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FOOTBALL TASK FORCE

PHYSIOLOGICAL BASIS OF FATIGUE RESISTANCE TRAINING IN COMPETITIVE FOOTBALL

Magni Mohr | Researcher | Department of Food and Nutrition, and Sport Science | University of Gothenburg | Gothenburg | Sweden
F. Marcello Iaia | Research Scientist | Department of Biomedical Sciences for Health | Università degli Studi di Milano | Milan | Italy

KEY POINTS

- Fatigue develops temporarily during the most intense periods of a football game, as well as towards the end of a game, and the two types of fatigue are related to different physiological systems.
- Temporary fatigue is proposed to be caused by muscle acidification and depolarization of the muscle resting membrane potential, and fatigue at the end of a game may associate with depleted muscle glycogen stores in individual muscle fibres or muscle cell compartments.
- Aerobic high-intensity training and speed-endurance training are efficient fatigue resistance training strategies in elite football.
- Intense intermittent training has been shown to improve a wide range of physiological systems directly or indirectly related to both endurance and high-intensity exercise performance in trained athletes.
- Large individual variations in game demands and fatigue profiles are present in football, which suggests a greater emphasis on individual fitness training for elite football players.

INTRODUCTION

Football match-play is an intermittent multiple-sprint sport with frequent changes in activity where prolonged intermittent exercise is conjoined with short-term periods encompassing high-intensity running and explosive football-specific actions (Mohr et al., 2003). Thus, a football game demands a high-endurance capacity, as well as ability to repeatedly perform at maximal and near-maximal exercise intensity. This notion is supported by a number of scientific studies reporting a high taxation of both the aerobic and anaerobic energy pathways during a football game (for review see Bangsbo et al., 2006a).

The high physiological loading has also been shown to provoke different types of fatigue throughout the course of a football game (Mohr et al., 2005). For example, it has been demonstrated that top-class football players fatigue temporarily during the most intense periods of a game, as well as in the final phase of a game, which is suggested to associate with different physiological mechanisms (Mohr et al., 2005; Mohr, 2008). The transient type of fatigue that players experience during the most intense game intervals appears to have a relatively short recovery and is suggested to relate physiological mechanisms having a fast recovery rate. Thus a high anaerobic energy turnover with resultant intramuscular accumulation of hydrogen ions (H^+) or inorganic phosphate (P_i) as well as depolarisation of the resting membrane potential induced by disturbances in the muscle sodium (Na^+), potassium (K^+) and chloride (Cl^-) homeostasis have been proposed as main candidates to this type of fatigue development (Bangsbo et al., 2006a; Mohr, 2008). In contrast the more permanent type of fatigue mainly accumulating in the second half and especially towards the end of a game has been shown to have long-lasting recovery. For example it has been shown in several studies that maximal voluntary force capacity is not fully recovered until 72 h after a game in trained football players (Mohr et al., 2005; Mohr 2008; Krustrup et al., 2011). Therefore, it is likely that end-game and post-game fatigue may partly be induced by depleted muscle glycogen stores in individual muscle fibres or in subcellular glycogen compartments with concomitant impairment in muscle calcium (Ca^{2+}) handling (Nielsen et al., 2011). In addition a critical degree of muscle damage potentially negatively affecting numerous neuro-muscular systems may also play a role for more permanent type of fatigue arising in the late stages of a football game (Mohr, 2008; Krustrup et al., 2011).

Thus, the principal aim of fitness training in football is to target the physiological mechanisms causing fatigue and thereby limiting physical football performance. A higher fatigue resistance will allow the players to utilize their technical and tactical capacity throughout a game and especially during the critical game periods. Therefore, the purpose of the present article is to briefly discuss the physiological basis of fatigue resistance training in elite football. Primary focus will be given to speed endurance training, and practical examples of individual fitness training in football will be provided.

TRAINING INTERVENTIONS IN FOOTBALL

Fitness training in any sport has to take account of the demands of the sport, and in team sports such as football the physical demands are multifactorial, which provides an additional challenge to coaches and fitness staff. From a practical point of view it is highly essential to have clear definitions of the fitness training categories. Moreover, these sub-components have to represent relevant physiological systems of importance for football match performance. Figure 1 shows an overview of the determinants of football performance in relation to different fitness training categories as well as underlying physiological mechanisms being the main targets of these training interventions. The figure is inspired by Bangsbo et al. (2006b).

Figure 1

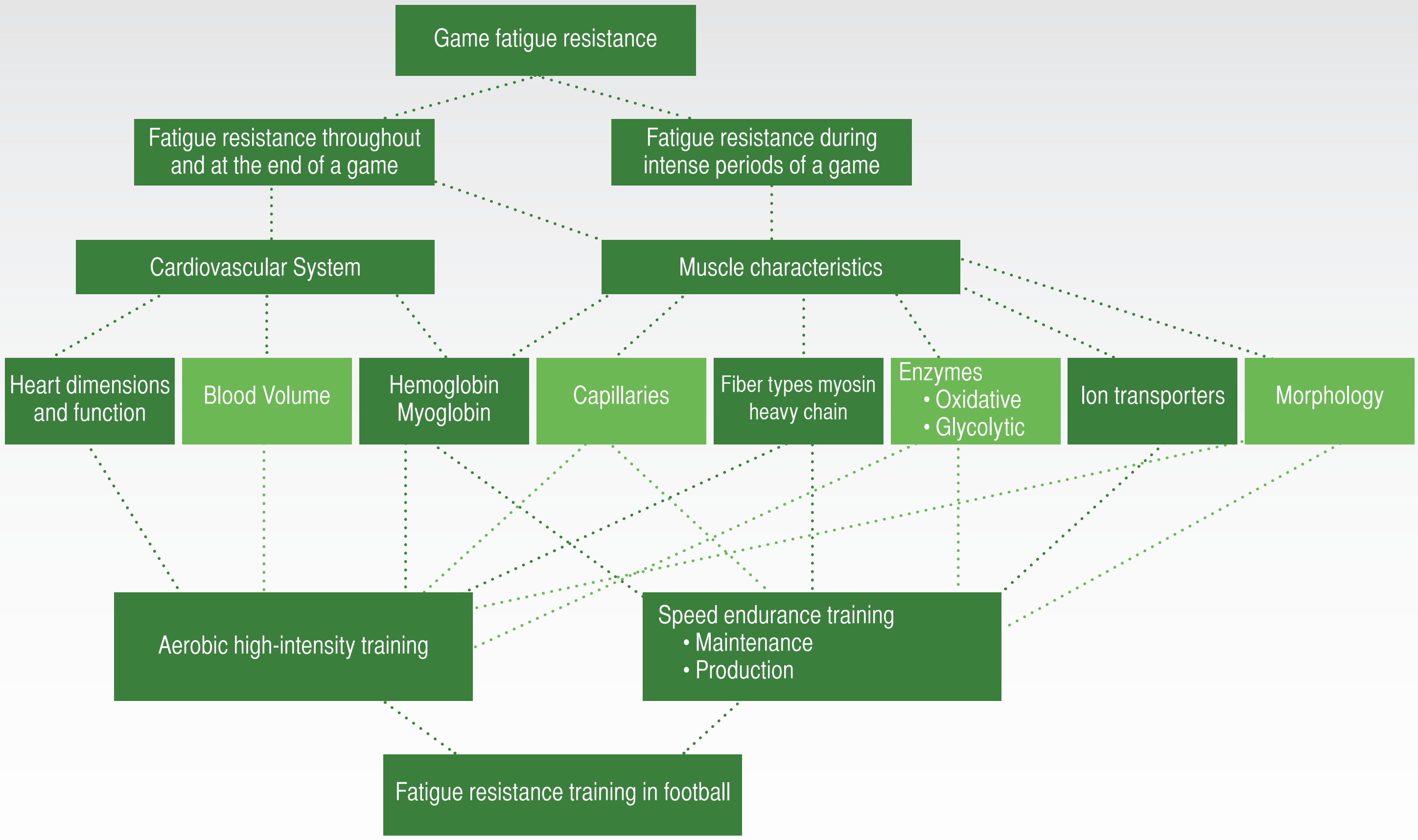


Figure 1. A model of the relationship between training category and physiological targets in fatigue resistance training in football.

Aerobic high-intensity training

Aerobic training in football is essential for the football endurance capacity and can be divided into aerobic training with low, moderate and high intensity (Figure 1). The two first sub-categories are primarily being utilised as recovery training and maintenance of physical fitness. For example most technical and tactical sessions will primarily have a physical loading that will classify it as aerobic moderate-intensity training. However, aerobic high-intensity training principally aims at improving physiological systems relating to the uptake, transportation and utilization of oxygen; thus, the different components of the cardiovascular system (Bangsbo et al., 2006a; 2006b). Aerobic high-intensity training is defined as training at an intensity corresponding to around 90% of the maximal heart rate (Bangsbo et al., 2006b), and in football is usually conducted as specifically designed small-sided games in exercise intervals ranging from 1-4 min separated by 1 min of recovery (Bangsbo et al., 2006b). In one study by it was shown that well-trained Scandinavian professional football players increased their VO_2Max markedly with concomitant improvements in match performance after a period with additional aerobic high-intensity training (Helgerud et al., 2001). The physiological effects from adding aerobic high-intensity interval training to already well-trained athletes have in other sports been shown to improve VO_2Max, ventilatory and lactate threshold, as well as an increased capacity to engage a higher volume of muscle mass and the ability to oxidize fat relative to carbohydrates (for review see Laursen, 2010). Moreover, football players display an improvement in VO_2Max (5-11%), running economy (3-7%) and demonstrate lower blood lactate levels during submaximal running after 8-12 wks of aerobic high-intensity running (Iaia et al., 2009). Thus, aerobic high-intensity training is a highly efficient training protocol for the elite football player. The training conducted in some of the studies mentioned above was performed as treadmill running (Helgerud et al., 2001), which normally is not recommended for team sport athletes such as football players due to the lack of specificity of the activity pattern in football and the missing technical and tactical component. Moreover, it has been substantiated that trained football players are able to reach higher heart rates during aerobic high-intensity small-sided games compared to generic running intervals, and that similar performance and physiological adaptations can be achieved with small-sided games as treadmill running (Impellizzeri et al., 2006). Thus, specially designed team drills also having a relevant technical and tactical focus are well-suited as an aerobic high-intensity training approach in competitive football (see also Bangsbo et al., 2006b).

Speed endurance training

Intensified training has drawn a lot of attention during the last decade. In a retrospective study on elite swimmers Mujika et al. (1995) reported that training intensity explained ~45% of the variance in performance improvement over a season with markedly less contribution from training volume and frequency. In a study on Italian football players Ferrari-Bravo et al. (2008) compared traditional aerobic high-intensity training (4x4min at 90-95% of HR_{max} separated by 3 min recovery) to speed endurance training (3 x 6 maximal shuttle sprints of 40 m). The intervention training was added to the normal training twice a week during a period of 7 wks. The study demonstrated that both groups improved their aerobic capacity, but the speed endurance training intervention induced greater improvements in Yo-Yo Intermittent Recovery test, level 1 and repeated sprint ability compared to the aerobic high-intensity training protocol. Thus, training intensity appears to be a key factor for improving football fitness in trained football players. Therefore, anaerobic training is an essential part of the physical preparation of elite football players.

Anaerobic training is separated into speed training and speed endurance training with the latter being sub-categorised into speed endurance production and maintenance training (Bangsbo et al., 2006b). Table 1 shows the training principals in anaerobic training in football.

***Table 1**. Principles of anaerobic training in football*

Anaerobic training categories	Exercise time	Recovery time	Intensity	Number of repetitions
Speed training	2-5 s	>10 times exercise time	Maximal (100%)	6-24
Speed endurance production training	10-40 s	>5 times exercise time	Very high (70-100%)	4-12
Speed endurance maintenance training	20-90 s	As exercise time	High (50-100%)	4-12

Table 1. Exercise and recovery time, exercise intensity and number of exercise intervals in anaerobic training in football. Exercise intensity is defined in relation to maximal (all-out) intensity, which in this situation is running speed.

While speed training is to be performed at maximal exercise, intensity speed endurance production and maintenance encompass a wider intensity range, especially speed endurance maintenance training. Besides the differences in range of exercise intensity between speed endurance maintenance and production training, there are other important differences. Speed endurance production training has to be performed according to principals relatively similar to speed training, only with lower exercise intensity and longer exercise time, but with long recovery periods between the exercise intervals. In contrast speed endurance maintenance training is carried out after principals comparable to aerobic high-intensity training with relatively short recovery intervals, only higher exercise intensity. This means from a practical point of view that speed endurance maintenance training is well-suited as training target in conventional small-sided games (1v1, 2v2 and 3v3). In contrast traditional small-sided games may not be the optimal approach for speed endurance production training where the exercise intensity has to be very high throughout the entire time of the drill. In a recent study, we compared speed endurance maintenance training conducted as small-sided games (2v2 with goals and goal keepers) to speed endurance production training organised as individual drills (running courses with technical ball challenges, see for example Bangsbo & Mohr, 2014 for drill examples). It was shown the peak and average running speed was ~30 and ~60% higher during the speed endurance production training drills in comparison to the speed endurance maintenance drills. In addition, the players displayed greater improvements in intermittent exercise capacity and repeated sprint ability after 4 wks of the speed endurance production training intervention compared to the speed endurance maintenance training (Mohr and Krustrup, unpublished observations). This is supported by others applying speed endurance production training to youth (Ingebrigtsen et al., 2013) and adult (Thomassen et al., 2010) elite players. In the study by Ingebrigtsen et al. (2013) speed endurance production training was added to the normal training for 4 wks resulting in improved Yo-Yo IR2 performance as well as 10-m sprint training ability. The study by Thomassen et al. (2010) was carried out during a 2 wk period where elite football players lowered their amount of training markedly (total training time was reduced ~30%), but emphasised speed endurance production training combined with aerobic high-intensity training. This intervention demonstrated a clear improvement in repeated sprint ability (10 x 20 m sprints), with concomitant muscle characteristic adaptations. For example the protein expression of Na^+-K^+ ATPase α_2 subunit and the resting phosphorylation status of the accessory and regulatory FXYD1 protein were significantly increased by intensified training despite a marked lowering in training volume (Thomassen et al., 2010). The Na^+-K^+ ATPase subunits have been shown to be adapt more efficiently to speed endurance production training compared to speed training (Mohr et al., 2007) as well as aerobic training (Iaia et al., 2009) with parallel increases in intense intermittent exercise capacity (for review see Iaia & Bangsbo, 2010). In addition, training-induced elevation in Na^+-K^+ ATPase subunits has been shown to increase the regulation of interstitial K^+ and fatigue resistance during intense exhaustive exercise (Nielsen et al., 2004). Moreover, the study by Thomassen et al. (2010) indicates that also the resting phosphorylation status of the regulatory FXYD1 subunit in trained football players can be changed with short-term prioritisation of speed endurance training. In support a significant correlation was found between the improvement in repeated sprint performance and the altered phosphorylation status of the FYXD1 subunit (Thomassen et al., 2010). This is suggested to elevate the Na^+-K^+ ATPase activity at the onset of exercise, which may contribute to improved fatigue resistance during repeated intense exercise such as the aforementioned peak intensity periods of a game where players experience temporary fatigue. In addition to the clear scientific evidence regarding up-regulation of the Na^+-K^+ ATPase potential after speed endurance production training, other sarcolemmal transport proteins have also been shown to respond to this type of training. Indeed the Na^+/H^+ exchanger isoform 1 (NHE1) and to a lesser degree the mono-carboxylate transporter (MCT) have been shown to increase after speed endurance training in already trained athletes (Iaia & Bangsbo, 2010). Thus, speed endurance training improves the capacity to regulate intramuscular pH, which may directly improve fatigue resistance during the high-intensity periods of a game. Moreover, an increased Na^+/H^+ exchange protein may also elevate the Na^+ uptake inside the muscle cell and thereby potentially further stimulate the Na^+-K^+ ATPase activity and cause a hyperpolarization of the resting membrane potential (Iaia & Bangsbo, 2010).

The physiological response to a standardised speed endurance training session was investigated in a study by Mohr et al. (2007) where participants completed eight 30 s runs at an exercise intensity corresponding to ~130% VO_{2max} with 150 s recovery. It was shown that blood lactate and plasma K^+ reached peak levels >16 and >6 mmol·L-1, respectively, while muscle lactate rose and muscle pH declined markedly (Mohr et al., 2007). Thus, the muscle ion transport systems (for example Na^+-K^+ ATPase, NHE1 and MCT) are highly stimulated during the speed endurance training, which is supported by clear improvements in fatigue resistance during repeated high-intensity exercise and concomitant increases in the protein expression of the respective ion transporters mentioned above. Table 2 provides a comprehensive summary of the change in high-intensity exercise performance (Table 2A) and muscle ion transport proteins playing key roles in regulating intramuscular pH and ion homeostasis (Table 2B) after periods of different high-intensity training interventions having speed endurance training elements.

Intensified training and endurance performance

Several studies applying speed endurance based training regimes have studied the effects on physiological variables associated with performance in endurance-based sports events. Studies using moderately trained subjects have demonstrated improvements ranging between 3-7% in VO_{2max} (Iaia & Bangsbo, 2010), as well as increased VO_{2max} speed (Esfarjani & Laursen, 2007). In a study by Bangsbo et al. (2009) well-trained distance runners demonstrated a ~3% increase in 3 and 10 km running performance as well as maintenance of VO_{2max} and both glycolytic and oxidative enzyme activity. However, running economy at continuous submaximal speeds rose by 3% and RER during fast speed running was significantly lowered, which indicated a higher fat oxidation capacity during intense exercise. This may exert a muscle glycogen sparring effect during intense exercise, which is supported by others showing a decrease in muscle glycogen degradation after a period with speed endurance training (Iaia et al., 2009). Moreover, it has been shown in elite football players that a short period with lowered training volume, but increased focus on speed endurance training, caused improvements in running economy (Christensen et al., 2011). Thus, speed endurance training seems also to improve mechanical efficiency during exercise in trained footballers, while the aerobic power and muscle oxidative capacity can be maintained. These adaptations may contribute to elevated fatigue resistance throughout and especially in the final stage of a football game.

Yet another physiological advantage of intensified training in football is to ensure that a greater portion of the muscle is being trained. For example it has been shown in runners after reducing their training volume and raising the training intensity that the area of the type IIx fibres was higher (Iaia et al., 2009). The muscle fibre type recruitment is highly dependent on exercise intensity and mode. Based on studies which have observed decrements in muscle glycogen in both type I and II fibres, we can assume that all fibre types are being used during a football game (Krustrup et al., 2006). Thus, by including aerobic high-intensity and speed-endurance training in your training strategy a more homogenous training response in all muscle fibre types may be expected.

INDIVIDUAL TRAINING IN FOOTBALL

It is necessary in team sports such as football to plan and organise the fitness training in relation to the individual demands of all the players in the team. Match analysis studies demonstrate large individual differences between the players in total distance covered, high-intensity running (Mohr, 2008; Mohr et al., 2003), as well as accelerations and sprint characteristics (Mohr, 2008; Di Salvo et al., 2009; Bangsbo & Mohr, 2014). Figure 2 shows the peak speed, length and duration of all sprints performed in a game by two different players (A and B). It is clear that player A performs markedly more sprinting during the game and several sprints are longer than 30 m and a peak speed higher than 30 km/h is reached. In contrast player B performed only few sprints whereas most are short accelerations.

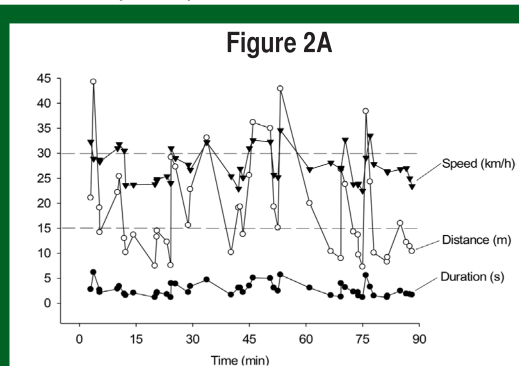


Figure 2. Peak speed, length and duration of all sprints performed by two top-class football players in the same game.

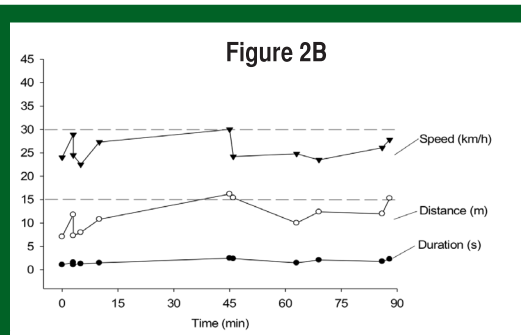
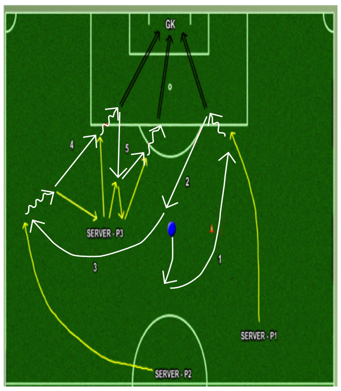


Figure 2. Peak speed, length and duration of all sprints performed by two top-class football players in the same game.

To a certain degree these differences are related to the playing position of the player, but also within the same playing position large differences are present (see for example Bangsbo & Mohr, 2014). In addition, similar variations are present in small-sided games (Dellal et al., 2012), and with some player types there is not consensus between the work profile in games and the training response during small-sided games (Mohr, unpublished observations). Thus, these players may not be sufficiently physically loaded during small-sided games to cope with their individual game demands. Therefore, fitness training in high-level football is proposed to include an individual player-specific approach. Some top-class teams have to our knowledge and experience player-specific fitness training as a regular part of their training model. Figure 3 shows an example of a speed endurance production drill used by a top-class team. The drill was constructed for a top-class attacker after detailed analysis of the game activity profile of the player including important technical challenges that were deemed as key performance indicators for the specific player. In the drill the player performs brief accelerations (~5 m), explosive directional changes and longer sprints (~30 m), which are similar to runs the player performs in important game situations (Figure 3). The player has a number of technical challenges including three shots at the goal (Figure 3). These are all similar to game situations for the respective player and are all performed at high speed, while the player is under physical stress.

Figure 3



1. Accelerate (maximally), explosive turn (~100°) and curved run (>28 km/h, control, dribble and shoot at the goal
2. Explosive turn (~90°), Defensive run (>22 km/h)
3. Curved run to left side (>28 km/h), control, dribble and wall-pass with server
4. Sprint to box (max acceleration), control the ball and shoot at the goal
5. Explosive turn (~150°), accelerate maximally to server, wall-pass and sprint to box (max acceleration) and shoot at the goal

~20 s exercise: 120 s recovery x 6 (2 sets separated by 10 min of low intense activity)

Figure 3. An example of an individual drill designed for a top-class attacker. The player performs a maximal acceleration, explosive turn and a curved sprint after the deep pass from the server/coach (position-1; P1) controls the ball using one touch and shoots the goal (1). The player turns, performs a defensive run at high speed (2), then sprints to the left side to the pass from the server/coach (position-2; P2) and controls the ball with one touch. The player dribbles, plays a wall-pass with the server/coach (position 3; P3), sprints, dribbles into the penalty area and shoots the goal (4). The player turn, sprints to the pass from the server/coach, plays another wall-pass, turns and sprints and shoots the goal (5). The exercise time is approximately 20 s and the recovery time is around 100 s. The player performs 12 intervals in total divided into two series separated by 10 min of low-intensity aerobic activities.

The drill shown above is constructed to fulfill the criteria of speed endurance production training with a very high intensity throughout the drill. The running speed is adjusted to peak speeds reached in a game based on match analysis data and can be monitored during the drill with, for example, real-time GPS technology. Finally, the technical football challenges are part of the key performance indicators of the specific player which partly are determined by the coaches and partly by detailed video analysis. From a physiological perspective the player is training systems associated with fatigue resistance during the demanding peak periods of a game and from a football perspective the player is being challenged within individual technical key components of performance in physically demanding conditions. From a motivational and educational point of view this type of training also has advantages in order to make the player aware of his/her own game demands and physical development.

SUMMARY

In summary football match-play is highly demanding and exerts a considerable taxation of aerobic and anaerobic energy systems, which has been demonstrated to provoke fatigue during and at the end of a game. Therefore, a principal aim of physical training in football is to improve physiological systems associated with game-specific fatigue resistance. Aerobic high-intensity and speed endurance training are suggested as main components of fatigue-resistance training in football, and have been demonstrated to be targeting a wide range of physiological systems linked to improved football fatigue resistance. Finally, large individual variations are present between the players in a team in physical and technical demands. Therefore, it is proposed that individual player-specific fitness training is incorporated into training regimes in elite football.

ACKNOWLEDGEMENT

The present paper is dedicated in memory of our late friend and colleague, Nick Broad.

Table 2a. Repeated sprints and exhaustive intermittent high-intensity performances

Study	Subjects					Training											Performance changes					
																	Repeated sprint			Intermittent HI to exh.		
Author	No./Sex	Age	Sport	VO2-max (ml/kg/min)	Fitness status	Type	Mode	Intensity	Exercise duration (s)	Rest (s)	No. reps	No. sets	Rec. Sets (min)	Frequency (days/wk)	Total duration (wk)	Training volume/ other training added	Best sprint/PPO (%)	Mean/Total sprint/ MPO (%)	Fatigue index/Sdec (%)	YYIR1 (%)	YYIR2 (%)	Others (%)
Serpiello et al. 2012	7M 3F	22	Team sports	53.7	NON-ATH	RS	Treadmill	Maximal	4	20	5	3	4.5	3	4	-	2.4	↑10.6	-2.5	-	-	-
Serpiello et al. 2011	7M 3F	22	Team sports	53.7	NON-ATH	RS	Treadmill	Maximal	4	20	5	2	4.5	3	3.3	n.r.	8.6	9.2	-	↑7.3	-	-
Fernandez et al. 2011	12M	21	Tennis	55.6	ATH	RS	Running	Maximal	~5	15	10	3	Active recovery (8 min of 2 vs. 1 tennis game)	3	6	In addition to training intervention: 1-2 low-intensity injury prevention training/wk	-	↑3.8	-13.9	-	-	-
Ferrari Bravo et al. 2007	13M	17-23	Soccer	55.7	ATH	RS	Running	Maximal	~7-8	20	6	3	3	2	7	Maintained/ In addition to training intervention: 1-2 training/wk	-	↑2.1	-10.4	↑28.1	-	-
Faiss et al. 2013	20M	35	Cycling	51.6	NON-ATH	SEM	Cycle ergometer	Maximal	10	20	5	3	5	2	4	In addition to training intervention: 5.1 h not specified training	↑5.6	↑5.9	-	-	-	-
Mohr et al. 2007	7M	25	-	49.0	NON-ATH	SEM	Running	130% VO2max	30	90	8	1	-	3-6	8	n.r.	1.0	↑2.4	↓53.8	-	↑28.7	-
Edge et al. 2010	6F	19	Team sports	45.6	NON-ATH	SEM	Cycle ergometer	92-111% VO2max	120	180	6-10	1	-	3	5	Maintained	-	↑12.0	-	-	-	-
Walklate et al. 2009	3M 3F	19	Badminton	n.r.	ATH	SEM	Badminton specific	Maximal	20	10	7-15	1	-	2	4	Maintained (4 sessions/wk of regular badminton training)	-	5	-7.5	-	-	-

NON-ATH = non-athletes, **ATH** = athletes, **S** = sprint training, RS = repeated sprint training **SEM** = speed endurance maintenance training, **SEP** = speed endurance production training.
n.r. = not reported, ↑ indicates significantly increased, ↓ indicates significantly decreased.
S_{dec} = percentage decrement score, **YYIR** = Yo-Yo intermittent recovery test.

Study	Subjects					Training											Performance changes					
																	Repeated sprint			Intermittent HI to exh.		
Author	No./Sex	Age	Sport	VO2-max (ml/kg/min)	Fitness status	Type	Mode	Intensity	Exercise duration (s)	Rest (s)	No. reps	No. sets	Rec. Sets (min)	Frequency (days/wk)	Total duration (wk)	Training volume/ other training added	Best sprint/PPO (%)	Mean/Total sprint/ MPO (%)	Fatigue index/Sdec (%)	YYIR1 (%)	YYIR2 (%)	Others (%)
Ortenblad et al. 2000	9M	24	-	n.r.	NON-ATH	SEP	Cycle ergometer	Maximal	10	50	20	1	-	3	5	-	-	↑12.0	-	-	-	-
Dawson et al. 1998	9M	22	-	57.0	ATH	SEP	Running	90-100% Maximal	<10	40-60	4-8	3-5	2-4	3	6	-	-	↑2.2	-16.9	-	-	-
McKenna et al. 1993	6M	19	-	51.1	NON-ATH	SEP	Cycle ergometer	Maximal	30	150-240	4-10	1	-	3	7	-	↑6.0	↑10.6	↓6.0	-	-	-
Thomassen et al. 2010	7M	23	Soccer	~55	ATH	SEP	Soccer specific	Maximal	25-30	~180	10-12	1	-	2	2	~-30% training volume/ Aerobic HI (SSG)	↔	↑1.9	-36.7	-	6.1	-
Gunnarsson et al. 2012	7M	23.3	Soccer	60.6	ATH	SEP	Running + Soccer specific	90-95% Maximal	30	180	5-9	1	-	1	5	+11% training volume/wk +80% no. Matches/wk	-	-	-	-	↑10.8	-
Ingebrigtsen et al. 2012	16M	17	Soccer	n.r.	ATH	SEP	Running	80-100% Maximal	30-40	180-240	5-6 or 8-10	1 or 2	5	2	6	Maintained	1.0	0.9	-	-	↑11.3	-
Iaia et al. 2008	8M	33.4	Endurance running	55.8	ATH	SEP	Running	93% Maximal speed during 30-s all-out sprint run	30	180	8-12	1	-	3-4	4	-64% training volume/wk	-	-	-	-	↑19	-
Gunnarsson et al. 2013	8M	34	Cycling	59.1	ATH	SEP	Bike	85-95% PPO	30	270	10-12	1	-	2-3	7	-70% training volume/wk. In addition to training intervention: 1-2/wk 4-5x3-4-min at 90-100% HRmax	↑4.0	↑3.0	-	-	-	-

NON-ATH = non-athletes, **ATH** = athletes, **S** = sprint training, RS = repeated sprint training **SEM** = speed endurance maintenance training, **SEP** = speed endurance production training.
n.r. = not reported, ↑ indicates significantly increased, ↓ indicates significantly decreased.
S_{dec} = percentage decrement score, **YYIR** = Yo-Yo intermittent recovery test.

Table 2b. Muscle pH regulatory proteins and in vitro muscle buffer capacity

Study: Author	Subjects: No./Sex	Age	Sport	VO2-max (ml/kg/min)	Fitness status	Training: Type	Mode	Intensity	Exercise duration (s)	Rest (s)	No. reps	No. sets	Rec. Sets (min)	Frequency (days/wk)	Total duration (wk)	Training volume/ other training added	Muscle pH regulatory proteins (% change): NHE1	MCT1	MCT4	NBCe1	NBCe2	CAII	CAIV	β (%)
Bell et al. 1988	8M 1F	26	-	52.9	NON-ATH	SEM	One-legged knee extension	150% thigh VO2max	20	60	15-20	1	-	4	7	-	-	-	-	-	-	-	-	↑16
Mohr et al. 2007	7M	25	-	49.0	NON-ATH	SEM	Running	130% VO2max	30	90	8	1	-	3-6	8	n.r.	↑31	↑28	12	-	-	-	-	-
Pilegaard et al. 1999	7M	20-24	-	n.r.	NON-ATH	SEM	One-legged knee extension	80 rpm (30-s), 60 rpm (60-s) Resistance: 100-120 N (30-s), 50-100 N (60-s)	30 60	120	2 3	3-5	n.r.	3-5	8	-	-	↑70	↑33	-	-	-	-	2
Juel et al. 2004	6M	25.3	-	50.2	NON-ATH	SEM	One-legged knee extension	150% thigh VO2max	60	180	15	1	-	3-5	7-8	-	↑16	↑15	11	-	-	-	-	-
Harmer et al. 2000	7M	22	-	~50	NON-ATH	SEP	Cycle ergometer	Maximal	30	180-240	4-10	1	-	3	7	-	-	-	-	-	-	-	-	8
Sharp et al. 1986	8M	22-29	-	52.8	NON-ATH	SEP	Cycle ergometer	Maximal	30	240	8	1	-	4	8	-	-	-	-	-	-	-	-	↑37
Gibala et al. 2006	8M	22	Various sports	~53	NON-ATH	SEP	Cycle ergometer	Maximal	30	240	4-6	1	-	3	2	Maintained (2-3 training/wk (~2.5 h))	-	-	-	-	-	-	-	8
Burgomaster et al. 2007	8M	22	Various sports	50	NON-ATH	SEP	Cycle ergometer	Maximal	30	240	4-6	1	-	3	6	n.r.	-	↑120	↑50	-	-	-	-	-
Thomassen et al. 2010	7M	23	Soccer	~55	ATH	SEP	Soccer specific	Maximal	25-30	~180	10-12	1	-	2	2	~-30% training volume/ Aerobic HI (SSG)	-5	13	12	-	-	-	-	-
Gunnarsson et al. 2012	7M	23.3	Soccer	60.6	ATH	SEP	Running + Soccer specific	90-95% Maximal	30	180	5-9	1	-	1	5	+11% training volume/wk +80% no. Matches/wk	-6	↑9	2	-	-	-	-	-
Iaia et al. 2008	8M	33.4	Endurance running	55.8	ATH	SEP	Running	93% Maximal speed during 30-s all-out sprint run	30	180	8-12	1	-	3-4	4	-64% training volume/wk	↑30	-3	3	-	-	-	-	-3
Puype et al. 2013	9M	25	Various sports	53.3	ATH	SEP	Cycle ergometer	80% MPO-Maximal	30	270	4-9	1	-	3	6	In addition to training intervention: 3-5 days/wk non-strenuous exercise training	-	66	-5	-	-	-	-	-
Gunnarsson et al. 2013	8M	34	Cycling	59.1	ATH	SEP	Bike	85-95% PPO	30	270	10-12	1	-	2-3	7	-70% training volume/wk. In addition to training intervention: 1-2/wk 4-5x3-4-min at 90-100% HRmax	30	-7	-19	-	-	-	-	-

NON-ATH = non-athletes, **ATH** = athletes, **S** = sprint training, RS = repeated sprint training **SEM** = speed endurance maintenance training, **SEP** = speed endurance production training.
n.r. = not reported, ↑ indicates significantly increased, ↓ indicates significantly decreased.
NHE1 = Na+/H+ exchanger isoform 1, **MCT** = monocarboxylate transporter, **NBCe** = sodium/bicarbonate co-transporter, **CA** = carbonic anhydrase, **β** = in vitro muscle buffer capacity.

Table 2b. Membrane potassium-transporting proteins in skeletal muscle.

Study	Subjects					Training											Potassium Transporting Proteins (% change)								
																	Na+,K+-ATPase pump subunits					Others			
Author	No./Sex	Age	Sport	VO2-max (ml/kg/min)	Fitness status	Type	Mode	Intensity	Exercise duration (s)	Rest (s)	No. reps	No. sets	Rec. Sets (min)	Frequency (days/wk)	Total duration (wk)	Training volume/ other training added	α1	α2	β1	β2	FXYD1	NKCC1	Kir2.1	$K_{Ca}1.1$	K_{ATP}
Mohr et al. 2007	7M	25	-	49.0	NON-ATH	SEM	Running	130% VO2max	30	90	8	1	-	3-6	8	n.r.	22	↑68	↑32	-	-	-	-	-	-
Nielsen et al. 2003	6M	25	-	50.2	NON-ATH	SEM	One-legged knee extension ergometer	Kicking frequency at 60 rpm 150% leg VO2max	60	180	15	1	-	3-5	7	-	↑29	↑15	16	-	-	-	-	-	-
Thomassen et al. 2010	7M	23	Soccer	~55	ATH	SEP	Soccer specific	Maximal	25-30	~180	10-12	1	-	2	2	-~30% training volume/ Aerobic HI (SSG)	18	↑15	3	-	↑27	↔	-	-	-
Gunnarsson et al. 2012	7M	23.3	Soccer	60.6	ATH	SEP	Running + Soccer specific	90-95% Maximal	30	180	5-9	1	-	1	5	+11% training volume/wk +80% no. Matches/wk	2	-5	↓13	-	-	-	-	-	-
Bangsbo et al. 2009	12M	35	Running	63	ATH	SEP	Running	95% Maximal speed	30	180	8-12	1	-	2-3	6-9	-~30% (from 50 to 35 km/wk). In addition to training intervention: 1/wk 4x4' at 85% Hrmax + 1-2/wk aerobic training	-8	↑68	10	-	-	-	-	-	-
Iaia et al. 2008	8M	33.4	Endurance running	55.8	ATH	SEP	Running	93% Maximal speed during 30-s all-out sprint run	30	180	8-12	1	-	3-4	4	-64% training volume/wk	↑29	17	2	-	-	14	-	-	-
Gunnarsson et al. 2013	8M	34	Cycling	59.1	ATH	SEP	Bike	85-95% PPO	30	270	10-12	1	-	2-3	7	-70% training volume/wk. In addition to training intervention: 1-2/wk 4-5x3-4-min at 90-100% HRmax	-10	-8	-3	-	-	-	18	↓14	-

NON-ATH = non-athletes, **ATH** = athletes, **S** = sprint training, RS = repeated sprint training **SEM** = speed endurance maintenance training, **SEP** = speed endurance production training.
n.r. = not reported, ↑ indicates significantly increased, ↓ indicates significantly decreased.
FXYD1 = Na^+,K^+ pump accessory and regulatory protein phospholemman, $\mathbf{K_{ATP}}$ = ATP-dependent K^+ channel, $\mathbf{K_{Ca}1.1}$ = big-conductance Ca^{2+} -dependent K^+ channel, **Kir2.1** = strong inward rectifier K^+ channel, **NKCC1** = Na^+-K^+- $2Cl^-$ 1 protein co-transporters.

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