Eur J Appl Physiol (2001) 85: 27–33
DOI 10.1007/s004210100425

ORIGINAL ARTICLE

Alexander Ferrauti · Michael F. Bergeron
Babette M. Pluim · Karl Weber

Physiological responses in tennis and running with similar oxygen uptake

Accepted: 6 March 2001 / Published online: 8 May 2001

Abstract The purpose of the study was to compare selected physiological responses during singles tennis match play and continuous running at a similar mean oxygen uptake ($\dot{V}O_2$). The study consisted of two main parts, which were separated by 1 week. In the first part, 12 nationally ranked senior tennis players [six females and six males; 47.2 (6.6) years old and 47.0 (5.4) years old, respectively] each completed a 2-h singles tennis match (TE). Mean $\dot{V}O_2$ during TE [23.1 (3.1) ml·kg^{-1} · min^{-1} for the women and 25.6 (2.8) ml·kg^{-1}·min^{-1} for the men] was measured by a portable spirometry-telemetry system and corresponded to 56% (women) or 54% (men) of their respective maximum $\dot{V}O_2$. In the second part, the relative $\dot{V}O_2$ data measured during TE were used to set a similar workload during a 2-h treadmill run at a constant level (RU). At the measured time points, heart rate [140.1 (15.5) beats·min^{-1} vs 126.4 (15.1) beats·min^{-1}], lactate concentration [1.53 (0.65) mmol·l^{-1} vs 1.01 (0.38) mmol·l^{-1}] and glucose concentration [5.45 (0.84) mmol·l^{-1} vs 4.34 (0.56) mmol·l^{-1}] in capillary blood, as well as the respiratory exchange ratio [0.93 (0.03) vs 0.88 (0.03)], were higher ($P < 0.05$) in TE compared to RU. Serum concentrations of free fatty acids increased ($P < 0.05$) during both work loads [from 0.25 (0.15) mmol·l^{-1} to 1.31 (0.44) mmol·l^{-1} in TE and from 0.22 (0.17) mmol·l^{-1} to 1.24 (0.35) mmol·l^{-1} in RU]. Post-exercise urine concentrations of epinephrine [0.17 (0.14) μmol·l^{-1} vs 0.08 (0.04) μmol·l^{-1}] and norepinephrine [1.27 (0.59) μmol·l^{-1} vs. 0.55 (0.33) μmol·l^{-1}] were higher in TE ($P < 0.05$). These results indicate a stronger metabolic emphasis on glycolysis and glycogenolysis and an overall enhanced sympathoadrenal activity during tennis match play compared to continuous running exercise at a similar mean $\dot{V}O_2$.

Keywords Portable spirometry · Intermittent exercise · Catecholamines · Carbohydrate · Fat metabolism

A. Ferrauti (✉) · K. Weber
German Sport University Cologne,
Institute of Sports Games, Carl-Diem-Weg 6,
50933 Cologne, Germany
E-mail: ferrauti@hrz.dshs-koeln.de
Tel.: +49-221-4982432
Fax: +49-221-4995637

M.F. Bergeron
Georgia Prevention Institute, Medical College of Georgia,
HS-1640, Augusta, GA 30912-3710, USA

B.M. Pluim
Royal Netherlands Lawn Tennis Association,
Displayweg 4, 3821 BT Amersfoort, The Netherlands

Introduction

The intermittent exercise profile in tennis consists of short, intense exercise bouts with a typical mean duration of 3–8 s, followed by longer resting periods of about 20–25 s. The nature of this type of workload may lead to different physiological responses (Bergeron et al. 1991) in comparison to continuous exercises such as running or cycling. From a preventive, health-risk profile perspective and a performance-oriented point of view, it would be beneficial to know the specific responses regarding substrate utilization (i.e., carbohydrate and fat metabolism) during such exercise.

Early studies have compared the energy metabolism during intermittent and continuous exercise (Åstrand et al. 1960; Essén 1978). For example, Essén showed that with respect to carbohydrate and fat utilization, no considerable differences exist between 60 min of intermittent intensive (15 s at 300 W with 15-s rest periods) and continuous moderate exercise (157 W). It has also been suggested that glycolysis is delayed at the beginning of each intermittent exercise bout, due to the enhanced acetyl-coenzyme A production from free fatty acid (FFA) oxidation during the rest periods (Essén 1978). Because many previous studies were performed using cycle ergometry, it is not entirely valid to extrapolate such findings to multiple sprint sports such as tennis or soccer. In addition, certain physiological effects related to higher mental stress in sports such as tennis

(prompted by factors such as the scoring system and stronger cognitive, technical and tactical demands) should be taken into account (Baron et al. 1992; Weber et al. 1996). For example, Richter et al. (1982) reported a close correlation between psychological strain and catecholamine release, with a subsequent acceleration of glycogenolysis and lipolysis.

In tennis, considerable lipolytic activity was demonstrated to occur during match play at a regional and national level, and a significant contribution of fat oxidation to meet the energy demand was suggested (Weber et al. 1994; Ferrauti et al. 1997). This perspective is supported by work showing a strong correlation between lipolysis, plasma fatty acid uptake and the rate of fat oxidation under steady-state conditions (Horowitz and Klein 2000). However, Mora-Rodriguez and Coyle (2000) demonstrated that an exogenously induced (intravenous infusion) elevation in plasma epinephrine concentration during low-level exercise (25% peak oxygen uptake, $\dot{V}O_{2peak}$) increases whole-body lipolysis, and the rate of FFA release into the plasma, yet decreases fatty acid oxidation to below control levels. Moreover, a higher intensity (45% $\dot{V}O_{2peak}$) exercise-induced increase in plasma epinephrine corresponded to a lower level of lipolysis than was induced by an equivalent infusion of epinephrine. Mora-Rodriguez and Coyle (2000) suggested that lipolysis (to the degree expected by the circulating level of epinephrine) is suppressed by increases in exercise intensity. Notably, fatty acid oxidation was still greater with the elevated intensity of exercise.

Therefore, it may be stated that a valid assessment of physiologic responses during tennis match play is only possible during real field test conditions while taking appropriate respiratory, metabolic and endocrine measurements into account. Moreover,a subsequent comparison of these data to those from continuous exercise requires that the total amount of work of both activities is similar. To this purpose, we utilized a portable spirometry-telemetry-system (Schulz et al. 1997) to specify the calorific cost and compare the respective substrate and respiratory changes that occur during tennis to those responses observed during a constant run with the same mean oxygen uptake ($\dot{V}O_2$) and exercise duration.

Methods

Subjects

Twelve nationally ranked senior tennis players (six females and six males) participated in the study. The mean (SD) age, height, and body mass of the subjects were 47.2 (6.6) years, 172 (3) cm, and 61.8 (4.5) kg, respectively for the females, and 47.0 (5.4) years, 182 (6) cm, and 79.0 (9.6) kg, respectively for the males. Maximum oxygen uptake ($\dot{V}O_{2max}$; 41.1 (6.0) $ml \cdot kg^{-1} \cdot min^{-1}$ for the women and 47.5 (4.3) $ml \cdot kg^{-1} \cdot min^{-1}$ for the men) was determined 2–6 weeks before beginning the main parts of the study by graded cycle ergometry until exhaustion. The subjects were not specifically trained in distance running, were non-smokers, and were not taking any medication during the experimental period.

Procedure

The study consisted of two main parts. In the first of these parts, on two occasions separated by 1 week, each subject played the same opponent during a 2-h singles tennis match on a clay court [23.5 (5.2)°C outside air temperature and 52.0 (7.0)% relative humidity]. Opponents were matched for ability and gender. Match play was conducted according to the rules of the International Tennis Federation (2000). A 10-min warm-up period was prescribed as the initial part of the 2-h workload. During match play, only one player (from eachmatched pair) wore a portable spirometry-telemetry system. This task was alternated between the two players for each of the two different occasions. For each player (from data collected while wearing the spirometry system), mean $\dot{V}O_2$ during the 2-h tennis workload ($\dot{V}O_{2ten}$), including the warm-up period,the rallies and all rest periods between the rallies and during court changeovers was calculated. These data were used as individual-specific workload determinants for the second part of the study.

In the second part of the study, separated by another week, each subject performed a 2-h treadmill run (Woodway-Geres, Lörrach, Germany) at a constant level of intensity, corresponding to their respective $\dot{V}O_{2ten}$. These tests were performed in a laboratory with an ambient temperature of 22.2 (1.9)°C and a relative humidity of 47.0 (4.0)%. Gas exchange during running was measured using the same portable spirometry system. Online control of $\dot{V}O_2$ and correction by running speed was ensured. The test began with a walking speed of 1.5 $m \cdot s^{-1}$, after which the treadmill speed was gradually increased (0.1 $m \cdot s^{-1} \cdot min^{-1}$). After 5:45 (1:45) min:s, $\dot{V}O_{2ten}$ was achieved for each individual and the treadmill speed was maintained. Thereafter, the $\dot{V}O_2$ during running ($\dot{V}O_{2run}$) was corrected by fine-tuning the treadmill speed at 5-min intervals. Overall, a decrease of about 0.1–0.2 $m \cdot s^{-1}$ was necessary to keep $\dot{V}O_{2run}$ at a steady state, resulting in a final running speed of 1.91 (0.21) $m \cdot s^{-1}$ in women and 2.02 (0.17) $m \cdot s^{-1}$ in men.

The subjects were asked to refrain from exercise for the 24 h immediately preceding each trial (tennis and running). On the test days, all subjects received a similar standardized carbohydrate-rich breakfast (7 a.m.) or lunch (1 p.m.). Each meal provided 2,300 kJ (550 kcal) of energy and 86 g of carbohydrate. The time of day for each exercise trial was kept consistent for each subject (either from 9 a.m. to 11 a.m. or from 3 p.m. to 5 p.m., depending on individual availability). During the exercise periods, water intake provided ad libitum, but no further intake of food was allowed.

Measurements and analyses

Blood samples were taken at rest and after 30, 60, 90 and 120 min during the exercise sessions (tennis and treadmill). Capillary blood was collected for glucose (Cobas-Bio-System, Hoffmann-La Roche, Basel, Switzerland) and lactate measurements (Eppendorf-Analyser 5060, Hamburg, Germany). Venous blood samples from an antecubital vein of the non-dominant arm were analyzed for FFA, glycerol (Cobas-Bio-System), insulin (Enzyme-Immunoassay ES300, Boehringer, Mannheim, Germany), and hematocrit (Sysmex Dualdilutor DD100, Digitana, Germany). Heart rate was monitored at 15-s intervals (Polar Sport-Tester, Kempele, Finland). The measurements performed during tennis and running were identical. Analysis during tennis, except for heart rate, only concerned the player whose $\dot{V}O_2$ was determined on that occasion.

Urine samples were taken pre- and post-exercise. Concentrations of urinary epinephrine and norepinephrine were determined by means of high-performance liquid chromatography (HPLC) with electrochemical detection (Chromsystems, München, Germany) after acquisition by an ion-exchange technique (Hjemdahl et al. 1989). The post-exercise urine sample represented urinary catecholamine accumulation during the experimental period. Aliquots of 50 ml urine (with 1 ml of 25% HCl added) were stored at –70°C before analysis.

The portable spirometry-telemetry system X1 (CORTEX, Leipzig, Germany) was used for respiratory measurements and was carried by the subjects in a backpack. The validity of this system

has been determined previously against a common breath-by-breath system (OXICONgamma, Mijnhardt, Bunnik, The Netherlands) during graded cycle ergometry (Schulz et al. 1997). The weight of the mobile device, including mask and backpack, was 4.5 kg. The system utilizes a mixing chamber for gas analysis, and the telemetric transfer of data took place every 10 s. In this study, the data regarding $\dot{V}O_2$ (measurement principle: zirconium, responsiveness <3 s) and carbon dioxide release ($\dot{V}CO_2$, measurement principle: infrared, responsiveness <5 s) were considered. Gas calibration was carried out at the beginning of each experimental day using a calibration gas mixture (nominal values: 16.0% oxygen, 5.0% carbon dioxide); every single measurement was preceded by a room air calibration.

Respiratory data and heart rate were calculated as mean values for a 5-min resting period prior to exercise and for the subsequent 30-min intervals during exercise. The post-exercise recovery period was not taken into consideration for analysis. Energy expenditure (for both tennis and running) and substrate utilization (only for the steady-state running part of the study) were estimated by means of indirect calorimetry, based on the results of the $\dot{V}O_2$ measurements and the respiratory exchange ratio (R; McArdle et al. 1996).

Validity of $\dot{V}O_2$ measurements

In this study, calculations of $\dot{V}O_{2ten}$ and the deductions for $\dot{V}O_{2run}$ were based on non-steady-state conditions. Thus, a systematic error cannot be completely excluded by the validation of Schulz et al. (1997). The validity of $\dot{V}O_{2ten}$ becomes quite dependent upon a correct alignment of the gas concentration measurements with the flow measurements under intermittent exercise conditions (Lamarra and Whipp 1995). According to the specifications of the manufacturer (CORTEX), the delay time between both signals is corrected mathematically by a time constant.

Our central assumption was that the metabolic loads of the tennis and running part of the study were essentially identical. In order to verify this assumption and to exclude systematic errors, six male subjects completed two different protocols (continuous vs intermittent) performing the same amount of work on a motor-driven treadmill (A: 12 min standing at rest, 6 min running, 2 min recovery; B: 36×10 s work, each interrupted by 20 s standing at rest, 2 min recovery). Mean $\dot{V}O_2$ during both 20-min time periods was 1,691 (338) ml·min^{-1} for A and 1,788 (298) ml·min^{-1} for B. These data may suggest a slight inaccuracy of the gas exchange measurements obtained during our main study (overestimation of $\dot{V}O_{2ten}$). On the other hand, the difference in $\dot{V}O_2$ may also be the result of an additional energy demand for the repeated starting and stopping processes required in protocol B. If the first assumption is correct, the metabolic load during the running part of our main study may have been overadjusted by about 5%.

Validity of tennis match play

One should take into account that the added weight of the spirometric device and the concomitant limit in the player's range of motion led to a prominent decline in the respective match results. Match statistics clearly demonstrated that the player with the spirometric device consistently won fewer points. Heart rate, withor without the measuring device, however, was similar and corresponded to previous reports for tennis match play (Morgans et al. 1987; Therminarias et al. 1991). Thus, we assume that the cardiocirculatoryand metabolic demands were influenced only minimally by the experimental design and that the calculation of the energy turnover is sufficiently valid.

Statistics

Data are presented as means (SD). A two-factorial analysis of variance (ANOVA) with repeated measurements was used to determine statistical differences between measurements (time periods) and types of exercise. In case of significance, simple effects were verified by means of the Newman-Keuls post-hoc test. Additional analysis was performed using Student's t-test for independent samples (men's versus women's tennis). The level of statistical significance was set at $P<0.05$.

Results

The average $\dot{V}O_2$ of the 30-min intervals during tennis match play ($\dot{V}O_{2ten}$) remained constant throughout the entire 120-min exercise period, and was maintained at a similar level during the treadmill running part of the study [$\dot{V}O_{2run}$); 1,642 (304) ml·min^{-1} vs 1,687 (414) ml·min^{-1}]. In spite of the similar average $\dot{V}O_2$, heart rate and blood lactate (ANOVA main factor: exercise type) were significantly higher in tennis compared to running (Fig. 1).

The relative mean $\dot{V}O_2$ during the entire period of tennis match play, which was similar between women and men (Table 1), corresponded to the $\dot{V}O_2$ at a running speed of 1.91 (0.21) m·s^{-1} in women (56% of $\dot{V}O_{2max}$) and 2.02 (0.17) m·s^{-1} in men (54% of $\dot{V}O_{2max}$). The estimated energy demand during tennis match play was similar in women 0.48 (0.06) kJ·kg·min^{-1} and men

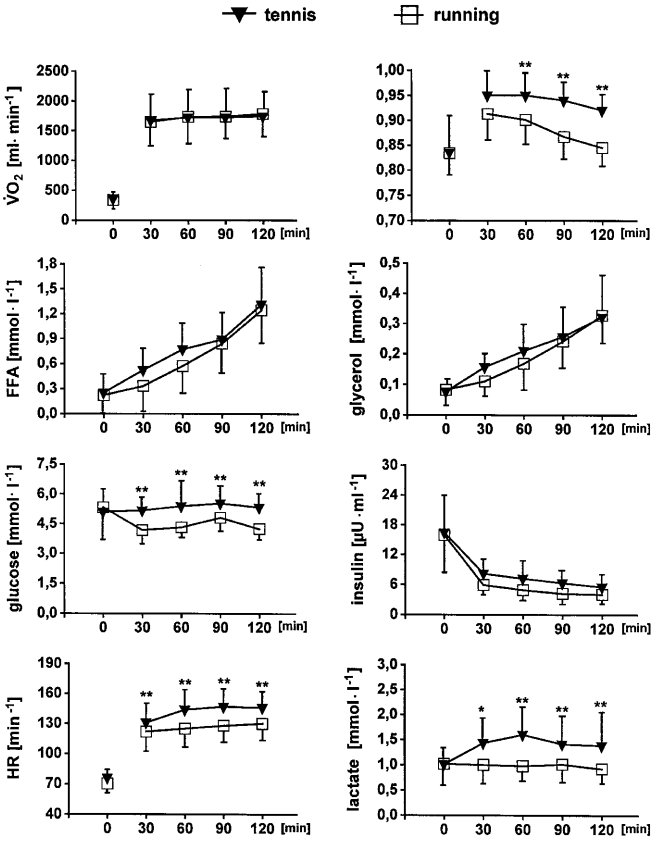

Fig. 1A–H Cardiocirculatory and metabolic parameters during tennis singles match play (*filled triangles*) compared to a run (*open squares*) with similar and constant oxygen uptake ($n=12$). ($\dot{V}O_2$ Oxygen uptake, R respiratory exchange ratio, *FFA* free fatty acids, *HR* heart rate). $^*P<0.05$, $^{**}P<0.01$; analysis of variance (ANOVA) of simple effects between running and tennis

0.53 (0.06) kJ·kg·min^{-1} (Table 1). During the 2-h match, the men metabolized an average of 5,000 kJ and women an average of 3,500 kJ.

The overall average *R* was significantly higher in tennis compared to running [0.93 (0.03) vs 0.88 (0.03), $P < 0.01$]. No significant differences in *R* were found between men and women (Table 1). After an initial increase from a resting value, the *R* decreased significantly in the course of both exercises. The rate and amount of decline was more pronounced during running [from 0.91 (0.04) to 0.85 (0.03)] than during tennis [from 0.94 (0.04) to 0.91 (0.03); Fig. 1]. Accordingly, estimated relative fat oxidation was significantly higher in running during the complete exercise period – it increased from 30 (12)% in the first 30 min of exercise to 52 (13)% during the last 30 min of exercise. For tennis, no calculations for substrate oxidation based on *R* values were performed.

Glucose in capillary blood remained at a constantly higher level in tennis, even showing a slight increase until 90 min of match play [from 4.95 (0.80) mmol·l^{-1} at the start to 5.45 (0.84) mmol·l^{-1}]. After 30 min of running [4.34 (0.56) mmol·l^{-1} vs 5.05 (0.48) mmol·l^{-1}], and at all subsequent measurement points until the end of the work load [4.12 (0.43) mmol·l^{-1} vs 5.29 (0.63) mmol·l^{-1}], blood glucose concentration was significantly lower in running compared to tennis (Fig. 1).

No differences in serum FFA, glycerol and insulin levels were found between tennis and running. FFA and glycerol significantly increased and insulin significantly decreased in the course of both types of exercise. The initial increases in serum FFA and glycerol appeared to be slightly greater in tennis than in running ($P > 0.05$) and showed an almost linear relationship to exercise duration. The drop in insulin levels occurred primarily during the first 30 min of exercise (Fig. 1). Hematocrit increased in running from 44.3 (4.9)% to 46.1 (4.8)%, yet remained constant during tennis. The correction of serum components for exercise-related changes in plasma volume (running: –7.1%; tennis: –1.2%) was of no statistical consequence (Van Beaumont 1972).

Post-exercise urine epinephrine and norepinephrine concentration increases were significantly greater as a result of tennis match play compared to running (Fig. 2). Since the creatinine concentrations were significantly higher at the end of tennis compared to running, both in urine [17.6 (8.3) mmol·l^{-1} vs 10.2 (6.2) mmol·l^{-1}] and in serum [0.10 (0.01) mmol·l^{-1} vs 0.07 (0.01) mmol·l^{-1}], a relationship between catecholamine and urinary creatinine levels was not calculated.

The overall average heart rate [140.1 (15.5) beats·min^{-1} vs 126.4 (15.1) beats·min^{-1}] and the mean individual maximum heart rate [177.4 (8.5) beats·min^{-1} vs 138.1 (12.5) beats·min^{-1}] were significantly higher in tennis compared to running ($P < 0.01$). No heart rate differences were found between men and women, during either tennis or running (Table 1).

$\dot{V}O_2$ and *R* varied during tennis according to different game situations. $\dot{V}O_2$ increased during warm-up [1,474 (296) ml·min^{-1}] compared to the resting level [341 (55) ml·min^{-1}] and went up significantly more ($P < 0.01$) during match play [1,719 (330) ml·min^{-1} in service games and 1,674 (291) ml·min^{-1} in return games] compared to the warm-up period. During the changeovers (as indicated by "rest"), the average $\dot{V}O_2$ dropped clearly

Table 1 Cardiocirculatory and metabolic parameters during tennis singles match play in male and female senior players. Data are given as the mean (SD). (*R* Respiratory exchange ratio, $\dot{V}O_2$ oxygen uptake, $\dot{V}CO_2$ carbon dioxide release)

Parameter	Women ($n = 6$)	Men ($n = 6$)	*P* values
Heart rate (beats·min^{-1})	141.5 (18.9)	142.5 (12.7)	0.913
Lactate concentration (mmol·l^{-1})	1.24 (0.37)	1.67 (0.49)	0.119
$\dot{V}O_2$ (ml·min^{-1})	1,423 (165)	2,011 (272)	0.002*
$\dot{V}O_2$ (ml·kg·min^{-1})	23.1 (3.1)	25.6 (2.8)	0.220
R ($\dot{V}O_2/\dot{V}CO_2$)	0.926 (0.023)	0.946 (0.028)	0.247
Energy cost (gross; kJ·min^{-1})	29.4 (3.4)	41.8 (5.8)	0.002*
Energy cost (gross; kJ·kg·min^{-1})	0.48 (0.06)	0.53 (0.06)	0.208

*$P < 0.01$; *t*-test for independent samples

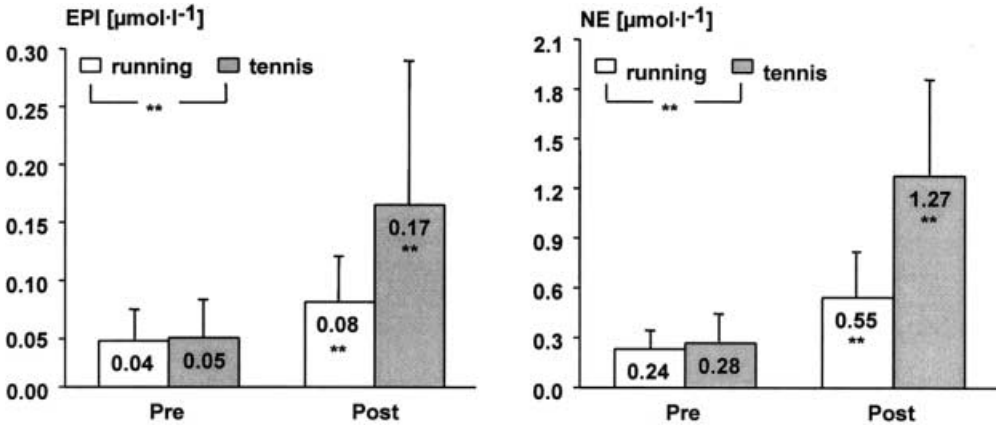

Fig. 2 Concentrations of epinephrine (*EPI*, **A**) and norepinephrine (*NE*, **B**) in pre- and post-exercise urine samples (*Pre* and *Post*, respectively) of subjects completing a 2-h singles tennis game (*filled bars*) or a 2-h run (*clear bars*) with similar and constant $\dot{V}O_2$ ($n = 12$). **$P < 0.01$; ANOVA main and simple effects

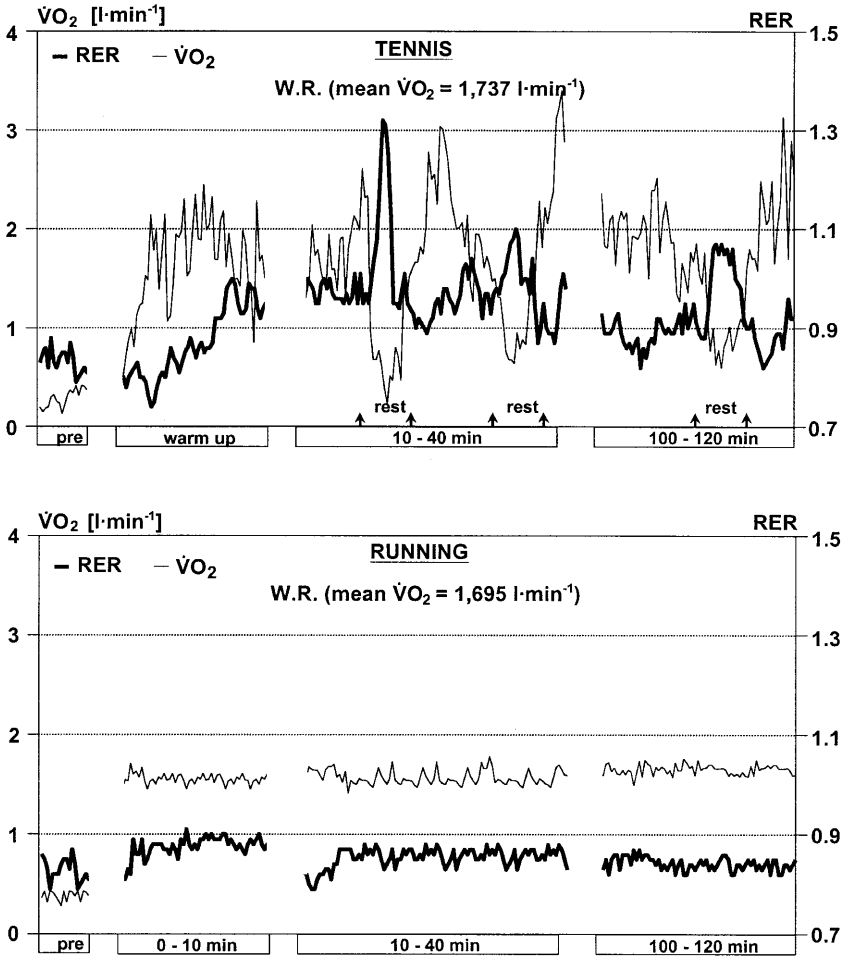

Fig. 3 $\dot{V}O_2$ (*thin lines*) and *R* values (*thick lines*) of subject W.R. during selected parts of a 2-h singles tennis match play (including the pre-exercise period, warm-up, playing and changeovers – rest; **A**) compared to during a run (**B**) with similar and constant $\dot{V}O_2$ values

compared to the playing phases [1,287 (351) ml·min^{-1}]. In contrast, the *R* reached significantly higher values [0.98 (0.05); $P < 0.01$] during the changeovers (which consisted primarily of sitting on chairs at midcourt), compared to during match play [0.93 (0.03)] and, incidentally increased to more than 1.3 (Fig. 3).

Discussion

The results of this study provide a novel insight regarding substrate changes and utilization as well as other metabolic aspects in tennis match play under "real" field conditions. This comparison of tennis, an intermittent and total body activity, to distance running, a continuous and predominantly lower extremity sport, leads to many points of discussion.

Of primary interest are the much higher post-exercise urinary epinephrine and norepinephrine concentrations observed after tennis match play (Fig. 2). Urinary catecholamine excretion provides insight into the concomitant catecholamine concentration in the tissues and blood during the collection period (Von Euler 1974). Our findings therefore suggest that the release of epinephrine can be higher during tennis match play compared to running at a similar overall $\dot{V}O_2$ level, which can possibly be traced back to different psychological and/or physiological demands. In addition, the intermittent and irregular nature of tennis match play periodically leads to considerable variation and high intensities, as indicated by $\dot{V}O_2$ (Fig. 3). Because plasma epinephrine rises linearly with increasing exercise intensity above 30–40% of $\dot{V}O_{2max}$ (Lehmann et al. 1981), we suspect that there were ongoing repetitive increases in catecholamine release, which accumulated during the collection period in the urine and led to the significantly elevated post-exercise concentrations. As a result of such enhanced sympathetic activity in tennis, an effect on numerous cardiocirculatory and metabolic factors can be expected.

The higher mean heart rate (about 15–20 beats·min^{-1}) and the greater concentrations of glucose and lactate in the capillary blood (Fig. 1), elucidate the metabolic influences of the enhanced sympathoadrenal activity during tennis. Catecholamines have a stimulating influence on glycogenolysis, induced by a β-adrenergicintracellular activation of the protein kinase and an α-adrenergic inhibition of insulin secretion (Richter et al. 1982; Weicker and Strobel 1994). Thus, the increases in epinephrine and blood glucose concentrations are strongly correlated.

The higher lactate concentration in tennis confirms that there are periodic increases in exercise intensity, resulting in more rapid glycolytic activity at times compared to running (Fig. 1). Several points with rallies of high intensity and long duration are likely to have caused a prompt increase in lactic acid production (Bergeron et al. 1991). This may have intermittently elevated blood lactate levels slightly, because the distribution and elimination of lactate occur with a time delay (Woll and Record 1979). In addition, an augmented recruitment of the glycolytic fast-twitch IIb fibers, as well as the β-adrenergic activation of protein kinases in the phosphofructokinase complex, play a role with respect to the enhanced glycolytic rate (Richter et al. 1982) in activities such as tennis.

After only 30 min of match play we recorded a sharp increase in serum FFA and glycerol, which progressed almost linearly (Fig. 1). In general, 20–30 min of exercise elapse before a significant rise of plasma FFA occurs (Pruett 1970). At higher exercise intensities, however, this rise is accelerated (Osness et al. 1971). In principal, epinephrine accomplishes its lipolytic action via β_2-adrenoceptors on the fat cells. With acute intense workloads, the sensitivity of these receptors increases (Weicker and Strobel 1994). Thus, the periodic moments of high-intensity activity at the beginning of match play might have prompted a more rapid initiation of lipolysis during tennis, compared to the responses to the more progressive and linear increase in workload during the running test. However, the apparently greater increase in circulating epinephrine during tennis (Fig. 2) did not yield significant differences in lipolysis or in the rate of FFA appearance between tennis and running (Fig. 1).

The decrease in R values suggests that the contribution of fat oxidation increased during both exercises. Accordingly, with a reduction in glycogen stores, a drop in the R value is to be expected (Heigenhauser et al. 1983). However, based on the observed R values, it appears that comparatively less fat was utilized for energy during the tennis. It is possible that the high availability of serum FFA (Fig. 1) is not totally coupled to a respective and proportional oxidation of fat in the muscle cells (Mora-Rodriguez and Coyle 2000). It may be that tennis players are periodically subjected to a catecholamine-related "stress-lipolysis" (Klein et al. 1994) in match play. This was in contrast to running, in which the degree of lipolysis seemed to be closer adjusted to the actual utilization of fats (Fig. 1). Our results are in accordance with other recent findings suggesting that anaerobic carbohydrate metabolism is more prevalent during high-intensity intermittent treadmill running as compared to continuous exercise with similar energy expenditure, despite a comparable increase in plasma FFA concentration (Christmass et al. 1999).

In addition to metabolic reasons, methodological factors (Cerretelli and Di Prampero 1987) may have contributed in part to the observed differences in R. It is difficult to interpret the R of interval exercise because of the distinct kinetics of $\dot{V}O_2$ and $\dot{V}CO_2$, the hyperventilation at the beginning of the breaks, as well as the expulsion of "non-metabolic" carbon dioxide out of the bicarbonate-buffer in the case of metabolic acidosis. At values above 70% of $\dot{V}O_{2max}$, $\dot{V}CO_2$ increases exponentially (Cerretelli and Di Prampero 1987). Notably, the ventilatory $\dot{V}CO_2$ may exceed the metabolic $\dot{V}CO_2$ during the breaks, and R could rise temporarily (Anderson 1960). During tennis match play, this effect can clearly be shown at the changeovers (Fig. 3). As a result, it is inappropriate to establish a chronological accordance between the measured R and the actual metabolic state. Thus, definitive statements regarding the substrate utilization (e.g., during changeovers) may not be possible since blood-gas-dependent R corrections were not calculated.

Conclusions

This study shows a significant participation of both carbohydrate and fat metabolism during singles tennis performed at the levels examined here. However, the apparently stronger sympathetic, glycolytic and glycogenolytic activity that occurred during tennis match play compared to continuous running is of practical interest. From a performance-oriented point of view, these aspects illuminate the importance of a sufficient carbohydrate supply in tournament tennis and the necessity of intermittent training drills for an adequate improvement of the tennis-specific metabolic pathways. From a health-oriented point of view, tennis is seemingly disadvantageous compared to continuous endurance exercises in some respects, due to the comparatively smaller amount of fat oxidation and potentially higher cardiac demands.

References

Anderson KL (1960) Respiration recovery from muscular exercise of short duration. Acta Physiol Scand Suppl 168:1–102

Åstrand I, Åstrand PO, Christensen EH, Hedman R (1960) Intermittent muscular work. Acta Physiol Scand 48:448–453

Baron R, Petschnig R, Bachl N, Raberger G, Smekal G, Kastner P (1992) Catecholamine excretion and heart rate as factors of psychophysical stress in table tennis. Int J Sports Med 13:501–505

Bergeron MF, Maresh CM, Kraemer WJ, Abraham A, Conroy B, Gabaree C (1991) Tennis: a physiological profile during match play. Int J Sports Med 12:474–479

Cerretelli P, Di Prampero PE (1987) Gas exchange in exercise. In: Farhi LE, Tenney SM (eds) Handbook of physiology. Section 3: The respiratory system. vol. IV, gas exchange. American Physiological Society, Bethesda, pp 297–339

Christmass MA, Dawson B, Passeretto P, Arthur PG (1999) A comparison of skeletal muscle oxygenation and fuel use in sustained continuous and intermittent exercise. Eur J Appl Physiol 80:423–435

Essén B (1978) Studies on the regulation of metabolism in human skeletal muscle using intermittent exercise as an experimental model. Acta Physiol Scand Suppl 454:1–32

Ferrauti A, Weber K, Strüder HK (1997) Effects of tennis training on lipid metabolism and lipoproteins in recreational players. Brit J Sports Med 31:322–327

Heigenhauser GJF, Sutton JR, Jones NL (1983) Effect of glycogen depletion on the ventilatory response to exercise. J Appl Physiol 54:470–474

Hjemdahl P, Larsson PT, Bradley T, Akerstedt T, Anderzen I, Sigurdsson K, Gillberg M, Lundberg U (1989) Catecholamine measurements in urine by high-performance liquid chromatography with amperometric detection – comparison with an autolyser fluorescence method. J Chromatogr 494:53–66

Horowitz JF, Klein S (2000) Lipid metabolism during endurance exercise. Am J Clin Nutr Suppl 72:558–563

International Tennis Federation (2000) Rules of tennis. International Tennis Federation, London

Klein S, Coyle EF, Wolfe RR (1994) Fat metabolism during low-intensity exercise in endurance-trained and untrained men. Am J Physiol 267:E934–E940

Lamarra N, Whipp B (1995) Measurement of pulmonary gas exchange. In: Maud PJ, Foster C (eds) Physiological assessment of human fitness. Human Kinetics, Champaign, pp 19–35

Lehmann M, Keul J, Huber G, Da Prada M (1981) Plasma catecholamines in trained and untrained volunteers during graduated exercise. Int J Sports Med 2:143–147

McArdle WD, Katch FI, Katch VL (1996) Exercise physiology: energy, nutrition, and human performance, 4th edn. Williams and Wilkins, Baltimore

Mora-Rodriguez R, Coyle EF (2000) Effects of plasma epinephrine on fat metabolism during exercise: interactions with exercise intensity. Am J Physiol Endocrinol Metab 278:669–676

Morgans LF, Jordan DL, Baeyens DA, Franciosa JA (1987) Heart rate responses during singles and doubles tennis competition. Physician Sportsmed 15:67–74

Osness WH, Blake B, Gordon ES, Rankin J, Nagle F, Breck W, Dempsey J (1971) Plasma fatty-acid-glycerol concentration changes during steady state exercise of varied intensity. Med Dello Sport 11:157–166

Pruett DER (1970) FFA mobilization during and after prolonged severe muscular work in men. J Appl Physiol 29:809–815

Richter EA, Ruderman NB, Galbo H (1982) Alpha and beta adrenergic effects on metabolism in contracting perfused muscle. Acta Physiol Scand 116:215–222

Schulz H, Helle S, Heck H (1997) The validity of the telemetric system CORTEX X1 in the ventilatory and gas exchange measurement during exercise. Int J Sports Med 18:454–457

Therminarias A, Dansou P, Chirpaz-Oddou MF, Gharib C, Quiron A (1991) Hormonal and metabolic changes during a strenuous tennis match. Effect of ageing. Int J Sports Med 12:10–16

Van Beaumont W (1972) Evaluation of hemoconcentration from hematocrit measurements. J Appl Physiol 32:712–713

Von Euler US (1974) Sympatho-adrenal activity in physical exercise. Med Sci Sports 6:166–173

Weber K, Ferrauti A, Strüder HK (1994) Fat metabolism in tennis especially under health orientated aspects. Int J Sports Med 15:366

Weber K, Ferrauti A, Strüder HK, Walber C (1996) Catecholamine secretion during a tennis match in training and during a tournament (abstract). Int J Sports Med 17 [Suppl 1]:S31

Weicker H, Strobel G (1994) Sportmedizin. Biochemisch-physiologische Grundlagen und ihre sportartspezifische Bedeutung. Fischer, Stuttgart Jena, New York

Woll PJ, Record CO (1979) Lactate elimination in man: effects of lactate concentration and hepatic dysfunction. Eur J Clin Invest 9:397–404