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ef-Upload tt.mm.jj | Datum 07.11.2005

G. Ravier[1]
B. Dugué[1,2]
F. Grappe[1]
J.-D. Rouillon[1]

Maximal Accumulated Oxygen Deficit and Blood Responses of Ammonia, Lactate and pH after Anaerobic Test: a Comparison between International and National Elite Karate Athletes

Abstract

The purpose of this study was to compare maximal accumulated oxygen deficit (MAOD) and the time course of blood markers of the anaerobic metabolism in response to exhaustive supramaximal test in two elite (international vs. national) class karate athletes. Ten male international competitors from the French national team (Int, age 21.2 ± 3.1 years, 71.9 ± 11.4 kg) and eight national class (Nat, 23.7 ± 2.4 years, 70.7 ± 12.2 kg) athletes with a similar maximal oxygen uptake of 57.6 and 59.4 ml · kg^{-1} · min^{-1}, respectively, were involved in this study. The MAOD was determined after an exhaustive supramaximal exercise (2 – 3 min at 140% of their $\dot{V}O_{2max}$ velocity) on a treadmill ergometer. Blood lactate, pH and plasma ammonia were determined at rest, immediately at the end of exercise and during the recovery period at 2, 4, 6, 8, 10 and 15 min. After the supramaximal exercise, a dramatic higher increase in the blood concentration of ammonia until its peak was observed in the Nat compared with the Int. Time course of [NH_4^+] and [La] reveals significant ($p < 0.01$) differences between the two groups. Peak values for [H^+] (89.2 ± 6.7 vs. 75.9 ± 8.8 nmol · l^{-1}; $p < 0.01$), [NH_4^+] (180 ± 67.9 vs. 118.7 ± 22.7 µmol · l^{-1}; $p < 0.05$) and [La] (20.7 ± 2.7 vs. 17.9 ± 1.1 mmol · l^{-1}; $p < 0.05$) were higher in Nat compared with Int group, respectively. However, the MAOD was similar in both groups (67.8 ± 8 ml · kg^{-1} and 64.5 ± 6.4 for Int and Nat groups, respectively). These data suggest that ammonia and lactate accumulation are sensitive to the level of performance in karate. Higher concentrations of these metabolites in blood after supramaximal exhaustive exercise may be related to either higher anaerobic contribution to energy supply in Nat or higher removal ability in the Int group.

Key words
Lactate · hydrogen · ammonia · anaerobic metabolism · karate

Introduction

Modern karate consists of many repetitions of bursts techniques (1 – 3 s) separated by hopping movements performed with low intensity (lasting 18 s). Such sequences are interrupted by breaks (9 s) decided by the referee [4]. Although karate fighting has an activity pattern comparable to intermittent exercise, karate fight-energetic stress is likely not stereotyped. The main energy pathway in karate has not really been identified. Previous investigations [1,17] assumed that karate involved an important contribution of anaerobic energy sources. However, it has recently been argued that aerobic metabolism is the main source of energy involved during karate fights [4]. Studies performed in highly trained karate athletes are rather rare and comparison between top athletes in regard to their physical performance are even rarer. This is unfortunate as karate training seems to be a good model for investigation on physical adaptations, and detailed physiological profiles of elite competitors have not been described so far.

Affiliation
[1] Unité de formation et de recherche en sciences et techniques des activités physiques et sportives, Laboratoire des Sciences du Sport, Place Saint-Jacques, Besançon cedex, France
[2] Laboratory of Exercise-Induced Physiological Adapatations (EA 3813), University of Poitiers, Poitiers, France

Correspondence
Gilles Ravier, Ph.D. · Université de Franche Comté · Laboratoire des Sciences du Sport · Place Saint-Jacques · 25030 Besançon · France · Fax: + 33 3 81 66 63 52 · E-mail: gilles.ravier@univ-fcomte.fr

Accepted after revision: September 20, 2005

Bibliography
Int J Sports Med 2005; 26: 1 – 8 © Georg Thieme Verlag KG · Stuttgart · New York · DOI 10.1055/s-2005-872965 · ISSN 0172-4622

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Anaerobic capacity has traditionally been estimated through the maximal accumulated oxygen deficit (MAOD) method [25]. Although now much debated [2,27], this method has been used to estimate the anaerobic energy release during high-intensity exercise [11,30]. Previous investigations demonstrated greater values in sprinters than in long distance runners [11,27] and higher MAOD values have also been observed after high-intensity intermittent training [27,37]. After intense exercise, the determination of blood markers of anaerobic metabolism may provide an insight into such metabolism. An accumulation of lactate [La] and proton [H^+] in plasma are well-known indicators of anaerobic glycolysis in active muscles. In addition, after short intense exercise, an increase in blood ammonia concentration [NH_4^+] indicates deamination of excess AMP derived from the breakdown of ATP and ADP, and suggests that the activation of the myokinase pathway to ATP synthesis in contracting muscles has occurred.

Based on oxygen uptake and blood lactate response, it has been assumed that anaerobic lactic metabolism is slightly involved during simulated karate fights [4]. Karate fight-energetic stress is certainly not stereotyped. In addition, no suitable exercise test specifically designed to evaluate karate energetic demands is available.

The present study was specifically designed to examine the impact of the karate level of practice on the adaptations concerning aerobic and anaerobic metabolisms and to describe the physiological profile of elite competitors. For this purpose, maximal oxygen uptake ($\dot{V}O_{2max}$), MAOD and the responses of blood anaerobic markers ([NH_4^+], [La] and [H^+]) were studied after a non-specific incremental exhaustive supramaximal treadmill test in international and national class karate athletes.

Methods

Subjects

Eighteen male (22.3 ± 3 years) karate practitioners participated in this study. Physiological measurements were made immediately following the competition period. Thus, all athletes participated in the National championship 1 to 3 weeks before our study. Ten (21.2 ± 3.1 years) were members of the French (Junior and Senior) National team (Int group) and 8 (23.7 ± 2.4 years) were of a national standard (Nat group). National athletes practised karate training 3 to 4 times a week. International competitors performed 4 to 5 karate training sessions weekly with, in addition, one aerobic and one strength training session. The characteristics of the subjects are presented in Table **1**. The study was approved by the local ethics committee. Written informed consent was obtained from each subject.

Table **1** Characteristics of international (Int) and national (Nat) level groups. Body fat was estimated from the skinfold measurements. Statistical analysis was performed with Mann-Whitney test. No significant difference was found between the two groups

	Int (n = 10)		*Nat (n = 8)*	
	Mean	*SD*	*Mean*	*SD*
Age (years)	21.2	3.1	23.7	2.4
Height (cm)	178.8	7.8	177.8	9.4
Body mass (kg)	71.9	11.4	70.7	12.2
Body fat (%)	13.7	4.1	13.6	4.5
$\dot{V}O_{2max}$ $(ml \cdot kg^{-1} \cdot min^{-1})$	57.6	3.0	59.4	2.7

Design of the study

All subjects particpated in four treadmill exercise tests which included two submaximal runs, one incremental test and a supramaximal test to exhaustion. The accumulated oxygen deficit measurement required a series of pre-tests involving steady-state submaximal runs to establish the relationship between exercise intensity and submaximal oxygen uptake. According to Medbø et al. [25], the linear relationship between exercise intensity (treadmill speed) and the steady-state $\dot{V}O_2$ can be accurately established by two submaximal intensities close to the maximal oxygen uptake and $\dot{V}O_2$ at rest. This relationship was extrapolated to predict the oxygen cost of the supramaximal run and to determine the speed for the supramaximal run to exhaustion.

Two treadmill runs (10 min at gradient of 10%) and an incremental exercise until exhaustion were performed on the same day. The first treadmill run was performed at 9 $km \cdot h^{-1}$ and after a period of rest (1 h) the subject chose the intensity of the second run between 8.5, 9.5 and 10 $km \cdot h^{-1}$. The $\dot{V}O_2$ ($ml \cdot min^{-1} \cdot kg^{-1}$) was averaged for the last 2 min of each 10 min period of exercise.

After a period of rest (2 – 3 h), an incremental exercise which lasted until exhaustion was performed in order to determine the $\dot{V}O_{2max}$ ($ml \cdot min^{-1} \cdot kg^{-1}$). This session started with a 15 min rest period while the subject was in a seated position. The average $\dot{V}O_2$ measured during the last 2 min of the resting period provided the resting $\dot{V}O_2$ value. The progressive exercise started at 9 $km \cdot h^{-1}$ (at gradient of 2%) and was incremented by 1 $km \cdot h^{-1}$ every 2 min. The average $\dot{V}O_2$ determined during the last minute before exhaustion was defined as the $\dot{V}O_{2max}$. Each exercise was preceded by a 10 min warm-up (3 min at 4 $km \cdot h^{-1}$ and 7 min at 8 $km \cdot h^{-1}$) on the treadmill at a 2% inclination.

Separated by at least 24 h the supramaximal exercise test was performed to determine the MAOD according to the method of Medbø et al. [25]. The MAOD corresponds to the difference between total energy demand (estimated from the oxygen cost of the surpamaximal exercise) and accumulated oxygen uptake. The supramaximal intensity to achieve exhaustion was set at 140% of the $\dot{V}O_{2max}$ velocity [35]. The duration of supramaximal exercise which enables us to calculate MAOD has been established to be 2 – 3 min [25,30]. However, tests which are lasting 1.5 min or longer than 3 min have been shown to be acceptable [12,25].

This session started with a 15 min rest period during which the subject was in the sitting position. Exercise was preceded by a 10-min warm-up (3 min at 4 $km \cdot h^{-1}$ and 7 min at 8 $km \cdot h^{-1}$) on the treadmill at 2% inclination followed by 10 min of recovery [25]. After a sign from one of the investigators the subject

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stepped on to the treadmill (at a gradient of 10%), which was moving at the predetermined velocity (leading to exhaustion after 2 – 3 min). Immediately after the end of exercise the subject recovered in the supine position for 30 min. A rating of perceived exertion (RPE) using a 6 – 20 scale [5] was requested immediately after the exhaustive running test.

Oxygen uptake measurement

All experiments were conducted on a treadmill ergometer (Gymrol 2500, Tecmachine, Andrézieux-Bouthéon, France). The $\dot{V}O_2$ was recorded breath-by-breath with an automatic gas analyser (CPX analyser-Medical Graphics Corporation-MSE, Strasbourg, France). A calibration procedure was completed before each test using certified commercial gas preparations. The $\dot{V}O_2$ and heart rate, which were displayed by an electrocardiogram (Nihon Kohden Cardiolife■*city?, country?*), were measured continuously.

Blood specimen collection and analyses

Blood specimens (2 ml) were collected using a catheter within the cephalic vein or in the superficial radial vein in the far distal third of the forearm when determining the $\dot{V}O_{2max}$ and the MAOD. Specimens were collected before the incremental run (at the end of the 15 min rest period), immediately after the end of exercise and during the active recovery ($8\,km \cdot h^{-1}$) at 2 and 10 min. Specimens were also collected before the supramaximal exhaustive run (at the end of the 15 min rest period), immediately after the end of exercise and during the passive recovery at 2, 4, 6, 8, 10 and 15 min post-exercise. The following analytes were determined: plasma ammonia ($[NH_4^+]$, $\mu mol \cdot l^{-1}$) was analysed with Amon (Dade Behring, ■ *city? country?*) apparatus, lactate ([La], $mmol \cdot l^{-1}$) with La (Dade Behring) apparatus and hydrogen ion from specimens collected into a heparinized syringe ($[H^+]$, $nmol \cdot l^{-1}$; Corning 178 blood gas analyser■ *city? country?*).

The highest recorded values of ammonia, lactate and hydrogen ion determined during the recovery period were defined as the peak concentrations ($[NH_4^+]_{peak}$, $[La]_{peak}$ and $[H^+]_{peak}$ respectively). The difference in the concentration of lactate between $[La]_{peak}$ and [La] measured immediately after the end of the exhaustive test ($[La]_{0\text{-}peak}$) was individually calculated (expressed in $mmol \cdot l^{-1}$, $mmol \cdot l^{-1} \cdot min^{-1}$ and in percentage) and the same applied for hydrogen ($[H^+]_{0\text{-}peak}$) and ammonia ($[NH_4^+]_{0\text{-}peak}$) in order to study the magnitude of the increase in the concentration of those markers in response to the anaerobic test. In the same way, the decrease of these markers was estimated from the differences between peak values and the concentrations obtained 15 min after the end of the exercise for lactate ($[La]_{peak\text{-}15}$), hydrogen ($[H^+]_{peak\text{-}15}$) and ammonia ($[NH_4^+]_{peak\text{-}15}$).

Statistics

Results are expressed as their mean and standard deviation. A Mann-Whitney's test was used to evaluate differences between the two groups. The time course of the blood metabolites concentrations (lactate, hydrogen and ammonia) after the end of the tests was studied with a two-way analyses of variance (time, group) for repeated measurements and Fisher's PLSD when appropriate. The relationships between [La], $[H^+]$, $[NH_4^+]$ and MAOD were analysed with the correlation of Spearman. The level of significance was set at $p < 0.05$.

Table **2** Supramaximal exercise profile. International (Int) and national (Nat) level groups were compared with Mann-Whitney test. No significant difference was found between the two groups

	Int (n = 10)		*Nat (n = 8)*	
	Mean	*SD*	*Mean*	*SD*
Maximal accumulated oxygen deficit ($ml \cdot kg^{-1}$)	67.76	8.00	64.50	6.40
Time to exhaustion (s)	133.5	26.0	116.5	24.7
Relative intensity ($\%\dot{V}O_{2max}$) for the supramaximal test	138.3	6.8	133.6	7.9
Oxygen demand ($ml \cdot kg^{-1} \cdot min^{-1}$) for the supramaximal test	79.5	4.5	79.1	2.2
Slope of regression lines ($ml \cdot kg^{-1} \cdot min^{-1}$)	0.310	0.01	0.316	0.01
RPE	17.3	0.75	16.9	0.64

Results

The volunteers characteristics are presented in Table **1**. No significant differences were detected between our two groups.

Submaximal, incremental and supramaximal tests data

The $\dot{V}O_2$ was measured during the two submaximal tests. The first submaximal run was at 80.9% (± 4.9) and 85.1% (± 3.8) of the subject's own $\dot{V}O_{2max}$ for Int and Nat groups respectively. The second submaximal run was at 89.7% (± 6.3) and 91.1% (± 4.6) of the subject's own $\dot{V}O_{2max}$ for Int and Nat groups respectively. No significant difference was found between the two groups. This result complied with methodological precisions specified by Green [14] concerning the validity of the "oxygen uptake-treadmill speed" regression.

The Int and Nat groups presented similar values for $\dot{V}O_{2max}$ and MAOD. The data concerning the time to exhaustion, the relative and absolute intensity of exhaustive supramaximal exercise and RPE are presented in Table **2**.

Blood variables after incremental test

Data reported below have been achieved in 8 Int and 8 Nat subjects. Blood specimens from 2 subjects were hemolyzed and therefore not analysed.

After the incremental exercise to determine $\dot{V}O_{2max}$ the two groups presented significant differences in the concentration of blood markers for anaerobic metabolism, especially in the concentration in lactate and ammonia which were found to be more elevated in the Nat than in the Int group. A higher concentration in blood lactate was found at 10 min time post-exercise ($11.9 \pm 3.2\,mmol \cdot l^{-1}$ vs. $7.3 \pm 2.2\,mmol \cdot l^{-1}$, $p < 0.01$) and also a higher concentration of ammonia ($104 \pm 23.8\,\mu mol \cdot l^{-1}$ vs. $76.6 \pm 21.1\,\mu mol \cdot l^{-1}$, $p < 0.05$), at the same time point, in the Nat compared with the Int, respectively. The time course of ammonia

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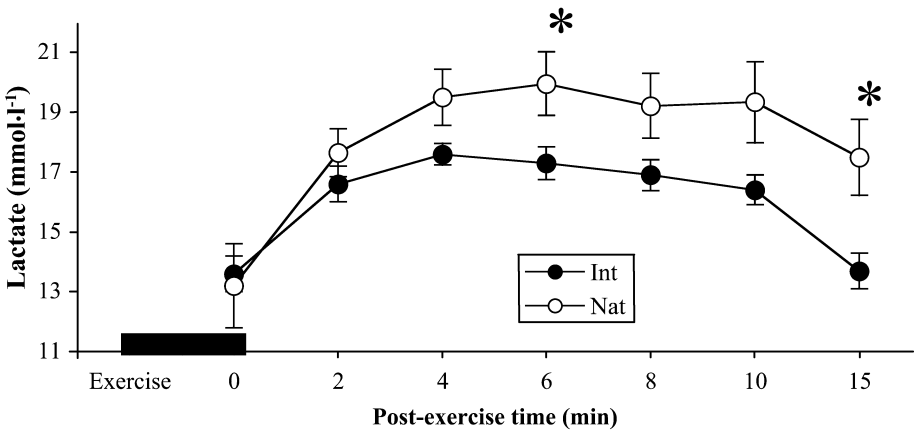

Fig. **1** Time course of plasma lactate after the supramaximal test. Plasma lactate response following the supramaximal test in Int (international level) (filled circles) and Nat (national level) group (open circles). Error bars denote standard error. The significant differences between the groups was specified for each time post-exercise (* $p < 0.05$; ** $p < 0.01$). Fisher's PLSD showed significant differences between end of exercise and 2, 4, 6, 8, 10 and 15 min.

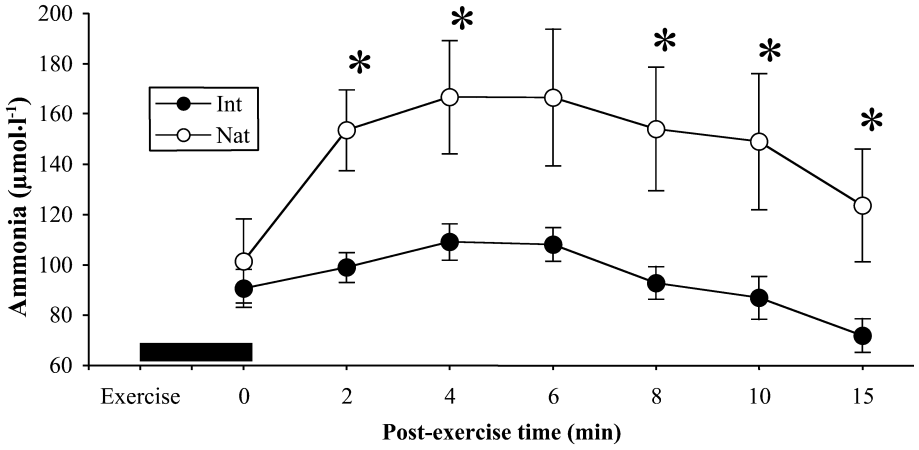

Fig. **2** Time course of plasma ammonia after the supramaximal test. Plasma ammonia response following the supramaximal test in Int (international level) (filled circles) and Nat (national level) group (open circles). Error bars denote standard error. The significant differences between the groups was specified for each time post-exercise (* $p < 0.05$; ** $p < 0.01$). Fisher's PLSD showed significant differences between end of exercise and 2, 4, 6, 8 and 10 min and between 15 min and 2, 4, 6, 8 and 10 min and between 4 min and 8 and 10 min and between 6 min and 8 and 10 min.

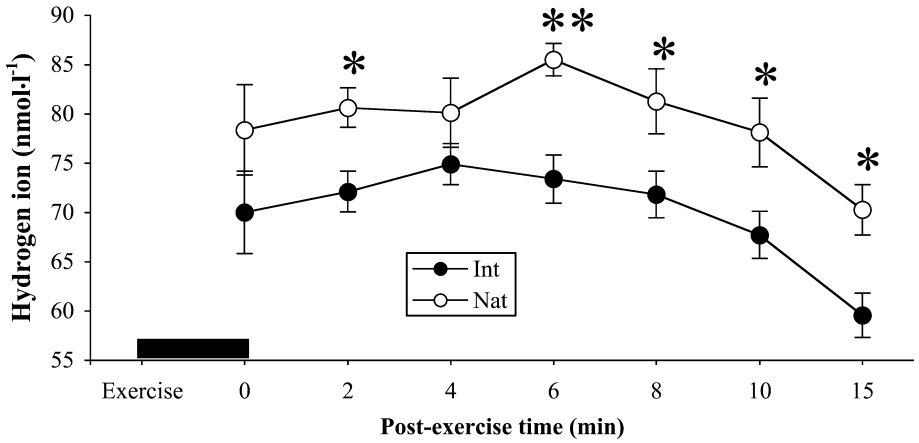

Fig. **3** Time course of hydrogen ion after the supramaximal test. Hydrogen ion response following the supramaximal test in Int (international level) (filled circles) and Nat (national level) group (open circles). Error bars denote standard error. The significant differences between the groups was specified for each time post-exercise (* $p < 0.05$; ** $p < 0.01$).

concentration during the recovery period presented a significant difference between the Int and Nat groups. When comparing peak values, the Nat group presented significantly higher concentration in lactate (16.9 ± 2.1 mmol·l^{-1} vs. 13.2 ± 2.2 mmol·l^{-1}, $p < 0.01$) than the Int group. The concentration of markers in blood at the other tested times were not different in those two groups. No differences were observed concerning [H^+] between the groups at any time.

Blood variables after supramaximal test

Blood specimens from 1 subject (Int group) were not analysed because of hemolyzed blood. The concentration of [La], [NH_4^+] and [H^+] in blood after the end of the exercise was significantly influenced by the international and the national experience of the karate practitioner. The time course of [La], [NH_4^+] and [H^+] in our two groups is presented in Figs. **1 – 3**.

The concentrations of ammonia and hydrogen ion during the entire recovery period were higher in the Nat group compared with the Int group ($p < 0.05$). The same trend in the lactate concentration during the entire recovery period was also observed (Fig. **1**), but the difference did not reach the significance level ($p = 0.069$).

The concentrations of the anaerobic markers measured immediately after the exhaustive supramaximal exercise markedly rose to the peak values in the two groups. Clear-cut differences were observed when comparing the $[La]_{peak}$, $[H^+]_{peak}$, $[NH_4^+]_{peak}$ in the two groups (Table **3**). The blood lactate, ammonia and hydrogen ion recovery curves displayed a transitory plateauing of the con-

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Table **3** Blood variables of exhaustive supramaximal exercise. The significant difference between international (Int) and national (Nat) groups was specified

	Int (n = 9)		*Nat (n = 8)*	
	Mean	*SD*	*Mean*	*SD*
$[La]_{peak}$ ($mmol \cdot l^{-1}$)	17.9	1.1	20.7*	2.7
$[H^+]_{peak}$ ($nmol \cdot l^{-1}$)	75.9	8.8	89.2**	6.7
$[NH_4^+]_{peak}$ ($\mu mol \cdot l^{-1}$)	118.7	22.7	180*	67.9
$[La]_{0\text{-}peak}$ (%)	33.5	15.3	67.8	47.2
$[La]_{0\text{-}peak}$ ($mmol \cdot l^{-1}$)	4.3	1.6	7.5*	3.8
$[H^+]_{0\text{-}peak}$ (%)	9.7	11.2	15.2	10.3
$[H^+]_{0\text{-}peak}$ ($nmol \cdot l^{-1}$)	5.9	6.1	10.8	7
$[NH_4^+]_{0\text{-}peak}$ (%)	33.9	23.1	89.2*	58
$[NH_4^+]_{0\text{-}peak}$ ($\mu mol \cdot l^{-1}$)	28.1	19.8	78.5**	51.9
$[La]_{peak\text{-}15}$ ($mmol \cdot l^{-1}$)	4.2	1	3.2*	1.8
$[H^+]_{peak\text{-}15}$ ($nmol \cdot l^{-1}$)	16.3	4.8	19	8.1
$[NH_4^+]_{peak\text{-}15}$ ($\mu mol \cdot l^{-1}$)	4.3	1.2	5.8	2

* $p < 0.05$; ** $p < 0.01$

centrations between the increasing and decreasing phases of the curves. The delayed peak after exertion was not significantly different between the two groups for ammonia, lactate and hydrogen, respectively (4 ± 2.2 Int vs. 5.5 ± 2.8 min Nat; 5.1 ± 1.8 Int vs. 6.5 ± 2.6 min Nat; 3.3 ± 2 Int vs. 4.2 ± 2.9 min Nat). However, the influence of time on the evolution of both blood lactate and ammonia concentrations significantly differed ($p < 0.01$) between the Int and the Nat groups (Fig. **3**). No significant difference between the two groups was observed concerning the influence of time on the concentration of hydrogen ion. The amount of ammonia ($[NH_4^+]_{0\text{-peak}}$ in $\mu mol \cdot l^{-1}$) and lactate ($[La]_{0\text{-peak}}$ in $mmol \cdot l^{-1}$) accumulated until the peaks were significantly higher in the Nat compared with the Int group (Table **3**) expressed in percentage, the increase in ammonia was 3-times higher in Nat than in Int ($p < 0.05$) (Table **3**). Although the increase in lactate was twice as high in Nat than in Int, the difference did not reach the significant level. The increased rates of ammonia ($[NH_4^+]_{0\text{-peak}} = 18.6 \pm 15.5$ vs. 7.7 ± 6.1 $\mu mol \cdot l^{-1} \cdot min^{-1}$, $p < 0.05$) and hydrogen ion ($[H^+]_{0\text{-peak}} = 2.4 \pm 0.6$ vs. 1.3 ± 1.1 $nmol \cdot l^{-1} \cdot min^{-1}$, $p < 0.05$) were higher in the Nat group compared with the Int group, respectively. The magnitude of the decrease was higher in the Int group compared with the Nat group only for lactate expressed both in $mmol \cdot l^{-1}$ and percentage ($[La]_{peak\text{-}15} = 4.2 \pm 1$ vs. 3.2 ± 1.8 $mmol \cdot l^{-1}$, $p < 0.05$; $[La]_{peak\text{-}15} = 23.6 \pm 6.3$ vs. 16.1 ± 9.6%, $p < 0.05$). No significance difference between the two groups was observed for the amount of disappearance neither in ammonia nor in hydrogen ion.

Correlations between variables of supramaximal test

Significant correlations were observed between [La] and $[NH_4^+]$ ($r = 0.76$, $p < 0.001$), [La] and $[H^+]$ ($r = 0.61$, $p < 0.001$) and $[NH_4^+]$ and $[H^+]$ ($r = 0.48$, $p < 0.001$) after supramaximal test. Also, significant correlations were observed between $[La]_{peak}$ and $[H^+]_{peak}$ ($r = 0.69$, $p < 0.01$), $[La]_{peak}$ and $[NH_4^+]_{peak}$ ($r = 0.72$, $p < 0.001$). The correlation between $[NH_4^+]_{peak}$ and $[H^+]_{peak}$ was not significant ($r = 0{,}47$; $p = 0.055$).

The relationships between MAOD and $[La]_{peak}$, $[H^+]_{peak}$ and $[NH_4^+]_{peak}$ were investigated but no significant correlations were found.

Discussion

The present study aimed to investigate the effects of aerobic and anaerobic tests until exhaustion in national and international class karate athletes on a series of aerobic and anaerobic markers: MAOD, lactate, ammonia and pH (expressed as hydrogen ion concentration). The changes of the concentrations of those markers in blood provides novel insights on the anaerobic components in this sport.

Clear-cut differences were observed when comparing the concentration of those analytes during the recovery period in those two groups. International class athletes presented much less [La], $[H^+]$ and $[NH_4^+]$ in their blood than the national class. Especially striking was the result obtained with $[NH_4^+]$ where the increase in its concentration until the peak (expressed in %) was roughly 3 times higher in Nat than in Int.

Maximal oxygen uptake and maximal accumulated oxygen deficit

The $\dot{V}O_{2max}$ was similar in both groups and close to values previously reported in karate competitors [17]. The results we obtained with the MAOD values were similar in both groups and close to the value reported for middle-distance runners [25], which is much lower than anaerobic trained male athletes and higher than aerobic experts [29,35]. Because the MAOD has been used to estimate the capacity of the anerobic energy releasing systems, it will be advantageous to have a high MAOD in intermittent sports. During high intensity intermittent contraction, anaerobic energy releasing systems occurred at a near-maximal rate and their ability to provid energy may limit the performance in intermittent sports [15,34]. It was assumed that the more demanding the training is the greater the fitness benefit will be. Therefore, results observed with MAOD in both Int and Nat groups suggested that karate training does not involve the anaerobic energy releasing system maximally.

Due to the needs of aerobic and anaerobic demands during karate competition, our athletes usually performed a mixed training combining both demands. The lack of difference in MAOD and $\dot{V}O_{2max}$ between the Int and the Nat groups does not necessarily suggest similar training status of our two groups. The longer supramaximal run time until exhaustion in the Int compared with the Nat group (Int sustained 16 s more than the Nat group), although non-significant, may reflect a greater aerobic energy contribution. Since the fraction of aerobic metabolism has been found to reach 65% of the energy demand during a supramaximal test lasting 2 – 3 min [26], the ability to sustain supramaximal effort seems more related to oxidative capacity than to anaerobic metabolism [23]. In response to 6 weeks of sprint training, Dawson et al. [8] showed a lack of change in blood lactate accumulation after a supramaximal test, despite a greater time to exhaustion (leading after 50 s).

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Potential relationships between MAOD and blood markers after the anaerobic test

A relationship between MAOD and anaerobic blood markers might have been expected since MAOD reflects the anaerobic energy released during high intensity exercise. Moreover, anaerobic glycolysis (leading to lactate production) provided 60 to 77% of the anaerobic energy (estimated from MAOD) during a 2 – 3 min exhaustive exercise [2,25]. However, MAOD and the peak in the blood markers concentrations after the supramaximal test were not correlated neither in the Int nor in the Nat group. It has been suggested that one possible explanation for the discrepancy between MAOD (similar in the two groups) and blood lactate, ammonia and hydrogen concentrations (different between the two groups) could be that metabolites concentrations do not only reflect the amount of metabolites produced in the active muscles, but also several peripheral adaptations. Thus, blood concentrations arise from competitive mechanisms (involved during and after exertion) of muscle production, exchange with the remaining space (in which metabolites are distributed) and removal processes.

Another explanation for the discrepancy between MAOD and the blood metabolites concentrations could be due to an artefact in the MAOD method. However, the "oxygen uptake – running intensity" relationship has been determined in accordance with the recommendations of Medbø et al. [25] and complied with the methodological precisions specified by Green [14]. Nevertheless, it has been shown that besides the running economy, the duration of the supramaximal exercise is an important source of methodological error [25]. Fatigue is a subjective experience that is influenced by motivation and is therefore difficult to assess objectively. However, the perception of exhaustion was similar in both groups.

The absence of differences between the groups in the performances observed in the aerobic and anaerobic tests is puzzling. However, it has been previously reported that a specific anaerobic training may not lead to any improvement in performance variables obtained in a laboratory, whereas this training induced enzymatic adapatations (e.g., increase in citrate synthase activity after 6 weeks of sprint training without changes in performance on a cycle-ergometer [18]). A similar figure might have happened in the present investigation. Furthermore, it has been previously reported that two groups with different track run performances (400 – 800 m) may achieve similar MAOD, with differences in the results concerning blood lactate and hydrogen ion accumulation after an anaerobic test (leading to exhaustion) in a laboratory [30].

Blood lactate and hydrogen ion responses after supramaximal test

The evolution of blood lactate concentration over the recovery period could be analysed in light of the two-compartment model consisting of the previously working muscles and the remaining space.

The Nat and Int groups accumulated higher peak in blood lactate than runners (sprint and middle distance) after similar kinds of exercise [30]. The value we obtained was close to that reported for well trained sprinters, which is much higher than the result obtained with endurance runners [35]. An increase in peak blood lactate concentration after the supramaximal test (lasting 30 s) has been reported to occur in conjunction with an increase in phosphofructokinase and lactate dehydrogenase activities in response to sprint training [18,23]. Blood lactate concentration is a useful index for exercise performance and generally reflects the potential of the anaerobic glycolysis energy providing process [6]. Our results suggest that karate training improved anaerobic metabolism.

Nevertheless, Int accumulated a significantly much lower peak lactate and hydrogen ion in response to supramaximal exercise test compared to Nat. In addition, the magnitude of the increase in blood lactate was higher in Nat than in Int. Such differences suggested a lower contribution of the anaerobic lactic energy releasing system during the supramaximal exercise in the Int than in the Nat. Although karate is ranked as a high intensity intermittent sport, the activity pattern during training could not be stereotyped and likely differed between the Int and Nat groups. This may, in part, explain the higher blood accumulation of lactate and hydrogen in Nat than in Int. Two intermittent sprint trainings involving brief efforts (< 10 s) with 55 s of rest (work recovery ratio = 1 : 11) [23] or a shorter period of rest (work recovery ratio = 1 : 4 – 6) [8] resulted in different glycolytic enzymes adaptation (i.e., phosphofructokinase activity increased in the first case or did not change in the second case).

Higher lactate concentration in blood may be caused by an enhanced ability of the body to exchange lactate between previously working muscles and blood compartment. Because the rate of the increase was similar in both groups, this reason could not be sustained. Lower lactate concentration in blood may also be caused by faster removal. Thus, the larger decrease in blood lactate in Int compared to Nat should stem from higher blood disappearance. It has been shown that endurance training increased the rate of lactate removal by oxidation which is known to be the major pathway of lactate disappearance [24]. The additional aerobic training performed weekly by Int athletes could lead to a reduced lactate accumulation over the recovery period after the supramaximal test. Furthermore, an increase in the activity of a mitochondrial skeletal muscle enzyme (i.e., citrate synthase) has been reported by Jacobs et al. [18] in response to high sprint training. In our study, this feature should stem from different specific karate training performed by Int and Nat groups.

Potential causes of the differences in ammonia accumulation between groups

In the present study, national athletes produced a higher blood ammonia concentration than the international competitors in response to the supramaximal exercise test. The 3-times lower increase in ammonia concentration until the peak and the lower peak blood ammonia observed in Int compared to Nat can be the result of a lower production of ammonia in muscle, a lower release of ammonia from the muscle, a higher removal in the ammonia from the blood, or any combination of the two.

Exercise-induced hyperammoniemia is usually attributed to an increased ammonia formation in contracting muscle either through activation of the purine nucleotide cycle or an increased metabolisation of branched-chain aminoacids (BCAA) [13]. In the

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present study, our exercise test lasted only 2 – 3 min. Therefore, the impact of amino acid metabolism is negligible. It has been suggested that one possible explanation for the higher peak in blood ammonia following the 2 – 3 min supramaximal exercise in Nat compared to Int, could be a greater activation of the myokinase pathway to the energy supply in response to specific karate training. However, it has been shown that 6 weeks of short maximal sprint interval training (10 s or less separated by recovery a period < 30 s) does not increase myokinase activity in muscle [8]. Nevertheless, status training could be involved to explain lower accumulation of blood ammonia in Int compared to Nat after tests. It has been shown that specific sprint training may reduce the activity of adenosine 5′-monophosphate (AMP deaminase) in muscle and therefore lower the accumulation of ammonia in blood [16,33]. Furthermore, AMP desaminase activity has been found to be lower in fast-twitch fiber and a lower ammonia concentration in blood has also been observed in endurance trained muscle [9,13].

Although debated [28,39], the clear-cut difference between the groups for ammonia accumulation could support that Nat utilised glycolysis to a greater extent than Int athletes during anaerobic performance. The occurrence of greater blood lactate and hydrogen ion response in Nat than in Int and the significant correlation between peak values of lactate and ammonia observed are consistent results with this hypothesis [18,28]. During supramaximal treadmill run, the rate of ATP turnover might be elevated, likely to increase products of ATP hydrolysis (i.e., free AMP and IMP) which are known activators of glycogen phosphorylase [15]. During test leading to exhaustion within 2 – 3 min, anaerobic glycolysis lower the pH which stimulates AMP desaminase, increases ammonia production and inhibits both mitochondrial respiration and glycolytic enzymes [36]. Thus, if the rate of ATP hydrolysis exceeds ATP resynthesis, this will lead to an increased muscle ammonia concentration [22].

A third possibility to explain the difference in blood ammonia between the Int and Nat groups concerns the fibre type distribution. The amount of muscle ammonia production has been shown to be related to anaerobic metabolism levels through type II fibres [10,19]. Lower values of ammonia in Int should stem from a lower amount of fast twitch fibre. However, in a previous study devoted to compare muscle mechanical properties in Int and Nat groups, we have shown that international karate experts were characterised with a higher performance in tests involving maximal velocity and explosive strength [31].

The above explanations should be treated with caution because it has also been reported that differences in plasma ammonia accumulation in reponse to sprint exercise may not necessarily stem from a difference in ammonia production in the muscle (e.g., smaller accumulation of plasma ammonia in a female group than in a male group, without difference in muscle inosine monophosphate accumulation between the two groups [10]). A smaller accumulation of ammonia in blood and particularly the 3-times lower increase of ammonia until the peak observed in Int compared with Nat could be due to an enhanced ammonia incorporation into amino acids (alanine and glutamine) leading to a reduced muscle ammonia efflux [13].

Furthermore, lower accumulation in blood ammonia concentration following supramaximal exercise in Int may also result from an increased removal of ammonia from the circulation, particularly in the liver, kidney, resting muscle or by sweat [13]. For example, Walsh et al. [38] found that intermittent high intensity exercise (20 bouts of 1 min exercise at 100% $\dot{V}O_{2max}$ separated by 2 min of active recovery) induced a decrease in plasma glutamine concentration in a recovery period. It could be expected that such intermittent training could enhance the activity of glutamine which is known to have a role of detoxification of ammonia and the maintenance of the acid-base balance during acidosis (i.e., the kidneys take up glutamine as a source of ammonia which can be used to buffer hydrogen ion excretion by formation of the ammonium ion).

Interest of monitoring ammonia in blood

Blood ammonia has been shown, in some contexts, to vary independently of lactate during exercise [21,39] and thereby it was expected to provide novel information about the physiological profile of elite competitors. After supramaximal test, the increase in ammonia concentration until the peak was 3-times higher in Nat than in Int, while non significant results were obtained for the changes in lactate concentration. In the absence of information regarding muscle ammonia production and ammonia removal, the mechanisms inducing a lower accumulation of ammonia in Int than in Nat remain speculative.

The importance of the difference between groups in ammonia accumulation lies in its negative effects on the functioning of the body. Ammonia has been reported as a new marker for exercise tolerance [7,32] and lies with adenine nucleotide degradation and thereby reveals an energetic stress during intense exercise. Lower ammonia accumulation in blood would suggest a higher capacity to perform exhaustive exercise. However, in our study, no significant difference was found between groups concerning such capacities. Regardless of the precise mechanism (lower amount of production, more effective elimination, influence on beta2-adrenergic receptors which are involved in the regulation of blood ammonia and lactate during exercise [6,20], …), this very specific adaptation of the international class athletes to have a rather low concentration of lactate and ammonia after aerobic and supramaximal tests provides them with a very advantageous physiological adaptation to perform in karate competition. Since the quantity of energy produced as a consequence of the deamination process is very small, it should hardly make a significant impact on performance in terms of energy supply. However, during intense exercise, accumulation of ammonia stimulates anaerobic glycolysis (increasing lactate production and acidosis) and decreases aerobic energy pathway. A high concentration of ammonia affects muscle metabolism and then may contribute to local muscle fatigue. In addition, this metabolite alters neuromuscular activity [32], which is an important factor of performance in sports based on bursting actions. Furthermore, ammonia may reach the brain and cause effects on the central nervous system, particularly affecting coordination function [3,7]. Karate competition consists of a series of fights (lasting 3 min, performed with short techniques and displacements performed with maximum intensity interrupted by breaks decided by the referee) separated by 10 to 15 min of rest [4]. Thus, recovery is one of the major factors involved in per-

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formance. Lower blood ammonia concentration in the Int group after exercise is definitely important for recovery, since exercise-induced ammonia accumulation has been associated with the development of fatigue [3].

In conclusion, we have shown that MAOD and maximal oxygen uptake seemed not to be influenced by the level of performance in karate athletes. In contrast, blood concentrations of lactate and ammonia after exhaustive exercises are lower in international than in national class karate athletes. Further studies are required to define the effectiveness of Int training to decrease ammonia accumulation after exhaustive supramaximal exercise.

Acknowledgements

The authors thank Dr. S Cappel for her assistance during the experiments. The authors wish particularly to acknowledge President F. Didier (French Karate Federation) and the French Ministry of Youth and Sports (Comité d'Orientation de la Recherche en Sport) which contributed to support this study.

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