International Journal of Sports Physiology and Performance, 2007;2:111-127

Metabolic Response and Fatigue in Soccer

Jens Bangsbo, Fedon Marcello Iaia, and Peter Krustrup

The physical demands in soccer have been studied intensively, and the aim of the present review is to provide an overview of metabolic changes during a game and their relation to the development of fatigue. Heart-rate and body-temperature measurements suggest that for elite soccer players the average oxygen uptake during a match is around 70% of maximum oxygen uptake (VO_2max). A top-class player has 150 to 250 brief intense actions during a game, indicating that the rates of creatine-phosphate (CP) utilization and glycolysis are frequently high during a game, which is supported by findings of reduced muscle CP levels and several-fold increases in blood and muscle lactate concentrations. Likewise, muscle pH is lowered and muscle inosine monophosphate (IMP) elevated during a soccer game. Fatigue appears to occur temporarily during a game, but it is not likely to be caused by elevated muscle lactate, lowered muscle pH, or change in muscle-energy status. It is unclear what causes the transient reduced ability of players to perform maximally. Muscle glycogen is reduced by 40% to 90% during a game and is probably the most important substrate for energy production, and fatigue toward the end of a game might be related to depletion of glycogen in some muscle fibers. Blood glucose and catecholamines are elevated and insulin lowered during a game. The blood free-fatty-acid levels increase progressively during a game, probably reflecting an increasing fat oxidation compensating for the lowering of muscle glycogen. Thus, elite soccer players have high aerobic requirements throughout a game and extensive anaerobic demands during periods of a match leading to major metabolic changes, which might contribute to the observed development of fatigue during and toward the end of a game.

Key Words: muscle lactate, glycogen, CP, ammonia, glucose, FFA, heart rate

A considerable number of scientific studies have focused on the overall physiological demands of soccer by performing physiological measurements before and after a game or at halftime.[1-6] Some studies have also examined changes in both performance and physiological response throughout the game, with special focus on the most demanding activities and periods.[6,7] This brief review deals with the present knowledge about the metabolic response during a soccer game, with a

The authors are with the Institute of Exercise and Sport Sciences, University of Copenhagen, Copenhagen Muscle Research Center, Universitetsparken 132 Copenhagen 2100, Denmark.

specific focus on the response of individual players and how metabolic processes might be related to the development of fatigue.

Heart-Rate and Oxygen Measurement in Soccer

Average heart rates have been found to be around 85% of maximal values, and peak heart rates have been close to maximal.[2,3,6-9] These values can be "converted" to oxygen uptake using the relation between heart rate and oxygen uptake obtained during treadmill running.[7,9-11] It is likely, however, that the heart-rate values during a match lead to an overestimation of the oxygen uptake, because a number of factors such as dehydration, hyperthermia, and mental stress elevate the heart rate without affecting oxygen uptake. Nevertheless, taking these factors into account, the heart-rate measurements during a game indicate that the average oxygen uptake is around 70% VO_2max. This is supported by measurements of core temperature, which is another indirect measurement of energy production. Core temperatures of 39°C to 40°C during a game suggest that the average aerobic loading during a game is 70% to 75% VO_2max.[3,12,13]

No study has been able to measure oxygen uptake during a soccer match, but in a number of investigations it has been measured by portable gas analyzers during soccer activities.[11,14,15] It was observed that oxygen uptake ranged from 2.5 to 4.5 L/min, with a corresponding relative aerobic loading around 70% and 85% to 95% VO_2max during moderate- and high-intensity activities, respectively. More important, the relation between oxygen uptake and heart rate was similar to that observed during treadmill running,[11] suggesting that heart-rate measurements during a match, with some limitations, can be used to estimate relative work intensity.

Muscle Creatine-Phosphate Utilization in Soccer

The observation that elite soccer players perform 150 to 250 brief, intense actions during a game[16] indicates that the rate of anaerobic-energy turnover is high during periods of a game. Even though it has not been studied directly, the intense exercise during a game would lead to a high rate of breakdown of creatine-phosphate (CP), which to a major extent is resynthesized in the subsequent periods of low-intensity exercise.[7] Measurements of CP in muscle biopsies obtained after intense-exercise periods during a game have shown average levels around 75% of the level at rest. This is, however, likely to be significantly lower during the match, because these values were obtained from biopsies taken 15 to 30 seconds after match activities in which a substantial resynthesis of CP undoubtedly has occurred.[6] Using proper values for resynthesis of CP and the measured CP values, as well as the delay time in obtaining the biopsies, it can be estimated that the CP concentration during the game would have been about 60% of the resting level.

There is evidence to suggest that soccer players experience fatigue temporarily during games.[6,16] The difficult question is what causes it. Fatigue during match play is probably a complex phenomenon with a number of contributing factors. It might be a result of low muscle CP concentrations, because performance in intense intermittent exercise is elevated after a period of creatine supplementation.[17,18] The question is whether CP is becoming critically low—that is, below a threshold for being able to perform maximally. The CP levels might during parts of a game become low, below 30% of resting level, if a number of intense bouts are performed with only short recovery periods. More important, CP might become very low in individual muscle fibers, because the stores of CP have been reported to be almost depleted in individual fibers at the point of fatigue after intense exercise.[19] During a Yo-Yo intermittent recovery test in which speed was progressively increased to the point of exhaustion, however, no changes were observed in muscle CP in the final phase of exercise.[20] This fact argues against low CP having a significant inhibitory effect on performance during intense intermittent exercise and during a soccer match. The breakdown of CP leads to a considerable accumulation of phosphate, and it has been suggested that phosphate could be involved in the development of fatigue during intense exercise.[21] With the same arguments as brought up for CP, however, it is not likely to be a major component in fatigue during intense periods of a soccer game, which is supported by findings of in vitro studies.[21,22]

Muscle Lactate and pH in Soccer

Average blood lactate concentrations of 2 to 10 mM have been observed during soccer games,[3,4,6-8,23-33] with individual values above 12 mM (Tables 1A and 1B). There are major individual changes during a match, as indicated in Figure 1, which to some extent reflects the activities of the players immediately before sampling.[4,10] Nevertheless, the findings of high blood lactate concentrations indicate that the rate of muscle lactate production is high during match play. Muscle lactate has been measured in a friendly game between nonprofessional teams and rose fourfold (to around 4 mmol/kg wet weight) compared with resting values after intense periods in both halves, with the highest value being 10 mmol/kg wet weight.[6] Nevertheless, the average value is less than one-fifth of the concentrations observed during short-term intermittent exhaustive exercise.[20]

An interesting finding was that muscle lactate was not correlated with blood lactate during a soccer game (Figure 2). A scattered relationship with a low correlation coefficient has also been observed between muscle and blood lactate when subjects performed repeated intense exercise during a Yo-Yo intermittent recovery test.[20] These observations are in contrast to those during continuous exercise, in which the blood lactate concentrations are lower but reflect the muscle lactate concentrations during exercise.[34] These differences between intermittent and continuous exercise are probably caused by different turnover rates of muscle and blood lactate during the 2 types of exercise, with the rate of lactate clearance being significantly higher in muscle than in blood.[35] An indication of the net rate of lactate clearance from the blood can be obtained from measurements of blood lactate at the start and the end of halftime, as well as after a game (Figure 3). In one study[6] the mean rate of blood lactate decrease at halftime was 0.1 mmol $\cdot$ L^{-1} $\cdot$ min^{-1}, which means that it would take 60 minutes to reduce the blood lactate concentration by 6 mmol/L. The rate of clearance also depends, however, on the level of blood lactate and is elevated during low-intensity exercise.

These factors can explain how 1 of the players whose data are shown in Figure 1 had a drop from 8.5 to 3 mmol/L within a 10-minute period of the game (5 to 15 minutes), corresponding to a net turnover rate of 0.55 mmol $\cdot$ L^{-1} $\cdot$ min^{-1}. The 2 other players only had a small reduction in blood lactate, probably because of higher

Table 1A Blood Lactate Concentration (mmol/L) in Sample Taken From a Fingertip, Earlobe, or Arm Vein During or After Competitive Soccer Matches in Male Players*

				Blood Lactate, First Half		Blood Lactate, Second Half	
Study	**Level (country)**	**Type of match**	**n**	**During**	**End**	**During**	**End**
Currie et al[23]	—	Competitive	5		5.7 ± 2.0	2.5 ± 0.5	
Carli et al[24]	Fourth division (Italy)	Competitive	11		3.4 ± 0.8		3.0 ± 0.7
Ekblom[3]	First division (Sweden)	Competitive	—		9.5 (6.9–14.3)		7.2 (4.5–10.8)
	Second division (Sweden)	Competitive	—		8.0 (5.1–11.5)		6.6 (3.1–11.0)
	Third division (Sweden)	Competitive	—		5.5 (3.0–12.6)		4.2 (3.2–8.0)
	Fourth division (Sweden)	Competitive	—		4.0 (1.9–6.3)		3.9 (1.0–8.5)
Rohde and Espersen[25]	First division (Denmark)	Competitive	22		5.1 ± 1.6		3.9 ± 1.6
Gerish et al[26]	Top amateur league (Germany)†	Competitive	59		5.6 ± 2.0		4.7 ± 2.2
Bangsbo et al[4]	First and second divisions (Denmark)	Competitive	14	4.9 (2.1–10.3)		3.7 (1.8–5.2)	4.4 (2.1–6.9)
Bangsbo[7,9]	League (Denmark)	Competitive	6	4.1 (2.9–6.0)	2.6 (2.0–3.6)	2.4 (1.6–3.9)	2.7 (1.6–4.6)
	League (Denmark)‡	Competitive		6.6 (4.3–9.3)	3.9 (2.8–5.4)	4.0 (2.5–6.2)	3.9 (2.3–6.4)
Capranica et al[27]	Youth, 11 years old (Italy)	Official game	6		3.1–8.1		
Roi et al[28]	First league (Italy)	Competitive	52				6.3 ± 2.4 (2.1–11.3)

*Values are mean ± SD or range (in parentheses).
†Median value.
‡Lactate analysis was performed using whole blood except in this case, in which plasma was used.

Table 1B Blood Lactate Concentration (mmol/L) in Sample Taken From a Fingertip, Earlobe, or Arm Vein During or After Friendly and Other Soccer Matches in Male Players*

Study	Level (country)	Type of match	n	Blood Lactate, First Half		Blood Lactate, Second Half	
				During	End	During	End
Agnevik[29]	First division (Sweden)	—	10				10.0
Smaros[30]	Second division (Finland)	—	7		4.9 ± 1.9		4.1 ± 1.3
Gerish et al[26]	University team (Germany)	Friendly	—	6.8 ± 1.0	5.9 ± 2.0	5.1 ± 1.6	4.9 ± 1.7
Tumilty et al[31]	Junior national (Australia)	Friendly	8				2.4 ± 2.0
Smith et al[32]	College players (England)	College league	6		5.2 ± 1.2 (1.9–11.7)		
Tessitore et al[33]	Recreational, 53–72 years old (Italy)	Friendly (70 min)	12		4.9 ± 1.9 (1.8–7.5)		3.6 ± 1.7 (1.1–7.5)
Krustrup et al[6]	Fourth division (Denmark)	Friendly	20	6.0 ± 0.4 (3.8–9.6)	4.1 ± 0.4 (1.3–6.0)	5.0 ± 0.4 (2.3–8.6)	3.9 ± 0.4 (2.1–5.9)

*Values are mean ± SD or range (in parentheses).

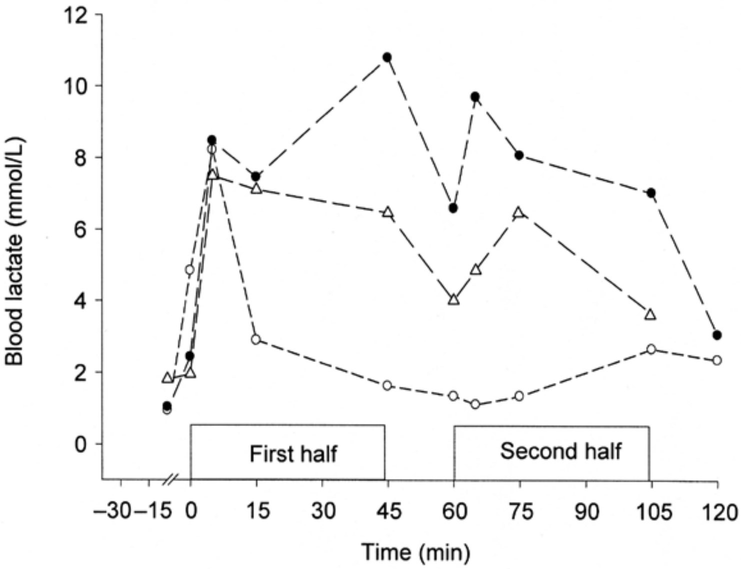

Figure 1 — Blood lactate concentrations before, during, and after a soccer game for 3 players.

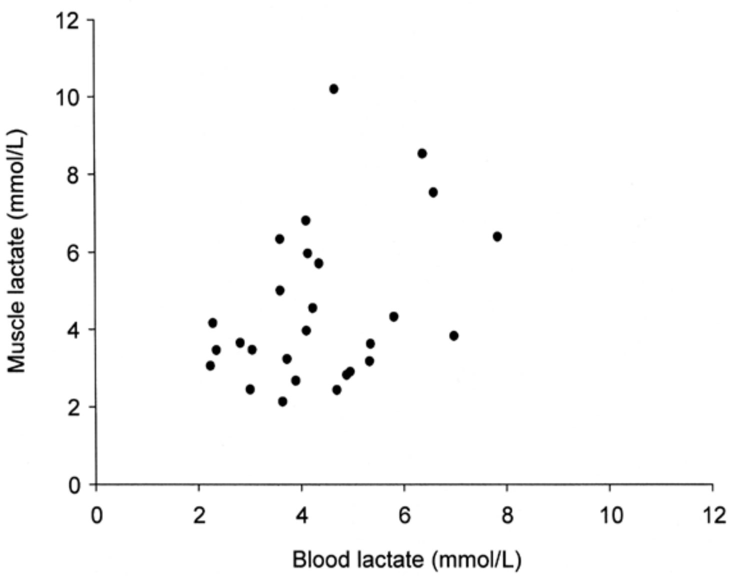

Figure 2 — Relationship between muscle and blood lactate concentration after intense exercise periods during a soccer match. Modified from Krustrup et al[6] and published with permission from *Medicine and Science in Sports and Exercise*.

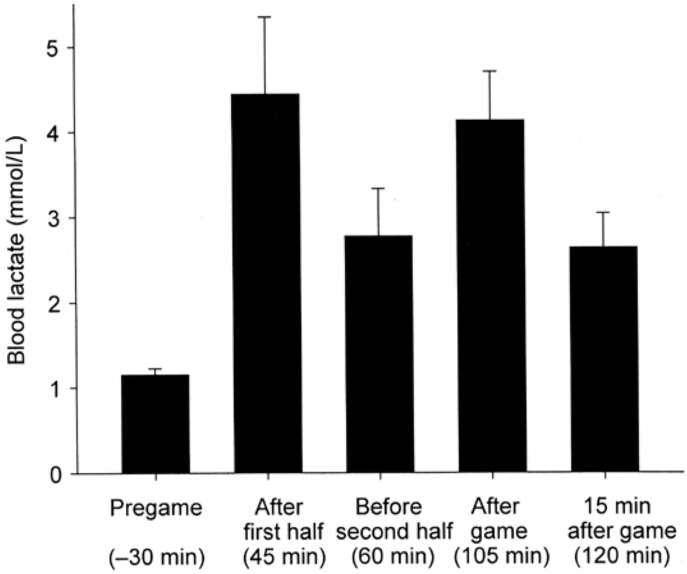

Figure 3 — Blood lactate at rest and before and after 15-minute periods of passive recovery at halftime and after the game. Values are mean ± SEM (n = 10).

production of lactate and a significant release of lactate from the active muscles. Apparently, during the intermittent exercise in soccer the blood lactate level can be high even though the muscle lactate concentration is relatively low. Thus, the rather high blood lactate concentration often seen in soccer[3,6,7] might not represent a high lactate production in a single action during the game but, rather, an accumulated, balanced response to a number of high-intensity activities. This response is important to take into account when interpreting blood lactate concentrations as a measure of muscle lactate concentrations. Nevertheless, based on numerous studies focusing on muscle lactate accumulation during short-term maximal exercise performed in a laboratory[36-38] and the finding of high blood lactate and moderate muscle lactate concentrations during match play, it appears that the rate of glycolysis is high for short periods of time during a game.

A role of accumulated muscle lactate and lowered muscle pH in the development of fatigue has been suggested.[21,39] In the study by Krustrup et al[6] the reduction in performance during the game was related to muscle lactate. The relationship was weak, however, and the changes in muscle lactate were moderate. Furthermore, several studies have shown that accumulation of lactate does not cause fatigue.[20,40-42] Another candidate for the cause of muscle fatigue during intense exercise is low muscle pH.[43] Muscle pH is only moderately reduced (>6.8) during a game, however, and no relationship with lowered performance has been observed.[6] Together, these findings suggest that temporary fatigue in soccer is not causally linked to high muscle lactate and acidosis.

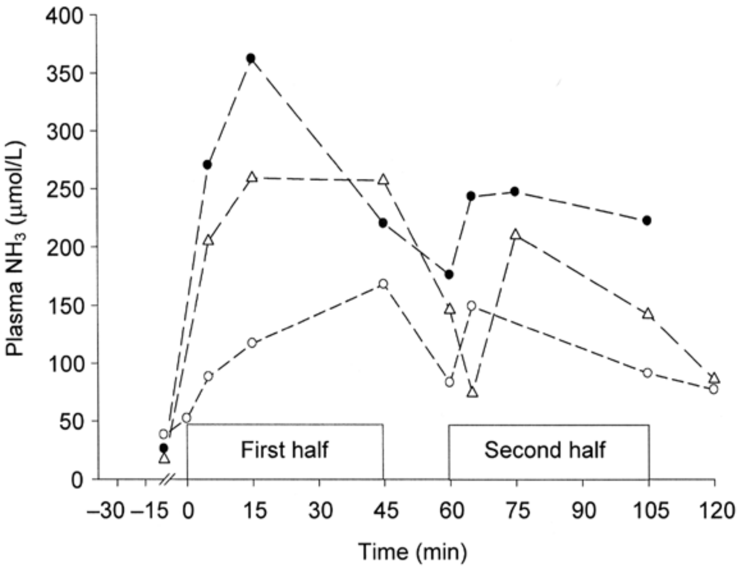

Figure 4 — Plasma ammonia concentrations before, during, and after a soccer game for 3 players.

Muscle ATP and IMP and Blood Ammonia in Soccer

During the match studied by Krustrup et al[6] muscle ATP was only moderately reduced (15%) during the game, which to some extent might have been a result of the 15- to 30-second delay in obtaining the biopsies. Even during intense short-term exhaustive exercise, however, muscle ATP is not lowered more than 30%, and the resynthesis rate is rather low in recovery.[6] Thus, the observed ATP concentrations might reflect true lowering of muscle ATP. A corresponding accumulation of muscle IMP is observed during a game.[6] In addition, plasma NH_3 concentration is higher,[7,9] supporting the suggestions of a significant activation of muscle AMP deaminase reaction. In addition, the concentrations of hypoxanthine and uric acid in the blood were significantly higher during match play than at rest, indicating a further breakdown of IMP.[7,9] As observed for lactate, considerable differences in plasma ammonia concentrations were observed, probably reflecting differences in activity levels and in energy turnover between players during a game (Figure 4). Nevertheless, muscle IMP levels were considerably lower than during exhaustive exercise,[44] and ATP was only moderately reduced. Thus, it not likely that fatigue occurred as a result of low energy status of the contracting muscles.

Muscle Glycogen Utilization During a Soccer Match

Muscle glycogen is an important substrate for soccer players, as illustrated from the various studies in which glycogen has been measured (Table 2). Saltin[1] observed that the muscle glycogen stores were almost depleted at halftime when the prematch

Table 2 Muscle-Glycogen Concentration (mmol/kg Wet Weight) Obtained From the Vastus Lateralis Before, During, and After a Soccer Match in Male Players*

Study	Level (country)	Type of match	Protocol	n	Before game	End of first half	After game	% Decrease
Karlsson[51]	Military team (Sweden)	Friendly	—	6	57.3 ± 26.3 (15.5–88.3)	18.6 ± 13.7 (5.0–40.5)	10.5 ± 5.7 (2.8–18.3)	82
Saltin[1]	(Sweden)	Friendly	Rest before the game	5	96	32	9	91
			Exhaustive exercise the day before the game	4	45	6	0	100
Currie et al[23]	—	Competitive	—	5	72.2 ± 16.7	—	50.0 ± 7.2	31
Smaros[30]	Second division (Finland)	—	—	—	84	63	43	49
Jacobs et al[45]	Top league (Sweden)	Competitive	—	15	—	—	45.9 ± 7.9 (35–63)	—
Leatt et al[46]	U21 national (Canada)	Semicompetitive	Glucose solution pregame and at halftime	5	87.8 ± 17.8	—	60.0 ± 14.0	32
			Placebo-treated	5	98.5 ± 22.0	—	53.3 ± 19.3	46
Krustrup et al[6]	Fourth division (Denmark)	Friendly	—	11	112 ± 20 (97–157)	—	64 ± 19 (42–94)	43

*Values are mean ± SD or range (in parentheses).

levels were low (~45 mmol/kg wet weight). In that study, some players also started the game with normal muscle glycogen levels (~100 mmol/kg wet weight), and the values were still rather high at halftime but below 10 mmol/kg wet weight at the end of the game. Others have found the concentrations to be 40 to 65 mmol/kg wet weight after a game,[6,23,30,45,46] indicating that muscle glycogen stores are not always depleted in a soccer game (Table 2). Analyses of single muscle fibers after a game, however, have revealed that a significant number of fibers are depleted or partly depleted at the end of the game (Figure 5).[6]

A number of studies have demonstrated that the amount of high-intensity running is reduced toward the end of a match,[5,16,47,48] and some studies have demonstrated that sprint and intermittent-exercise performance after a soccer game are lowered.[6,13] The question is what causes that type of fatigue in soccer. One candidate is depletion of glycogen stores, because development of fatigue during prolonged intermittent exercise has been associated with lack of muscle glycogen. Moreover, elevating muscle glycogen before exercise through a carbohydrate diet enhances performance during such exercise.[49,50] Some[1,51] but not all investigations[6,23,30,45,46] have indicated that muscle glycogen during a game decreases to levels below the required value to maintain maximal glycolytic rate (~50 mmol/kg wet weight).[48] In the study by Krustrup et al[6] the muscle glycogen concentration at the end of the game was reduced to 40 to 60 mmol/kg wet weight, indicating that there was still glycogen available. Histochemical analysis revealed, however, that about half the individual muscle fibers of both types were almost depleted or depleted of glycogen (Figure 5). This reduction was associated with a decrease in sprint performance

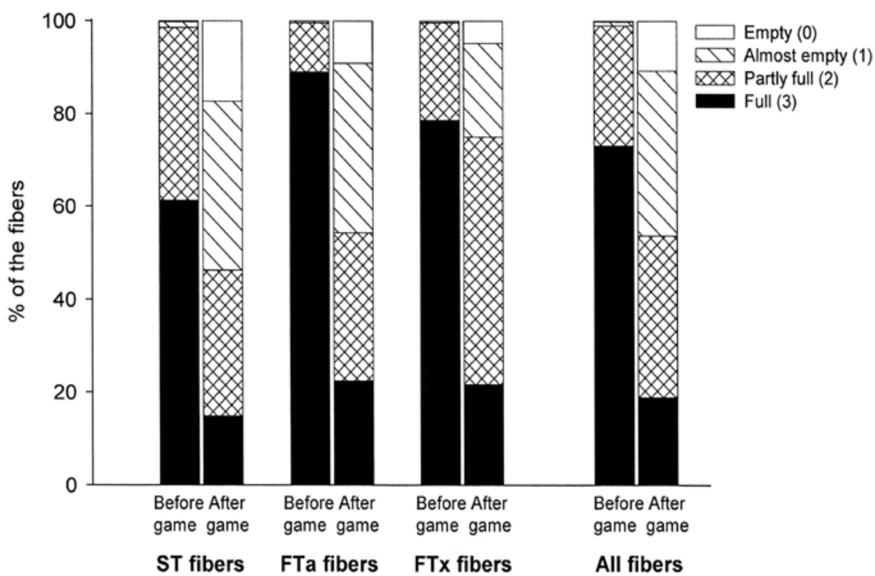

Figure 5 — Relative glycogen content in slow-twitch (ST) and fast-twitch (FT) a and x fibers, as well as all fibers, before and immediately after a soccer match. Values are mean (n = 10). Modified from Krustrup et al[6] and published with permission from *Medicine and Science in Sports and Exercise*.

immediately after the game. Therefore, it is possible that such a depletion of glycogen in some fibers does not allow for a maximal effort in single and repeated sprints. Nevertheless, it appears unclear what the mechanisms are behind a possible causal relationship between muscle glycogen levels and fatigue during prolonged intermittent exercise.

Blood Glucose, Free Fatty Acids, and Hormones in Soccer

Blood glucose is elevated in soccer players during games,[52] and only in a few cases has it been observed to decrease to a level that might affect performance (Table 3). These findings suggest that the rate of glucose release from the liver is high enough to compensate for the use of blood glucose throughout a game. It is interesting that at halftime almost all players had a reduction in blood glucose (Figure 6), probably reflecting a significant glucose uptake by the previously active muscles and a reduced stimulation of liver glycogenolysis through, among other things, lowered catecholamine levels. Free-fatty-acid (FFA) concentration in the blood increases progressively during a game, and more so during the second half (Figure 7).[6,7] The frequent rest and low-intensity periods of a game allow for significant blood flow to adipose tissue, which promotes release of FFA. This effect is also illustrated by the finding of even higher FFA concentrations at the end of the halftime and after the game (Figure 7). The suggestion of a high rate of lipolysis during a game is supported by the observations of elevated levels of glycerol, even though the increases are smaller than during continuous exercise, which probably reflects a high turnover of glycerol—for example, as a gluconeogenic precursor in the liver.[7] Hormonal changes might play a major role in the progressive increase in FFA. Insulin concentrations are lowered and catecholamine levels are progressively elevated during a match,[7] stimulating a high rate of lipolysis and, thus, release of FFA into the blood.[7,52] The effect is reinforced by lowered lactate levels toward the end of a game, leading to less suppression of mobilization of fatty acid from the adipose tissue.[6,7,53,54] The changes in FFA during a match might reflect a higher uptake and oxidation of FFA by the contracting muscles, especially during recovery periods in a game.[55] In addition, higher utilization of muscle triglycerides might occur in the second half as a result of elevated catecholamine concentrations.[56] Both processes might be compensatory mechanisms for the progressive lowering of muscle glycogen and are favorable in maintaining blood glucose concentration at a high level.

Summary

The intense exercise periods during a soccer game lead to high anaerobic-energy turnover with an associated accumulation of lactate and lowering of pH in the exercised muscles. These factors are probably not, however, the main factors in the temporary fatigue that occurs during a game, which is probably caused by a complex interplay between a number of factors. Recent data from human studies support an old theory about accumulation of potassium in muscle interstitium and a concomitant change in muscle-membrane potential playing an important

Table 3 Blood Glucose Concentration (mmol/L) in Sample Taken From a Fingertip or Arm Vein During or After a Soccer Match in Male Players*

Study	Level (country)	Type of match	Protocol	n	Before game	Halftime	After game
Currie et al[23]	—	Competitive	—	5	5.11 ± 0.24	7.75 ± 3.60	6.14 ± 0.24
Carli et al[24]	Fourth division (Italy)	Competitive	—	11	5.8 ± 0.3	8.2 ± 0.6	6.5 ± 0.2
Smaros[30]	Second division (Finland)	—	—	—	—	—	(6–7)
Ekblom[3]	First division (Sweden)	Competitive	—	—	—	—	3.8 ± 0.8
				3	—	—	(3.0- 3.2)
Leatt et al[46]	U21 national (Canada)	Semicompetitive	Glucose solution pregame and at halftime	5	4.2 ± 0.3	6.1 ± 0.7	5.3 ± 0.7
			Placebo-treated	5	5.0 ± 1.1	5.7 ± 1.3	4.7 ± 0.5
Bangsbo[52]	Elite players (Denmark)	Competitive	—	6	4.4 ± 0.2	5.9 ± 0.4	5.5 ± 0.3
Krustrup et al[6]	Fourth division (Denmark)	Friendly	—	14	4.5 ± 0.1 (3.2–5.8)	5.4 ± 0.4 (2.8–8.9)	4.9 ± 0.2 (4.0–6.3)

*Values are mean ± SD or range (in parentheses).

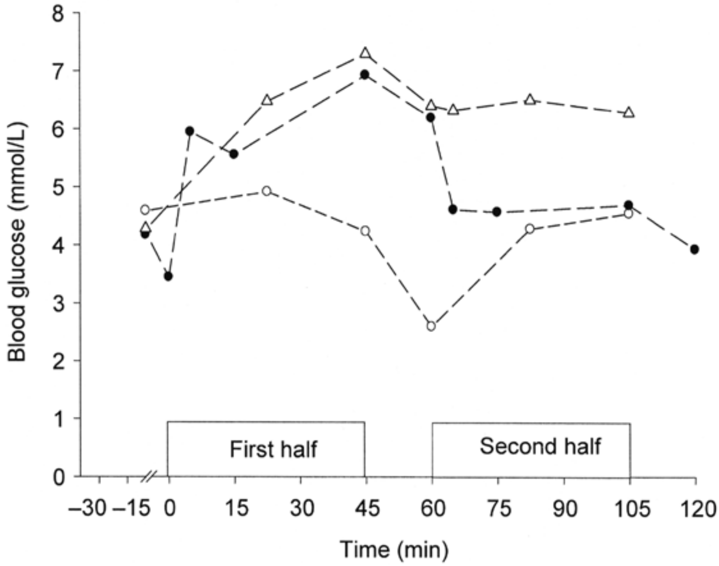

Figure 6 — Blood glucose concentrations before, during, and after a soccer game for 3 players.

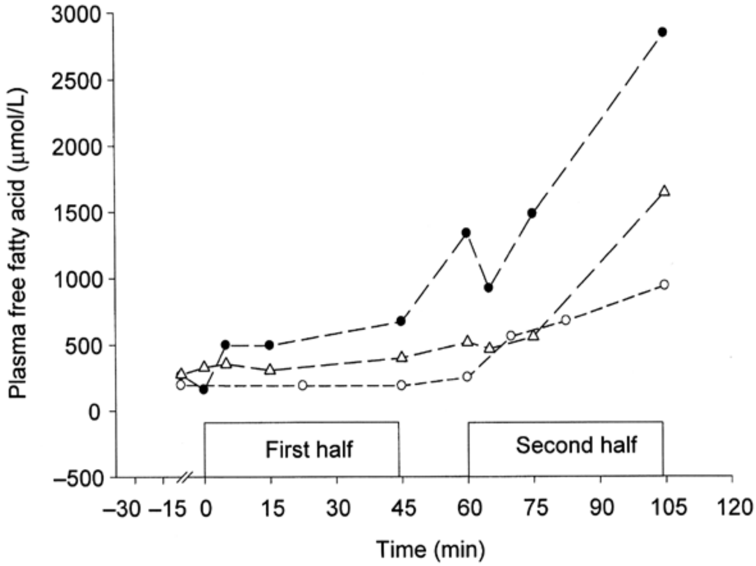

Figure 7 — Plasma free-fatty-acid concentrations before and during a soccer game for 3 players.

role in the development of fatigue during intense exercise.[57,58] Plasma potassium has been shown to be elevated during a soccer match, but sufficient information was not provided about the accumulation in muscle interstitium.[6] Soccer players also appear to be fatigued toward the end of a game, and even though it is unclear what causes this fatigue, depletion of glycogen in individual fibers might play an important role. Thus, players should develop proper nutritional strategies to elevate muscle glycogen before games[9,59] and perform appropriate training to reduce the loss of muscle glycogen during games.[60,61]

Perspectives

The intense research on the metabolic response during soccer has provided many answers but also given rise to a number of important questions. For example, it would be valuable to have more information about the cause of temporary fatigue during a match and whether it is linked to the metabolic response.[61] Such investigations should be performed based on information from research studies done in the laboratory and incorporate some of the experimental designs and methods used in such studies.

Acknowledgment

The original studies by the authors of this review were supported by Team Denmark and the Sports Research Council, Ministry of Culture, Denmark.

References

1. Saltin B. Metabolic fundamentals in exercise. *Med Sci Sports Exerc*. 1973;5:137-146.
2. Reilly T, Thomas V. Estimated energy expenditures of professional association footballers. *Ergonomics*. 1979;22:541-548.
3. Ekblom B. Applied physiology of soccer. *Sports Med*. 1986;3:50-60.
4. Bangsbo J, Nørregaard L, Thorsøe F. Activity profile of competition soccer. *Can J Sport Sci*. 1991;16:110-116.
5. Krustrup P, Mohr M, Ellingsgaard H, Bangsbo J. Physical demands during an elite female soccer game: importance of training status. *Med Sci Sports Exerc*. 2005;37(7):1242-1248.
6. Krustrup P, Mohr M, Steensberg A, Bencke J, Kjaer M, Bangsbo J. Muscle and blood metabolites during a soccer game: implications for sprint performance. *Med Sci Sports Exerc*. 2006;38(6):1165-1174.
7. Bangsbo J. The physiology of soccer—with special reference to intense intermittent exercise. *Acta Physiol Scand*. 1994;151(suppl 619):1-156.
8. Ali A, Farrally M. Recording soccer players' heart rates during matches. *J Sports Sci*. 1991;9(2):183-189.
9. Bangsbo J. Energy demands in competitive soccer. *J Sports Sci*. 1994;12:S5-S12.
10. Krustrup P, Bangsbo J. Physiological demands of top class soccer refereeing in relation to physical capacity and training. *J Sports Sci*. 2001;19:881-891.
11. Esposito F, Impellizzeri FM, Margonato V, Vanni R, Pizzini G, Veicsteinas A. Validity of heart rate as an indicator of aerobic demand during soccer activities in amateur soccer players. *Eur J Appl Physiol*. 2004;93(1-2):167-172.

12. Smodlaka VJ. Cardiovascular aspects of soccer. *Physician Sportsmed*. 1978;18:66-70.
13. Mohr M, Krustrup P, Nybo L, Nielsen JJ, Bangsbo J. Muscle temperature and sprint performance during soccer matches—beneficial effects of re-warm-up at half time. *Scand J Med Sci Sports*. 2004;14(3):156-162.
14. Hoff J, Wisloff U, Engen LC, Kemi OJ, Helgerud J. Soccer specific aerobic endurance training. *Br J Sports Med*. 2002;36(3):218-212.
15. Castagna C, Belardinelli R, Abt G. The VO_2 and HR response to training with the ball in youth soccer players. In: Reilly T, Cabri J, Araújo D, eds. *Science and Football V*. London/New York: Routledge, Taylor & Francis Group; 2005:462-464.
16. Mohr M, Krustrup P, Bangsbo J. Match performance of high-standard soccer players with special reference to development of fatigue. *J Sports Sci*. 2003;21:519-528.
17. Balsom PD, Seger JY, Sjödin B, Ekblom B. Physiological responses to maximal intensity intermittent exercise. *Eur J Appl Physiol*. 1992;65:144-149.
18. Greenhaff PL, Bodin K, Soderlund K, Hultman E. Effect of oral creatine supplementation on skeletal muscle phosphocreatine resynthesis. *Am J Physiol*. 1994;266(5):E725-E730.
19. Søderlund K, Hultman E. ATP and phosphocreatine changes in single human muscle fibers after intense electrical stimulation. *Am J Physiol*. 1991;261:E737-E741.
20. Krustrup P, Mohr M, Amstrup T, et al. The Yo-Yo intermittent recovery test: physiological response, reliability and validity. *Med Sci Sports Exerc*. 2003;35(4):697-705.
21. Westerblad H, Allen D, Lännergren J. Muscle fatigue: lactic acid or inorganic phosphate the major cause? *News Physiol Sci*. 2002;17:17-21.
22. Fitts RH**.** The muscular system: fatigue processes. In: Tipton CM, ed. *ACSM's Advanced Exercise Physiology*. Baltimore, Md, Philadelphia, Pa: Lippincott Williams & Wilkins; 2006:178-196.
23. Currie D, Bonen A, Belcastro AN, Kirby RL, Sopper M, Richards AL. Glycogen utilization and circulating substrate responses during match play soccer and soccer training sessions [abstract]. *Int J Sports Med*. 1981;2:271.
24. Carli G, Baldi L, Lodi L, Lupo di Prisco C, Martelli G, Viti A. Hormonal and metabolic changes following a football match [abstract]. *Bollettino Società Italiana Biologia Sperimentale*. 1984;LX(suppl 3):78-79.
25. Rohde HC, Espersen T. Work intensity during soccer-match play. In: Reilly T, Lees A, Davids K, Murphy WJ, eds. *Science and Football*. London/New York: E & FN Spon; 1988:68-75.
26. Gerisch G, RutermÖller E, Weber K. Sportsmedical measurements of performance in soccer. In: Reilly T, Lees A, Davids K, Murphy WJ, eds. *Science and Football*. London/New York: E & FN Spon; 1988:60-67.
27. Capranica L, Tessitore A, Guidetti L, Figura F. Heart rate and match analysis in prepubescent soccer players. *J Sports Sci*. 2001;19(6):379-384.
28. Roi GS, Sisca G, Perondi F, Diamante A, Nanni G. Post competition blood lactate accumulation during a First League soccer season [abstract]. *J Sports Sci*. 2004;22(6):560.
29. Agnevik G. *Fotboll*. Rapport idrottsfysiologi. Stockholm: Trygg-Hansa; 1970.
30. Smaros G. Energy usage during a football match. In: Guanello D, ed. *Proceedings of the 1st International Congress on Sports Medicine Applied to Football*. Rome: Vecchiet L; 1980:795-801.
31. Tumilty DM, Hahn AG, Telford RD, Smith RA. Is lactic acid tolerance an important component of fitness for soccer? In: Reilly T, Lees A, Davids K, Murphy WJ, eds. *Science and Football*. London/New York: E & FN Spon; 1988:81-86.
32. Smith M, Clarke G, Hale T, McMorris T. Blood lactate levels in college soccer players during match-play. In: Reilly T, Clarys J, Stibbe A, eds. *Science and Football II*. London/New York: E & FN Spon; 1993:129-134.

33. Tessitore A, Meeusen R, Tiberi M, Cortis C, Pagano R, Capranica L. Aerobic and anaerobic profiles, heart rate and match analysis in older soccer players. *Ergonomics*. 2005;15:48(11-14):1365-1377.
34. Krustrup P, Söderlund K, Mohr M, Bangsbo J. The slow component of oxygen uptake during intense sub-maximal exercise in man is associated with additional fibre recruitment. *Pflugers Arch*. 2004;447(6):855-866.
35. Bangsbo J, Johansen L, Graham T, Saltin B. Lactate and H^+ effluxes from human skeletal muscles during intense, dynamic exercise. *J Physiol*. 1993;462:115-133.
36. Nevill ME, Boobis LH, Brooks S, Williams C. Effect of training on muscle metabolism during treadmill sprinting. *J Appl Physiol*. 1989;67:2376-2382.
37. Gaitanos GC, Williams C, Boobis LH, Brooks S. Human muscle metabolism during intermittent maximal exercise. *J Appl Physiol*. 1993;75:712-719.
38. Bogdanis GC, Nevill ME, Boobis LH, Lakomy HK, Nevill AM. Recovery of power output and muscle metabolites following 30 s maximal sprint cycling in man. *J Physiol*. 1995;482:467-480.
39. Allen DG, Westerblad H, Lannergren J. The role of intracellular acidosis in muscle fatigue. *Adv Exp Med Biol*. 1995;384:57-68.
40. Bangsbo J, Graham T, Johansen L, Strange S, Christensen C, Saltin B. Elevated muscle acidity and energy production during exhaustive exercise in man. *Am J Physiol*. 1992;263:R881-R899.
41. Mohr M, Nordsborg N, Nielsen JJ, et al. Potassium kinetics in human interstitium during repeated intense exercise in relation to fatigue development—effect of muscle acidosis. *Pflugers Arch*. 2004;448(4):452-456.
42. Bangsbo J, Juel C. Counterpoint: lactic acid accumulation is a disadvantage during muscle activity. *J Appl Physiol*. 2006;100(4):1412-1413.
43. Sahlin K. Metabolic factors in fatigue. *Sports Med*. 1992;13(2):99-107.
44. Hellsten Y, Richter EA, Kiens B, Bangsbo J. AMP deamination and purine exchange in human skeletal muscle during and after intense exercise. *J Physiol*. 1999;529(3):909-920.
45. Jacobs I, Westlin N, Karlson J, Rasmusson M, Houghton B. Muscle glycogen and diet in elite soccer players. *Eur J Appl Physiol*. 1982;48:297-302.
46. Leatt PB, Jacobs I. Effect of glucose polymer ingestion on glycogen depletion during a soccer match. *Can J Sport Sci*. 1989;14(2):112-116.
47. Rienzi E, Drust B, Reilly T, Carter JE, Martin A. Investigation of anthropometric and work-rate profiles of elite South American international soccer players. *J Sports Med Phys Fitness*. 2000;40:162-169.
48. Di Salvo V, Baron R, Tschan H, Calderon Montero FJ, Bachl N, Pigozzi F. Performance characteristics according to playing position in elite soccer. *Int J Sports Med*. 2007;28(3):222-227.
49. Balsom PD, Gaitanos GC, Søderlund K, Ekblom B. High-intensity exercise and muscle glycogen availability in humans. *Acta Physiol Scand*. 1999;165:337-345.
50. Bangsbo J, Graham T, Kiens B, Saltin B. Elevated muscle glycogen and anaerobic energy production during exhaustive exercise in man. *J Physiol (Lond)*. 1992;451:205-227.
51. Karlsson HG. Kohlydratomsattning under en fotbollsmatch. *Report of the Department of Physiology III*. Stockholm: Karolinska Institute; 1969.
52. Bangsbo J. Metabolism in soccer [abstract]. In: *European Congress on Football*. Stockholm: Karolinska Institute; 1992:21.
53. Galbo H. *Hormonal and Metabolic Adaptations to Exercise*. New York: Thime-Stratton; 1983.
54. Bülow J, Madsen J. Influence of blood flow on fatty acid mobilization form lipolytically active adipose tissue. *Pflugers Arch*. 1981;390(2):169-174.
55. Turcotte LP, Kiens B, Richter EA. Saturation kinetics of palmitate uptake in perfused skeletal muscle. *Fed Eur Biochem Soc*. 1991;279:327-329.

56. Galbo H. Exercise physiology: humoral function. *Sport Sci Rev*. 1992;1:65-93.
57. Nordsborg N, Mohr M, Pedersen LD, Nielsen JJ, Langberg H, Bangsbo J. Muscle interstitial potassium kinetics during intense exhaustive exercise: effect of previous arm exercise. *Am J Physiol Regul Integr Comp Physiol*. 2003;285(1):R143-R148.
58. Nielsen JJ, Mohr M, Klarskov C, et al. Effects of high-intensity intermittent training on potassium kinetics and performance in human skeletal muscle. *J Physiol*. 2004;554(pt 3):857-870.
59. Bangsbo J, Nørregaard L, Thorsøe F. The effect of carbohydrate diet on intermittent exercise performance. *Int J Sports Med*. 1992;13(2):152-157.
60. Bangsbo J. *Aerobic and Anaerobic Training in Soccer—With Special Emphasis on Training of Youth Players*. Bagsværd, Denmark: HO+Storm; 2007.
61. Bangsbo J, Mohr M, Krustrup P. Physical and metabolic demands of training and match-play in the elite football player. *J Sports Sci*. 2006;24(7):665-674.