The effect of inspiratory muscle training on high-intensity, intermittent running performance to exhaustion

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The effect of inspiratory muscle training on high-intensity, intermittent running performance to exhaustion

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Abstract: The effects of inspiratory muscle (IM) training on maximal 20 m shuttle run performance (Ex) during Yo-Yo intermittent recovery test and on the physiological and perceptual responses to the running test were examined. Thirty men were randomly allocated to 1 of 3 groups. The experimental group underwent a 6 week pressure threshold IM training program by performing 30 inspiratory efforts twice daily, 6 d/week, against a load equivalent to 50% maximal static inspiratory pressure. The placebo group performed the same training procedure but with a minimal inspiratory load. The control group received no training. In post-intervention assessments, IM function was enhanced by >30% in the experimental group. The Ex was improved by 16.3% ± 3.9%, while the rate of increase in intensity of breathlessness (RPB/4i) was reduced by 11.0% ± 6.2%. Further, the whole-body metabolic stress reflected by the accumulations of plasma ammonia, uric acid, and blood lactate during the Yo-Yo test at the same absolute intensity was attenuated. For the control and placebo groups, no significant change in these variables was observed. In comparison with previous observations that the reduced RPB/4i resulting from IM warm-up was the major reason for improved Ex, the reduced RPB/4i resulting from the IM training program was lower despite the greater enhancement of IM function, whereas improvement in Ex was similar. Such findings suggest that although both IM training and warm-up improve the tolerance of intense intermittent exercise, the underlying mechanisms may be different.

Key words: training, inspiratory muscle, muscle function, breathlessness, metabolic stress, intermittent exercise.

Résumé : Dans cette étude, nous analysons l’effet de l’entraînement des muscles de l’inspiration (IM) sur le nombre de répétitions d’une course de 20 m (Ex) au cours du test Yo-Yo constitué de périodes intermittentes de récupération ; au cours de l’épreuve de course, on évalue aussi les ajustements physiologiques et perceptuels. Trente sujets sont répartis aléatoirement dans l’un des trois groupes : le groupe expérimental participe à un entraînement des muscles de l’inspiration d’une durée de six semaines consistant en 30 inspirations exécutées deux fois par jour, 6 fois par semaine à un seuil de pression équivalant à 50 % de la pression statique maximale observée au cours de l’inspiration. Le groupe placebo fait le même entraînement, mais contre une résistance minimale à l’inspiration et le groupe de contrôle de s’entraîne pas. À la suite du programme d’entraînement, on observe une amélioration de la fonction IM de plus 30 % chez le groupe expérimental. Le nombre de répétitions d’une course de 20 m augmente de 16,3 % ± 3,9 % et la vitesse de l’installation de la sensation d’essoufflement (RPB/4i) diminue de 11,0 % ± 6,2 %. De plus, on observe une diminution du stress métabolique global de l’organisme comme le révèlent les valeurs des concentrations plasmatiques d’ammoniac, d’acide urique et des concentrations sanguines de lactate au cours du test Yo-Yo réalisé à la même intensité absolue de travail. On n’observe aucune modification significative des valeurs de ces variables chez les deux autres groupes. Dans une étude antérieure, les auteurs ont observé que l’augmentation de Ex était due à la diminution de RPB/4i causée par l’échauffement des muscles de l’inspiration. Dans cette étude, on observe une moins grande diminution de RPB/4i et ce, même en présence d’une plus grande amélioration de la fonction IM et d’une même amélioration de Ex. D’après ces observations, l’entraînement et l’échauffement des muscles de l’inspiration améliorent la tolérance à la fatigue au cours d’un vigoureux exercice intermittent, mais les mécanismes semblent différents.

Mots-clés : entraînement, muscles de l’inspiration, fonction musculaire, essoufflement, stress métabolique, exercice intermittent.

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Introduction

During high-intensity intermittent exercise, the sensation of breathlessness experienced when the subject approaches the point of volitional exhaustion has been shown to be a significant factor limiting exercise tolerance (Tong et al. 2003, 2004). Recently published study has shown that moderate-intensity inspiratory muscle (IM) warm-up activity attenuates the sensation of breathlessness and the rating of perceived exertion during high-intensity intermittent bouts of exercise (Tong and Fu 2006). These findings have been largely attributed to an enhanced IM function resulting from the IM warm-up activity, explaining 80% of the variance in exercise tolerance. The ergogenic effect of specific IM warm-up activity on the attenuation of breathlessness has been further confirmed during high-intensity intermittent footwork drills used for badminton training (Lin et al. 2007).

Longer-term IM training involving the principles of overload has resulted in significant and long-lasting changes in IM strength and power (McConnell and Lomax 2006; Romer and McConnell 2003; Romer et al. 2002*a*; Volianitis et al. 2001). The enhanced IM function resulting from IM training has been shown to improve continuous rowing and cycling performance (Romer et al. 2002*a*; Volianitis et al. 2001). Although it is acknowledged that the attenuation in the sensation of breathlessness after IM training is a significant factor for improved performance during high-intensity exercise, it is not the sole factor for improved performance. Volianitis et al. (2001) found that the enhanced IM strength following IM training results in an improved resistance to IM fatigue during all-out rowing exercise. A reduction in blood lactate concentration at a given intensity of exercise has also been observed with IM training (McConnell and Sharpe 2005).

The competition in oxygen demand between the locomotor and inspiratory muscle groups during high-intensity incremental exercise on a cycle ergometer leads to limited oxygen availability in locomotor muscles during maximal exercise (Harms et al. 1997, 1998). This phenomenon has also been observed during high-intensity submaximal exercise corresponding to ~85% $\dot{V}O_{2\ max}$ (Legrand et al. 2007). The limited blood flow through the locomotor muscle and consequent oxygen availability during exercise is largely attributable to reflex vasoconstriction in the muscles (Dempsey et al. 2006). This metaboreflex response is evoked by the accumulation of metabolic byproducts in the respiratory muscles when the work of breathing becomes severe during exercise. The increased type III/IV phrenic afferent discharge enhances the sympathetic vasoconstrictor outflow to the locomotor muscles, thereby reducing muscle blood flow and accelerating the rate of peripheral fatigue of these muscles (Romer et al. 2006). The mechanisms for the improved performance following IM training also includes an attenuation of the metaboreflex response, which is secondary to the biochemical and structural adaptations resulting from IM training (McConnell and Lomax 2006).

The purposes of this study were to examine the change in IM function after specific IM training, and the associated changes in the sensation of breathlessness, perceived exertion, and resistance to fatigue during bouts of high-intensity intermittent running to exhaustion. We were also interested in examining the changes in the respiratory response and metabolic stress during the exercise as a result of IM training. The effects of familiarization, concurrent athletic training, and psychological influence on the variables were also considered. It was hypothesized that specific IM training would augment the IM function, attenuate the sensation of breathlessness, and improve exercise tolerance during an exhaustive intense intermittent run to a greater extent in comparison with previous findings of IM warm-up (Tong and Fu 2006).

Materials and methods

Subjects

Thirty male university students who were asymptomatic for cardiovascular or respiratory disease and engaged in regular training in either soccer or rugby team play volunteered for the study (Table 1). After being fully informed of the experimental procedures and possible discomfort associated with the exercise test, subjects gave their written consent. Ethical approval for this study was obtained from the Committee on the Use of Human and Animal Subjects in Teaching and Research of Hong Kong Baptist University.

Procedures

Preliminary testing and familiarization

Before the experimental trials, forced spirometry and aerobic capacity were assessed. The details of these assessments have been reported previously (Tong et al. 2001). After the preliminary testing, familiarization trials of the IM function test and intense intermittent run to exhaustion were undertaken to familiarize the subject with the testing equipment and procedures, and with the sensation of exercising to exhaustion.

Experimental trials

Subjects were randomly assigned to 1 of 3 groups. The control group received no IM training (CON). The other two groups underwent either specific IM training (IMT) or sham training (PLA). This study was carried out in 3 different pre-season periods of the university soccer and rugby teams with which the subjects were affiliated. In each preseason period, the number of subjects recruited for each group was the same. The physical characteristics of subjects among the 3 groups were not different (Table 1). During the intervention period, the intensity and volume of regular physical training were similar in all groups.

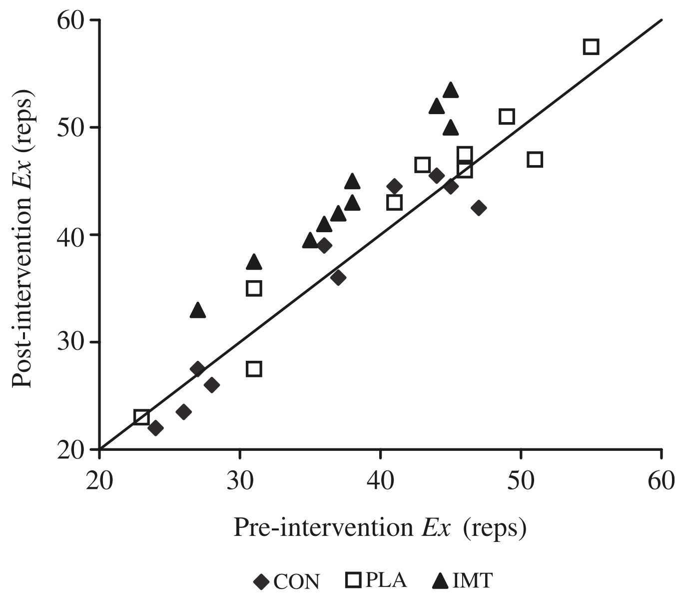
Each subject was required to perform identical maximal dynamic IM function and Yo-Yo intermittent recovery tests pre- and post-intervention. The Yo-Yo test was repeated 2 and 3 times pre- and post-intervention, respectively, to assess the repeatability of the perceptual responses and tolerance to high-intensity intermittent running. Ventilatory and metabolic responses to the Yo-Yo test were assessed in an additional trial pre- and post-intervention. This was to avoid interference from the instrumentation on the intensity of breathlessness and exercise tolerance during the test. In an attempt to examine the change in whole-body metabolic stress after IM training in the IMT group, the post-intervention Yo-Yo test was further repeated with repetitions

Table 1. Physical characteristics of the subjects in CON, PLA, and IMT groups.

Group	Age (y)	Height (cm)	Body mass (kg)	FVC (L)	FEV_1 (L)	FEV_1/FVC (%)	12 s MVV ($L \cdot min^{-1}$)	$\dot{V}O_{2\,max}$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	HR_{max} ($beats \cdot min^{-1}$)	$\dot{V}_E$ ($L \cdot min^{-1}$)
CON (n = 10)	22.0±1.9	176.4±6.1	65.8±6.2	4.80±0.36	4.04±0.30	84.2±2.7	179.4±20.3	59.1±5.2	197.6±8.2	141.2±14.1
PLA (n = 10)	21.5±2.1	174.7±6.8	65.8±7.9	4.77±0.64	3.99±0.51	84.3±6.1	186.3±27.9	55.8±7.9	197.5±6.3	140.9±18.4
IMT (n = 10)	21.3±0.9	175.0±5.4	67.8±7.2	4.53±0.65	3.79±0.41	84.2±7.0	174.9±23.5	60.8±4.7	194.6±6.1	144.8±22.7

Note: FVC, forced vital capacity; FEV_1, forced expiratory volume in 1 s; 12 s MVV, maximum voluntary ventilation measured in 12 s; $\dot{V}O_{2\,max}$, $\dot{V}_E$, and HR_{max}, maximum oxygen consumption, maximum minute ventilation, and maximum heart rate, respectively, recorded in the maximum graded treadmill running test. Data are presented as means ± SD. Differences in all parameters among groups are not significant, $p > 0.05$

Fig. 1. Changes in exercise tolerance (Ex) after intervention in individual subjects in CON, PLA, and IMT groups. Oblique line is line of identity.



of a 20 m shuttle run identical to the pre-intervention value (ISO). For the testing venues and conditions, details have been reported previously (Tong and Fu 2006).

Protocols

Prior to either the IM function assessment or the Yo-Yo test, the subject performed a standardized whole-body warm-up exercise after reporting to the laboratory. The protocol of the standardized warm-up exercise was described previously (Tong and Fu 2006).

To assess maximal dynamic IM function, the method originated by Romer and McConnell (2003) was applied. The major parameters selected for the assessment were maximal inspiratory pressure at zero flow (P_0 in cm H_2O) and maximal rate of pressure development (MRPD, in cm $H_2O \cdot ms^{-1}$). Maximal inspiratory flow ($\dot{V}_{max}$, in $L \cdot s^{-1}$), maximal IM power (W_{Imax}, in cm $H_2O \cdot L \cdot s^{-1}$), optimal pressure ($P_{opt}$ in cm H_2O and $\%P_0$) and flow ($\dot{V}_{opt}$ in $L \cdot s^{-1}$ and $\%\dot{V}_{max}$) derived from the linear regression of inspiratory flow – pressure and the polynomial regression of flow–power were also evaluated. The two regressions were fitted by curves drawn according to the peak pressure and flow measured during maximum inhalation against 6 discrete loads (~0%, 20%, 25%, 35%, 50%, and 65% P_0) of a pressure-threshold device (POWERbreathe, Gaiam Ltd., Warwickshire, UK). The definitions and measurements of the inspiratory pressure – flow – power parameters were previously reported (Romer and McConnell 2003).

The tolerance of intense intermittent run (Ex) was assessed using the Yo-Yo intermittent recovery test (level 1). Details of the testing protocol were reported previously (Krustrup et al. 2003). In this study, Ex was defined as the maximum number of repetitions (reps) of the 20 m shuttle run.

During the Yo-Yo test, whole-body metabolic stress was examined by measuring plasma ammonia ($[NH_3]_{pl}$), uric acid ($[UA]_{pl}$), and blood lactate ($[La^-]_b$) accumulation. A

Table 2. Maximum dynamic inspiratory muscle function and perceptual responses to the Yo-Yo test pre- (Pre) and post-intervention (Post)

		Maximum dynamic IM function					
Group	Intervention	P_0 (cm H_2O)	$\dot{V}_{max}$ ($L \cdot s^{-1}$)	W_{Imax} (cm $H_2O \cdot L \cdot s^{-1}$)	P_{opt} (cm H_2O)	P_{opt}/P_0 (%)	$\dot{V}_{opt}$ ($L \cdot s^{-1}$)
CON (n = 10)	Pre	153.4±19.4	8.01±0.84	326.0±46.6	84.1±13.7	55.2±8.7	3.91±0.51
	Post	154.6±20.2	8.14±0.69	338.5±42.2	85.8±9.3	56.1±7.3	3.96±0.43
PLA (n = 10)	Pre	160.2±25.0	8.07±1.30	352.1±73.9	90.5±11.3	57.6±11.1	3.89±0.62
	Post	156.9±25.5	8.31±1.45	360.1±100.0	89.2±18.5	56.7±5.5	4.02±0.68
IMT (n = 10)	Pre	145.1±19.6	7.48±1.11	290.9±75.6	79.2±15.4	55.4±10.2	3.66±0.60
	Post	191.3*±22.2	7.67±0.97	406.4*±80.8	109.4*±19.6	57.5±10.2	3.73±0.49

Note: P_0, maximal inspiratory pressure at zero flow; $\dot{V}_{max}$, maximal inspiratory flow; $W_{I\,max}$, maximal inspiratory muscle power; P_{opt}, optimal tive to $\dot{V}_{max}$; MRPD, maximal rate of pressure development; RPE, rating of perceived exertion; RPB, rating of perceived breathlessness; breathlessness and exertion, respectively, for every 4th exercise interval during the Yo-Yo test. Data are presented as means ±SD.

*Significantly different from corresponding pre-intervention value, $p < 0.05$

pre-exercise blood sample was collected before the standardized warm-up exercise. For obtaining the post-exercise peak values of plasma $[NH_3]_{pl}$ and $[UA]_{pl}$, blood samples were taken immediately and 1 h after the exercise. The blood sample taken immediately after exercise was also used for $[La^-]_b$ analysis. In this study, blood sampling for the assessment of metabolite accumulation were taken in the 2nd pre-intervention trial and the 2nd and 3rd post-intervention trials.

Inspiratory muscle training

The IMT group performed 30 inspiratory efforts twice per day, 6 d/week, for 6 weeks. Each effort required the subject to inspire against a pressure-threshold load equivalent to 50% P_0 using the POWERbreathe device. A similar protocol has been reported as effective for improving IM functional capacity (Romer et al. 2002*a*). During training, subjects were instructed to initiate every breath from the residual volume in a powerful manner. The inspiratory effort was continued until the inspiratory capacity for the preset loading limited further excursion of the thorax. The inspiratory pressure, flow, and volume of each effort were monitored throughout the training. The breathing pattern was one of low breathing frequency and duty cycle to avoid hyperventilation and resulting hypocapnia. For training progression, the inspiratory load would be increased by 10–15 cm H_2O once the subject had adapted (i.e., the subject was able to complete 30 maneuvers without a break). For the PLA group, the subject performed the same training procedure with a load equivalent to 15% P_0, a load known to lead to only negligible change in IM function (Romer et al. 2002*a*). The initial load was maintained throughout the training period. The inspiratory efforts were performed gently and the respiratory time of each breath was protracted. The IM training in both the IMT and PLA groups were conducted in the laboratory. The subjects were blinded to the true purpose of the study by a message that suggested a comparison of the effects of the powerful-type and the endurance-type IM training protocols on intermittent exercise performance. In the present study, the adherence to the IM training was close to 100% in both groups. One week after the completion of the 6 week training, the post-intervention trials were started in all groups.

Measurement

For assessing maximum dynamic IM function, inspiratory flow was measured using a bidirectional gas flow meter (UVM 17125, Cafif.) that was connected between a mouthpiece and the POWERbreathe pressure-threshold valve. Inspiratory mouth pressure was measured with a differential pressure transducer coupled with a signal conditioner (Collins, Mass.) that was connected by polyethylene tubing to a 4 mm ID vent located near the mouthpiece. The calibrations of the measuring instruments were previously described (Tong and Fu 2006). The inspiratory flow and pressure signals were digitized at 50 ms intervals with the PowerLab data recording system (ML785, ADInstruments, Sydney NSW, Australia). The flow was integrated on-line to provide the inspiratory volume.

During the Yo-Yo test, the ratings of the perceived breathlessness (RPB) and perceived exertion (RPE) were recorded before the exercise, at the subsequent 10 s recovery of every 4th exercise bout starting from the 13th level of the Yo-Yo test, and at exhaustion. The RPB and RPE were assessed with the aid of Borg category scales 0–10 and 6–20, respectively (Borg 1998). The details were reported previously (Tong et al. 2004). For examining the respiratory response to the Yo-Yo test, minute ventilation ($\dot{V}_E$), mean inspiratory flow (V_T/t_i), and O_2 consumption ($\dot{V}O_2$) were recorded with a portable cardio-pulmonary measuring instrument (MetaMax, Cortex, Leipzig, Germany).

The procedure and equipment used for measuring metabolite accumulation in the blood were previously reported (Tong et al. 2003). Briefly, at each blood sampling, a 2–3 mL venous blood was drawn from the antecubital vein using a venous puncture with the subjects in a sitting position. A 25 µL blood sample was drawn for analyzing $[La^-]_b$ using the YSI 1500 Sport Analyzer (Yellow Springs, Dayton, Ohio). The remaining portion of the blood sample was immediately centrifuged and the plasma was separated to use for the assay of $[NH_3]_{pl}$ and $[UA]_{pl}$ with the Vitros DT60 II Chemistry System (Johnson & Johnson Clinical Diagnostics, Rochester, N.Y.). Before the main trials, all equipment was calibrated and verified with standard solutions the manufacturers had provided.

Statistical analysis

The within-subject coefficient of variation, intra-class correlation coefficient, and 95% ratio limits of agreement were calculated for determining the reliability of Ex and perceptual responses in the repeated trials. Two-way analyfor CON, PLA, and IMT groups.

		Perceptual responses			
$\dot{V}_{opt}/\dot{V}_{max}$ (%)	*MRPD* ($cm\,H_2O{\cdot}ms^{-1}$)	RPE	RPB	RPE/4i	RPB/4i
48.8±2.0	0.43±0.05	19.3±1.1	9.70±0.48	0.40±0.10	0.29±0.07
48.6±1.6	0.43±0.05	19.4±0.7	9.75±0.35	0.42±0.13	0.30±0.09
48.3±2.3	0.49±0.07	19.7±0.7	9.80±0.42	0.37±0.11	0.27±0.08
48.4±1.2	0.50±0.07	19.8±0.8	9.90±0.32	0.37±0.13	0.26±0.09
48.9±2.2	0.41±0.06	19.9±0.3	10.00±0.00	0.38±0.07	0.26±0.05
48.6±1.9	0.57*±0.08	19.9±0.3	9.95±0.16	0.34*±0.05	0.23*±0.03

pressure; P_{opt}/P_0, optimal pressure relative to P_0; $\dot{V}_{opt}$, optimal flow; $\dot{V}_{opt}/\dot{V}_{max}$ is optimal flow rela-
RPB/4i and RPE/4i, the slopes of the linear relationship of the increase in ratings of perceived

sis of variance (ANOVA) was computed to examine the between-group effects due to groups (CON, PLA, and IMT) and within-group effects due to intervention (pre and post), 20 m shuttle run (11th, 15th, 19th, and 23rd) and Ex (80, 90 and 100% Ex) on most of the dependent variables. One-way ANOVA with repeated measurements was used to examine the difference in metabolite accumulation among the pre- and post-intervention trials and ISO trial in the IMT group. Newman–Keuls post-hoc analyses were performed when main effects of ANOVA were significant. Relationships between variables were determined using simple regression. All tests for statistical significance were standardized at an α level of $p < 0.05$, and all results were expressed as the mean ± SD.

Results

Maximal dynamic IM function

IM function measures for the CON, PLA, and IMT groups pre- and post-intervention are shown in Table 2. The measures for the CON and PLA groups remained unchanged post-intervention ($p > 0.05$). In contrast, substantial improvements in P_0, $W_{I\,max}$, P_{opt}, and MRPD were observed in the IMT group after IM training ($p < 0.01$). The others were not changed.

Intense intermittent run to exhaustion

Exercise tolerance

The within-subject coefficient of variation and intra-class correlation coefficients for the pre-intervention Ex were 5.3% (95% CI = 3.8% to 6.8%) and 0.97 (95% CI = 0.94 to 0.99); for the post-intervention Ex they were 4.5% (95% CI = 3.4% to 5.7%) and 0.99 (95% CI = 0.98 to 0.99), respectively.

In this study, since blood tests for the assessment of metabolite accumulation were performed in the 2nd pre-intervention trial and the 2nd and 3rd post-intervention trials, all the variables recorded in the 2nd pre-intervention trial and the average of those recorded in the two post-intervention trials were selected for analysis. Figure 1 shows the change in the Ex of each subject for CON, PLA, and IMT groups. The pre-intervention Ex among the 3 groups was not different ($p > 0.05$). Further, it was not changed in the CON (Pre: 35.5 ±8.7 reps; Post: 35.1 ±9.4 reps) and PLA (Pre: 41.6 ±10.2 reps; Post: 42.4 ±10.7 reps) groups post-intervention ($p > 0.05$). For the IMT group, improvement in Ex after specific IM training was found in all subjects with a group mean change from 37.6 ± 5.9 reps to 43.7 ± 6.6 reps ($p < 0.05$).

Perceptual responses

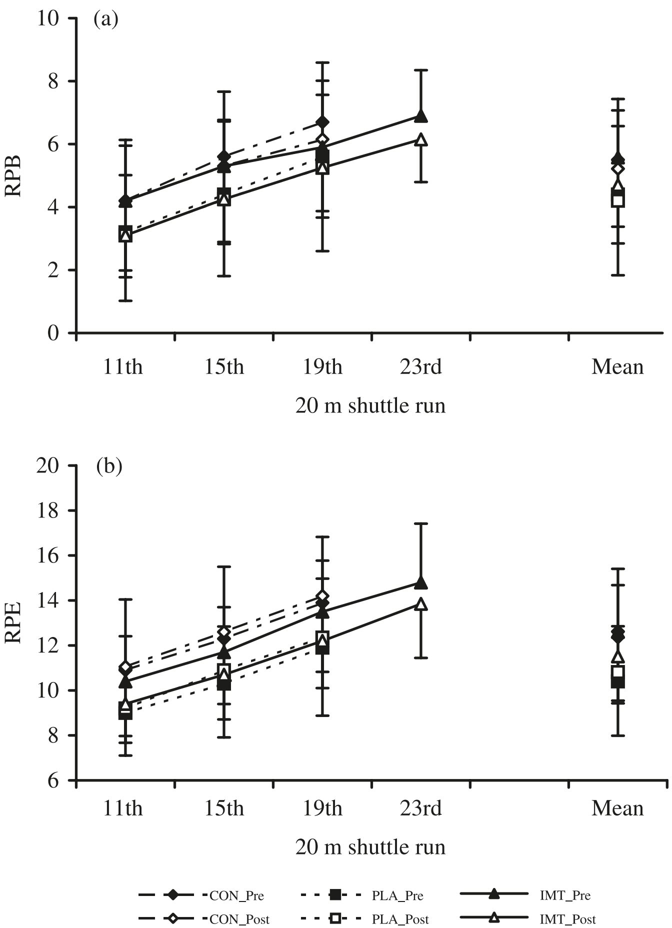
The rates of increase in the RPB and RPE during the Yo-Yo test are expressed as the slopes of the linear relationship of the increase in RPB (RPB/4i) and RPE (RPE/4i) for every 4th exercise interval. The within-subject coefficient of variation and intra-class correlation coefficients for the pre-intervention RPB/4i were 7.2% (95% CI = 4.9% to 9.5%) and 0.94 (95% CI = 0.88 to 0.97); for the post-intervention RPB/4i were 6.4% (95% CI = 4.8% to 7.9%) and 0.94 (95% CI = 0.88 to 0.97), respectively. The two coefficients for the pre- and post-intervention RPE/4i were 5.9% (95% CI = 4.0% to 7.8%) and 0.95 (95% CI = 0.90 to 0.98); and 6.3% (95% CI = 5.2 to 7.5%) and 0.95 (95% CI = 0.90 to 0.98), respectively.

For the IMT group, significant reductions in the RPB/4i and RPE/4i were observed post-intervention ($p < 0.05$), whereas the RPB and RPE at exhaustion, which were close to maximum, were not changed ($p > 0.05$) (Table 2). The reductions in the RPB and RPE ($p < 0.05$) were also revealed in the symptom profiles and average values composed of data at which all subjects had not been exhausted (Fig. 2). For the CON and PLA groups, the perceptual responses to the exercise test were not altered post-intervention ($p > 0.05$).

Metabolic stress

The whole-body metabolic stress experienced by the subjects during the Yo-Yo test was severe. Marked accumulations of $[NH_3]_{pl}$, $[UA]_{pl}$, and $[La^-]_b$ were observed in all groups after the exercise (Table 3). Following the intervention, the CON group did not exhibit any change in metabolite accumulation ($p > 0.05$). The metabolite accumulation for the PLA group tended to be reduced, but did not reach statistical significance ($p > 0.05$). For the IMT group, although Ex was increased post-intervention, the metabolite accumulations were not altered significantly ($p > 0.05$). Rather, the $[NH_3]_{pl}$, $[UA]_{pl}$, and $[La^-]_b$ accumulations in the ISO trial were significantly lower than the pre-intervention values and those recorded in the exhaustive post-intervention trial ($p < 0.05$).

Fig. 2. The symptom profiles and average values of pre- (Pre) and post-intervention (Post) (*a*) RPB and (*b*) RPE at selected 20 m shuttle runs for which all subjects in CON, PLA, and IMT groups were not exhausted. Note that all the RPB and RPE at 19th and 23rd are significantly greater than corresponding values at 11th and 15th 20- m shuttle run in all groups. Post-intervention RPB and RPB at all selected 20 m shuttle runs in the IMT group were significantly lower than corresponding pre-intervention values, $p < 0.05$.



Respiratory response

The pre- and post-intervention respiratory responses at 80%, 90%, and 100% pre-intervention Ex were compared for the IMT group (Fig. 3). During the pre- and post-intervention Yo-Yo tests, the $\dot{V}_E$ and V_T/t_i, but not the $\dot{V}O_2$, for the 20 m shuttle run increased continuously from 80% to 100% Ex. However, the increases in the $\dot{V}_E$ and V_T/t_i in the post-intervention trial were lessened, with significant differences found at 100% Ex ($p < 0.05$). The changes in the post-intervention $\dot{V}_E$ and V_T/t_i were not correlated ($r = 0.37$, $n = 10$, $p > 0.05$). In subsequent recovery intervals, similar changes in the $\dot{V}_E$ and V_T/t_i were also found, but the differences were not statistically significant. For the CON and PLA groups (Table 4), none of the variables for the 20 m shuttle run and the subsequent recovery of the pre-intervention Yo-Yo test near exhaustion were altered post-intervention ($p > 0.05$).

Correlations among variables with IM training

The inter-individual correlations among the changes (Δ) in the IM function measures, RPB/4i, RPE/4i, metabolite accumulation, and Ex post-intervention, which were expressed as percentages of the pre-intervention values, were examined. For the IMT group, the ΔRPB/4i and the improved IM function measures were not significantly correlated (Fig. 4). The correlation was not significant between the ΔEx and ΔRPB/4i (r = –0.50, n = 10, $p > 0.05$) and between the ΔEx and ΔRPE/4i (r = –0.49, n = 10, $p > 0.05$), whereas it was significant between the ΔRPB/4i and ΔRPE/4i (r = 0.75, n = 10, $p < 0.05$). The ΔEx and the changes in metabolite accumulation recorded in the ISO trial were also not correlated ($[NH_3]_{pl}$: r = 0.42, $[UA]_{pl}$: r = –0.16, $[La^-]_b$: r = –0.06, n = 10, $p > 0.05$). For the CON and PLA groups, however, the ΔEx was negatively correlated to the ΔRPB/4i (CON: r = –0.78, PLA: r = –0.90, n = 10, $p < 0.05$) and ΔRPE/4i (CON: r = –0.71, PLA: r = –0.85, n = 10, $p < 0.05$).

Discussion

The major findings of this study are that specific IM training augmented IM function and improved metabolic stress, perceptual responses, and exercise tolerance during an exhaustive, intense, intermittent run. The effects of familiarization, concurrent athletic training, and psychological influence on the variables are minimal.

Maximal dynamic IM function

In this study, the maximal dynamic IM function was enhanced significantly in the IMT group, but not in the PLA or CON groups. The enhancement in IM function was mainly found in the pressure parameters of P_0, $W_{I\ max}$, P_{opt}, and MRPD, and was negligible in the flow parameters of $\dot{V}_{max}$ and $\dot{V}_{opt}$ (Table 2). The inferior improvement in the flow parameters resulting from the specific pressure-threshold IM training was in contrast to the 17% increase in $\dot{V}_{max}$ reported in a previous study after similar IM training (Romer et al. 2002*a*). Romer and McConnell (2003) observed that the flow-pressure specificity of IM training is such that high-pressure – low-flow IM training can result in increases in maximal inspiratory pressure and power with no change in maximal inspiratory flow. It is likely that the IM training used in the present study tended towards the high-pressure – low-flow specific condition rather than the intermediate flow-pressure specific that was used previously (Romer et al. 2002*a*).

In the IMT group, although the unchanged $\dot{V}_{max}$ and $\dot{V}_{opt}$ after IM training contrasted with previous findings, the increase in the P_0 of 33.6% (±21.4%) was consistent with the 28%–45% improvements reported in healthy individuals using pressure-threshold IM training (Huang et al. 2003; Romer et al. 2002*a*; Volianitis et al. 2001). The improvements in $W_{I\ max}$ (45.2% ± 33.9%), P_{opt} (41.2% ± 27.7%), and MRPD (41.9% ± 26.7%), which were in line with the increase in P_0, were also in agreement with the adaptations observed in previous studies (Romer and McConnell 2003; Romer et al. 2002*a*). In comparison with IM warm-up (Tong and Fu 2006), the improvements in IM function after the specific IM training were greater.

Table 3. Plasma ammonia ($[NH_3]_{pl}$), uric acid ($[UA]_{pl}$), and blood lactate ($[La^-]_b$) accumulation during the Yo-Yo test pre- (Pre) and post-intervention (Post) for CON, PLA, and IMT groups.

	$[NH_3]_{pl}$ (μmol·L^{-1})		$[UA]_{pl}$ (μmol·L^{-1})		$[La^-]_b$ (mmol·L^{-1})	
Group	Pre	Post	Pre	Post	Pre	Post
CON (n = 10)	124.8±26.3	117.5±23.2	91.3±35.9	99.7±46.6	8.59±1.58	8.21±1.19
PLA (n = 10)	122.9±33.1	107.8±23.3	79.3±16.7	67.7±28.8	9.04±1.09	7.53±0.62
IMT (n = 10)	114.3±35.4	122.7±38.1	61.8±24.1	68.2±25.1	7.64±1.80	8.31±1.62
ISO (n = 10)		87.4±24.3*		44.0±18.9*		6.50±1.65*

Note: Data are presented as means ± SD. ISO, post-intervention trial in the IMT group with repetitions of 20 m shuttle run identical to the pre-intervention value.

*Significantly different from IMT pre- and post-intervention values, $p < 0.05$.

Intense intermittent run to exhaustion

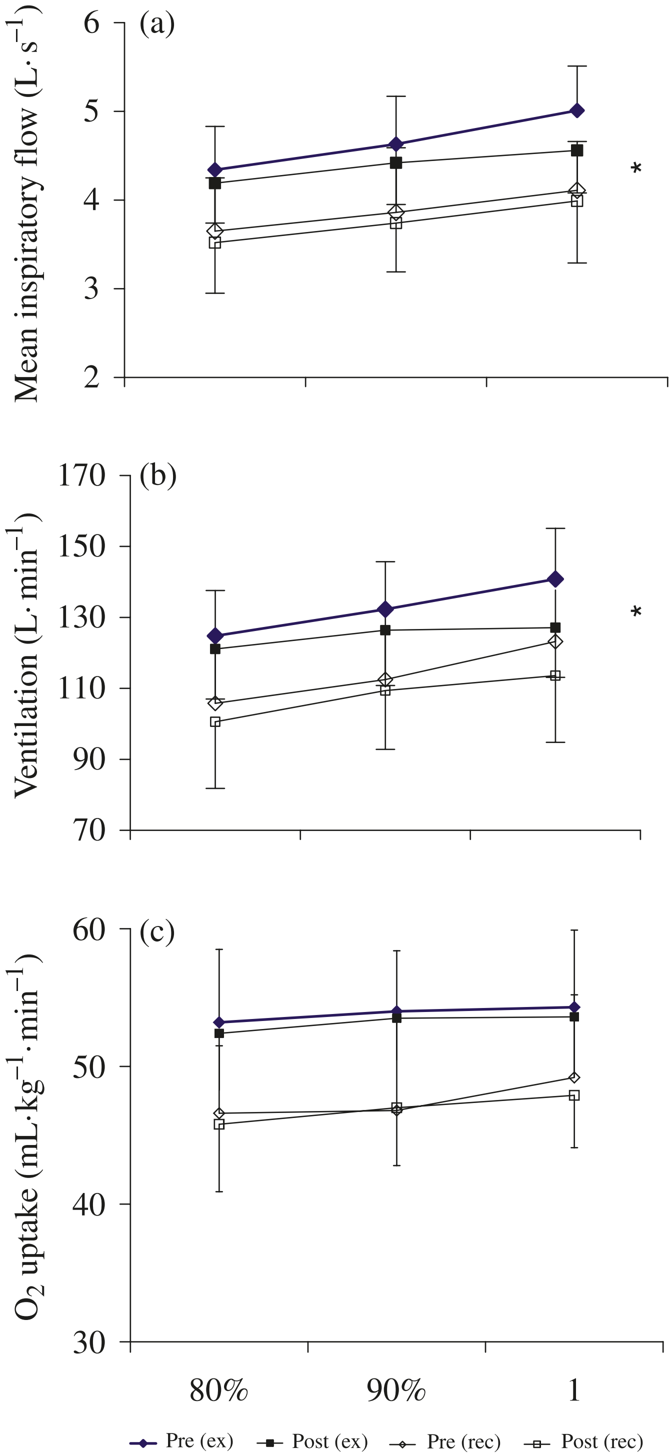
Intensity of breathlessness

During the Yo-Yo test, the physical demand of repeating the 20 m shuttle run increased progressively from mild to intense. The vigorous physical exertion during the test was accompanied with a huge ventilatory demand (Table 4). At exhaustion, the ventilatory levels attained during the 20 m shuttle run (102.1% ±13.9% (ranging from 77.1% to 147.8%)) and the subsequent 10 s recovery (90.5% ±11.2% (ranging from 78.6% to 133.3%)) were almost the same as the maximum $\dot{V}_E$ recorded in the preceding $\dot{V}O_{2\ max}$ test. The corresponding breathlessness intensity in most subjects was at maximum. In post-intervention trials, RPB was reduced in the IMT group (Fig. 2). The RPB/4i, which was the rate of increase in intensity of breathlessness during the Yo-Yo test, was reduced to 89.0% ± 6.2% of pre-intervention value (ranging from 74.4% to 97.5%). The reduced RPB/4i is considered to be an adaptation to the IM training rather than due to familiarization, concurrent athletic training, or psychological influence, as the RPB/4i was consistent in repeated trials and it was unchanged post-intervention in the CON and PLA groups.

It has been shown that the intensity of the sensation of breathlessness is an analog of the magnitude of the central respiratory motor drive (el-Manshawi et al. 1986). In the IMT group, the V_T/t_i, which has been used to indicate the central inspiratory drive (Lind 1984), was reduced concomitantly with the reduction in $\dot{V}_E$ during the post-intervention trial (Fig. 3), but these changes were not correlated. Such findings implied that the diminished inspiratory drive that resulted in the amelioration of RPB/4i was not just a consequence of the concomitant reduction in ventilatory demand. It is postulated that it may be an independent physiological adaptation to IM training, as an increase in IM strength reduces the fraction of maximal tension generated with each breath. Negative correlations between improved IM strength and reduced inspiratory motor drive revealed by mouth occlusion pressure at 0.1 s and reduced RPB during repeated sprints have been demonstrated previously after pressure-threshold IM training (Huang et al. 2003; Romer et al. 2002*b*). However, in the present study, the relationship between the reduction in RPB/4i during the Yo-Yo test and the improvement in IM function post-intervention was not statistically significant. This observation is in contrast to the findings of Romer et al. (2002*b*), although it should be noted that their findings were obtained from a fixed-time, non-exhaustive, shuttle run test and the reduction in the breathlessness intensity after IM training was reflected by the difference in the RPB rather than in the rate of RPB increase. Figure 4 shows that the large inter-individual variations of the enhancement of the IM function resulted in a relatively consistent reduction in the RPB/4i among the subjects in the IMT group. The magnitude of reduction in RPB/4i was limited to ~10% of pre-intervention value. It was relatively less than the ~20% reduction in RPB/4i in an identical Yo-Yo test subsequent to the specific IM warm-up (Tong and Fu 2006).

The limitation for further reductions in RPB/4i with improved IM strength cannot be explained precisely in this study. An acute bout of submaximal inspiratory loading, which is generally applied in IM warm-up, has been shown to optimize the IM activation pattern and enhance the muscle excitability during subsequent maximum inspiratory effort (Hawkes et al. 2007; Ross et al. 2007). The IM warm-up activity was also suggested to decrease the degree of antagonist co-contraction during inspiration (Volianitis et al. 1999). These transient physiological responses, which could augment the absolute inspiratory strength and lessen the demand of IM force generation in each breath, may facilitate the attenuation of the sensation of breathlessness during subsequent exercise (Tong and Fu 2006; Volianitis et al. 2001). Moreover, prior loaded respiratory activity has been demonstrated to cause a temporary alteration in the “memorized” association between breathlessness and respiratory load (Wilson and Jones 1990). The desensitizing effect may reduce the sensation of breathlessness independently of the enhanced IM function. In the IMT group, the enhanced IM function after the IM training was a result of both slow neurogenic and myogenic adaptations in the muscles to the specific training (Downey et al. 2007; Sale 1988). Those acute neural changes resulting from specific IM warm-up were not likely to occur in the post-intervention Yo-Yo test. The reduced RPB/4i post-intervention was mainly attributed to the decrease in relative tension for a given level of ventilation resulting from the improvement in IM force-generation capacity (Kellerman et al. 2000). It is reasonable to postulate that the attenuation of the sensation of breathlessness during the Yo-Yo test, subsequent to acute and chronic loaded inspiratory activities, is attributable to different underlying mechanisms. The difference in the mechanisms may potentially lead to the discrepancy in the RPB/4i reduction. However, these results should be interpreted with caution as the discrepancy in the attenuation of the intensity of breathlessness was observed only in the RPB/4i variable and resulted from two independent subject groups. Whether

Fig. 3. Pre- and post-intervention (*a*) mean inspiratory flow rate, (*b*) minute ventilation, and (*c*) volume of O_2 uptake during the 20 m shuttle run (ex) and the subsequent 10 s recovery (rec) of the Yo-Yo test at 80%, 90%, and 100% of the pre-intervention exercise tolerance (Ex) in IMT group are shown. Note that the values of all parameters, except the volume of O_2 uptake at 90% and 100% Ex, are significantly greater than corresponding values at 80%. Asterisk (*) indicates a significant difference from corresponding pre-intervention value, $p < 0.05$.



the discrepancy was biased by expressing the change in breathlessness intensity as a rate of change or due to inter-individual variations awaits further investigation.

Exercise tolerance

In the IMT group, Ex was enhanced by 16.3% ± 3.9% (ranging from 11.1% to 22.2%) post-intervention. The Ex score, which was repeatable in the pre- and post-intervention trials, was enhanced in the IMT group, but not in the CON and PLA groups. This provides evidence that the improved tolerance can be attributed to an adaptative response to the specific IM training, rather than a result of familiarization, concurrent athletic training, or psychological phenomena. It has been noted in previous studies that the severe sensation of breathlessness elicited during intense intermittent exercise at exhaustion in normal active persons plays a part in limiting exercise tolerance (Tong et al. 2003, 2004). The notion was further supported by the recent findings that the ΔRPB/4i resulting from the IM warm-up accounted for more than 80% of the variance in the ΔEx in the Yo-Yo test (Tong and Fu 2006). In the IMT group, however, the correlation between the ΔRPB/4i and the ΔEx post-intervention was not statistically significant. This contrast in findings may be partly due to the similar reduction in the RPB/4i among the subjects. In Fig. 5, all except one data point comprising both ΔRPB/4i and ΔEx are clustered. The ΔRPB/4i and ΔEx within the homogeneous subjects in this study may mask the true relationship between the two variables, and consequently lead to a type II error. Indeed, the ΔRPB/4i in the CON and PLA groups, which was probably due to daily variation, was correlated to the ΔEx ($r = -0.85$, $n = 20$, $p < 0.05$). It was therefore considered that the Ex enhancement in the IMT group after the specific IM training was partly attributable to the reduction in RPB/4i.

In Fig. 5, it is notable that the ΔEx in the IMT group deviated upwardly from the regression formulated by the ΔEx and ΔRPB/4i of the CON and PLA groups. The upward deviation, in contrast to the previous findings of IM warm-up, indicated that there might be factors independent of attenuation of the sensation of breathlessness that contributed to the enhancement in Ex. These factors, which are separate from the acute physiological responses to the IM warm-up, are probably associated with the training adaptations in IM structure and biochemical properties. This may explain the reduction in RPB/4i after the IM training, which was only half of that observed subsequent to the IM warm-up, and may explain the similar Ex enhancement of 19% previously reported by Tong and Fu (2006).

Recently, Legrand et al. (2007) demonstrated that the rise in accessory IM O_2 demand during maximal incremental exercise limits further increase in O_2 utilization in locomotor muscles in active men. The respiratory steal phenomenon occurs not only at maximal-intensity exercise, but also at lower-intensity exercise, down to ~85% $\dot{V}O_{2\,max}$, which is close to the respiratory compensation point (Legrand et al. 2007). As indicated previously, this phenomenon is attributable to vasoconstriction within the locomotor muscles, which is a consequence of the metaboreflex elicited from the respiratory muscles when the work of breathing becomes severe (Dempsey et al. 2006). The increased sympathetic vasoconstrictor outflow, evoked by the accumulation of met-

Table 4. Respiratory response to the exercise bout of 20 m shuttle run and the subsequent 10 s recovery in pre-intervention Yo-Yo test near exhaustion (Pre) and at corresponding periods in post-intervention test (Post) for CON, PLA, and IMT groups.

	$\dot{V}O_2$ (mL·kg^{-1}·min^{-1})		$\dot{V}_E$ (L·min^{-1})		V_T/t_i (L·s^{-1})	
Group	Pre	Post	Pre	Post	Pre	Post
20 m shuttle run						
CON (n = 10)	54.6±5.4	55.2±6.8	142.3±19.6	142.9±15.2	4.85±0.80	4.95±0.73
PLA (n = 10)	53.5±8.4	52.4±4.8	147.1±9.4	141.8±13.3	5.15±0.41	4.98±0.56
IMT (n = 10)	54.3±5.6	53.6±4.3	140.8±14.3	127.1±14.0*	5.01±0.51	4.56±0.48*
10 s recovery						
CON (n = 10)	49.1±6.0	48.2±3.9	129.9±19.1	127.2±18.9	4.37±0.81	4.34±0.80
PLA (n = 10)	48.4±6.9	45.4±2.7	129.5±13.4	122.4±17.9	4.40±0.60	4.17±0.74
IMT (n = 10)	49.2±6.0	47.9±3.8	123.2±14.5	113.6±18.8	4.11±0.55	3.99±0.70

*Significantly different from corresponding pre-intervention value (p < 0.05).

Fig. 4. The relationships between the percentage changes in the pre-intervention P_0, $W_{I\,max}$, P_{opt}, and MRPD, and the percentage change in the pre-intervention RPB/4i during the Yo-Yo test in the IMT group. Data for each subject in the IMT group are plotted. Note that correlations are not significant in all variables, $p > 0.05$.

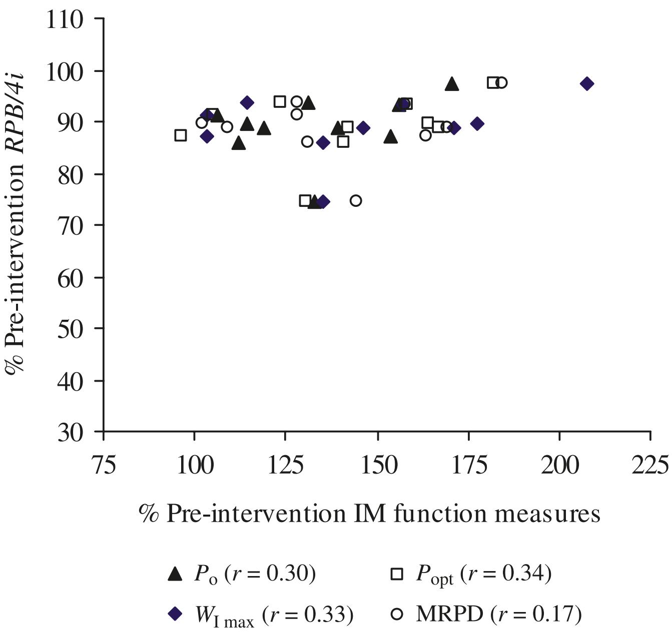
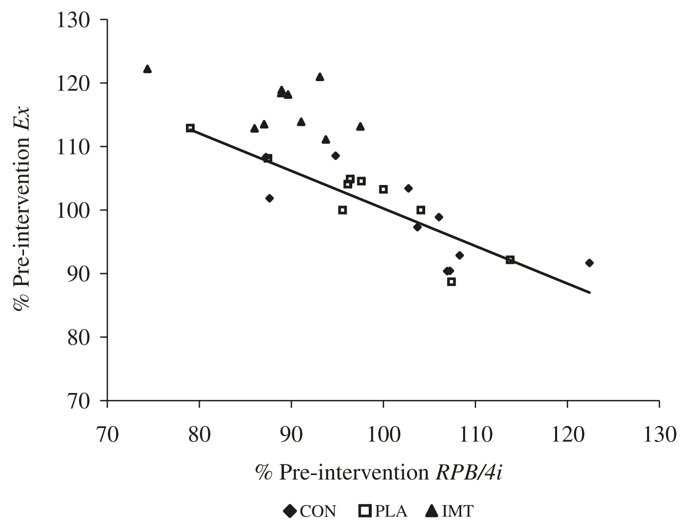


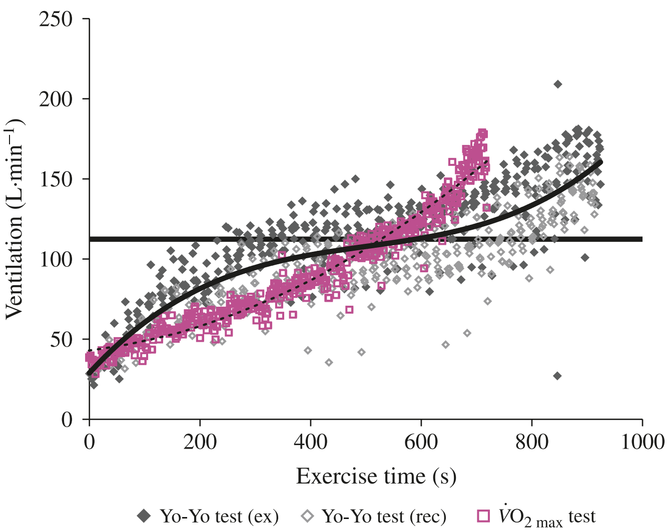
Fig. 5. The relationship between the percentage change in the pre-intervention RPB/4i and that in the pre-intervention Ex in the IMT, PLA, and CON groups are shown. Note that the correlation in IMT group is not significant (r = –0.50, n = 10, p > 0.05), although it is significant in PLA and CON groups (r = –0.85, n = 20, regression equation: y = –0.591x + 159.35, p < 0.05).



abolic by-products in IM, reduces blood flow to locomotor muscles (Rodman et al. 2003). In comparison, the degree of vasoconstriction in the respiratory muscles in response to the increased sympathetic activity is less pronounced. This is probably due to the lower sensitivity to the vasoconstrictor influences in the vasculature in the inspiratory muscles (Aaker and Laughlin 2002). Eventually, the reduced blood flow in locomotor muscles accelerates the rate of peripheral fatigue (McConnell and Lomax 2006; Romer et al. 2006). In the present study, taking into account the rise of ventilation of a typical subject in response to the Yo-Yo test and the preceding $\dot{V}O_{2\,max}$ test (Fig. 6), it was observed that the $\dot{V}_E$ increased rapidly during the Yo-Yo test and the maintenance of $\dot{V}_E$ at the level corresponding to or higher than that attained at 85% $\dot{V}O_{2\,max}$ was relatively longer compared with that during the $\dot{V}O_{2\,max}$ test. Although we did not assess the change in blood flow in respiratory and locomotor muscles during the Yo-Yo test, it is likely that the heavy respiratory muscle work induced the metaboreflex in subjects.

It has been shown that improved IM function increases the work threshold required to elicit the IM metaboreflex (McConnell and Lomax 2006; Witt et al. 2007). Based on this concept, the relative reduction in the IM work during the post-intervention Yo-Yo test resulting from the reduction in $\dot{V}_E$ and augmentation of IM function in the IMT group might delay initiation of the IM metaboreflex. As a result, the blood flow and thus the O_2 availability in the locomotor muscles were improved. Such a scenario is supported by the attenuation of whole-body metabolic stress during the post-intervention Yo-Yo test, as reflected by the reduction in the $[NH_3]_{pl}$, $[UA]_{pl}$, and $[La^{-}]_b$ accumulation with no change in total $\dot{V}O_2$ compared with those measured at the same absolute intensity pre-intervention. The reductions in metabolite accumulation, resulting from the decrease in adenine nucleotide degradation and relative contribution of anaerobic metabolism to ATP resynthesis, has been shown to be sec-

Fig. 6. The time courses for ventilation of a typical subject during the Yo-Yo test and the $VO_{2\,max}$ test are shown. Solid horizontal line indicates the ventilatory level corresponding to 85%$VO_{2\,max}$. Solid curve indicates the time course for mean ventilation during the Yo-Yo test. Dotted curve indicates the time course for mean ventilation during the $VO_{2\,max}$ test.



ondary to the improved O_2 availability in the locomotor muscles during intense intermittent exercise (Balsom et al. 1994). In the post-intervention Yo-Yo test in the IMT group, the improved RPE/4i and Ex are in line with the previous findings that the attenuation of the IM metaboreflex consequent upon the IM training decreased the rate of calf fatigue during repeated plantar flexions by improving local perfusion in these muscles (McConnell and Lomax 2006). It is postulated that the attenuation of the IM metaboreflex, other than RPB/4i reduction, may be another underlying mechanism for improving the Ex after the IM training.

In conclusion, 6 weeks of pressure-threshold IM training augmented maximal dynamic IM function, mainly in the parameters of P_0, $W_{I\,max}$, P_{opt}, and MRPD. It reduced mean inspiratory flow, minute ventilation, RPB/4i, and whole-body metabolic stress during the Yo-Yo test and enhanced exercise tolerance. In comparison with the IM warm-up previously reported, the RPB/4i reduction resulting from specific IM training was relatively smaller in magnitude despite the greater enhancement of IM strength, whereas the improvement in exercise tolerance was similar. Such findings suggest that both chronic (training) and acute (warm-up) ventilatory activity applied to the inspiratory muscles improve the tolerance of intense intermittent exercise, although the underlying mechanisms are different.

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References

Aaker, A., and Laughlin, M.H. 2002. Diaphragm arterioles are less responsive to alpha1- adrenergic constriction than gastrocnemius arterioles. J. Appl. Physiol. **92**: 1808–1816. PMID:11960928.

Balsom, P.D., Ekblom, B., and Sjodin, B. 1994. Enhanced oxygen availability during high intensity intermittent exercise decreases anaerobic metabolite concentrations in blood. Acta Physiol. Scand. **150**: 455–456. PMID:8036914.

Borg, G. 1998. Borg's perceived exertion and pain scales. Human Kinetics, Champaign, Ill.

Dempsey, J.A., Romer, L., Rodman, J., Miller, J., and Smith, C. 2006. Consequences of exercise-induced respiratory muscle work. Respir. Physiol. Neurobiol. **151**: 242–250. doi:10.1016/j.resp.2005.12.015. PMID:16616716.

Downey, A.E., Chenoweth, L.M., Townsend, D.K., Ranum, J.D., Ferguson, C.S., and Harms, C.A. 2007. Effects of inspiratory muscle training on exercise responses in normoxia and hypoxia. Respir. Physiol. Neurobiol. **156**: 137–146. doi:10.1016/j.resp.2006.08.006. PMID:16996322.

el-Manshawi, A., Killian, K.J., Summers, E., and Jones, N.L. 1986. Breathlessness during exercise with and without resistive loading. J. Appl. Physiol. **61**: 896–905. PMID:3759774.

Harms, C.A., Babcock, M.A., McClaran, S.R., Pegelow, D.F., Nickele, G.A., Nelson, W.B., and Dempsey, J.A. 1997. Respiratory muscle work compromises leg blood flow during maximal exercise. J. Appl. Physiol. **82**: 1573–1583. PMID:9134907.

Harms, C.A., Wetter, T.J., McClaran, S.R., Pegelow, D.F., Nickele, G.A., Nelson, W.B., et al. 1998. Effects of respiratory muscle work on cardiac output and its distribution during maximal exercise. J. Appl. Physiol. **85**: 609–618. PMID:9688739.

Hawkes, E.Z., Nowicky, A.V., and McConnell, A.K. 2007. Diaphragm and intercostal surface EMG and muscle performance after acute inspiratory muscle loading. Respir. Physiol. Neurobiol. **155**: 213–219. doi:10.1016/j.resp.2006.06.002. PMID:16846758.

Huang, C.H., Martin, A.D., and Davenport, P.W. 2003. Effect of inspiratory muscle strength training on inspiratory motor drive and RREP early peak components. J. Appl. Physiol. **94**: 462–468. PMID:12391135.

Kellerman, B.A., Martin, A.D., and Davenport, P.W. 2000. Inspiratory strengthening effect on resistive load detection and magnitude estimation. Med. Sci. Sports Exerc. **32**: 1859–1867. doi:10.1097/00005768-200011000-00007. PMID:11079514.

Krustrup, P., Mohr, M., Amstrup, T., Rysgaard, T., Johansen, J., Steensberg, A., et al. 2003. The yo-yo intermittent recovery test: physiological response, reliability, and validity. Med. Sci. Sports Exerc. **35**: 697–705. doi:10.1249/01.MSS.0000058441.94520.32. PMID:12673156.

Legrand, R., Marles, A., Prieur, F., Lazzari, S., Blondel, N., and Mucci, P. 2007. Related trends in locomotor and respiratory muscle oxygenation during exercise. Med. Sci. Sports Exerc. **39**: 91–100. doi:10.1249/01.mss.0000241638.90348.67. PMID:17218889.

Lin, H., Tong, T.K., Huang, C., Nie, J., Lu, K., and Quach, B. 2007. Specific inspiratory muscle warm-up enhances badminton footwork performance. Appl. Physiol. Nutr. Metab. **32**: 1082–1088. doi:10.1139/H07-077. PMID:18059581.

Lind, F.G. 1984. Respiratory drive and breathing pattern during exercise in man. Acta Physiol. Scand. Suppl. **533**: 1–47. PMID:6594031.

McConnell, A.K., and Sharpe, G.R. 2005. The effect of inspiratory muscle training upon maximum lactate steady-state and blood lactate concentration. Eur. J. Appl. Physiol. **94**: 277–284. doi:10.1007/s00421-004-1282-3. PMID:15765241.

McConnell, A.K., and Lomax, M. 2006. The influence of inspiratory muscle work history and specific inspiratory muscle training upon human limb muscle fatigue. J. Physiol. **577**: 445–457. doi:10.1113/jphysiol.2006.117614. PMID:16973699.

Rodman, J.R., Henderson, K.S., Smith, C.A., and Dempsey, J.A. 2003. Cardiovascular effects of the respiratory muscle metaboreflexes in dogs: rest and exercise. J. Appl. Physiol. **95**: 1159–1169. PMID: 12754173.

Romer, L.M., and McConnell, A.K. 2003. Specificity and reversibility of inspiratory muscle training. Med. Sci. Sports Exerc. **35**: 237–244. doi:10.1249/01.MSS.0000048642.58419.1E. PMID:12569211.

Romer, L.M., McConnell, A.K., and Jones, D.A. 2002*a*. Effects of inspiratory muscle training on time-trial performance in trained cyclists. J. Sports Sci. **20**: 547–562. doi:10.1080/026404102760000053. PMID:12166881.

Romer, L.M., McConnell, A.K., and Jones, D.A. 2002*b*. Effects of inspiratory muscle training upon recovery time during high intensity, repetitive sprint activity. Int. J. Sports Med. **23**: 353–360. doi:10.1055/s-2002-33143. PMID:12165887.

Romer, L.M., Lovering, A.T., Haverkamp, H.C., Pegelow, D.F., and Dempsey, J.A. 2006. Effect of inspiratory muscle work on peripheral fatigue of locomotor muscles in healthy humans. J. Physiol. **571**: 425–439. doi:10.1113/jphysiol.2005.099697. PMID:16373384.

Ross, E.Z., Nowicky, A.V., and McConnell, A.K. 2007. Influence of acute inspiratory loading upon diaphragm motor-evoked potentials in healthy humans. J. Appl. Physiol. **102**: 1883–1890. doi:10.1152/japplphysiol.00694.2006. PMID:17234806.

Sale, D.G. 1988. Neural adaptation to resistance training. Med. Sci. Sports Exerc. **20**(5 Suppl): S135–S145. doi:10.1249/00005768-198810001-00009. PMID:3057313.

Tong, T.K., and Fu, F.H. 2006. Effect of specific inspiratory muscle warm-up on intense intermittent run to exhaustion. Eur. J. Appl. Physiol. **97**: 673–680. doi:10.1007/s00421-006-0233-6. PMID:16770567.

Tong, T.K., Fu, F.H., and Chow, B.C. 2001. Nostril dilatation increases capacity to sustain moderate exercise under nasal breathing condition. J. Sports Med. Phys. Fitness, **41**: 470–478. PMID: 11687766.

Tong, T.K., Fu, F.H., Chow, B.C., Quach, B., and Lu, K. 2003. Increased sensations of intensity of breathlessness impairs maintenance of intense intermittent exercise. Eur. J. Appl. Physiol. **88**: 370–379. doi:10.1007/s00421-002-0724-z. PMID:12527965.

Tong, T.K., Fu, F.H., Quach, B., and Lu, K. 2004. Reduced sensations of intensity of breathlessness enhances maintenance of intense intermittent exercise. Eur. J. Appl. Physiol. **92**: 275–284. doi:10.1007/s00421-004-1094-5. PMID:15083370.

Volianitis, S., McConnell, A.K., Koutedakis, Y., and Jones, D.A. 1999. The influence of prior activity upon inspiratory muscle strength in rowers and non-rowers. Int. J. Sports Med. **20**: 542–547. doi:10.1055/s-1999-9464. PMID:10606219.

Volianitis, S., McConnell, A.K., Koutedakis, Y., McNaughton, L., Backx, K., and Jones, D.A. 2001. Inspiratory muscle training improves rowing performance. Med. Sci. Sports Exerc. **33**: 803–809. PMID:11323552.

Wilson, R.C., and Jones, P.W. 1990. Influence of prior ventilatory experience on the estimation of breathlessness during exercise. Clin. Sci. **78**: 149–153. PMID:2155740.

Witt, J.D., Guenette, J.A., Rupert, J.L., McKenzie, D.C., and Sheel, A.W. 2007. Inspiratory muscle training attenuates the human respiratory muscle metaboreflex. J. Physiol. **584**: 1019–1028. doi:10.1113/jphysiol.2007.140855. PMID:17855758.