscle,” and “shell” temperatures; with individual compartments within each model weighted for their relative influence upon the change in body heat content ($\Delta H_b$) during moderate-intensity exercise (40% of $V\dot{O}_2$ peak) on a cycle ergometer and a sum-to-one constraint. Fifty-two participants performed 90 min of exercise and calorimetry data were used to derive optimally fitting two- and three-compartment thermometry models. The traditional two-compartment model was found to be statistically biased, systematically underestimating $\Delta H_b$ by 10.2 ± 0.3°C on 30°C and 5.4% (SD 30.0) at 24°C. The thermometry model greatly underestimates $\Delta H_b$, with an adjusted R$^2$ of 0.48 and 0.51, respectively. It is concluded that a major source of error in the estimation of $\Delta H_b$ using the traditional two-compartment thermometry model is the lack of an expression independently representing the heat storage in muscle during exercise.

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with ~5% skin mass (44), and the specific heat capacity of muscle tissue is very similar to that of skin (13). Despite this, temperature of the skin is independently considered in the two-compartment thermometry model (i.e., “shell”), whereas muscle temperature is not. Furthermore, the traditional two-compartment thermometric approach arbitrarily includes muscle mass as part of the “core.” However, active muscle tissue can be the primary source of thermogenesis during exercise, and inactive muscle may be a major heat sink during exercise. Therefore, overall muscle tissue temperature is typically subject to a greater change relative to measures of core and skin temperature.

The aim of the present study was to compare the change in body heat content, as estimated using a two-compartment thermometry model, and a three-compartment model, incorporating the thermal influences of muscle mass, with those values directly measured using whole body direct calorimetry. It was hypothesized that the difference between the estimates for change in body heat content by a three-compartment thermometry model relative to direct calorimetry, will be less than by the two-compartment approach.

METHODS

Participants

After approval of the experimental protocol from the University of Ottawa Research Ethics Committee, 52 healthy, nonsmoking normotensive participants volunteered (26 males, 26 females) for the study. Of the participants, 22 (10 males, 12 females) were exposed to an air temperature of 30°C and relative humidity (RH) of 30%; 6 (3 males, 3 females) to 30°C, 60% RH; and 10 (4 males, 6 females) to 24°C, 30% RH; and 14 (9 males, 5 females) to 24°C, 60% RH. The characteristics of the participants are given in Table 1.

The body composition of each participant was measured using dual energy X-ray absorptiometry (DEXA) by which the body mass is partitioned into fat tissue mass (mf), lean tissue mass (ml), and bone mass (mb). Lean tissue mass (ml) is further subdivided into muscle mass (51.0% of ml), skin mass (11.0%), white matter, gray matter, eye, nerve, lens, and cartilage mass (12.9%), blood mass (25.0%), and cerebral spinal fluid mass (0.1%) (12, 37). Using these components (13), we determined the mean average specific heat of the body (Cp) (Table 2).

Instrumentation

Esophageal temperature (Tes) was measured by placing a pediatric thermocouple probe of ~2 mm in diameter (Mon-a-therm General Purpose Temperature Probe; Mallinckrodt Medical, St. Louis, MO) through the participant’s nostril while they were asked to sip water through a straw. The location of the probe tip in the esophagus was estimated to be at the T8/T9 level, in proximity to the left ventricle and aorta. This position is based upon the equation of Mekjavic and Rempel (27). Rectal temperature (Tre) was measured using a pediatric thermocouple probe (Mon-a-therm Tympanic) placed in the aural canal until resting against the tympanic membrane (determined by the participant reporting an audible scratching sound), following which it was withdrawn slightly. The aural canal probe was held in position and isolated from the external environment with cotton and ear protectors. Skin temperature was measured at 12 points over the body surface using 0.3-mm diameter T-type (copper/constantan) thermocouples integrated into heat flow sensors (Concept Engineering, Old Saybrook, CT). Thermocouples were attached using surgical tape (Blenderm, 3M, St. Paul, MN). Mean skin temperature (Tm) was measured using the anterior superior iliac spine and the superior aspect of the centre of the patella (23–25). The triceps brachii muscle temperature probe was inserted approximately midway between, and lateral to, a line joining the greater

<p>| Table 1. Mean descriptive characteristics for male and female participants |
|-----------------------------|------------------|-------------------|-------------------|-----------------|-------------------|-------------------|</p>
<table>
<thead>
<tr>
<th>n</th>
<th>Age, yr</th>
<th>Weight, kg</th>
<th>Height, cm</th>
<th>BSA, m²</th>
<th>BMI, kg/m²</th>
<th>V̇O₂peak, ml·kg⁻¹·min⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>26</td>
<td>25.8 (9.0)</td>
<td>78.8 (12.9)</td>
<td>179.0 (6.0)</td>
<td>1.97 (0.17)</td>
<td>24.5 (3.5)</td>
</tr>
<tr>
<td>Female</td>
<td>26</td>
<td>51–18</td>
<td>106.8–60.1</td>
<td>193.0–167.6</td>
<td>2.37–1.69</td>
<td>31.8–19.6</td>
</tr>
<tr>
<td></td>
<td>38–18</td>
<td>63.1 (10.0)</td>
<td>167.3 (6.2)</td>
<td>2.71 (0.14)</td>
<td>22.7 (3.5)</td>
<td>40.5 (8.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>97.2–41.5</td>
<td>180.0–154.9</td>
<td>2.04–1.35</td>
<td>35.7–17.3</td>
<td>56.7–28.0</td>
</tr>
</tbody>
</table>

Values given are means, standard deviation (in parentheses), and range (maximum–minimum). Body surface area (BSA) is estimated using the equation of DuBois and DuBois (8). BMIs, body mass indices; V̇O₂peak, volume of peak oxygen consumption.

with assigned specific heat for each tissue component (12, 13, 37). DEXA, dual energy X-ray absorptiometry.
tubercle of the humerus and the superior aspect of the olecranon of the ulna (23, 25). The upper trapezius muscle temperature probe was inserted 3 cm superior to the center point between the acromion process and superior angle of the scapula.

All temperature data were collected using a HP Agilent data acquisition module (model 3497A) at 15-s intervals. These data were simultaneously displayed and recorded in spreadsheet format on a personal computer (IBM ThinkCentre M50) with LabVIEW software (Version 7.0, National Instruments, Austin, TX).

**Direct calorimetry.** The modified Snellen whole body air calorimeter was employed for the purpose of measuring whole body changes in evaporative and dry heat loss, yielding an accuracy ± 2.3 W for the measurement of total body heat loss. A full technical description of the fundamental principles of the original Snellen calorimeter has been published (39), and a further technical report describing all modifications and performance characteristics is also available (34).

In summary, the calorimeter incorporates a semirecumbent constant load cycle ergometer and is housed within a climatic chamber slightly pressurized (+8.25 mmHg) to nullify potential air leakage through the calorimeter walls. Differential air temperature and humidity are measured over the calorimeter by sampling the influent and effluent air. The water content is measured using precision dew point thermometry (model 3733H; RH Systems, Albuquerque, NM), while the air temperature is measured using RTD high-precision thermistors (±0.002°C, Black Stack model 1560, Hart Electronics, American Fork, UT). Air mass flow through the calorimeter is estimated by differential thermometry over a known heat source (2 × 750 W heating elements) placed in the effluent air stream. Differential temperature over the heater is measured using a third aforementioned high-precision thermistor placed downstream from the heater. Air mass flow rate (kg air/min) is continuously measured during each trial. Data from the calorimeter were collected continuously at 8-s intervals throughout the trials. The real-time data were displayed and recorded on a personal computer (Dell OPTIPLEX GX270) with LabVIEW software (Version 7.0, National Instruments).

Evaporative heat loss per minute was calculated using the following equation:

\[
\text{Evaporative Heat Loss} = \text{Mass flow} \times (\text{Humidity}_{\text{out}} - \text{Humidity}_{\text{in}}) \times 2.427 \tag{1}
\]

where (Humidity\textsubscript{out} - Humidity\textsubscript{in}) is the difference in absolute humidity across the calorimeter (g water•kg air\textsuperscript{-1}), and 2.427 is the latent heat of vaporization of sweat (kJ•kg sweat\textsuperscript{-1}) (50).

Dry heat loss per minute from radiation, conduction, and convection was calculated using the following equation:

\[
\text{Dry Heat Loss} = \text{Mass flow} \times (\text{Temperature}_{\text{out}} - \text{Temperature}_{\text{in}}) \times 1.005 \tag{2}
\]

where (Temperature\textsubscript{out} - Temperature\textsubscript{in}) is the difference in air temperature across the calorimeter (°C), and 1.005 is the specific heat of air [kJ•(kg air•°C\textsuperscript{-1})].

**Indirect calorimetry.** Oxygen consumption ($\dot{V}$O\textsubscript{2}) was measured by the open circuit technique using expired gas samples drawn from a 6-liter fluted mixing box. Expired gas was analyzed using calibrated electrochemical gas analyzers (AMETEK model S-3A/1 and CD 3A, Applied Electrochemistry, Pittsburgh, PA). Expired air was recycled back into the calorimeter chamber to account for respiratory conductive and evaporative heat loss. Before each session, gas mixtures of 4% CO\textsubscript{2}, 17% O\textsubscript{2}, balance N\textsubscript{2} were used to calibrate the gas analyzers and a 3-liter syringe was used to calibrate the turbine ventilator.

Metabolic energy expenditure (M) was calculated from minute-average values for $\dot{V}$O\textsubscript{2} and respiratory exchange ratio using the following equation:

\[
M = \left[ \dot{V}_O^2 \times \left( \frac{(RER - 0.7)}{0.3} - e_r \right) + \left(1 - RER\right) \times e_p \right] 
\tag{3}
\]

where $e_r$ is the caloric equivalent per liter of oxygen for the oxidation of carbohydrates (21.13 kJ), and $e_p$ is the caloric equivalent per liter of oxygen for the oxidation of fat (19.62 kJ).

**Change in body heat content.** Change in body heat content ($\Delta$H\textsubscript{b}) was measured using the temporal summation of metabolic heat production by indirect calorimetry and the net evaporative and dry heat exchange of the body with the environment by direct calorimetry. The cumulative change in heat storage over the exercise period was therefore calculated using the following equation:

\[
\Delta H_b = \int \left[ M - (R + C + K) - \dot{E} - W \right] dt \tag{4}
\]

where $M$ = metabolic rate, $(R + C + K) =$ rate of dry heat loss (radiation, convection, and conduction), $\dot{E}$ = rate evaporative heat loss, and $W$ = rate of external work being performed.

**Experimental Protocol**

All participants volunteered for two separate testing sessions. On the first day, an incremental cycle ergometer $\dot{V}$O\textsubscript{2\_peak} test was performed. On the second day, the calorimetry experimental protocol was performed. Testing days were separated by a minimum of 72 h. All calorimeter trials were performed at the same time of day, with each participant entering the calorimeter at 8:45 AM. Participants were asked to arrive at the laboratory in a fasted state, consuming no tea, coffee, or food that morning, and also avoiding any major thermal stimuli on their way to the laboratory. Participants were also asked to not drink alcohol or exercise for 24 h before experimentation.

Following instrumentation, the participant entered the calorimeter regulated to an ambient air temperature of either 24°C or 30°C and either 30% or 60% relative humidity. The participant, seated in the semirecumbent position, rested for a 45-min habituation period until either 30% or 60% relative humidity. The participant entering the calorimeter at 8:45 AM. Participants were asked to arrive at the laboratory in a fasted state, consuming no tea, coffee, or food that morning, and also avoiding any major thermal stimuli on their way to the laboratory. Participants were also asked to not drink alcohol or exercise for 24 h before experimentation.

For all experimentation, clothing insulation was standardized at ~0.2 to 0.3 clo [i.e., cotton underwear, shorts, socks, sports bra (for women) and athletic shoes].

**Statistical Analyses**

The data from all participants were pooled and analyzed according to ambient air temperature (24 and 30°C). Data were not separated further according to relative humidity due to the confounding effect of a reduced number of data points upon predictive power, and the traditional two-compartment thermometry approach employing weighting coefficients based upon air temperature not relative humidity (4). This also ensures an optimal statistical validity by attaining a wide variation in the calorimetric and thermometric measures between participants, under each air temperature condition.

Change in body heat content ($\Delta$H\textsubscript{b}) as measured using calorimetry was solved for mean body temperature ($\Delta$T\textsubscript{b}) using the following equation:

\[
\Delta T_b = \left( \frac{\Delta H_b}{M} \right) \tag{5}
\]
\[ \Delta T_b = \Delta H_b / (b_m - C_p) \]  

where \( \Delta H_b \) is the change in body heat content by calorimetry (kJ), \( b_m \) is total body mass (kg), and \( C_p \) is specific heat of the human body as estimated using DEXA (in kJ·kg\(^{-1} \cdot °C^{-1}\)).

Two-compartment thermometry model of mean body temperature.

The traditional two-compartment thermometry model (4) for mean body temperature (\( \Delta T_b \)) is

\[ \Delta T_b = (X \cdot \Delta T_c) + ((1 - X) \cdot \Delta T_s) \]

where \( \Delta T_c \) is the change in core temperature and \( \Delta T_s \) is the change in mean skin temperature. The value for \( X \) is the proportion of the body representing the body “core.” The value of \( X \) may not exceed 1 or be less than 0.

Three-compartment thermometry model of mean body temperature.

The three-compartment thermometry model (28, 45) for mean body temperature (\( \Delta T_b \)) is

\[ \Delta T_b = (X_1 \cdot \Delta T_{core}) + (X_2 \cdot \Delta T_s) + (X_3 \cdot \Delta T_{mus}) \]

where \( \Delta T_{core} \) is the change in core temperature represented by either rectal (\( T_{re} \)), esophageal (\( T_{es} \)), or aural (\( T_{au} \)) temperature or an unweighted mean of the three measurements (\( T_c \)); \( \Delta T_s \) is the change in mean skin temperature; and \( \Delta T_{mus} \) is the change in muscle temperature represented by either vastus lateralis (\( T_{vl} \)), trapezius (\( T_{tr} \)), triceps brachii (\( T_{tb} \)), or an unweighted mean of all three measurements (\( T_{mus} \)).

Values for coefficients \( X_1 \), \( X_2 \), and \( X_3 \) may not exceed 1 or be less than 0, and the sum of all coefficients must equal 1.

Derivation of optimal two- and three-compartment models for mean body temperature.

The two- and three-compartment thermometry models were individually fit to the mean body temperature data obtained using calorimetry with the optimization technique of quadratic programming. In summary, the quadratic programming problem is to derive coefficient values that minimize a quadratic function while simultaneously satisfying the set of linear constraints (32). These constraints were that individual coefficients within each model may not exceed 1, be less than 0, and the sum of all coefficients within each model must equal 1. Quadratic programming was performed using the statistical programming language “R” (the open-source software R can be downloaded at http://www.r-project.org/).

Goodness-of-fit. To demonstrate and compare the predictive power of the optimal two- and three-compartment thermometry models for \( \Delta T_b \), the goodness-of-fit was measured for each by simply adapting the \( R^2 \) statistic from linear regression. For \( n \) observations and \( k \) parameters in a given model, the quadratic programming problem incorporates \( j \) equality constraints (in the present case, \( j = 1 \)). Let the \( j \)th response be denoted by \( y_j \), (for each thermometry model, \( y_j = \Delta T_{b,j} \)), the \( j \)th fitted value be denoted by \( \hat{y}_j \), and let the mean response be denoted by \( \bar{y} \). Then the variance of the response about the mean is estimated by \( \text{SSM} = (1/n) \sum \bar{y}^2 - (1/n \sum y_j^2)(n - 1) \) and the residual variance, with respect to the quadratic programming model, is estimated by

\[ \text{SSE} = \sum (y_j - \hat{y}_j)^2 / (n - k - j). \]

Defined as the proportion of the variance in the response explained by the model, the \( R^2 \) statistic is given by the expression \( 1 - \text{SSE/SSM} \). As with linear regression, the \( R^2 \) statistic is a quadratic programming model has a maximum value of 1. However, as \( SSE \) may be greater than \( SSM, R^2 \) may be less than 0. It is possible for \( R^2 \) to be greater than \( SSM \) as the model does not contain a constant intercept. In the event of this, the model is considered biased, that is, a systematic under- or overestimation of the response. For a biased model, the average observed response will actually perform better as a predictor than the model itself. In other words, the variance about the mean (\( SSM \)) will be less than the variance about the fitted values (\( SSE \)) and \( R^2 \) will be negative.

As is the case with linear regression, if there are many parameters in the model, it is possible for the \( R^2 \) statistic to be biased by overfitting. The adjusted \( R^2 \) statistic, which takes into account the possibility of overfitting, is given by the following expression:

\[ 1 - \frac{(n - 1)\text{SSE}/(n - k - j)\text{SSM}}{(n - k - j)}. \]

RESULTS

Thermometry Data

Mean values for mean skin temperature and all of the measurements of core and regional muscle temperature at each air temperature condition are given for baseline preexercise rest and across the final 10 min of exercise (Table 3). These data show that during the final 10 min of exercise, rectal temperature (\( T_{re} \)) was 0.24°C (SD 0.23) and 0.25°C (0.15) higher than esophageal temperature (\( T_{es} \)) and 0.62°C (0.23) and 0.45°C (0.27) higher than aural canal temperature (\( T_{au} \)) at 24°C and 30°C, respectively. Active muscle temperature, vastus lateralis (\( T_{vl} \)), was higher than the two inactive muscle temperature sites of the triceps brachii (\( T_{tb} \)) and the upper trapezius (\( T_{tr} \)) by 1.23°C (0.98) and 0.53°C (0.99), respectively, at 24°C, and by 0.63°C (0.74) and 0.62 (0.87), respectively at 30°C. Mean core temperature (\( T_c \)), \( T_{es} \), and \( T_{au} \) was higher than \( T_{vl} \) by 0.29°C (0.53), 0.33°C (0.59), and 0.57°C (0.56), respectively, at 24°C, and by 0.08°C (0.37), 0.07°C (0.42), and 0.32°C (0.39), respectively, at 30°C. Whereas \( T_{au} \) was 0.03°C (0.23) and 0.14°C (0.36) lower than \( T_{vl} \) at 24° and 30°C, respectively.

Comparison of Thermometry with Calorimetry

An example of the minute-by-minute calorimetry data with concurrent thermometry data is given in Fig. 1. The mean differences between calorimetry and the two thermometric models for the change in mean body temperature (\( \Delta T_b \)) and change in body heat content (\( \Delta H_b \)) at 24 and 30°C are detailed in Table 4.

The optimal coefficients for the estimation of \( \Delta T_b \) using the traditional two-compartment thermometry model of “core” represented by \( T_{re} \) and “shell” represented by \( T_{sk} \) for the direct, whole body calorimetry data measured in the present study were

\[ 24°C; \Delta T_{b} = (0.52 \Delta T_{m}) + (0.48 \Delta T_{a}) \]

Adjusted R-squared: 0.07

\[ 30°C; \Delta T_{b} = (0.90 \Delta T_{m}) + (0.10 \Delta T_{a}) \]

Adjusted R-squared: −0.37

The resultant estimation of \( \Delta H_b \) using the two-compartment model for \( \Delta T_b \) shows a very poor predictive capability at 24°C and a systematic shortfall compared with calorimetry (as indicated by the negative adjusted \( R^2 \) value) at 30°C. Change in body heat content (\( \Delta H_b \)) is below the line of identity between thermometry and calorimetry in 43 of the 52 total participants, and in 26 of the 28 participants at 30°C (Fig. 2A).

Results for the quadratic programming analyses of the three-compartment model of core, muscle, and skin for the estimation of \( \Delta T_b \) are detailed for 24°C (Table 5) and 30°C (Table 6). At 24°C, it is evident that in all of the models \( T_{sk} \) has a consistent influence with a weighting coefficient between...
Models employing Tre as a representation of the "core" yield the higher adjusted $R^2$ statistics, with "muscle" effectively represented by Tvl, Ttb, and Tinact. In contrast, the three-compartment models at 30°C are minimally influenced by Tsk; however, Tre again provides the best representation of the "core" relative to Tes, Tau, and Tc. By incorporating Tre as "core," Tvl, Ttb, and Tinact again provide effective representations of the "muscle" compartment. At both 24 and 30°C, all models using Tut as "muscle" yielded the lowest adjusted $R^2$ statistics. The optimal three-compartment models for the data in the present study were:

- Baseline (24°C): $T_{es}$, $T_{re}$, and $T_{es}$,
- Steady-state (24°C): $T_{es}$, $T_{re}$, and $T_{es}$,
- Delta (24°C): $T_{es}$, $T_{re}$, and $T_{es}$,
- Baseline (30°C): $T_{es}$, $T_{re}$, and $T_{es}$,
- Steady-state (30°C): $T_{es}$, $T_{re}$, and $T_{es}$,
- Delta (30°C): $T_{es}$, $T_{re}$, and $T_{es}$.

### Table 3. Mean values for skin temperature and all of the measurements of core and regional muscle temperature

<table>
<thead>
<tr>
<th></th>
<th>Core Temperatures</th>
<th>Regional Muscle Temperatures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>T$_{es}$</td>
<td>T$_{re}$</td>
</tr>
<tr>
<td>Skin T$_{sk}$</td>
<td>Baseline (24°C)</td>
<td>36.64 (0.30)</td>
</tr>
<tr>
<td></td>
<td>Steady-state (24°C)</td>
<td>37.27 (0.25)</td>
</tr>
<tr>
<td></td>
<td>Delta (24°C)</td>
<td>0.63 (0.23)</td>
</tr>
<tr>
<td></td>
<td>Baseline (30°C)</td>
<td>36.81 (0.23)</td>
</tr>
<tr>
<td></td>
<td>Steady-state (30°C)</td>
<td>37.43 (0.39)</td>
</tr>
<tr>
<td></td>
<td>Delta (30°C)</td>
<td>0.62 (0.31)</td>
</tr>
</tbody>
</table>

All values are means, standard deviation (in parentheses) for baseline preexercise rest, final 10-min of exercise (steady state) and changes between steady state and baseline (Delta $\Delta$). Data are presented for $n = 24$ at 24°C and $n = 28$ at 30°C. Core temperature measured in the esophagus ($T_{es}$), rectum ($T_{re}$), aural canal ($T_{au}$), and an unweighted mean of all three measurements ($T_{c}$). Regional muscle temperature measured in the vastus lateralis ($T_{vl}$), triceps brachii ($T_{tb}$), upper trapezius ($T_{ut}$), an unweighted mean of inactive ($T_{in}$ and $T_{ut}$) muscle temperature ($T_{m}$), and an unweighted mean all muscle temperature measurements ($T_{m}$). Skin temperature ($T_{sk}$) measured as a weighted mean of 12 sites (14).

---

**Table 3. Mean values for skin temperature and all of the measurements of core and regional muscle temperature**

- **Core Temperatures**
  - Baseline: 36.64 (0.30), 36.82 (0.20), 36.48 (0.30), 36.65 (0.23)
  - Steady-state: 37.27 (0.25), 37.51 (0.25), 36.90 (0.32), 37.23 (0.22)
  - Delta: 0.63 (0.23), 0.69 (0.23), 0.42 (0.18), 0.58 (0.22)

- **Regional Muscle Temperatures**
  - Baseline: 34.17 (0.75), 32.77 (0.83), 35.11 (0.67), 34.01 (0.65)
  - Steady-state: 36.94 (0.64), 35.71 (1.12), 36.38 (0.76), 36.06 (0.82)
  - Delta: 2.78 (0.79), 2.94 (0.88), 1.27 (0.42), 2.04 (0.64)

---

**Adjusted $R^2$ values**

- Baseline: 0.30
- Steady-state: 0.30
- Delta: 0.20

---

**Adjusted $R^2$, delta (24°C)**

- Core: 0.51
- Muscle: 0.48

---

**Adjusted $R^2$, delta (30°C)**

- Core: 0.51
- Muscle: 0.48

---

**Fig. 1. Example of the minute-by-minute whole body direct calorimetry data**

Temperature change from end of rest ($^\circ$C) vs. Time (min) and Rate of Total Gain / Loss (W) vs. Time (min).
The resultant estimation of $\Delta H_b$ using the optimal three-compartment thermometry model for $\Delta T_b$ shows an unbiased relationship with calorimetry at both 24 and 30°C (Fig. 2B).

**DISCUSSION**

The main findings from this study show that the traditional two-compartment thermometry model of “core” and “shell” underestimates changes in body heat content ($\Delta H_b$) during moderate-intensity, steady-state exercise by between 15 and 35%. Upon investigating change in mean body temperature ($\Delta T_b$) within the two-compartment thermometry model, there was a systematic underestimation of $\Delta T_b$ relative to calorimetry. At 30°C, the adjusted $R$-squared statistic for the two-compartment model was negative (~0.37), indicating a bias, that is, simply using the group mean value for $\Delta T_b$ of 1.11°C measured using calorimetry provides a better estimation than the two-compartment model. The three-compartment thermometry model of core, muscle, and skin at both 24 and 30°C was unbiased and was found to consistently yield a more precise estimate of $\Delta T_b$ and therefore $\Delta H_b$ than the two-compartment model.

The notion of a three-compartment thermometry model for the improved estimation of $\Delta H_b$ has been supported for some time. However, the present study, with the exception of Snellen (38), is the first to use whole body direct air calorimetry to assess such a concept. Nadel et al. (28) developed the following theoretical three-compartment model for the calculation of absolute mean body temperature ($T_b$) within positive and negative work on a semirecumbent bicycle ergometer, by estimating the mass of working muscles from the data of Stolwijk and Hardy (42)

$$T_b = 0.67T_e + 0.23T_m + 0.10T_{sk}$$

where $T_e$ is esophageal temperature; $T_m$ is quadriceps temperature, and $T_{sk}$ is mean skin temperature.

Webb (45) proposed an alternative three-compartment thermometry model for the estimation of change in mean body temperature ($\Delta T_b$) during level and uphill walking with a suit calorimeter. While muscle temperature was not measured, the estimated weighting coefficients for muscle suggested substantial heat storage during exercise

$$\Delta T_b = 0.5\Delta T_e + 0.4\Delta T_m + 0.1\Delta T_{sk}$$

where $\Delta T_e$ is the change in rectal temperature, $\Delta T_m$ is the change in mean muscle temperature; and $\Delta T_{sk}$ is change in mean skin temperature.

The three-compartment models derived in the present study suggest that the role of skin temperature in the estimation of $\Delta T_b$ becomes progressively less with increasing ambient air temperature as is the case with the traditional two-compartment approach (4). As such, the model derived at 30°C is similar to that proposed by both Webb (45) and Nadel et al. (28). Furthermore, the “core” weighting coefficient derived by Webb (45) is almost identical to the 30°C model in our study, while the weighting coefficient derived by Nadel et al. (28) is closer to that of the 24°C model; however, $T_{re}$ provided the best representation of the “core” compartment at both 24 and 30°C. The “muscle” compartment weighting coefficient of 0.46 at 30°C is very similar to that proposed previously by Webb (45), but the coefficient of 0.13 at 24°C is lower than previously suggested with the body “shell” (i.e., $\Delta T_{sk}$) having a more prominent effect.

Whole body, direct air calorimetry was used by Snellen (38) to develop an improved estimation of $\Delta H_b$ and therefore $\Delta T_b$. This was a unique study that incorporated multiple tissue measurements, including the estimation of subcutaneous temperature, for individuals exposed to ambient conditions from 12.3 to 35.0°C. However, there were considerable limitations of the methodology, in that only seven young male subjects were tested and subcutaneous temperatures were not directly measured, but estimated, using zero-flux heat devices, which have been since demonstrated not to give a reliable estimate of muscle temperature (3). Furthermore, the multiple linear regression method used for deriving the improved estimating equation for $\Delta T_b$ appears statistically unstable due to the number of variables introduced for such a small sample size, potential collinearity between variables, and the use of a nonintercept design, giving disproportionate $R$-squared statistics. In the case of the present study, a large subject group of 52 was used, ranging in age and physical characteristics; active and inactive muscle temperatures were directly measured using intramuscular probes; and the analytical techniques for deriving an improved estimation of $\Delta T_b$ were meticulously considered, so that collinearity between variables was avoided and fallacious $R$-squared statistics were not attained.

Mean body temperature is defined as the average temperature of the tissues of the body (4). In the two-compartment thermometry model, change in mean skin temperature is inde-

---

**Table 4. Comparison of whole body, direct calorimetry, and traditional thermometry**

<table>
<thead>
<tr>
<th></th>
<th>Calorimetry</th>
<th>Two-compartment</th>
<th>Three-compartment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Change in body heat content in kJ, $\Delta H_b$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24°C</td>
<td>260.7 (94.1)</td>
<td>220.0 (108.1)</td>
<td>259.6 (109.1)</td>
</tr>
<tr>
<td>30°C</td>
<td>258.7 (95.7)</td>
<td>161.7 (61.1)</td>
<td>261.6 (82.6)</td>
</tr>
<tr>
<td>Change in mean body temperature in °C, $\Delta T_b$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24°C</td>
<td>1.06 (0.36)</td>
<td>0.87 (0.35)</td>
<td>1.04 (0.34)</td>
</tr>
<tr>
<td>30°C</td>
<td>1.11 (0.47)</td>
<td>0.68 (0.30)</td>
<td>1.09 (0.35)</td>
</tr>
<tr>
<td>%Difference between thermometry and calorimetry for $\Delta H_b$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24°C</td>
<td>—</td>
<td>−15.5% (31.3)</td>
<td>−1.1% (29.5)</td>
</tr>
<tr>
<td>30°C</td>
<td>—</td>
<td>−35.5% (21.9)</td>
<td>+5.4% (30.0)</td>
</tr>
</tbody>
</table>

Values for calorimetry obtained using direct whole body calorimetry. Values for thermometry obtained using $\Delta H_b = \Delta T_b \cdot b_m \cdot C_p$, where $b_m$ is total body mass (kg), $C_p$ is specific heat of the human body (kJ·kg⁻¹·°C⁻¹), and $\Delta T_b$ is change in mean body temperature. Optimal two-compartment models: $\Delta T_b = (0.52 \cdot \Delta T_{es}) + (0.48 \cdot \Delta T_{sk})$ for 24°C, and $\Delta T_b = (0.90 \cdot \Delta T_{es}) + (0.10 \cdot \Delta T_{sk})$ for 30°C; Optimal three-compartment models: $\Delta T_b = (0.63 \cdot \Delta T_{es}) + (0.24 \cdot \Delta T_{sk}) + (0.13 \cdot \Delta T_m)$ for 24°C and $\Delta T_b = (0.51 \cdot \Delta T_{es}) + (0.03 \cdot \Delta T_m) + (0.46 \cdot \Delta T_{sk})$ for 30°C, where $\Delta T_{es}$ is change in rectal temperature, $\Delta T_m$ is change in mean skin temperature, $\Delta T_{sk}$ is change in vastus lateralis temperature and $\Delta T_{es}$ is change the unweighted mean of the two inactive muscle sites.
The specific heat of muscle (3.639 kJ/kg°C) is muscle mass, whereas only independently included in the estimation of the change mean body temperature. However, in a typical person, ~40% of total body mass is muscle mass, where as only ~5% is skin mass (44). The specific heat of muscle (3.639 kJ·kg⁻¹·°C⁻¹) is very similar to that of skin (3.662 kJ·kg⁻¹·°C⁻¹), and in the present study, change in mean muscle temperature was 2.08 and 3.35 times greater than the change in mean skin temperature at 24°C and 30°C, respectively. It therefore seems logical to consider changes in muscle temperature when estimating changes in mean body temperature. It has previously been viewed in the two-compartment thermometry model that the “muscle” com-

![Fig. 2. A comparison between change in body heat content measured by whole body and direct calorimetry and estimated by thermometry using the optimal two-compartment model (A) and the optimal 3-compartment model (B). Triangle (△) denotes 24°C; Circle (○) denotes 30°C. Solid line indicates the line of identity (y = x).](image)

Table 5. Results for quadratic fitting of three-compartment model of core (ΔTcore), skin (ΔTk), and muscle (ΔTmus) for 24°C

<table>
<thead>
<tr>
<th>Measures</th>
<th>Optimal Coefficients</th>
<th>Adjusted R-Squared</th>
</tr>
</thead>
<tbody>
<tr>
<td>ΔTcore</td>
<td>ΔTmus X1 (ΔTcore) X2 (ΔTk) X3 (ΔTmus)</td>
<td></td>
</tr>
<tr>
<td>Tc</td>
<td>Ta 0.58 Ta 0.23 Ta 0.23 0.23 0.37</td>
<td></td>
</tr>
<tr>
<td>Tres</td>
<td>Td 0.61 Te 0.23 Te 0.16 0.16 0.37</td>
<td></td>
</tr>
<tr>
<td>Td</td>
<td>Tb 0.62 Te 0.24 Te 0.14 0.14 0.33</td>
<td></td>
</tr>
<tr>
<td>Tm</td>
<td>Tb 0.31 Te 0.30 Ta 0.40 0.40 0.22</td>
<td></td>
</tr>
<tr>
<td>Ta</td>
<td>Tm 0.54 Tmus 0.25 Ta 0.22 0.22 0.32</td>
<td></td>
</tr>
<tr>
<td>Tmus</td>
<td>Tm 0.63 Tmus 0.24 Ta 0.13 0.13 0.48</td>
<td></td>
</tr>
<tr>
<td>Tmus</td>
<td>Tm 0.64 Tmus 0.24 Te 0.12 0.12 0.47</td>
<td></td>
</tr>
<tr>
<td>Tinact</td>
<td>Tm 0.37 Tmus 0.29 Ta 0.34 0.34 0.32</td>
<td></td>
</tr>
<tr>
<td>Tmus</td>
<td>Tm 0.57 Tmus 0.24 Te 0.19 0.19 0.45</td>
<td></td>
</tr>
<tr>
<td>Tmus</td>
<td>Tm 0.58 Tmus 0.20 Ta 0.22 0.22 0.44</td>
<td></td>
</tr>
<tr>
<td>Tinact</td>
<td>Tm 0.59 Tmus 0.21 Ta 0.20 0.20 0.38</td>
<td></td>
</tr>
<tr>
<td>Taus</td>
<td>Tm 0.24 Tmus 0.30 Ta 0.46 0.46 0.20</td>
<td></td>
</tr>
<tr>
<td>Tinact</td>
<td>Tm 0.49 Tmus 0.22 Ta 0.29 0.29 0.36</td>
<td></td>
</tr>
</tbody>
</table>

Data obtained for the model of ΔTk = (X1 ∗ ΔTcore) + (X2 ∗ ΔTk) + (X3 ∗ ΔTmus). The term ΔTcore is represented by esophageal (Tes), rectal (Tre), aural canal temperature (Tam), or the unweighted mean of all three core temperature measures (Tc). The term ΔTk is represented by mean skin temperature. The term ΔTmus is represented by vastus lateralis (Tvl), triceps brachii (Tb), upper trapezius (Tut) temperature, the unweighted mean of all three measurements (Tm) or the unweighted mean of the two inactive muscle sites (Tinact). Model constraints are the sum of X1, X2, and X3 must equal 1, and all coefficients must be between 0 and 1.

Table 6. Results for quadratic fitting of three-compartment model of core (ΔTcore), skin (ΔTk), and muscle (ΔTmus) for 30°C

<table>
<thead>
<tr>
<th>Measures</th>
<th>Optimal Coefficients</th>
<th>Adjusted R-Squared</th>
</tr>
</thead>
<tbody>
<tr>
<td>ΔTcore</td>
<td>ΔTmus X1 (ΔTcore) X2 (ΔTk) X3 (ΔTmus)</td>
<td></td>
</tr>
<tr>
<td>Tc</td>
<td>Ta 0.49 Ta 0.10 Ta 0.41 0.41 0.45</td>
<td></td>
</tr>
<tr>
<td>Tres</td>
<td>Td 0.51 Td 0.23 Td 0.27 0.27 0.25</td>
<td></td>
</tr>
<tr>
<td>Td</td>
<td>Tb 0.48 Tb 0.20 Tb 0.31 0.31 0.31</td>
<td></td>
</tr>
<tr>
<td>Tm</td>
<td>Tb 0.00 Tb 0.00 Tb 1.00 1.00 0.17</td>
<td></td>
</tr>
<tr>
<td>Ta</td>
<td>Tm 0.36 Tmus 0.11 Ta 0.52 0.52 0.40</td>
<td></td>
</tr>
<tr>
<td>Tmus</td>
<td>Td 0.65 Td 0.12 Ta 0.23 0.23 0.42</td>
<td></td>
</tr>
<tr>
<td>Tmus</td>
<td>Td 0.63 Td 0.10 Ta 0.27 0.27 0.48</td>
<td></td>
</tr>
<tr>
<td>Tinact</td>
<td>Td 0.13 Td 0.00 Tb 0.87 0.87 0.19</td>
<td></td>
</tr>
<tr>
<td>Tmus</td>
<td>Td 0.51 Tmus 0.03 Ta 0.46 0.46 0.51</td>
<td></td>
</tr>
<tr>
<td>Tinact</td>
<td>Td 0.51 Tmus 0.19 Ta 0.30 0.30 0.32</td>
<td></td>
</tr>
<tr>
<td>Taus</td>
<td>Td 0.49 Tmus 0.17 Ta 0.35 0.35 0.39</td>
<td></td>
</tr>
<tr>
<td>Tinact</td>
<td>Td 0.00 Tmus 0.00 Ta 1.00 1.00 0.17</td>
<td></td>
</tr>
<tr>
<td>Tinact</td>
<td>Td 0.37 Tmus 0.08 Ta 0.56 0.56 0.45</td>
<td></td>
</tr>
</tbody>
</table>

Data obtained for the model of ΔTk = (X1 ∗ ΔTcore) + (X2 ∗ ΔTk) + (X3 ∗ ΔTmus). The term ΔTcore is represented by esophageal (Tes), rectal (Tre), aural canal temperature (Tam), or the unweighted mean of all three core temperature measures (Tc). The term ΔTk is represented by mean skin temperature. The term ΔTmus is represented by vastus lateralis (Tvl), triceps brachii (Tb), upper trapezius (Tut) temperature, the unweighted mean of all three measurements (Tm) or the unweighted mean of the two inactive muscle sites (Tinact). Model constraints are the sum of X1, X2, and X3 must equal 1, and all coefficients must be between 0 and 1.
The findings of the present study suggest that the source of error observed with the two-compartment thermometry model for the estimation of ΔTb and therefore ΔHb is an underestimation of the tissue temperature transients of the body during exercise. The three-compartment model by no means reflects the level of complexity of the thermal interactions between various tissues of the body; however, the inclusion of a “muscle” compartment does give a degree of representation to the considerable influences of muscle heat load upon body heat content. Indeed, regional muscle temperature at any point in time is the result of regional differences in metabolic rate, conductive heat loss to adjacent tissue, and deep and peripheral convective blood flow. Furthermore, the convective transfer of muscle heat load to cooler tissues in the body has been demonstrated to significantly prolong the elevation of core temperature and presumably body heat content after exercise, with hyperemically previously active musculature considered to have the most profound influence.

When using a “muscle” compartment for the estimation of ΔTb, the present findings suggest a minimal predictive role of the “shell” compartment at warmer ambient temperatures. In addition to the fact that total body mass is composed of a relatively small proportion of skin mass, the contribution of mean skin temperature to the estimation of ΔTb is further confounded by several factors. Skin temperature is strongly influenced by skin blood flow, which itself can be significantly modified independently of whole body thermal state. For example, varying levels of exercise intensity result in different skin-to-muscle perfusion ratios, with increasing blood flow shunted away from skin to working muscle groups with greater levels of exercise. Furthermore, factors such as hydration status, training status, level of acclimatization, and the administration of topically applied medications, such as corticosteroids and nicotinates, have been demonstrated to alter skin blood flow during exercise. The use of mean skin temperature as an estimate of the thermal status of the skin is itself also subject to potential error. Measurement methods range from as few as four sites to as many as 12 sites, and mean skin temperature is in reality an interface temperature between the body surface with the external environment, factors such as clothing and environmental conditions will also have an influence.

Similarly, as with the two-compartment thermometry model, the data from the present study indicated that Tms was the “core” measurement that best associated with ΔTb within the three-compartment thermometry model. Models using Tms as an indicator of “core” temperature provided the worst association with ΔTb. This is thought to be a consequence of Tms generally representing the central arterial blood temperature. Although a response lag is inevitable with Tms, it is suggested that during steady-state exercise Tms provides a better representation of equilibrated tissue temperatures of the deep visceral/splanchnic region. The use of Tam also provided an acceptable means by which changes in core temperature could be represented in the three-compartment thermometry model; however, Tam was consistently lower than both Tms and Tes, possibly due to insufficient insulation of the probe in the aural canal from the air within the calorimeter and are therefore thought to be less reliable.

The present study does have limitations in terms of the range of ambient conditions tested and the employment of only one workload. Indeed core and active muscle temperature has been demonstrated to be dependent upon relative workload; therefore, thermometry models for ΔHb may also differ across the range of workloads that steady-state exercise is possible. Furthermore, the employment of the three-compartment thermometry model does require the direct measurement of intramuscular temperature; however, in many cases, such an invasive technique may not be possible. The development of an accurate noninvasive method of estimating muscle temperature using novel zero-heat-flux methods is ongoing.

Despite the inclusion of a “muscle” compartment yielding an improved estimation of ΔTb relative to the traditional two-compartment thermometry model, the optimal models only explained 48% and 51% of the variation found in ΔTb at 24°C and 30°C, respectively. Increasing the number of tissue temperature measurements intermediate to the “core” and “shell” may further improve the estimation of ΔTb somewhat; however, the determination of the primary sources of individual variability in body heat content is of paramount importance for its more precise estimation. Further research must therefore be conducted to elucidate the relative effects of factors such as adiposity, age, gender, physical fitness, and acclimation upon ΔHb.

In conclusion, whole body direct air calorimetry shows that a two-compartment thermometry model of “core” and “shell” for the derivation of ΔTb underestimates ΔHb by between 15 and 35% under the conditions tested in this study. A three-compartment thermometry model independently removed the statistical bias seen with the two-compartment model, including the thermal influences of “muscle,” and consistently yielded a more precise estimate of ΔTb and therefore ΔHb.

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REFERENCES
