

Research article

INSPIRATORY MUSCLE FATIGUE FOLLOWING MODERATE-INTENSITY EXERCISE IN THE HEAT

James S. Williams^{1,2} ✉, Kendra A. O'Keefe¹ and Lee T. Ferris²

¹Department of Health, Exercise, and Sport Sciences and ²Department of Physiology, Texas Tech University/TTU Health Sciences Center, Lubbock, TX, USA

Received: 05 April 2005 / Accepted: 10 May 2005 / Published (online): 01 September 2005

ABSTRACT

Heavy exercise has been shown to elicit reductions in inspiratory muscle strength in healthy subjects. Our purpose was to determine the combined effects of moderate-intensity endurance exercise and a thermal load on inspiratory muscle strength in active subjects. Eight active, non heat-acclimatized female subjects (23.5 ± 1.4 yr; $VO_{2max} = 39.8 \pm 2.4$ ml \cdot kg⁻¹ \cdot min⁻¹) randomly performed two 40 min endurance exercise bouts (60% VO_{2max}) in either a thermo-neutral (22°C/21% RH) or hot (37°C/33% RH) environment on separate days. Maximal sustained inspiratory mouth pressure (PI_{max}) was obtained pre and post exercise as an index of inspiratory muscle strength. Additional variables obtained every 10 min during the endurance exercise bouts included: rectal temperature (T_{RE}), heart rate (HR), minute ventilation (V_E), oxygen uptake (VO_2), tidal volume (V_T), breathing frequency (F_b), and ratings of perceived exertion and dyspnea (RPE/RPD). Data were analyzed with repeated measures ANOVA. PI_{max} was significantly reduced ($p < 0.05$) after exercise in the hot environment when compared to baseline and when compared to post exercise values in the thermo-neutral environment. PI_{max} was unchanged from baseline following exercise in the thermo-neutral environment. HR and T_{RE} were significantly higher ($p < 0.05$) in the hot compared to the thermo-neutral environment. V_E and VO_2 were not significantly different between conditions. V_T was unchanged between conditions whereas F_b was higher ($p < 0.05$) in the hot condition compared to thermo-neutral. RPE was not significantly different between conditions. RPD was significantly higher ($p < 0.05$) in the hot compared to the thermo-neutral environment. We conclude that moderate-intensity endurance exercise (60% VO_{2max}) in a hot environment elicits significant reductions in inspiratory muscle strength in unfit females. This finding is novel in that previous studies conducted in a thermo-neutral environment have shown that an exercise intensity of >80% VO_{2max} is required to elicit reductions in inspiratory muscle strength. In addition, dyspnea perception during exercise is greater in a hot environment, compared to thermo-neutral, at a similar level of V_E and VO_2 .

KEY WORDS: Control of breathing, endurance, respiratory function, thermal load.

INTRODUCTION

Inspiratory muscle fatigue (IMF) has been demonstrated following maximal or near-maximal exercise in both trained and untrained subjects (Babcock et al., 1995a; 1995b; Coast et al., 1999; Johnson et al., 1996; Mador et al., 1993). In general, it appears that the intensity of exercise must be very

high (>80% VO_{2max}) and the duration of exercise lasting at least 10 min in order to elicit IMF in male and female subjects with a wide range of fitness levels (Babcock et al., 1996; 2002; Johnson et al., 1996). We have recently shown that IMF occurs in both male and female unfit subjects at an exercise intensity of >80% VO_{2max} and that the magnitude of decrease in inspiratory muscle strength is similar

between genders (Gonzales et al., 2003). Likewise, it is generally accepted that the pulmonary system does not limit exercise performance in healthy subjects during prolonged submaximal exercise (Powers and Howley, 2004). However, limited data suggests that inspiratory muscle function may be compromised during submaximal exercise performed in various environmental conditions (e.g. heat or altitude) (Cibella et al., 1996; Romer et al., 2004).

Several hypotheses have been suggested as possible causes of IMF following heavy exercise. These include an accumulation of exercise-induced metabolites in the diaphragm (Babcock et al., 1995a; Yanos et al., 1993), reductions in available energy substrate (Ianuzzo et al., 1987), and competition for blood flow between respiratory and locomotor muscles (Babcock et al., 1995a; Babcock et al., 1995b; Harms et al., 1997; Johnson et al., 1996). Babcock et al. (2002) have further suggested a dual cause of exercise-induced IMF. These authors postulated that the development of IMF during heavy exercise is related to the magnitude of both resistive and elastic inspiratory muscle work incurred and the adequacy of its blood supply. They further suggest that greater reductions in available inspiratory muscle blood supply would require less muscle work to produce IMF.

Exercise in a hot environment results in substantial alterations in cardiovascular function with a progressive increase in cutaneous blood flow as core temperature rises (Rowell, 1986). Consequently, blood flow to the inspiratory musculature may be further compromised during exercise in the heat which could exacerbate IMF, even at a moderate intensity of exertion. The purpose of this study was to test the hypothesis that the magnitude of IMF would be greater following moderate-intensity exercise in a hot environment compared to exercise at the same exercise intensity under a thermo-neutral environmental condition. We were interested in the effects of prolonged moderate-intensity exercise in a hot environment as this type of exercise is more typical of a daily training situation as opposed to an incremental exercise test to exhaustion. We chose to study females because: 1) considerably less exercise data, including that on inspiratory muscle function, has been collected in women (Sheel et al., 2004); 2) previous studies have demonstrated that women differ from men with respect to ventilatory control (White et al., 1983); and 3) women differ from men in the oxygen cost of breathing (Topin et al., 2003), which may influence inspiratory muscle function during exercise.

METHODS

Subjects

The study population consisted of eight females (age 23.5 ± 4.1 yr; height 1.66 ± 0.07 m; weight 59.2 ± 5.6 kg; mean \pm SD) who were physically active but not engaged in competitive sports. Based on a detailed medical history questionnaire, all subjects were free of cardiopulmonary, metabolic or musculoskeletal disease and were nonsmokers. All subjects signed an informed consent form and the local institutional review board approved the study.

General testing procedures

Subjects reported to the laboratory on four separate occasions. On the first visit, the subjects practiced a maximal inspiratory mouth pressure maneuver (10-15 trials) (Larson et al., 1993) and were familiarized with the exercise testing equipment. Maximal inspiratory mouth pressure (PI_{max}) has been commonly used as an index of inspiratory muscle fatigue (Chen et al., 1989; Inbar et al., 2000; Romer et al., 2002a; Sonetti et al., 2001; Volianitis et al., 2001; Williams et al., 2002). Though this measurement technique does not provide information as to the specific site of fatigue (central vs. peripheral) or to the specific inspiratory muscles involved, it is sufficient to determine global inspiratory muscle force generation. The second visit to the laboratory consisted of a spirometric screening test for normal pulmonary function and completion of a graded maximal exercise test (GXT). On the last two visits, the subjects performed an endurance exercise test (EET) in either a thermo-neutral or hot environment. Testing sessions for the GXT and EET were separated by 48 hours and the EET was randomized between environmental conditions. All testing was conducted during the follicular phase of the menstrual cycle (days 6-14 following menses) and at the same time of the day. Subjects were asked not to drink coffee or other caffeine-containing beverages on testing days and to refrain from strenuous exercise for 24 h prior to testing.

Graded maximal exercise and pulmonary function testing

All subjects performed a GXT on an electronically-braked cycle ergometer (Lode, Corival, Groningen, Holland). After a brief warm-up period, the exercise test began at 25 W and the subjects maintained a 70 rpm pace. The ergometer resistance was increased every 2 min by 25 W until the subjects were unable to keep the set pace or volitional fatigue. Ventilatory and gas exchange values were obtained on a breath-by-breath basis during the GXT and averaged over 30-sec intervals via an automated metabolic cart (MedGraphics, CPX/D, St. Paul, MN). Heart rate (HR) was monitored continuously throughout the GXT via electrocardiography (Quinton, Q4000,

Bothell, WA). Prior to the GXT, standard pulmonary function testing (Knudson et al., 1983) was performed to determine forced vital capacity (FVC), forced expired volume in one second (FEV₁) and the 12-second maximal voluntary ventilation (MVV₁₂) utilizing the automated metabolic/pulmonary function system described above. Calibration of the metabolic cart was performed prior to each testing session as per the manufacturer's specifications. The system pneumotach was calibrated with a 3-L volume syringe and the gas analyzers were calibrated with certified gases of known concentration (5% CO₂; 12% O₂).

Endurance exercise testing

On separate days, all subjects completed a 40-min ride on the cycle ergometer in either a thermo-neutral (22°C-21% RH) or hot (37°C-33% RH) environment. The hot condition was performed in an environmental chamber. The endurance rides were randomized and performed at a work rate that corresponded to 60% of the subject's VO_{2max} as determined from the GXT. Oxygen uptake (VO₂), heart rate (HR), minute ventilation (V_E), tidal volume (V_T), breathing frequency (F_b), and ratings of perceived exertion (RPE; Borg 6-20 scale) and perceived dyspnea (RPD; Borg 0-10 scale) were determined immediately before and at 10 min intervals during the endurance rides as described above. Additionally, rectal temperature (T_{RE}) was continuously monitored and recorded at 10-min intervals during the endurance rides with a thermistor inserted to the depth of 12 cm (YSI, Yellow Springs, OH). Subjects were allowed to consume a commercial sports drink of their choice before and ad libitum during the endurance rides to prevent severe dehydration. FVC and PI_{max} measurements were obtained before and immediately after the endurance exercise rides. As an index of effort and general motivation (Coast et al., 1990), hand grip strength (HG) was also obtained before and after the endurance rides with a standard handgrip dynamometer (Takei, Kogyo, Japan). Three attempts were allowed with the dominant hand and the single best value was used for analysis.

Inspiratory muscle strength testing

As an index of global inspiratory muscle strength, PI_{max} generated at the mouth was recorded starting from residual volume as described previously (Black and Hyatt, 1969). Mouth pressures were recorded with a differential pressure transducer (Validyne, DP-45, Northridge, CA) that was calibrated with a certified pressure manometer prior to each test. A computer screen provided visual feedback of the

pressure signal. Subjects sustained each inspiratory effort for at least 1 s. To ensure repeatable results, 3-5 trials were performed with at least 1 min of rest between each trial to prevent testing-induced fatigue. The greatest static negative inspiratory pressure recorded (cm H₂O) within 5% of three other trials was used for data analysis.

Statistical analysis

Data were analyzed with repeated-measures ANOVA. Significant main effects were further analyzed with Student-Newman *post hoc* tests. Results are presented as means (±SE). A *p*-value of < 0.05 was considered significant. Statistical analyses were conducted using SigmaStat for Windows (Jandel Scientific Software, SPSS Inc., Chicago IL).

RESULTS

Results from the GXT and pulmonary function testing are presented in Table 1. All subjects demonstrated essentially normal lung function and normal cardiopulmonary responses to graded exercise. The mean values for PI_{max} before and after the EET for both environmental conditions are presented in Figure 1. Baseline values were not significantly different between environmental conditions. No significant reductions in PI_{max} were observed following the EET in the thermo-neutral condition compared to baseline. PI_{max} was significantly reduced (*p* = 0.001) following the EET in the hot condition compared to baseline and also when compared to the post EET value in the thermo-neutral condition (*p* = 0.003). All eight subjects showed a reduction in PI_{max} following exercise in the hot condition. There were no significant differences in FVC or HG values before and after the EET for either environmental condition.

Table 1. Graded exercise test and spirometry values. Data are means (± SE).

VO_{2max} (ml·kg⁻¹·min⁻¹)	39.8 (2.4)
% predicted VO_{2max}	120.6 (9.3)
HRmax	184 (2)
% predicted HRmax	93.2 (1.3)
RER	1.20 (.01)
FVC (L)	4.2 (.2)
% predicted FVC	111.8 (4.4)
FEV₁/FVC (%)	83.9 (2.3)
MVV (L·min⁻¹)	122.0 (5.9)
% predicted MVV	106.3 (5.2)

The T_{RE} and HR responses during the EET for both environmental conditions are presented in Figure 2. Baseline values for both variables were not significantly different between environmental

conditions. Significant differences ($p = 0.023$) in T_{RE} were detected between conditions at the 40-min measurement period during the EET. Significant differences in HR were detected between conditions at the 20-min ($p = 0.008$), 30-min ($p = 0.003$), and 40-min ($p = 0.001$) measurement periods during the EET.

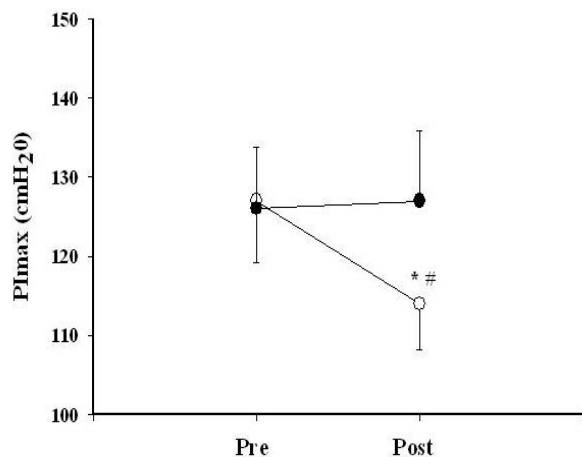


Figure 1. Maximal sustained inspiratory mouth pressure (PI_{max}) obtained pre and post endurance exercise during the thermo-neutral (closed circles) and hot (open circles) environmental conditions. Values are means \pm SE. # significantly different from baseline ($p = 0.001$); * significantly different from the thermo-neutral condition ($p = 0.003$).

No significant differences were detected between conditions at any measurement time point for V_E or VO_2 . The V_T and F_b responses during the EET for both conditions are shown in Figure 3. No significant differences between conditions were noted across time for V_T . The F_b tended to be higher at each measurement point during exercise in the hot condition compared to thermo-neutral and this reached statistical significance at the 30-min ($p = 0.026$) and 40-min ($p = 0.005$) measurement periods.

The reported values for RPE were not significantly different between conditions (Figure 4). RPD was statistically higher in the hot condition compared to the thermo-neutral condition at the 30-min ($p = 0.012$) and 40-min ($p = 0.002$) measurement time points.

DISCUSSION

The novel finding of this study was that moderate-intensity (60% VO_{2max}) endurance exercise in a hot environment elicited significant reductions in inspiratory muscle strength in untrained female subjects. In contrast, previous studies (Babcock et al., 1996; 2002; Johnson et al., 1996) have shown that an exercise intensity of $>80\%$ VO_{2max} is generally necessary to elicit significant IMF when exercise is performed in a thermo-neutral

environment. In addition, dyspnea perception was greater in the hot compared to the thermo-neutral environment at a similar level of V_E or VO_2 . Our measured handgrip strength data further suggest that the reductions in inspiratory muscle strength did not result from generalized fatigue or poor subject motivation.

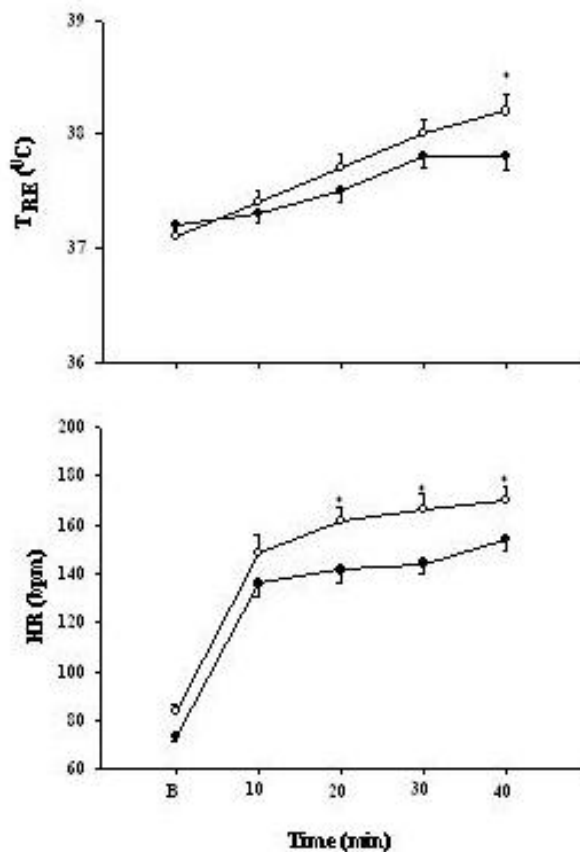


Figure 2. Rectal temperature (T_{RE}) and heart rate (HR) responses during the endurance rides for both thermo-neutral (closed circles) and hot (open circles) environmental conditions. Values are means \pm SE. * significantly different from the thermo-neutral condition ($p < 0.01$).

To the best of our knowledge, only one other study has investigated the combined effects of endurance exercise and a heat load on IMF. Results from this study (Romer et al., 2004) suggest that endurance exercise in the heat (66% maximal work rate/40 min) impaired a subsequent cycle time trial performance but did not exacerbate IMF when compared to exercise performed in a cool environment. Though direct comparisons between our study and the study of Romer et al. are difficult as their subjects were endurance trained males, the findings that inspiratory muscles are susceptible to fatigue following moderate-intensity endurance exercise in the heat are in partial agreement. However, our results suggest a significant difference

between environmental conditions, and we were unable to detect the presence of IMF following exercise in our thermo-neutral condition. This disparity in results may be the result of methodological differences between the studies. In the Romer et al. study (2004), inspiratory muscle strength was determined after a cycle time trial that was preceded by a constant load exercise bout. Thus, considerably more inspiratory muscle work was performed in this study compared to our study. In addition, the temperature was higher during both the heat (37° vs 35° C) and thermo-neutral (22° vs 15° C) conditions in the present study when compared to the study by Romer et al. (2004). This degree of a heat load coupled with our untrained subjects was adequate to result in a significant difference between environmental conditions in the present study.

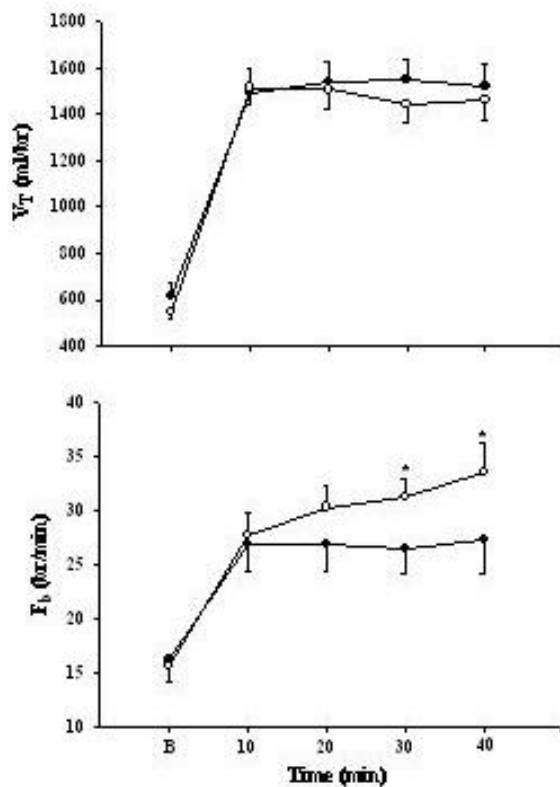


Figure 3. Tidal volume (V_T) and breathing frequency (F_b) responses during the endurance rides for both thermo-neutral (closed circles) and hot (open circles) environmental conditions. Values are means \pm SE. * significantly different from the thermo-neutral condition ($p < 0.05$).

In both of our endurance exercise conditions, the exercise intensity was well below the previously reported threshold ($>80\%$ $\text{VO}_{2\text{max}}$) for exercise-induced IMF (Babcock et al., 1996; 2002; Johnson et al., 1996). No evidence of IMF was present following exercise in the thermo-neutral environment whereas a significant reduction in inspiratory muscle strength was demonstrated

following exercise in the hot environment. Harms et al. (1997) have demonstrated that locomotor muscles and the diaphragm compete for the available cardiac output during heavy exercise. Changes in inspiratory muscle work appear to effect limb muscle blood flow via a sympathetically mediated reflex arc originating from type III/IV receptors in the fatiguing inspiratory muscles (St Croix et al., 2000). With the addition of a heat load during exercise, it is not clear which vascular bed would be compromised as an additional portion of the cardiac output would now be directed to the cutaneous circulation for thermoregulation. Though indirect, our data suggests that inspiratory muscle blood flow was compromised during exercise in the heat as evidenced by a greater degree of IMF in this condition compared to the thermo-neutral exercise condition. These differences were present at a similar level of V_E and VO_2 and presumably a similar level of inspiratory muscle work. It is possible that the above mentioned reflex arc resulting in compromised limb blood flow also resulted in compromised inspiratory muscle blood flow which may have further exacerbated IMF.

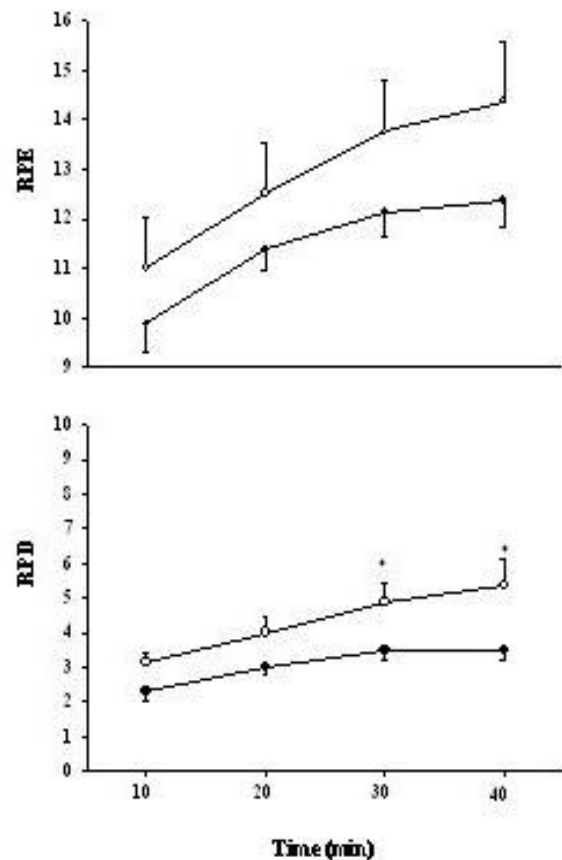


Figure 4. Ratings of perceived exertion (RPE) and dyspnea (RPD) during the endurance rides for both thermo-neutral (closed circles) and hot (open circles) environmental conditions. Values are means \pm SE. * significantly different from the thermo-neutral condition ($p < 0.05$).

Elevated T_{RE} and HR responses to moderate-intensity exercise in a hot environment are well established and the magnitude of increase in the present study is comparable to those values previously reported (Powers et al., 1982; Romer et al., 2004). Elevated HR in a hot environment is the consequence of increased blood flow to the skin and a subsequent reduction in central blood volume resulting in a decreased stroke volume and a compensatory rise in HR. Our VO_2 values are also in agreement with a previous study demonstrating a small but insignificant increase in VO_2 in response to moderate-intensity exercise in a hot environment (Powers et al., 1982).

A progressive increase in V_E occurs in response to prolonged constant-load exercise in a thermo-neutral environment (Martin et al., 1981) and increased V_E has also been reported in a hot or humid exercise environment. This upward "drift" in V_E in a hot environment may be the result of increased blood temperature influencing the respiratory control center (Powers et al., 1982). Altered ventilatory responses in the heat appear to be the result of an increase in F_b and fall in V_T (Martin et al., 1979) and this tachypneic pattern has also been observed after the induction of IMF (Mador, 1991). Our results are in agreement with these previous finding in that V_E was slightly augmented at each measurement period in the hot condition compared to the thermo-neutral condition, and our subjects developed a tachypneic pattern toward the end of the EET in the hot condition. We view it likely that the significant increase in F_b during the hot condition, with V_T remaining constant, occurred in response to ensuing IMF (Mador, 1991; Mador and Acevedo, 1991; Syabbalo et al., 1994).

Previous studies have shown that experimentally induced IMF effects respiratory effort sensation (Gandevia et al., 1981). Our data are in agreement with these finding in that RPD was significantly elevated during exercise in the hot condition compared to thermo-neutral, at a similar level of V_E and VO_2 . We suggest that the elevated RPD is related to the ensuing IMF as evidenced by the reduction in PI_{max} following the exercise bout. In addition, recent studies have demonstrated reductions in respiratory effort sensation during exercise following a period of specific inspiratory muscle training (Romer et al., 2002a; 2002b; Williams et al., 2002). In a recent review article (McConnell and Romer, 2004), evidence is presented suggesting that the contractile properties of the respiratory muscles modify the intensity of perceived dyspnea via changes in motor outflow to the respiratory muscles. Accordingly, in the presence of IMF, central motor outflow to the

respiratory muscles would be increased to maintain a given level of mechanical output from the muscles and dyspnea would be enhanced (Gandevia et al., 1981). Alternatively, a peripheral hypothesis has been suggested involving enhanced muscle metaboreceptor afferent activity from respiratory muscles during IMF that is related to increased dyspnea (Jammes and Balzamo, 1992).

The reductions in PI_{max} in the present study following exercise in the heat could be secondary to dehydration and/or substrate availability (Febbraio, 2000). However, we think this unlikely as our subjects consumed a commercial sports drink before and during the endurance rides and no significant reduction in body mass was noted following exercise in either condition. Exercise in a hot environment is associated with increased carbohydrate oxidation and lactate production (Gonzalez-Alonso et al., 1999). Lactate is one of several circulating metabolites of muscle metabolism that is associated with muscle fatigue. Though speculative as we did not measure blood lactate levels in our study, it is possible that increased blood lactate contributed to the reductions in inspiratory muscle strength observed following exercise in the heat condition whereas these reductions were not present in the thermo-neutral condition. Increases in core body temperature ranging from 38-40°C are associated with fatigue during exercise in the heat and may be related to central nervous system function (Gonzalez-Alonso et al., 1999; Nybo and Nielson, 2001). As all of the subjects in our study were able to complete the 40-min ride in the hot environment and RPE values were not significantly different between conditions, we feel that the contribution of central fatigue to the observed IMF in this study were minimal. Furthermore, our HG data suggest that subject effort and motivation were well preserved following exercise in both environmental conditions. In addition, changes in PI_{max} are sensitive to changes in lung volume (Coast and Weise, 1990). FVC values were unchanged before and after the endurance rides in both environmental conditions suggesting that the reductions in PI_{max} truly represented IMF and not an increase in residual volume.

CONCLUSIONS

Results from the present study suggest that moderate-intensity prolonged exercise in a hot environment with ad lib fluid intake results in significant reductions in global inspiratory muscle strength in untrained females. The mechanism whereby this reduction in inspiratory muscle function occurs may be related to compromised inspiratory muscle blood flow. The precise

mechanism whereby exercise-induced IMF occurs in a hot environment will require further research. In addition, the perception of dyspnea is augmented during exercise in the heat, compared to a thermo-neutral condition, at a similar level of exercise V_E and VO_2 .

ACKNOWLEDGEMENTS

The authors thank the female subjects for their enthusiastic participation in this study, the technical assistance of K.A. Hale during the data collection phase of the project, and the helpful comments provided by Dr. Robert Sawyer during the preparation of the manuscript.

REFERENCES

- Babcock, M.A., Johnson, B.D., Pegelow, D.F., Suman, O.E., Griffin, D. and Dempsey, J.A. (1995a) Hypoxic effects on exercise-induced diaphragmatic fatigue in normal healthy humans. *Journal of Applied Physiology* **78**, 82-92.
- Babcock, M.A., Pegelow, D.F., Harms, C.A. and Dempsey, J.A. (2002) Effects of respiratory muscle unloading on exercise-induced diaphragm fatigue. *Journal of Applied Physiology* **93**, 201-206.
- Babcock, M.A., Pegelow, D.F., Johnson, B.D. and Dempsey, J.A. (1996) Aerobic fitness effects on exercise-induced low-frequency diaphragm fatigue. *Journal of Applied Physiology* **81**, 2156-2164.
- Babcock, M.A., Pegelow, D.F., McClaran, S.R., Suman, O.E. and Dempsey, J.A. (1995b) Contribution of diaphragmatic power output to exercise-induced diaphragm fatigue. *Journal of Applied Physiology* **78**, 1710-1719.
- Black, L.F. and Hyatt, R.E. (1969) Maximal respiratory pressures: Normal values and relationship to age and sex. *American Review of Respiratory Disease* **99**, 696-702.
- Chen, H. and Kuo, C. (1989) Relationship between respiratory muscle function and age, sex, and other factors. *Journal of Applied Physiology* **66**, 943-948.
- Cibella, F., Cuttitta, G., Kayser, B., Narici, M., Romano, S. and Saibene, F. (1996) Respiratory mechanics during exhaustive submaximal exercise at high altitude in healthy humans. *Journal of Physiology* **494**, 881-890.
- Coast, J.R., Haverkamp, H.C., Finkbone, C.M., Anderson, K.L., George, S.O. and Herb, R.A. (1999) Alterations in pulmonary function following exercise are not caused by the work of breathing alone. *International Journal of Sports Medicine* **20**, 470-475.
- Coast, J.R. and Weise, S.D. (1990) Lung volume changes and maximal inspiratory pressure. *Journal of Cardiopulmonary Rehabilitation* **10**, 461-464.
- Febbraio MA. (2000) Does muscle function and metabolism affect exercise performance in the heat? *Exercise and Sport Science Reviews* **28**, 171-176.
- Gandevia, S.C., Killian, K.J. and Campbell, E.J. (1981) The effect of respiratory muscle fatigue on respiratory sensations. *Clinical Science (London)* **60**, 463-466.
- Gonzales, J.U., Williams, J.S., Scheuermann, B.W. and James, C.R. (2003) Gender differences in respiratory muscle function following exhaustive exercise. *50th Annual Meeting of the American College of Sports Medicine, May 28-31, San Francisco, California. Medicine and Science in Sports and Exercise* **35 (Suppl.)**, 834.
- Gonzalez-Alonso, J., Teller, C., Andersen, S.L., Jensen, F.B., Hyldig, T. and Nielsen, B. (1999) Influence of body temperature on the development of fatigue during prolonged exercise in the heat. *Journal of Applied Physiology* **86**, 1032-1039.
- Harms, C.A., Babcock, M.A., McClaran, S.R., Pegelow, D.F., Nিকে, G.A., Nelson, W.B. and Dempsey, J.A. (1997) Respiratory muscle work compromises leg blood flow during maximal exercise. *Journal of Applied Physiology* **82**, 1573-1583.
- Ianuzzo, C.D., Spalding, M.J. and Williams, H. (1987) Exercise-induced glycogen utilization by the respiratory muscles. *Journal of Applied Physiology* **62**, 1405-1409.
- Inbar, O., Weiner, P., Azgad, Y., Rotstein, A. and Weinstein, Y. (2000) Specific inspiratory muscle training in well-trained endurance athletes. *Medicine and Science in Sports and Exercise* **32**, 1233-1237.
- Jammes, Y. and Balzamo, E. (1992) Changes in afferent and efferent phrenic activities with electrically induced diaphragmatic fatigue. *Journal of Applied Physiology* **73**, 894-902.
- Johnson, B.D., Aaron, E.A., Babcock, M.A. and Dempsey, J.A. (1996) Respiratory muscle fatigue during exercise: implications for performance. *Medicine and Science in Sports and Exercise* **28**, 1129-1137.
- Knudson, R.J., Lebowitz, M.D., Holberg, C.J. and Burrows, B. (1983) Changes in the normal maximal expiratory flow-volume curve with growth and aging. *American Review of Respiratory Disease* **127**, 725-734.
- Larson, J.L., Covey, M.K., Vitalo, C.A., Alex C.G., Patel, M. and Kim, M.J. (1993) Maximal inspiratory pressure: learning effect and test-retest reliability in patients with chronic obstructive pulmonary disease. *Chest* **104**, 448-453.
- Mador, M.J. (1991) Respiratory muscle fatigue and breathing pattern. *Chest* **100**, 1430-1435.
- Mador, M.J. and Acevedo, F.A. (1991) Effect of respiratory muscle fatigue on breathing pattern during incremental exercise. *American Review of Respiratory Disease* **143**, 462-468.
- Mador, M.J., Magalang, U.J., Rodis, A. and Kufel, T.J. (1993) Diaphragmatic fatigue after exercise in healthy human subjects. *American Review of Respiratory Disease* **148**, 1571-1575.
- Martin, B.J., Morgan, E.J., Zwillich, C.W. and Weil, J.V. (1979) Influence of exercise hyperthermia on

- exercise breathing pattern. *Journal of Applied Physiology* **47**, 1039-1042.
- Martin, B.J., Morgan, E.J., Zwillich, C.W. and Weil, J.V. (1981) Control of breathing during prolonged exercise. *Journal of Applied Physiology* **50**, 27-31.
- McConnell, A.K. and Romer, L.M. (2004) Dyspnoea in health and obstructive pulmonary disease: The role of respiratory muscle function and training. *Sports Medicine* **34**, 117-132.
- Nybo, L. and Nielsen, B. (2001) Hyperthermia and central fatigue during prolonged exercise in humans. *Journal of Applied Physiology* **91**, 1055-1060.
- Powers, S.K. and Howley, E.T. (2004) *Exercise Physiology: Theory and application to fitness and performance*. 5th ed. McGraw-Hill, New York, 216-217.
- Powers, S.K., Howley, E.T. and Cox, R. (1982) Ventilatory and metabolic reactions to heat stress during prolonged exercise. *Journal of Sports Medicine and Physical Fitness* **22**, 32-36.
- Romer, L.M., Bridge, M.W., McConnell, A.K. and Jones, D.A. (2004) Influence of environmental temperature on exercise-induced inspiratory muscle fatigue. *European Journal of Applied Physiology* **91**, 656-663.
- Romer, L.M., McConnell, A.K. and Jones, D.A. (2002a) Effects of inspiratory muscle training upon recovery time during high intensity, repetitive sprint activity. *International Journal of Sports Medicine* **23**, 353-360.
- Romer, L.M., McConnell, A.K. and Jones, D.A. (2002b) Effects of inspiratory muscle training on time-trial performance in trained cyclists. *Journal of Sports Science* **20**, 547-562.
- Rowell, L.B. (1986) *Human Circulation: Regulation during physical stress*. New York: Oxford University Press. 174-406.
- Sheel, A.W., Richards, J.C., Foster, G.E. and Guenette, J.A. (2004) Sex differences in respiratory exercise physiology. *Sports Medicine* **34**, 567-579.
- Sonetti, D.A., Wetter, T.J., Pegelow, D.F. and Dempsey, J.A. (2001) Effects of respiratory muscle training versus placebo on endurance exercise performance. *Respiration Physiology* **127**, 185-199.
- St Croix, C.M., Morgan, B.J., Wetter, T.J. and Dempsey, J.A. (2000) Fatiguing inspiratory muscle work causes reflex sympathetic activation in humans. *Journal of Physiology* **529** Pt 2, 493-504.
- Syabbalo, N.C., Krishnan, B., Zintel, T. and Gallagher, G.C. (1994) Differential ventilatory control during constant work rate and incremental exercise. *Respiration Physiology* **97**, 175-187.
- Topin, N., Mucci, P., Hayot, M., Prefaut, C. and Ramonatxo, M. (2003) Gender influence on the oxygen consumption of the respiratory muscles in young and older healthy individuals. *International Journal of Sports Medicine* **24**, 559-564.
- Volianitis, S., McConnell, A.K., Koutedakis, Y., McNaughton, L., Backx, K. and Jones, D.A. (2001) Inspiratory muscle training improves rowing performance. *Medicine and Science in Sports and Exercise* **33**, 803-809.
- White, D.P., Douglas N.J., Pickett, C.W., Weil, J.V. and Zwillich, C.W. (1983) Sexual influence on the control of breathing. *Journal of Applied Physiology* **54**, 874-879.
- Williams, J.S., Wongsathikun, J., Boon, S.M. and Acevedo, E.O. (2002) Inspiratory muscle training fails to improve endurance capacity in athletes. *Medicine and Science in Sports and Exercise* **34**, 1194-1198.
- Yanos, J., Wood, L.D., Davis, K. and Keamy, M. (1993) The effect of respiratory and lactic acidosis on diaphragm function. *American Review of Respiratory Disease* **147**, 616-619.

AUTHORS BIOGRAPHY

James S. WILLIAMS

Employment

Dept. of Health, Exercise, and Sport Sciences and Physiology, Texas Tech University/Texas Tech Univ. Health Sciences Center, USA.

Degree

PhD

Research interests

Cardiopulmonary limitations to exercise, control of breathing during exercise.

E-mail: jim.williams@ttu.edu

Kendra A. O'KEEFE

Employment

Dept. of Health, Exercise and Sport Sciences, Texas Tech University, USA

Degree

MS

Research interests

Exercise testing and training, metabolism, fitness.

E-mail: kokeefe@frontstrat.com

Lee T. FERRIS

Employment

Department of Physiology, Texas Tech University Health Sciences Center, USA.

Degree

MS (PhD candidate)

Research Interests

Exercise training, cognitive function, neurotrophins

E-mail: lee.ferris@ttuhsc.edu

KEY POINTS

- The combined effects of a heat load and exercise on inspiratory muscle strength were investigated in untrained female subjects.
- Previous studies have shown that a very high exercise intensity (> 80% VO₂max) is required to elicit reductions in inspiratory muscle strength.
- Prolonged submaximal exercise (40-min/60% VO₂max) in a hot environment significantly reduced inspiratory muscle strength in untrained females whereas the same intensity in a thermo-neutral environment had no effect on inspiratory muscle function.
- These reductions in inspiratory muscle strength may be related to competition for blood flow among the locomotor, inspiratory, and cutaneous circulations.

✉ James S. Williams, PhD

Associate Professor, Department of Health, Exercise, and Sports Sciences, Box 43011 Texas Tech University, Lubbock, Texas 79409-3011, USA