



UTILISATION OF DIFFERENT ENERGY SOURCES DURING EXERCISE AND NUTRITIONAL STRATEGIES FOR EFFECTIVE RECOVERY

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SUMMARY

In this text, we will examine how the body uses the nutrients in food to produce energy during exercise, and whether these processes differ between the sexes. If they do, does this mean that the nutritional requirements should be different for men and women? We will also present current knowledge on the effects of nutrition on recovery after physical activity, a topic that has attracted much interest in the sports world. Finally, we will briefly discuss the nutritional requirements of physically active women and the common nutritional problems they encounter.

TAKE HOME MESSAGES:

- Women appear to oxidise relatively more fat than men do during submaximal endurance exercise. However, it is difficult to match male and female subjects perfectly with regard to fitness level, which may explain—at least in part—this apparent sex difference.
- During repeated bouts of high-intensity exercise, fatigability and changes in muscle metabolism are similar in men and women when they exercise at the same initial peak power output. However, because women generally perform at a lower peak power output, they become less fatigued during repeated 10-second or 30-second sprints.
- The contribution of protein to energy production is estimated to be less than 5% during exercise under normal physiological conditions, and women seem to oxidise protein to a lesser extent than men do.
- To promote effective recovery, carbohydrates should be ingested shortly after exercise, especially if additional training is to be performed on the same day.
- To maximise the effect of training and optimise recovery, essential amino acids or protein should be ingested shortly after, or even during, exercise to stimulate the formation of new muscle protein.
- The differences observed between the sexes with respect to utilisation of different energy sources during exercise provide no basis for different dietary recommendations regarding intake of carbohydrates, fat and protein for men and women.
- Physically active women often consume too little calcium and iron, as well as other nutrients. Such deficiencies can be avoided by eating a wellbalanced and varied diet.

INTRODUCTION

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Energy is stored in the body as phosphocreatine, glycogen (in muscle and liver) and fat (in adipose tissue and muscle). The main biochemical fuels, termed *substrates*, used by muscles to provide energy are blood glucose, muscle glycogen, free fatty acids from the blood and triglycerides stored within the muscles. Phosphocreatine is an important fuel during very intense short-term exercise. It provides energy very rapidly through breakdown that can occur in the absence of oxygen (anaerobic metabolism). Glycogen can also be degraded anaerobically to rapidly produce energy, with lactate as the end product. In addition, glycogen can be oxidised, that is, degraded in the presence of oxygen (aerobic metabolism), which produces water and carbon dioxide as end products. However, the maximal rate of energy delivery is only 30% of the rate of anaerobically produced energy. Fat can only be oxidised—there is no anaerobic degradation of fat—and the rate of energy delivery is only half that of the aerobic breakdown of muscle glycogen.

The degradation processes include: (1) glycolysis; (2) the citric acid cycle; and (3) the electron transport chain. The reactions of glycolysis occur in the cytoplasm (the fluid matrix) of the cells. The reactions of the citric acid cycle and the electron transport chain occur in the mitochondria (small organelles in the cell that are referred to as the cell's 'powerhouses'). The reactions are all catalysed (facilitated) by proteins called enzymes, some of which are considered 'rate-limiting' for the different processes. The energy generated by these processes is transferred into adenosine triphosphate (ATP), which subsequently is used for processes in the cells that require energy.

Proteins and their constituents, amino acids, can also supply energy through oxidation. Their contribution to energy metabolism can be as high as 20% at rest; however, during exercise the contribution of protein is low, and is estimated to be less than 5% of energy production under normal physiological conditions.

FACTORS INFLUENCING WHICH SUBSTRATES ARE UTILISED FOR ENERGY PRODUCTION

Endurance exercise

Exercising muscles use mainly carbohydrates and fat as substrates for energy production, except during very intense short-term exercise. The relative amounts of fat and carbohydrates that are oxidised by muscle to produce energy depend on the intensity and duration of the exercise, on how well-trained the individual is, and on dietary habits. During low-intensity exercise, oxidation of carbohydrates accounts for approximately 50–60% of energy metabolism, but as the exercise intensity increases, the carbohydrate contribution gradually increases, reaching 100% when exercising at maximal intensity. The better trained an individual is, the more fat is oxidised at any given sub-maximal rate of work. Ingestion of a diet high in fat leads to enhanced fat oxidation, and when the diet contains large amounts of carbohydrates, their relative contribution to energy production is elevated.

There is some evidence that women use proportionally more fat than men do during submaximal exercise. Several studies on recreationally active individuals reveal that during light to moderately intense exercise (i.e. 45–75% of peak oxygen uptake), the respiratory exchange ratio (RER) is lower, and thus the relative oxidation of fat is higher in women, even when expressed per kilogram lean body mass. Moreover, in some studies, the blood concentration of free fatty acids rises more in women than in men during exercise, and women also express the fatty acid transporter CD36 at higher levels in their muscle. These two factors may promote more rapid uptake and oxidation of fatty acids. In some investigations, the lower oxidation of carbohydrates by women appears to reflect less breakdown of muscle glycogen, whereas other studies report reduced uptake of glucose by the muscle, but no effect on glycogen breakdown. Administration of oestrogen to male subjects increases the relative contribution of fat to energy metabolism during moderate to intense exercise. Simultaneously, both release of glucose from the liver and glucose uptake by muscle are attenuated. These observations reveal that oestrogen is involved in regulating substrate utilisation, and support the view that women oxidise proportionally more fat than men do, although the mechanisms underlying this effect of the female hormone are presently unclear.

However, not all studies have found a sex difference in the proportion of carbohydrates and fat oxidised during exercise. For example, well-trained men and women (matched on the basis of their maximal oxygen uptake per kilogram lean body mass, their level of physical activity and training routine) demonstrated the same RER during exercise, which indicates the same relative oxidation of fat. At the same time, the women utilised intramuscular triglycerides to a greater extent than the men did, which may reflect their higher levels of this form of energy storage. Thus, a sex difference may exist in the *type* of fat metabolised, rather than in the total oxidation of fat.

Moreover, in another study, the more extensive oxidation of fat by women was actually related to the higher oxidative capacity of their muscles (as a result of a larger proportion of slow-twitch type I fibres and higher capillary density), rather than directly to a genetic difference between the sexes. This finding illustrates the great difficulty in matching female and male subjects perfectly, even when great care is taken to match their levels of fitness and activity, as well as factors in the period preceding the exercise (e.g. diet and physical activity). Consequently, the variation between men and women with regard to utilisation of different energy sources cannot definitively be explained by sexual dimorphism.

With regard to protein as a substrate, women appear to utilise this energy source during sustained exercise to a lesser extent than men do. This is indicated by less oxidation of leucine, one of the three branched-chain amino acids and lower total loss of nitrogen (a component of proteins) during exercise days. The reason for this difference is not clear, but there is some support for the involvement of oestrogen in protein metabolism as well: oestrogen supplementation to male subjects has been reported to decrease whole body leucine oxidation during exercise.

High-intensity exercise

During short-term intensive exercise, phosphocreatine and anaerobic breakdown of muscle glycogen are the primary sources of energy for the contracting muscles. Compared with the vast number of reports on endurance exercise, relatively little is known concerning possible sex differences in substrate utilisation during high-intensity exercise. Most such studies have involved either a single or repeated 10-second or 30-second sprints. For example, during a 30-second sprint, the levels of ATP and phosphocreatine in the quadriceps muscle were reduced to the same extent in men and women. However, the level of ATP increased more rapidly in the women, primarily in their fast-twitch (type II) fibres, during the 20-minute recovery periods between the sprints. This more rapid recovery in the ATP level resulted in a smaller *overall* reduction in ATP, despite similar reductions in phosphocreatine. On the whole, only relatively minor sex differences in muscle metabolism were observed during this type of repeated high-intensity exercise.

Peak power output during sprinting is generally 30% lower in women than in men, but women can maintain their peak power output during repeated sprints to a greater extent, that is, they become less fatigued. At the same time, blood levels of catecholamines (e.g. adrenalin), ammonia and lactate are less elevated in women, suggesting that their lower level of fatigue is related to the less pronounced changes in muscle metabolism because they are exercising at a lower work rate. Accordingly, women's less pronounced reduction in sprint performance was recently shown to result from their lower initial peak power output, as revealed by the observation that during repeated 10-second sprints a similar reduction in force occurred in subgroups of men and women with the same *initial* peak force. This finding strongly supports the proposal that men and women have a similar capacity for recovery, in contrast to previous suggestions that women are more resistant to fatigue.

Resistance exercise

Knowledge about the relative proportions of fat and carbohydrates oxidised during resistance exercise (e.g. weight training) is considerably less than our knowledge of these processes in endurance training. This deficiency is most likely because of the difficulty in obtaining reliable measurements of oxygen uptake (and RER) during this type of non-steady-state exercise. Muscle glycogen is used to large extent, especially by the type II fibres, but no data are available on differences between the sexes. The increase in blood lactate concentration (an indication of the anaerobic breakdown of glycogen) at a given *relative* work load during, for example, leg press exercise is less in women than in men. This may partly be due to the slightly lower glycolytic capacity in women (see below), although the fact that the *absolute* load is less for women is probably the major reason for this difference.

Characteristics of skeletal muscle related to substrate metabolism

Human skeletal muscle contains a mixture of fibre types that exhibit different contractile and metabolic properties; the slow-twitch type I fibres have higher levels of oxidative enzymes and a greater capacity to oxidise fat and carbohydrates, whereas the fast-twitch type II fibres contain higher levels of glycolytic enzymes and, consequently, have higher anaerobic capacity. The most frequently studied muscle in humans is the lateral part of the quadriceps muscle, the vastus lateralis, and the following information therefore relates to this specific muscle. The content (maximal activities) of the mitochondrial enzymes that control carbohydrate and fat oxidation has been reported to be similar in men and women. However, the levels of glycolytic enzymes are slightly lower in women, which probably is related to the smaller area occupied by type II fibres (see below). The average proportion of type I fibres in the quadriceps is similar in young men and women (about 50%, with a wide range from 15 to 85%). Possibly, the proportion is slightly higher in women. The cross-sectional area of these fibres is comparable in men and women, whereas the area of the type II fibres is 40-50% larger in men. The capillary density, expressed per square millimetre, is the same in men and women, although because of their larger fibre areas, the number of capillaries per fibre is higher in men.

The most important factor responsible for women's generally lower maximal strength and power output during resistance and high-intensity exercise, respectively, is their smaller muscle mass. The slightly lower glycolytic capacity and, possibly, a slightly higher proportion of type I fibres in the quadriceps muscles of women may also contribute, but to lesser extent.

Variations throughout the menstrual cycle

Several investigators have examined how variations in the levels of oestrogen and progesterone during the menstrual cycle might influence substrate metabolism during exercise. In agreement with the fact that oestrogen reduces oxidation of carbohydrates and increases the availability of free fatty acids, some studies have found differences in substrate utilisation during various phases of the menstrual cycle; however, others observed no variation. This discrepancy might be explained, at least in part, by differences in the intensity and duration of the exercise, as well as in nutritional intake. These factors have been proposed to exert a more pronounced influence on substrate utilisation than that of hormonal variations.

The marked variation in hormone levels across the menstrual cycle is not reflected in different rates of muscle protein synthesis and, indeed, only small variations in protein metabolism occur during the menstrual cycle in young women.

RECOVERY FROM EXERCISE

Replenishing energy stores

In preparation for the next training session, it is important to refill both muscular and hepatic (liver) stores of glycogen. Rapid ingestion of carbohydrates following exercise elevates the rate of glycogen synthesis nearly four-fold (from 0.4 to 1.4 g/h/kg bodyweight), whereas waiting for 2 hours before such ingestion only increases this rate about half as much. The more pronounced effect of immediate ingestion can be explained by more rapid glucose uptake and stimulation of glycogen synthesis in the exercised muscle. Intake of carbohydrates soon after the exercise is especially important when the next training session or competitive event is performed on the same day.

Intake of hydrolysed protein or of specific amino acids in combination with carbohydrates has been observed to further augment glycogen re-synthesis in some recent studies, but not in others. These divergent findings can largely be explained by the greater amount of energy supplied after the addition of protein. Increasing the amount of carbohydrates consumed eliminates the additional effect of protein intake. One practical consequence is that maximal re-synthesis can be achieved even when some of the carbohydrate is replaced by protein. Athletes are advised to eat 70–100 g of carbohydrates (or, alternatively, 1.2–1.5 g/kg bodyweight) within the first 30 minutes after exercise, with an additional intake of 150–200 g during the next 2 hours. An hourly energy intake of 5–6 kcal/kg bodyweight is recommended, with about 20% of the calorie intake in the form of protein if desired. Furthermore, intake of the supplement as a drink is convenient directly after exercise and results in a more rapid uptake of glucose and amino acids than solid food.

Glycogen loading

Most studies on strategies for glycogen loading have used male subjects and the results are assumed valid for women as well. In an early investigation on both men and women, the intake of carbohydrates was increased from 55–60% to 75% of the daily energy requirement for 4 days. This procedure elevated the level of muscle glycogen in male endurance athletes by 40%, but had no effect on the glycogen stores in female athletes. The original conclusion that women lack the capacity to load muscle glycogen was later rejected; instead, the findings were explained by the smaller amounts of carbohydrates ingested by the women. In later reports, the elevation in muscle glycogen levels was the same in men and women

following intake of 11–12 g of carbohydrates per kg lean body mass, an intake within the range recommended during periods of intensive training (7–12 g/kg bodyweight/day).

Stimulation of protein synthesis

Resistance exercise has marked effects on protein turnover, with increases in protein synthesis lasting up to 2 days after a single bout of exercise. However, resistance exercise also increases protein breakdown. Therefore, in order to attain a positive net balance, nutritional stimulus in the form of amino acids or a protein supplement must be provided. Moreover, only the essential amino acids are required for stimulation of protein synthesis, whereas the nonessential amino acids have no further effect. For maximal stimulation of protein synthesis, the recommended intake of essential amino acids or intact protein is approximately 10 g or 20 g, respectively. Simultaneous ingestion of carbohydrates provides no additional stimulation of protein synthesis, and ingestion of carbohydrates alone has only a minor effect compared to that of amino acids.

Also, a single bout of endurance exercise such as treadmill walking, dynamic knee-extensor exercise or ergometer cycling increases the rate of protein synthesis for several hours—sometimes up to 72 hours—after the exercise. However, the effect on the rate of protein degradation following exercise is less clear. The conclusion from the few studies available is that ingestion of protein and carbohydrates during and after endurance exercise stimulates the rate of synthesis further, creating a positive net balance. There are no studies on the separate effects of protein, amino acid or carbohydrate supplementation, but the combined effect of carbohydrates and protein is larger than that of carbohydrates alone. This finding of a more pronounced effect in the presence of protein agrees with that following resistance exercise, although it should be noted that no comparisons with a placebo were made in the endurance exercise studies.

Most studies on protein turnover have been performed in men, but women have been included in a number of studies. Although these studies were not specifically designed to explore possible sex differences, no obvious differences were noted in the stimulation of protein synthesis by exercise or nutrition. This conclusion was confirmed by recent experiments actually designed to test for sex differences. The basal rate of muscle protein synthesis appears to be the same in men and women and, furthermore, regular strength training for a period of 12 weeks leads to similar relative increases in muscle mass, independent of sex. Following a session of high-intensity resistance exercise, the rate of protein synthesis increased 50% and the activation of enzymes known to stimulate protein synthesis increased more than two-fold during recovery in both men and women. Furthermore, stimulation of muscle protein synthesis following infusion of insulin and amino acids into young men and women at rest has been reported to be the same anabolic (muscle-building) response in both sexes.

The long-term effects of protein intake soon after training are not well investigated, but three studies — two reports on young men and one on young women — document beneficial long-term effects. In two studies, one on male and one on female subjects, the increase in muscle fibre area following 12–14 weeks of training was greater when a protein supplement, rather than a carbohydrate supplement, was taken immediately after each session. In another study on young men, 8 weeks of resistance training in combination with a leucine and whey protein supplement induced a greater increase in muscle strength compared to the effect of a carbohydrate supplement. However, the increase in cross-sectional area of the

quadriceps muscle was similar with both supplements. Overall, these observations indicate that a protein supplement ingested in connection with exercise also enhances the anabolic effect of training in the longer term.

Molecular signalling

The adaptive responses of skeletal muscle to exercise and nutritional supplements in the form of protein or amino acids are both likely to be mediated, at least in part, by the mammalian target of rapamycin (mTOR) signalling pathway. Following resistance exercise, activation of this pathway, which appears to be a major regulator of muscle mass, occurs in parallel with an elevation in the rate of protein synthesis in both men and women. Furthermore, in both men and women, intake of essential amino acids in combination with resistance exercise markedly enhances the phosphorylation of mTOR and its downstream effector, p70S6 kinase, which is indicative of activation of this pathway.

The few investigations involving both men and women have revealed no obvious disparity in the response to exercise and nutrition—at least with regard to the signalling pathways that have been studied. However, many more studies on a larger number of signalling proteins are required to elucidate possible sex differences, including investigating the role of female hormones in adaptation to training.

NUTRITIONAL REQUIREMENTS FOR ATHLETES

Carbohydrates

According to the Nordic Nutrition Recommendations from 2012, carbohydrates in the diet should provide 45–60% of the energy requirement for a normally active individual, which corresponds to 250–450 grams per day. For elite endurance athletes, the corresponding recommendation is that approximately 70% of the energy required daily should be provided by carbohydrates, which equates to 600–800 grams per day (i.e. 6–10 g/kg bodyweight/ day), depending on the type, intensity and duration of training. The lower amounts are recommended for women, because of their smaller muscle mass. For balanced energy intake, however, these quantities can be somewhat problematic for women who do not expend large amounts of energy. To consume the recommended amount of carbohydrates *and* adequate amounts of protein and fat without being in energy surplus can be difficult for female athletes. A constant energy surplus will ultimately lead to weight gain, which may hamper performance.

Protein

The general recommendation with respect to daily protein intake is the same for men and women, that is, a minimum of 0.8 g/kg bodyweight for a normally active individual. Because protein turnover is enhanced by training (see also above), a higher intake (1.2–1.8 g/kg bodyweight) is often recommended for athletes. Although protein oxidation during endurance exercise has been reported to be lower in women than in men, this difference is of relatively minor importance due to the small contribution of protein to energy metabolism. Thus, any distinction between the protein requirement for men and women in connection with physical activity appears unnecessary. The recommended protein intake can easily be achieved with a balanced and varied diet without special attention to dietary protein, as long as the energy intake is adequate. In fact, individuals who perform endurance and strength training generally consume amounts of protein within or above the recommended range.

Fat

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In general, the intake of carbohydrates and protein should be a priority for physically active individuals. Any remaining energy needs can be covered by intake of fat, which then accounts for about 25–30% of the energy intake. This figure is within the Nordic Nutrition Recommendations for normally active individuals (25–40% of energy intake).

There is no evidence that high-fat diets improve performance. Therefore, high fat consumption is not recommended at the expense of a carbohydrate-rich diet. Usually, active individuals are advised to eat enough fat to provide at least 15% of their total energy intake to minimise the risk of consuming insufficient energy and other nutrients such as fat-soluble vitamins and essential fatty acids.

With respect to the type of fat to consume, the recommendations for physically active individuals and the general public are the same: approximately 5–10% of the total energy intake as polyunsaturated fat and 10–20 % as monounsaturated fat, while the consumption of saturated fat should be limited to 10%. The intake of industrially produced 'trans' fatty acids should be limited as far as possible. There is no evidence that the recommended fat intake for men and women should differ.

Vitamin and minerals

Vitamins and minerals do not provide energy but are essential for good health and body function. They must be supplied by the diet, since our bodies cannot produce them. Many physically active women consume too little of various B vitamins and bone-building nutrients such as calcium, zinc and magnesium. Calcium is a key component of bone mass and inadequate intake elevates the risk of low bone density and stress fractures. However, optimal bone density requires not only an adequate intake of calcium but also adequate ingestion of vitamin D, as well as normal levels of oestrogen in the blood.

Moreover, physically active women often consume too little iron and lack of iron is the most common nutritional deficiency among women in general. It has been reported that 15–60% of physically active women have inadequate stores of iron in the body, mainly because they seem to avoid foods rich in the form of iron that is well absorbed (haeme iron). Vegetarian diets also worsen the iron status, since the form of iron in this type of diet is generally not well absorbed.

NUTRITIONAL DEFICIENCIES

As a group, women who are training intensively appear to be exposed to nutritional deficiencies. These risks are probably not due to sex per se, but rather to inadequate intake of energy and nutrients. Several studies have recently identified physically active women as particularly prone to a variety of unhealthy conditions. These include, to varying degrees, irregular menstruation, low bone mineral density and low energy intake. In extreme conditions in these women, amenorrhoea (absence of menstruation) and osteoporosis (thinning of the bones) may result. These risks can be minimised by a balanced diet that includes dairy products containing bone-building nutrients such as calcium and vitamin D, as well as red meat, which contains iron in an easily absorbed form.

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