THE ENERGETICS OF 'BENT-HIP, BENT-KNEE' WALKING IN HUMANS: IMPLICATIONS FOR THE EVOLUTION OF BIPEDALISM IN EARLY HOMINIDS

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ABSTRACT

Bipedalism is the defining feature of a hominid. Humans remain the single primate adapted to habitual bipedal gait. The first fossils discovered to show conclusive evidence of a bipedal gait are the australopithecine hominids from Africa. The most complete skeleton displaying bipedal characteristics is the australopithecine, AL 288-1, named 'Lucy'. To this day an argument still exists over the probable mode of locomotion in these early hominids. The argument revolves around a central theme: was 'Lucy' habitually using fully upright bipedalism; or was she displaying a flexed posture during locomotion, in addition to displaying some arboreal adaptations? The current study aims to assess the energy cost of these two forms of locomotion in modern humans and goes on to examine the likely cost of a flexed posture to our hominid ancestors. Using this information the study then attempts to resolve the argument over the probable mode of locomotion in 'Lucy'. This work follows on from previous work which assessed the mechanical consequences of a flexed-joint bipedal gait. Computer modelling techniques were previously employed in simulating a flexed gait, both in 'Lucy', non-human primates and in modern humans. Results from a biomechanical model of 'Lucy' walking in a flexed gait (Crompton et al. 1998) show that mechanical energy costs increase substantially with a change in posture.

A combination of physiological techniques were used in this study to assess the cost of a 'bent-hip, bent-knee' (BHBK) gait in modern humans. Oxygen consumption data revealed that BHBK walking in modern humans caused a significant (50%) increase in total energy cost of locomotion over the average cost during normal upright walking. Data for heart rate, core temperature and lactate production was also recorded during both normal and BHBK walking. Heart rate showed a 30% increase during BHBK walking. The physiological index of walking and lactate production both increased by 200% during the BHBK gait when compared to normal upright walking. Rate of perceived exertion increased by two units for the same speed during a BHBK gait. The thermal cost of exercise in a BHBK gait was also significantly higher than the thermal cost of an upright posture. The total increase in temperature during a specific exercise routine in the BHBK gait was more then twice that of normal walking. It was estimated that a recovery period totalling approximately 150% of the time spent active should be assumed for individuals using the BHBK gait.

It was evident during this study that the flexed hip, flexed knee posture in BHBK walking requires substantial muscular stress in order to maintain equilibrium. Electromyographic data predicted that the length of time during the gait cycle in which the major superficial muscles of the lower leg were producing force increased by 50% during BHBK walking.

After taking all the data produced during this study into consideration, it is predicted that the uneconomical nature of BHBK bipedal posture prevent it being maintained by early hominids for long periods of time. This type of locomotion, therefore, cannot represent sustained (habitual) bipedalism. For this reason, it seems very unlikely that this BHBK posture would have been a precursor of the erect posture seen in modern man.

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CHAPTER ONE

INTRODUCTION

Locomotion is "the translation of the centre of gravity through space along a path requiring the least expenditure of energy"

Basmajian (1978)

"Bipedalism is of great functional, morphological, and phylogenetic significance in hominid evolution"

Foley (1992)

1.1 Hominid Evolution and Bipedalism

Bipedalism is by definition characteristic of all hominids, since it is generally accepted to be the principal defining feature of a hominid (Jones et al., 1992). The anatomical changes that were necessary for habitual bipedalism to evolve separate all hominids from habitually quadrupedal hominoids. These morphological changes are distributed throughout the hominid skeleton, and therefore bipedalism is of great functional and phylogenetic significance in the evolution of the human lineage.

Exactly how many species of hominid there have been, which of these first made stone tools, and how they walked remain the three major conundrums of human evolution. Day (1986: p191) concluded from a survey of the literature that "we really have no clear idea of what form of locomotion, in what creature, preceded, or was immediately pre-adaptive for, upright posture and bipedal gait".

AL 288-1, or 'Lucy', a fossil hominid approximately 3.1 million years old (see section 1.3.1), represents the best model for early hominid locomotor morphology (Johanson et al., 1982a; Leakey and Walker, 1997). There is general agreement that the postcranial features of the skeleton are adapted to bipedalism, along with some features which might be better adapted to arboreal climbing. The actual nature of Lucy's locomotion, however, has not been agreed upon. Lovejoy and colleagues (Lovejoy, 1981, 1988; Latimer et al. 1987; Latimer and Lovejoy, 1989; Latimer, 1991, Ohman et al., 1997) hold the view that this early hominid was a completely erect terrestrial biped. They further argue that any adaptations to climbing were primitive features retained from a basically 'quadrupedal' morphology. Lovejoy supports his view with an interpretation of the function of the gluteal muscles as abductors of the hip, which indicates a function of the glutei that is analogous to modern humans. This view is consistent with some of the australopithecine morphology, such as a small acetabulum and femoral head (see section 1.3.6). Latimer and Lovejoy (1989, 1990a, b) and Ohman et al. (1997) present physical evidence (namely specialised morphology of the calcaneus, metatarsophalangeal joint and femoral neck, see section 1.3.6) that the suite of features displayed by the Hadar specimens (AL 288) can only be accounted for by habitual terrestrial bipedality.

An opposing view was presented by Napier back as long ago as 1967, and more recently by Stern and Susman (1983) with respect to the functional morphology of *Australopithecus afarensis*. They argued that the early australopithecines were non-striding bipeds, who were physiologically inefficient, and who walked with their knees and hips slightly bent. Stern and Susman indicate early australopithecine morphology is adapted to climbing as well as to a less than human form of bipedalism. Napier claims this gait would impart a high energy cost to australopithecines and indeed would make long distance travel impossible (Napier, 1967). Napier (p 59) suggests the possibility that "*Australopithecus* walking could be something of a jog-trot". Stern and Susman (1983) argue that the anterior position of the iliac pillar, along with a coronally and posteriorly oriented iliac blade indicate that pelvis stabilisation during bipedalism was more similar to that of apes than humans.

Energetics can provide answers to some of the most important questions in the evolution of bipedalism. One question in particular: 'what are the benefits of upright walking to those species capable of bipedalism?' can and probably must be approached from the energetic viewpoint. It has been proposed that bipedalism (under certain conditions) should confer an energetic advantage in the population (see section 1.2 for other views), compared with other forms of possible locomotion, for it to evolve (Foley, 1992). If bipedalism has evolved because it is energetically advantageous, it should be an 'efficient' gait. While in essence, the efficiency of a gait is the work done during that gait divided by the energy expended (see section 1.5.6), actually measuring efficiency is extremely difficult (Saibene and Minetti, 1992). There are a number of types of efficiency, including muscle efficiency, muscular efficiency and mechanical efficiency, which each have their own definitions and may or may not have different meanings (Saibene and Minetti, 1992).

In the analysis of hominid locomotion therefore, the approach should be an integrative one, adapting the viewpoints of both energetics and mechanics (Saibene and Minetti, 1992).

1.2 Theories for the Evolution of Bipedalism

It has been noted that development of bipedal gait is recognised as a crucial element in the process of hominid evolution. Many studies have therefore aimed at uncovering the primary reasons behind the evolution of bipedalism, and many schools of thought exist on the advantages that an upright posture may have bestowed upon early hominids. It is likely that pressure for the evolution of bipedalism lay in a survival advantage of bipedal animals, in comparison to counterparts practising a different locomotor mode (Day, 1986). The selective pressures identified for development of a bipedal gait fall into 5 major categories (Day, 1986):

i) improved food acquisition and carrying
ii) improved predator avoidance
iii) improved reproductive success
iv) greater energetic efficiency
v) reduced thermal stress

The idea that bipedalism conferred an advantage in foraging and food gathering techniques is an old one (e.g. see DuBrul, 1962). Many studies have linked origins of bipedalism to behaviour during positional food gathering in terrestrial and arboreal environments. Advantages in gathering food are also linked to hypotheses concerning improved carrying of food or young, and the effectiveness of a bipedal gait in freeing the hands for carrying of food or infants is indisputable (DuBrul, 1962; Jolly, 1970; Wrangham, 1980). Hunt (1994, 1996) however, views the postural bipedalism seen in chimpanzees feeding as a vital clue towards our understanding of the origin of bipedalism. He suggests that pre-hominids were already using vertical climbing and an upright bipedal stance in trees for fruit gathering. This enabled a shift to terrestrial environments where hominids would reach into trees from the ground in a bipedal stance whilst using over-hanging branches for balance. Bipedalism in bonobos is strongly linked to food carrying. This may have significance in the evolution of bipedalism (Susman, 1984). Rodman and McHenry (1980) conclude bipedalism evolved from quadrupedalism when foraging activity necessitated increased travel between food patches; therefore suggesting that bipedalism evolved as an efficient foraging tactic. Rose (1991) linked the importance of food gathering strategies to the probable extension and complex opening of habitats during hominid evolution.

Various studies link foraging theory with an increase in social activity. Kurland and Beckerman (1985) speculate that a combination of tool use, social co-operation and environmental modification transformed apes into humans. According to their studies, social foraging increased the success of foraging strategy in patchy environment. A change in habitat from forest to savannah led to more widely dispersed foraging patches, which ultimately led to an increase foraging group size. This theory surmises that the sociality of hominids powered the move to bipedalism.

Hypotheses concerning predator avoidance are largely connected with an assumption that there was a shift from more closed to more open habitats around the time of the early evolution of bipedalism. An upright stance increases visual distance, which is more useful in savannah rather than forested habitats. Some studies (e.g. Day, 1996) link increased predator avoidance with other theories such as tool use and increased efficiency of bipedal gait. The freeing of hands for weapons (Kortlandt,

1980) and the ability to run for long periods are two scenarios where bipeds could gain an advantage in avoiding predators.

There are thus many social and behavioural theories connected with bipedal evolution. There may also be an increase in reproductive success for possessing a bipedal stance, since many primates utilise bipedal stance in aggressive behaviours (Jablonski and Chaplin, 1993; Thorpe, 1997). Bipedal threat displays represent a non-violent alternative to aggressive behaviour in primates, reducing morbidity and mortality in social conflicts, and hence increasing reproductive success (Jablonski and Chaplin, 1993). Jablonski and Chaplin (1993) concluded that habitual bipedalism enhances display behaviour and therefore evolved as an aid in appeasement during group conflict.

The high degree of sexual dimorphism exhibited by early hominids (Häusler and Schmid, 1995; McHenry, 1991b; also see section 3.2) influences some theories concerning behavioural drives behind the evolution of bipedalism. Schich and Toth (1993) developed a hypothesis based around the possibility of a strong monogamous bond between male and female, leading to social organisation where males go out collecting food, while females forage locally. Schich and Toth (1993) consider that this type of reproductive strategy implies a better chance of survival for the offspring, as females stay around a central area looking after the young. Bipedal locomotion is therefore seen as an advantage in carrying out provisioning behaviour for the young in males. This hypothesis seems unlikely, as it implies that bipedalism is only advantageous for males. With no selection pressure existing for females to become bipedal, this does not infer a substantial advantage for the species as a whole.

Many studies have supposed that bipedalism conferred an energetic advantage to early hominids (e.g. Rodman and McHenry, 1980; McHenry, 1991a; Foley, 1992).

The potential energetic advantages of bipedalism will be covered in more detail in section 1.5.8. Upright posture saves 50% of energy expenditure compared to the joint-flexed bipedal posture more commonly observed in chimpanzees (Ishida, 1991). Energetic advantages would therefore be conferred on completely upright bipedal hominids if they regularly employed bipedal locomotion. It is difficult for habitually quadrupedal chimpanzees to sustain upright walking, but a move to bipedalism would have only required a simple postural adjustment in early hominids (Ishida, 1991). Isbell and Young (1996) pose that bipedal walking may have evolved due to decreasing resource availability. Efficient bipedalism may have been a preferable alternative to small-group sizes in response to resource scarcity during the Miocene.

Wheeler (1984, 1991a, b) suggests that bipedalism would have significantly reduced thermal stress in early hominids. This conclusion is based on experiments with a model hominid, and predictions for solar heat gain in both quadrupedal and bipedal postures. He argues that lack of body hair and effective use of evaporative cooling by perspiration aided in reducing thermal stresses in bipedal hominids. Carrier (1984), with a similar perspective, proposes that early hominids were diurnal hunters, gaining a thermal advantage over potential prey by possessing an efficient thermoregulatory system.

While many of these behaviours have been hypothesised as primary selection pressures towards bipedalism, many of them taken singly might appear to lack the selective strength to bring about bipedalism. Others, based on the use of stone tools, are now deemed obsolete, as they contravene evidence gathered concerning the temporal placement of the first stone tools (Isaac, 1983; Blumenschine, 1987, 1991).

However, it is most unlikely that the first manufactured tools were made of stone (Yamakoshi, 1998).

Several of these theories concern carrying as a selective pressure for bipedal evolution. It should be noted, however, Goodall (1986) has claimed that carrying of food and infants is performed effectively by chimpanzees and other primates while practising tripedal postures. However, carrying by chimpanzees in tripedal postures is unlikely to allow locomotion at high speeds.

Although several theories use the efficiency of bipedalism as a selection pressure towards its evolution, many believe that in the first stages of an upright gait, bipedalism would have been inefficient (Susman and Stern, 1983; Preuschoft and Witte, 1991). Since it is usually assumed that early bipedalism was inefficient, it is often stated that increasing commitment to a modern human striding bipedalism occurred due to the opening up of habitats, the emergence of terrestrial food gathering techniques or the appearance of tool use and hunting (Brace, 1979; Rose, 1991).

One single selective factor is unlikely to have brought about such a large modification in habitual locomotion. It is likely that many factors, over a long period, continued to select for the various behavioural, ecological and energetic benefits that bipedalism bestowed.

It is likely that as more and more fossils are discovered, the number of alternative theories for the evolution of bipedalism will be reduced. Each fossil serves as evidence for or against theories concerning the origin of bipedal gait. As research into the origins of bipedalism continues, improved knowledge about the climate, flora and fauna of early hominid habitats will serve as an aid in piecing together hominid ecology. Better information about early hominid habitat preferences and more accurate estimates of ranging behaviours will assist in predictions concerning the origin of bipedalism (Wood, 1993).

1.3 Skeletal Evidence and "Lucy"

1.3.1 Lucy

The hominid partial skeleton (AL-288-1, see Figure 1.1) known as "Lucy" was discovered in Hadar, Ethiopia in 1974. "Lucy" remains the best skeletal evidence of the species *Australopithecus afarensis*, and has been dated to approximately 3.1 million years old (Johanson et al., 1982).

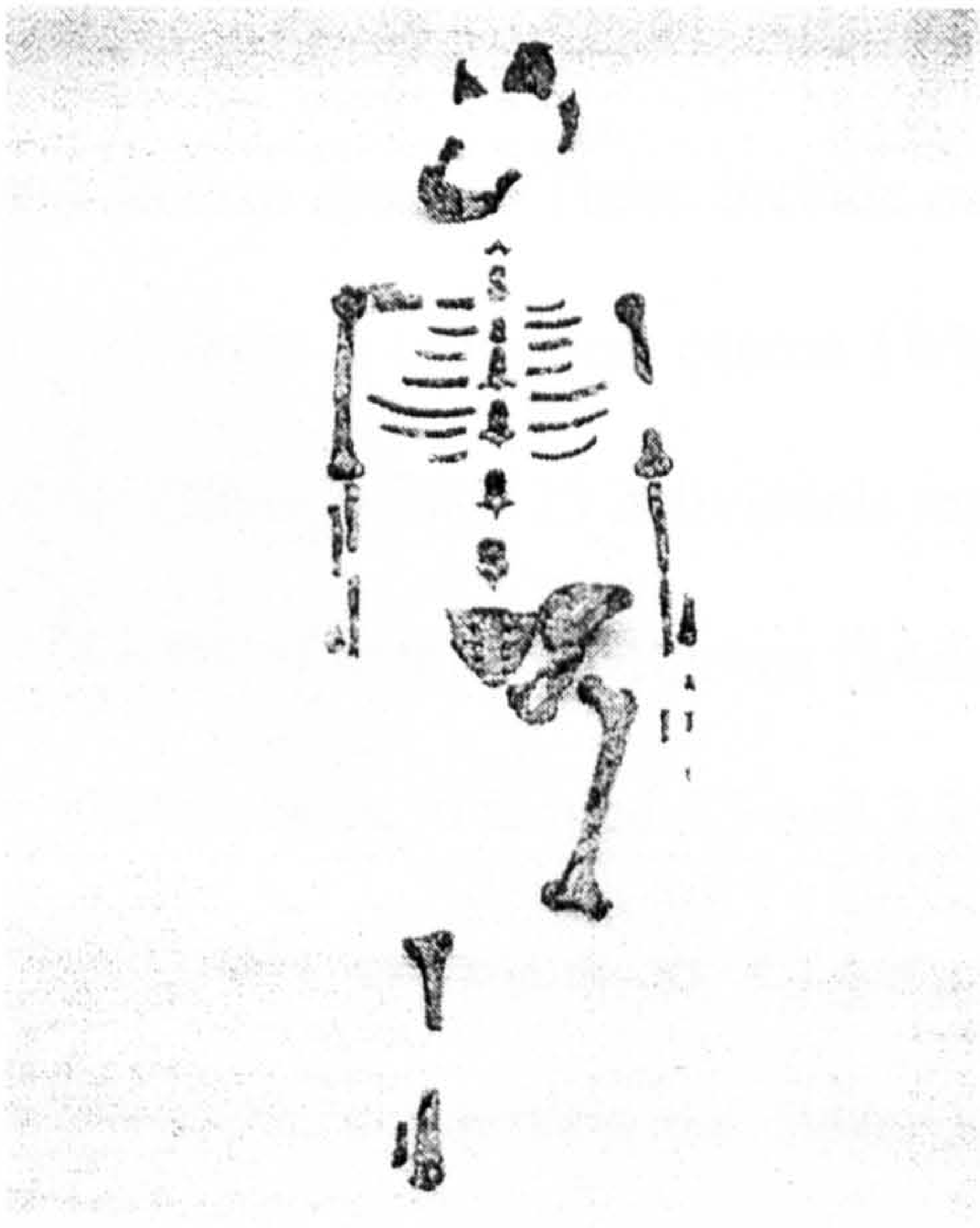


Figure 1.1

The remarkably complete skeleton of the female australopithecine (*Australopithecus afarensis*) called Lucy (AL 288-1), discovered at Hadar in 1974.(From Wood, 1992)

The "Lucy" specimen represents a small, gracile female, with a mass estimated at 27 kg, and stature 1.05 m (McHenry, 1992; Wood, 1992). The view that the pelvis of AL 288-1 (Lucy) belongs to a female has rarely been questioned. However, a recent assessment of the "Lucy" skeleton concluded that the remains belonged to a male, not a female (Häusler and Schmid, 1995). Wood and Quinney (1996) consequently reassessed the evidence and conclude that in this paper insufficient evidence was given to construct a reasonable argument against "Lucy" being female.

The humerofemoral index has been calculated at 85 for AL 288-1 (Jungers 1982). This clearly indicates a ratio of limb lengths intermediate between that humans and that of African apes (Hartwig-Scherer and Martin, 1991).

1.3.2 *Australopithecus afarensis*

The species *Australopithecus afarensis* encompasses many fossils discovered over the last few decades, which cover 3.0 to 3.9 million years ago (MYA) during the Pliocene era (see Appendix XI). Although AL 288-1 is the most complete skeleton that represents the species *Australopithecus afarensis*, there are other fossils attributed to this species. These include some specimens discovered in the Laetoli area of Tanzania: a lower left canine (White, 1980), a right maxilla with P^{3-4}, an isolated M^2 (Boaz, 1988), 23 individuals represented mainly by isolated teeth (White, 1980) and a set of hominid footprints (Leakey and Hay, 1979). All discoveries in the Laetoli area are dated to around 3.5 to 3.8 MYA (Boaz, 1988).

Specimens belonging to *A. afarensis* were also discovered in the Afar triangle, Ethiopia, comprising the Hadar and the Awash areas. Specifically in the Hadar area, in addition to the well known partial Lucy skeleton (AL 288-1), there were a number of other fossil discoveries. This includes two femoral fragments (AL 128-1 and 129-1c) and distal femoral fragments (AL 129-1b, 1c) forming a partial knee joint (Johanson et al., 1982b). A temporal fragment (AL 166-9), mandibular and maxillary remains (inc. AL 200-1) and a collection of a minimum of 13 hominid individuals named the "first family" have been found from the AL 333 site in this area, and dated to around 3.1 to 3.3 MYA (Boaz, 1988). From the middle Awash area, two early hominid fossils were uncovered, comprising a proximal femur (MAK-VP-1/1) and a frontal (BEL-VP-1/1) dated to *circa* 4.0 MYA (Asfaw, 1987).

Other sites have also contributed fossils attributed to *A. afarensis*. The Lower Omo Basin in Ethiopia revealed fragments including a right molar (W 508) and a right P^3 (W 978) (Howell, 1969). From the east of Lake Turkana, Kenya, an occipital (KNM-ER 2602) and fragment with P^3-M^2 (KNM-ER 5431) were discovered at the Koobi Foora region, dating from 3.3 to 3.4 MYA (Boaz, 1988). A small fragment of mandible (right with M^{1-2}) was uncovered in Tabarin, near Baringo in Kenya which possibly dates back to 5 - 5.3 MYA, and could represent the earliest record of *A. afarensis* (Ward and Hill, 1987).

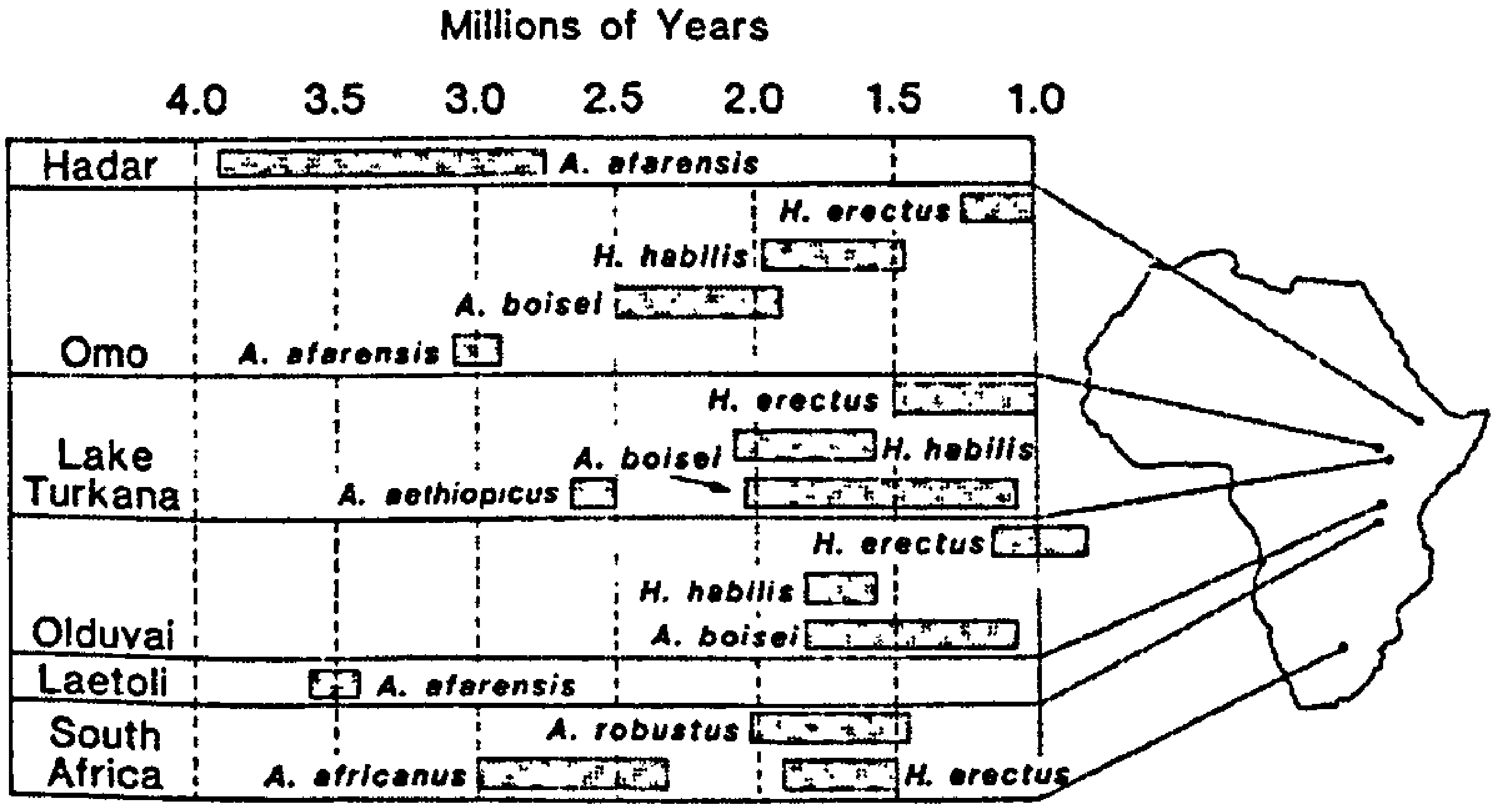


Figure 1.2 Geographic and temporal placement of early hominid sites in Africa. After Fleagle (1988)

1.3.3 Other australopithecine species

Ancestors of the human line are usually assigned to the genus *Australopithecus*, and all further species will be described as such. The origins of *Australopithecus* are not clear from the evidence of *A. afarensis* alone, and before *A. anamensis* and *Ardipithecus* were uncovered (see below), there was still a large gap between the earliest well-known species (*A. afarensis*), and the last common ancestor between humans and chimpanzees between 5 and 6 MYA. Small fragments of bone possibly belonging to an earlier species were dated to around 4 or 5 MYA, but up to 1995 only these small pieces existed to satisfy our curiosity concerning the earliest hominids (White et al, 1994). Evidence indicated that there were at least 4 species of australopithecine capable of upright bipedalism (Boaz, 1988). See Figure 1.2 for geographical and temporal placement of some hominid species before 1 MYA. *A. africanus* and *A. robustus* were relatively small-brained, and possessed canine teeth that differed from those of modern apes. *A. robustus*, the younger of these two species (1.5 to 2 MYA), had very large molar and pre-molar teeth combined with strongly marked bony crests on the skull, which indicate that this species had very powerful chewing muscles (Robinson, 1972). *A. africanus* from South Africa (2 to 3 MYA) is in some cases combined with the East African *A. afarensis* as a single species (Boaz, 1988; Strait et al., 1997). *A. afarensis* and *A. africanus* are known as 'gracile' australopithecines due to their relatively light build, especially of the skull and teeth. *A. aeopithecus*, a more 'robust' hominid, probably existed between 2.6 and 2.3 MYA. It resembles *A. afarensis* in many ways, with a small brain and some primitive features of the skull. However in other features it is similar to *A. boisei*, especially in the strength of the jaws (Lewin, 1987). *A. aeopithecus* may be an ancestor to both *A. robustus* and *A. boisei* (see section 1.3.4). The latter, similar in many ways to *A. robustus*, lived from 1.1 to 2.1 MYA, and some consider these two as variants of the same species (see Boaz, 1992 for a review). *A. aeopithecus*, *robustus* and *boisei* are together known as the 'robust' australopithecines. There is direct evidence that australopithecines gave rise to the lineage of *Homo*, which has lasted between approximately 2.4 MYA to the present day. The *Homo* lineage is usually divided into species *H. habilis*, *H. erectus* and *H. sapiens*, and their appearance is believed to have occurred is this order. *H. habilis* being the oldest species regarded as 'human'.

Since 1995, discoveries in Kenya have helped to fill in some of the missing information about our earliest ancestors. Another species of australopithecine was identified from Kanapoi, which pushed the origin of bipedalism back to around four million years ago. This species was named *Australopithecus anamensis*, and consisted of a number of fragments (KP 292), including upper and lower jaw bones, bits of skull and teeth, and the proximal and distal end of a tibia (Leakey et al., 1995). These fossils have been dated to between 4.2 and 3.9 MYA. The nearly complete tibia closely resembles that of *A. afarensis* from Hadar, although *A. anamensis* may be a million years older (Leakey and Walker, 1997). It displays some human-like characteristics in the tibia, and Andrews (1995) has described *A. anamensis* as morphologically 'more advanced' than other australopithecines. *A. anamensis* has been summarised as a habitual biped that retained some primitive features in the forelimb (Leakey and Ward, 1997).

At Aramis in Ethiopia, White and colleagues (1994) discovered fragments of skull, teeth, and arm bones, comprising 17 individual hominids (ARA-VP), which have been dated around 4.4 MYA (White et al., 1994). These fossils were also designated australopithecines, but named *Australopithecus ramidus*, subsequently moved to a new genus, *Ardipithecus*. This species represents the most primitive hominid yet found, and possesses more ape-like features than other hominids, including thin dental enamel and robust upper limbs.

Some attempts have been made to reconstruct the habitat of these new hominids, and with the evidence of other fossil animals found close to the hominid site, it has been concluded that they both lived within or close to riparian habitats, possibly in a closed-canopy woodland (Andrews, 1995; Leakey and Walker, 1997). These discoveries are too recent, however to warrant major conclusions about locomotor style, or behaviour. After further analysis it is hoped that they will help with piecing together the history of human ancestors.

1.3.4 Phylogeny

The Pliocene australopithecines from East Africa, such as 'Lucy', form an excellent model for an early hominid species from which to derive all subsequent hominids (Brace, 1979). There are a large range of views concerning the evolutionary history of the australopithecines. Many are involved with resolving which, if any, of all species discovered present the best model for a direct ancestor to the *Homo* lineage. *A. afarensis* is often described as the 'basal' hominid, or the species that first diverged from the common ape-hominid ancestor (Johanson and White, 1979).

Four alternate phylogenies are presented here (see Figure 1.3), all of which place *A. afarensis* as ancestral to the human lineage. Olson (1985) suggests that the Hadar and Laetoli '*A. afarensis*' samples do not represent one species, but agrees that *A. africanus* is positioned in the lineage of *Homo*. Tobias (1983) suggests, in agreement with Boaz (1988) that both *A. africanus* and *A. afarensis* are in the *Homo* lineage, but regards *A. afarensis* and *A. africanus* as a single species. Boaz's interpretation was supported by Skelton and McHenry (1992) and subsequently by Foley (1993), while Grine (1985) added *A. aeopithecus* as a separate species, rather than a variant of *A. boisei*. Since recent reappraisals of *A. aeopithecus* (or *Paranthropus aeopithecus*) (Strait et al., 1997; Skelton and McHenry, 1998; Strait and Grine, 1998) have not brought light onto this problem, this species has been left out of the figure for simplicity. Lewin (1986) proposed *A. afarensis* as the common ancestor of all other species. *A. afarensis* gave rise to the *Homo* lineage through an as yet undiscovered intermediary. *A. africanus* is positioned as the ancestor to the robust lineage, while *A. boisei* is assumed to have evolved in parallel to *A. robustus*, but from different ancestral population (Lewin, 1986), a proposal which is strengthened by an assessment of evolutionary patterns in cranial venous sinuses (Kimbel, 1984).

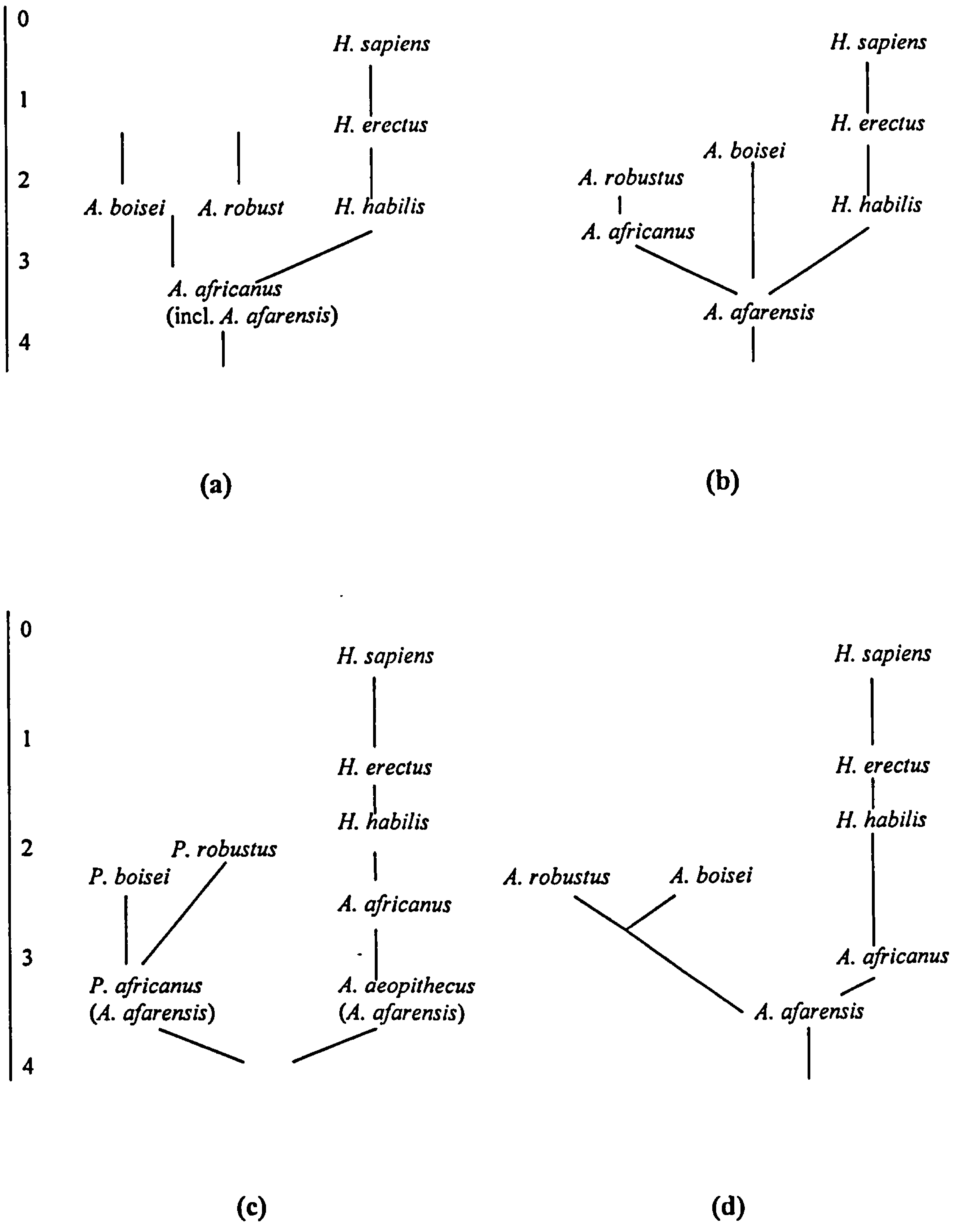


Figure 1.3 (a-d) Four proposed phylogenetic relationships incorporating *A. afarensis* as ancestral to the human lineage. Time lines indicate million years (MYA) from present. Adapted from Boaz (1988)

a - from Tobias (1983)
b - from Lewin (1986)
c - from Olson (1985)
d - from Boaz (1988)

1.3.5 Miocene hominoids

A relatively large number of fossils known from the Miocene period (see Figure AXI.1 in Appendix for geological epochs), are regarded as hominoids. Knowledge of the pre-hominid morphotype is important to piecing together the origins of a bipedal gait (Harrison, 1991). These hominoids may represent ancestors of some extant primate species, as they share some functional morphological features (Rose, 1993). Major Miocene hominoids (i.e. those with relevance to hominid evolution) are discussed here with reference to their similarities to each other, to Plio-Pleistocene hominids and to extant species. Inferences concerning the positional behaviour of Miocene hominoids can only be tentative, especially since there is a lack of detailed information on the links between morphology and positional behaviour, even in extant species (Rose, 1993).

Proconsul

Proconsul (18 MYA) is probably the best known of all Miocene hominoids, due to the quantity of postcranial material available (see Figure 1.4 for a reconstruction). *Proconsul,* as described here, comprises five species from the early to middle Miocene, including *P. hesloni*, *P. nyanzae*, *P. major* and P. '*afropithecus*' *turkanensis.* Major size differences are apparent between these species, but all possess a relatively similar morphology (Rose, 1993). A combination of features of the postcranial skeleton (especially in the pelvis) suggest a predominantly quadrupedal gait, with climbing also included in their behaviour (Rose; 1991,1993). The forelimbs and feet are similar in most respects to those of arboreal primates (e.g. the calcaneus, radius, ulna, hand bones), with some features (metatarsals and hallux) showing particular similarity to those of extant African primates.

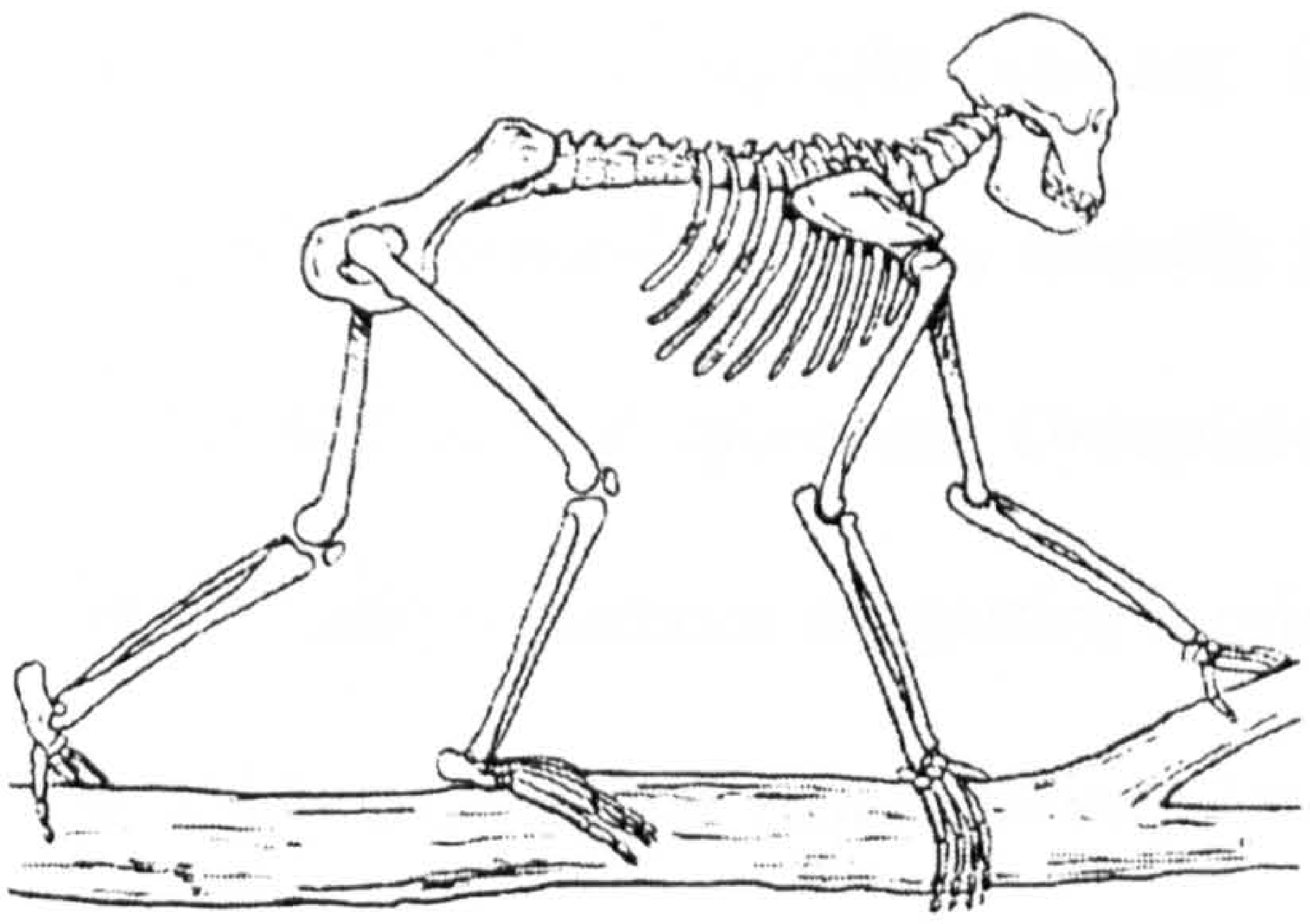


Figure 1.4 A reconstructed skeleton of Proconsul. Note the monkey-like proportions (From Fleagle, 1988)

Figure 1.5 A skeleton of Oreopithecus in a reconstruction of its locomotor habit (From Fleagle, 1988)

Oreopithecus

A major discovery in the form of a proto-hominid from the late Miocene (8.5 - 9.0 MYA), which was possibly capable of walking upright, may help us to understand the evolution of bipedalism in early hominids. The almost complete skeleton of *Oreopithecus bambolii* (see Figure 1.5 for a reconstruction), which is attributed to the ape-human clade Hominoidea, could be one of the most important fossil discoveries connected with hominid evolution from the Miocene period (Harrison, 1987). It is the only one of all Miocene hominids discussed here that closely resembles modern hominoids (Rose, 1993). Fossils of this Italian species, have been excavated for more than a century. A recent analysis of the *O. bambolii* postcranial material has revealed new implications for the interpretation of the origin of bipedalism. This ape-like animal of 8.5 to 9 million years old could have been habitually bipedal, according to new research (Köhler and Moyà-Solà, 1997). The overall morphology of *Oreopithecus* is intermediate between modern apes and australopithecines. It possessed a lower back and knee morphology that include features crucial to upright walking (e.g. robust cervical vertebrae, relatively symmetrical femoral condyles, laterally tilted femur shaft), along with a pelvis that resembled that of *A. afarensis*. *Oreopithecus* approximates the common chimpanzee in size, with proportions suggesting a primarily arboreal adaptation (Harrison, 1991). Some workers suggest that relatively long forelimbs, as seen in *Oreopithecus*, form part of an adaptive complex associated with vertical climbing and forelimb suspension (Fleagle et al., 1981). It seems then that *Oreopithecus* had a functionally generalised morphology, which conforms to most interpretations of the ancestral hominoid morphotype (Beard, 1991; Harrison, 1991). However, several important features of the pelvis and hindlimb are functionally associated with bipedalism. These features could also be interpreted as adaptations for vertical climbing (Harrison, 1991), but since these characteristics are structurally and functionally related to terrestrial bipedalism, the transformation from *Oreopithecus* morphology to a bipedally adapted hominid may not have been as dramatic as once thought. Köhler and Moyà-Solà (1997) view *Oreopithecus* morphology from another perspective. They state that as the *Oreopithecus* environment is characterised by an absence of predators, and therefore subject to high competition for food (as were all Miocene Mediterranean islands), habitual bipedalism could have evolved as a response to a necessity for energy efficient locomotion with an increase in mobility and speed. The similarities and differences seen between australopithecines and *Oreopithecus* deem this Miocene hominoid important to the evolution of hominid bipedality.

Dryopithecus

With the exception of *Oreopithecus*, very little fossil evidence has been discovered with hominid-like anatomy and locomotion prior to the oldest *Australopithecus*. Further, until recently, no skeletal material documenting hominoid skeletal anatomy was uncovered for the period between *Proconsul* and the appearance of *Oreopithecus*, some 10 million years later. A partial skeleton of a 9.5 MYA ape *Dryopithecus laietanus*, however, was recently discovered in Europe. This exceptional find provides additional evidence concerning the origins of modern ape morphology and locomotion (Moyà-Solà and Köhler, 1996). *Dryopithecus* morphology differs from the generalised quadrupedal characteristics apparent in *Proconsul*, as several features indicate a more upright posture. The situation of the scapula is similar to that in extant hominoids, and the orientation of the clavicle suggests suspensory postures, perhaps akin to those employed by the orang-utan (Moyà-Solà and Köhler, 1996). The possibility that *Dryopithecus* was a member of the ancestry of the great apes is supported by cranial evidence (Begun, 1994), but is it not yet clear whether it should be positioned within the Asian (orang-utan) or African (chimpanzee, gorilla) groupings.

Kenyapithecus

Kenyapithecus, a large-bodied hominid from the middle Miocene may provide evidence for a semi-terrestrial ancestor to the australopithecines of the Pliocene (McCrossin, 1997). Analysis of the recently discovered postcranial skeleton has been interpreted as suggesting that *Kenyapithecus* was semi-terrestrial with cursorial (i.e. adapted for walking/running) adaptations. However, the newly discovered and more complete *Kenyapithecus* from Nachola, northern Kenya has some postcranial features similar to those of *Proconsul* (Nakatsukasa et al., 1998). From this new evidence *Kenyapithecus* has been characterised as an arboreal climber and quadruped (Nakatsukasa et al., 1998). Terrestrial behaviour is not ruled out, but the latest analysis indicates that periods of terrestrialism would have been short-lived (Nakatsukasa et al., 1998). There are indications that this 20 - 30 kg species lived in woodland areas, and ate mostly fruit and nuts, similar to the reconstructed ecological characteristics of *Ardipithecus ramidus* and *Australopithecus anamensis*. *Kenyapithecus* therefore may represent a possible precursor to *A. anamensis*, and therefore to *A. afarensis* (McCrossin, 1997).

It has been suggested (Moyà-Solà and Köhler, 1996) that Asian and African apes diverged in their locomotor strategies after separation from an as yet undiscovered common ancestor. The ancestor to all extant great apes is supposed to be a generalised climber, more primitive than any of the extant forms. The Asian group is argued to have become adapted to suspensory postures and slow climbing, apparent in *Dryopithecus*, while the African group utilised two alternate strategies, one for terrestrial quadrupedalism (i.e. chimpanzee, gorilla), the other specialising in bipedalism (australopithecines and man).

1.3.6 Postcranial data

Morphological features of Lucy and other australopithecines

Morphological comparisons between the hominids, modern humans and African apes can identify the anatomical and mechanical changes that occurred as a consequence of the evolutionary transition to habitual bipedality. Since the major morphological changes for a shift to habitual bipedalism will be evident in the pelvis and the lower limb, detailed analysis of the characteristics of fossil hominids will be primarily restricted to these areas. See Figure 1.6 for a comparison of a human skeleton with a reconstruction of the 'Lucy' skeleton and Figures AXII.1, 2, 3 in Appendix XII for a general comparison of the anatomy of an upright biped, an arboreal quadruped and a terrestrial quadruped showing some of their distinctive anatomical features associated with each type of locomotion.

The general pelvic morphology of australopithecines is more like human pelves than the pelves of living African apes (Aiello and Dean, 1990). Their exact morphology, however, has no living counterpart. They share similar features with humans, for example: the short, wide ilium (Langdon et al., 1991); a well-developed sciatic notch (McHenry, 1991); a well-developed anterior inferior iliac spine (Aiello and Dean, 1990); a robust posterior superior spine (McHenry, 1991); a wide sacrum and a short ischium. The sub-pubic angle is intermediate between that of human males and females according to Tague and Lovejoy (1986). Schmid (1991) regarded the sacrum as possessing mostly human-like features and argued that the orientation of the sacrum implies lumbar curvature. This is indicative that the spinal column functioned in a similar manner to the way it does in modern humans.

Australopithecine pelves differs from modern humans in certain features, such as their relative width (they are wide at the level of the acetabulae as well as at the iliac crests, Aiello and Dean, 1990); large sub-pubic angles; small sacral and acetabular joint surfaces (McHenry, 1991); a flat sacrum with a small sacral angle; posteriorly facing iliac blades (McHenry, 1991) and a relatively small iliac tuberosity (Aiello and Dean, 1990). The hominid pelvis also has a relatively long pubis, which has a different angular relationship to both the ilium and the ischium, when compared with modern humans (Berge and Katzmierczak, 1986).

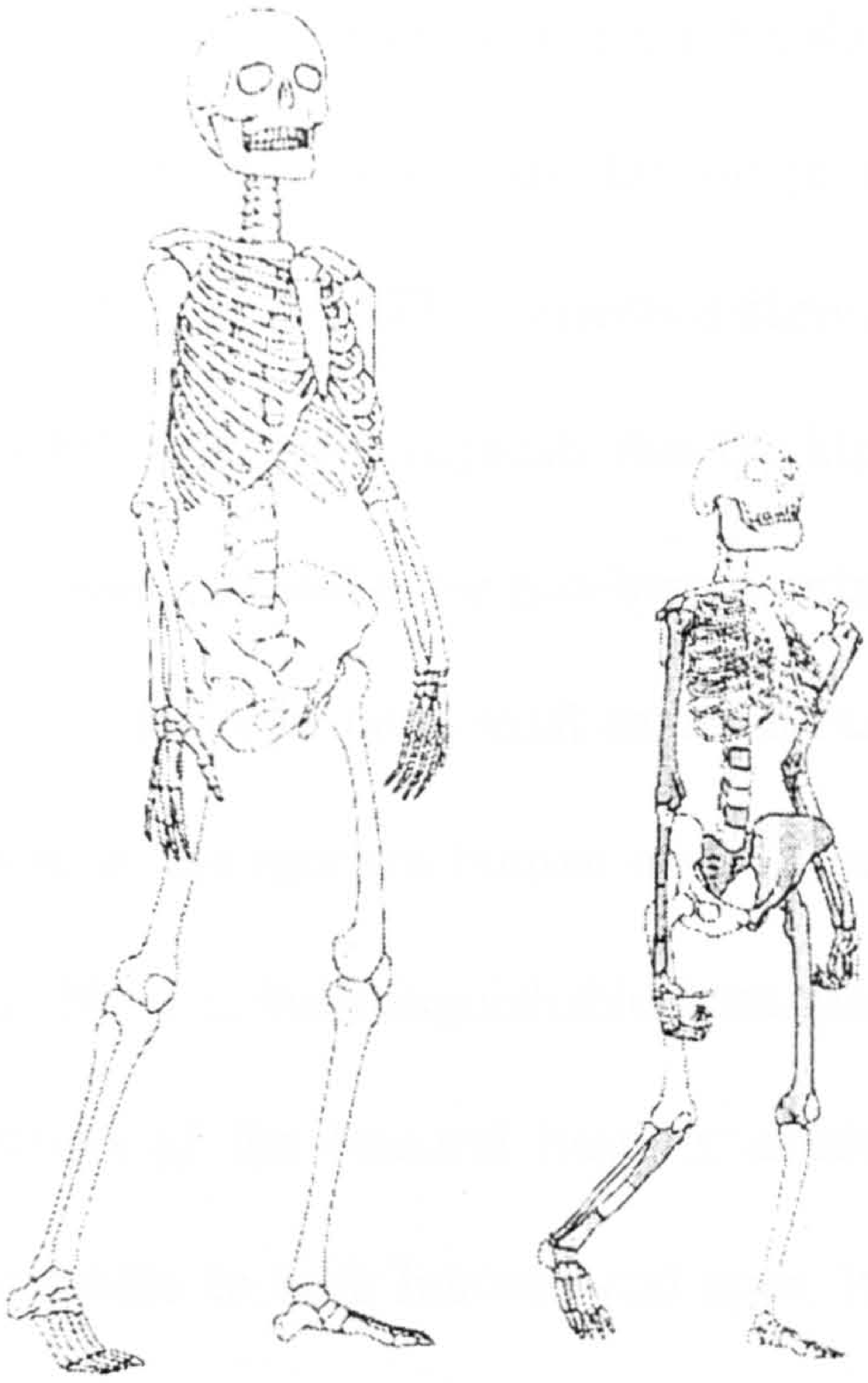


Figure 1.6

The reconstructed Lucy skeleton (*right*) compared to a modern female human skeleton (*left*) of average height. This version of Lucy was reconstructed at Kent State University, Ohio. The original parts are shown in grey, and mirror images of known bones and some parts based on other fossils are in white. The cranium has been left white for clarity, although this was not found complete. Here Lucy is shown at about 105 cm in height. Notice her relatively long arms if compared with the human skeleton. (After Wood, 1992)

In general the australopithecine proximal femur is very different in morphology to both humans and chimpanzees. The most pronounced differences are the longer relative length of the femoral neck, and the relatively small femoral head (Walker, 1973). However, there is much debate over the relative size of the femoral head in australopithecines. Some suggest that the small relative size of the femoral head is an allometric response to body weight, and is therefore expected to be smaller in small-bodied hominids, particularly in AL 288-1 (Jungers, 1988c). However Wolpoff (1976), who included a human Amerindian group in his analysis, disputes this. The femoral head morphology in AL 288-1 resembles that in the chimpanzee femur, according to Aiello and Dean (1990), where the femoral head extends onto the posterior surface of the femoral neck. However this condition may be simply due to sexual dimorphism (Asfaw, 1985) rather than suggesting a marked difference in locomotor function (Aiello and Dean, 1990). Three dimensional simulations of posture and maximum abduction (MacLatchy, 1996) indicate that AL 288-1 had an adducted hip with a similar range of motion to modern humans. Limited hip abduction in AL 288-1 reflects a diminished ability to climb according to MacLatchy (1996), or at least suggests that the kinematics of climbing are dissimilar to those in chimpanzees and other non-human primates.

Femoral neck-shaft angles measured in AL 288 (Stern and Susman, 1983) are close to the modern human mean. Cortical bone distribution at the femoral neck of AL 288-1 is indistinguishable from modern humans (Ohman et al., 1997). The cross-section of the femoral head is unusual in being ellipsoid. This shape, which is dissimilar to both humans and apes, is likely to be due to higher bending moments incurred by increased neck length (Aiello and Dean, 1990).

The fragmentary nature of the femoral shaft in australopithecines precludes major conclusions about their general morphology. However, Walker (1973) suggested that early the hominid femur shaft is more robust than that of modern humans.

The australopithecine distal femur shares some features with that of modern humans, possessing a high bicondylar angle, a deep patellar groove and a lateral condyle with an elliptical profile (McHenry, 1991; Tardieu and Preuschoft, 1996). Stern and Susman (1983), however, suggest that the smaller australopithecines (such as AL 288) share very few features with modern humans, with the exception of the high bicondylar angle. Further, they assert that analysis of the femoral and tibial plateau points towards an adaptation for arboreal locomotion, and that the knee articulation differs from the human condition (Stern and Susman, 1983). Aiello and Dean (1990) disagree, and propose that certain characteristics in the *A. afarensis* knee indicate that it was used in extension. Boaz (1988) inferred that *A. afarensis* possessed a valgus knee (i.e. knees positioned directly beneath centre of gravity), which is characteristic of humans, and hence of bipedality.

Lower leg bones are rare discoveries in the fossil record (Aiello and Dean, 1990). However, the tibia and fibula are present in AL 288-1. Many features of the *A. afarensis* tibia and fibula show great similarity with modern apes, while other aspects are consistent with modern human morphology. Features of the distal tibia, in particular are consistent with the demands of bipedal locomotion (Aiello and Dean, 1990). Many features of the proximal tibia are ape-like, such as a hollow in the lateral shaft below the epicondyle, a pit on the medial epicondyle and the shape if the posterior border to the lateral condyle (Aiello and Dean, 1990). A posterior tilt of the distal tibia is also characteristic of chimpanzee morphology (McHenry, 1991). The distal fibula also has a number of ape-like features. The proximal border of the distal articular surface runs obliquely (McHenry, 1991), there is a deep peroneal groove with a well-developed medial lip (Aiello and Dean, 1990) and the articular surface faces inferomedially (McHenry, 1991). Stern and Susman (1983) again suggest that these ape-like features are indicative of arboreal locomotion. However, some of the ape-like features can be explained simply by an increase in joint movement and an increased weight transfer through the fibula (Aiello and Dean, 1990). Latimer et al. (1987) point out that the orientation of the distal tibial joint is extremely variable even in modern human populations, and therefore such morphology does not necessarily signify arboreal locomotion. Some of these ape-like features may remain as archaisms from a quadrupedal ancestor (Aiello and Dean, 1990). Two primary features of the distal tibia and fibula are consistent with those of modern humans. The articular surface of the distal tibia is nearly perpendicular to the shaft axis (McHenry, 1991). Also the axis of rotation of the ankle joint is reasonably parallel with the ground and the distal tibial articular surface (Aiello and Dean, 1990; Latimer et al., 1987).

AL-288-1 represents the best evidence of pedal morphology of any species of *Australopithecus* (Aiello and Dean, 1990). Again the features of the australopithecine foot are a mosaic of features, some closer to the morphology of modern humans, while others are more similar to that of African apes. Some view this as evidence for a model of australopithecine locomotion that included periods of terrestrial locomotion, interspersed with time spent climbing (Duncan et al., 1994). A number of features of the talus suggest a human-like ankle joint, including the shape of the talar trochlea, and the orientation of the groove for the flexor hallucis longus (Aiello and Dean, 1990). These human-like characteristics of the ankle joint would enable the *A. afarensis* leg to move in a relatively saggital plane with relation to the foot, providing evidence against a chimpanzee-like bipedal gait (Aiello and Dean, 1990). A large calcaneus with a deep dorso-plantar. dimension is also human-like in morphology (McHenry, 1991). The orientation of the posterior articular surface of the calcaneus is a unique adaptation to bipedal locomotion according to Latimer and Lovejoy (1989), and further the sizeable calcaneal volume in *A. afarensis* is argued to be an adaptation for energy dissipation in animals walking bipedally with a valgus knee. An enhanced ability to dorsiflex the toes in *A. afarensis*, may be suggested by the human-like morphology of the second to the fifth metatarsals. This is dissimilar to function in the feet of modern apes and is consistent with the demands of a bipedal gait (Aiello and Dean, 1990; McHenry, 1991). According to Latimer and Lovejoy (1990), dorsal expansion of the metatarsal heads, a dorsal orientation of the articular surfaces of the proximal phalanges and a non-abductable hallux reflect bipedal locomotion, and conflict with any possibility of pedal grasping (which would reflect arboreal behaviour). It is further claimed that certain features of the australopithecine foot point towards primary development of the longitudinal arch, and therefore also towards bipedalism. These include the well developed insertion points for the plantar-cubonavicular and calcaneonavicular ligaments, and the elongated lateral cuneiform (Aiello and Dean, 1990).

More primitive features of the australopithecine foot include long, curved proximal phalanges with broad bases (McHenry, 1991); a long middle phalanx and a rounded head on the first metatarsal (Stern and Susman, 1983). Some contested features of the australopithecine foot (tarso-metatarsal flexion, varus stance and abducted hallux) might suggest prehensile abilities (Deloison, 1991). Opposing the interpretation of McHenry (1991), Stern and Susman describe the calcaneus as exhibiting more similarities to modern apes. The more primitive features include an oval orientation of the tuberosity and a massive peroneal tubercle (Stern and Susman, 1983). McHenry (1991) regards the cuneiform plantar tuberosity to be characteristic of the more primitive ape condition. A functional analysis of the metatarsophalangeal joint of *A. afarensis* (Duncan et al., 1994) suggested that *A. afarensis* was capable to some extent of a greater degree of plantarflexion than modern humans, but results were not conclusive regarding the functional significance of this feature. Langdon et al. (1991) examined the foot bones of a number of australopithecine specimens, including AL-288-1. Their interpretation of the talus was that the tarsal joint closely resembles that of modern humans. Further investigation revealed features consistent with 'efficient' bipedalism. The evidence they present substantiate a view that the transition to bipedalism with extensive morphological adaptations occurred very early, before the occurrence of *Australopithecus* (Langdon et al., 1991). Furthermore, Wolpoff (1983) considers that the morphology of the pelvis and femur indicate Lucy was exclusively bipedal.

Berge (1994) reconstructed the gluteal musculature around the australopithecine pelvis and found no major obstacles for extension of the lower limb. We may therefore suppose that Hadar hominids in particular could walk with extended and adducted lower limbs as do humans. In addition, the femoral morphology and the valgus position of the early hominid knee joint (see section 1.5.6) are considered to be a functional consequence of habitual bipedalism ordinarily in extended postures (Preuschoft and Tardieu, 1996).

1.3.7 Summary

In summary there are two current interpretations of the functional morphology of early hominids, of 'Lucy' in particular. Lovejoy and colleagues (Lovejoy, 1981, 1988; Latimer and Lovejoy 1989, 1990a, b; Latimer et al., 1987) argue on the one hand that differences in the morphology of australopithecines (when compared with modern humans) does not necessarily indicate a difference in gait, and therefore could function as habitual completely upright bipeds. On the other hand, Stern, Susman and co-workers (Fleagle et al., 1981; Stern and Susman 1981, 1983) and Prost (1980) argue that australopithecine morphology indicates a compromise morphology between an adaptation to climbing as well as to a less than human form of bipedal locomotion.

1.4 Reconstructing Early Hominids

Among many interpretations of the origins of human bipedalism (see section 1.2), increased efficiency during locomotion has been suggested as a contributing factor to the evolution of an upright gait. Remarkably few studies, however, have directly examined the energetic costs of human bipedal locomotion in an evolutionary context (Leonard and Robertson, 1997b). Although some studies (e.g. Taylor et al., 1970; Taylor and Rowntree, 1973; Ishida, 1991) have investigated the comparative economy of human bipedalism versus primate bipedalism and quadrupedalism, there has been no consensus regarding the possible benefits that may have accrued to early hominids for bipedal locomotion. Fedak et al. (1974) concluded that energetic "economy might be one important factor in determining the effects of natural selection on the mechanical characteristics of running animals".

Some recent studies (Leonard and Robertson, 1995, 1997a, b; Steudel, 1995, 1996) have notably advanced the understanding of primate energetics by using a variety of sources of information on which to base energetic comparisons between human and primate species (more details in section 1.5.7). However, very few studies of comparative energetics between species have analysed direct comparisons of energy cost in alternative postures. However, see section 4.3.1 for some exceptions.

One of the most valid methods with which to determine the ability of an individual to perform physical exercise is to measure the rate of energy expended. Energy is defined as the capacity or ability to perform work (Fox, Bowers and Foss, 1993). A further parameter of importance is power. Power is the rate of doing work (i.e. work done per unit of time), and is therefore related to energy.

Since there are no surviving counterparts of the first bipedal hominids, how is it possible to study their ecology, and make inferences about behaviour? Quantitative comparative investigations of great apes and humans are generally regarded as an essential tool for investigating human evolution and for interpreting hominid fossils (Hartwig-Scherer and Martin, 1992).

1.4.1 Analogy to chimpanzees

To gain insight from extant non-human primates, it is first necessary to consider both phylogenetic relationships between primates and their adaptation to environment (Brace, 1979). Since research into Plio-Pleistocene environments has recently rejected the concept that the first bipedal hominids lived in a savannah environment (Reed, 1997; Spencer, 1997), the savannah baboon often suggested as a model for human evolution (Wrangham, 1980), is no longer considered as a suitable model for early hominids. Chimpanzees and gorillas are phylogenetically closest to humans (Martin, 1990), and chimpanzees are possibly the best ecological counterparts for early hominids (Hunt, 1994). Chimpanzee ecology is now more commonly supposed to show the most parallels to supposed early hominid lifestyle and therefore chimpanzees are most often selected as the best non-human primate model.

1.4.2 Analogy to humans

Considering the fact that none of the extant non-human primates are habitually bipedal, and that modern humans are direct descendants from one species of early hominid, it is essential to employ modern humans as an alternate model. Carrier (1984) stated that studying human locomotion could prove to be one of the more insightful approaches to the field of hominid evolution. Modern human societies which are considered to show similarities to early hominid subsistence ecology include the !Kung, Hadza, and pygmy hunter-gatherer societies from Africa. The !Kung San are a modern hunter-gatherer society based in the Dobe area of the Kalahari desert in Botswana (Lee, 1979). The Hadza are a small group of hunter-gatherers (probably only around 750 in number), living in northern Tanzania (O'Connell et al., 1988). The pygmy hunter-gatherers are more numerous and comprise various groups. The Aka pygmies from the Congo, for example, number around 30,000. Other pygmy groups live in Cameroon and north-east Zaire. The Eke and Beni pygmies are probably the oldest pure ethnic group of people in the world. The ≠Kade San population lives in a Southern African habitat bordering both areas of forest and open land. The modern hunter-gatherer subsistence ecology, land-use pattern and habitat provide a useful insight into 'primitive' human life. As a consequence they provide a reasonable model for a human ancestor living in similar habitats (Lee and DeVore, 1976). It should be noted, however, that we cannot assume that modern humans are a direct representation of early hominids. It is important not to make the mistake of classifying hominids as too 'human' (Isaac, 1983).

1.5 Biomechanics of Locomotion

Mechanics is the behaviour of matter under the action of a force, and biomechanics refers to the mechanics of movement in living creatures. The pioneer in quantification of locomotion was E. J. Marey (1838-1904), who developed numerous measuring devices and employed cine photography extensively. He also developed what must be regarded as the first 'gait laboratory', in Paris.

Force systems can be classified in various ways. Static force systems are those in which forces balance and there is no motion. These can be used to describe a body that is in equilibrium, for example a box upon a floor. Dynamic force systems are those in which motion occurs, involving velocity and other such changes over time and are therefore more complex.

Description and analysis of motion

Kinesiology is a broad term meaning the study of human movement. The description of human motion encompasses two elements, kinetics and kinematics. Kinetics is the study of mass, force and acceleration of a body, while kinematics is concerned with the study of the motion of the body, without reference to the forces involved. For a complete biomechanical analysis of any form of locomotion both kinetics and kinematics are needed, plus knowledge of the functional anatomy of the limbs involved (Alexander and Goldspink, 1977).

1.5.1 Kinetics

Kinetic analysis is an important technique in the biomechanical analysis of movement. Forces and accelerations of a body can be measured with relative ease.

Studying forces acting on a body usually involves the use of a force plate. Force plates measure the force exerted by a limb upon the ground, by recording the equal and opposite 'ground reaction force' (Alexander, 1981). Force plates usually measure forces in three directions, vertical, anteroposterior and mediolateral forces. Therefore in addition to measuring the magnitude of force, they also assess the relative importance of the forces acting in the saggital, horizontal and transverse planes. Kinetic studies are extremely useful in comparing differing locomotor modes within the same individual, as they can provide force data from both fore and hind limbs, and also give an indication of limb loading (Swartz, 1993).

1.5.2 Kinematics

Body motion, is usually considered in terms of parts of the body moving with respect to others. The body is described as series of segments, usually including the head and neck, trunk, thigh, leg, foot, arm, forearm and hand. While the proportion and mass characteristics of each body segment vary greatly between one individual and another, describing a segment as a percentage of the whole body substantially reduces inter-individual differences (Low and Reed, 1996). Motion at joints between segments is usually described reasonably accurately by angular motion around a fixed axis (Low and Reed, 1996).

Using a combination of kinematics and kinetics, it is possible to find the relationship between the limb segments and the ground force vector. There is then the potential to perform mechanical calculations to describe the moments of force, and the power generated or absorbed at all of the major joints of the lower limb. These calculations require data (such as limb segment masses, and the location of segment centre of gravity) that is not directly measurable in fossil species, but knowledge of these can be obtained by mathematical and computer modelling. Mathematical modelling can also be used to estimate the forces transmitted across joints, and through the ligaments, tendons and articular surfaces associated with the joints. There are always some unknowns associated with this type of modelling, such as the internal moment generated by the muscles (Whittle, 1991), but nevertheless such data, although approximate, can be very useful in biomechanics research.

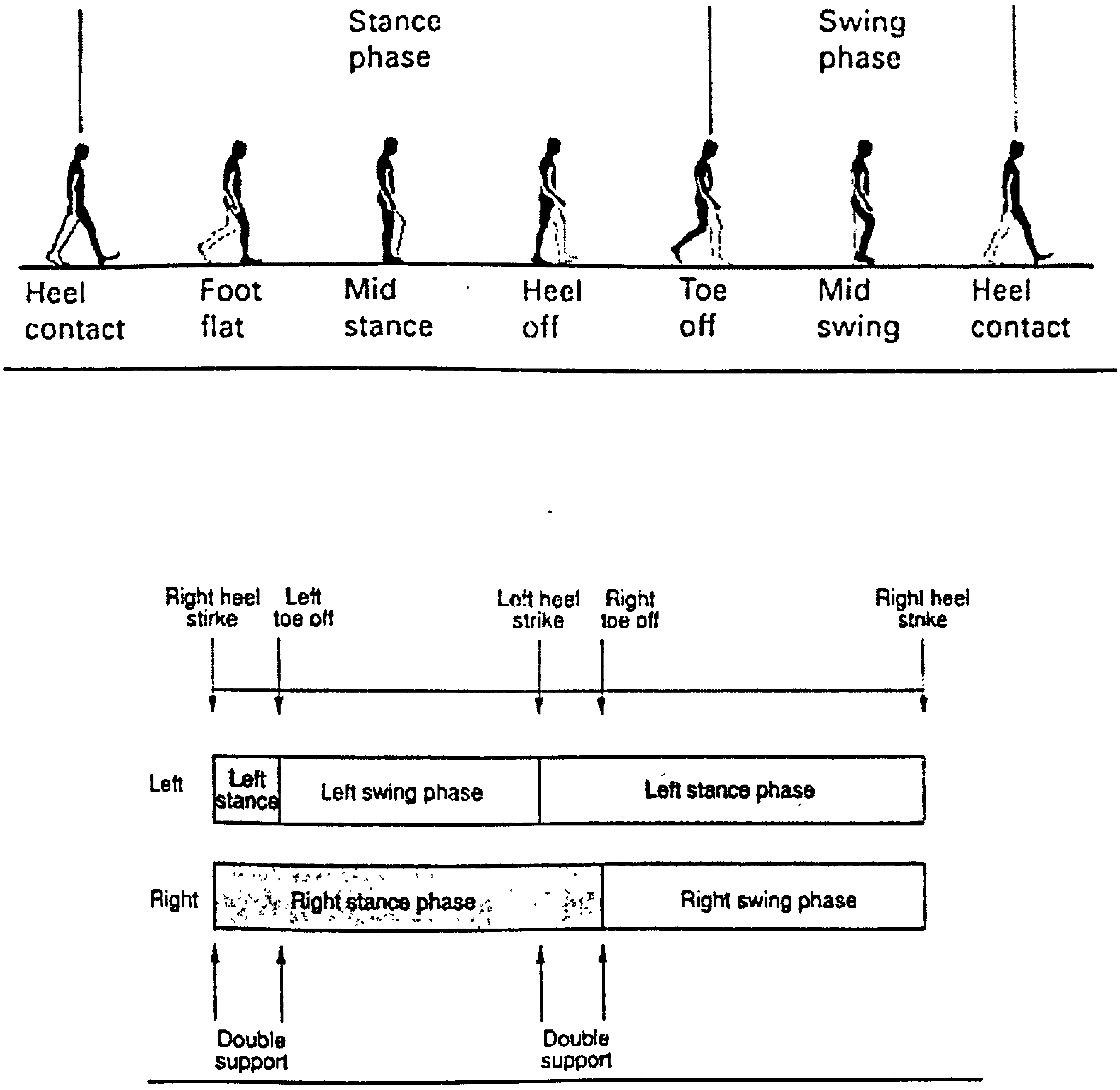


Figure 1.7 The gait cycle. (ABOVE) Figure diagrams to show different phases during one gait cycle (Whittle, 1991). (BELOW) Details of the phases of the gait cycle. (Low and Reed, 1993)

1.5.3 The gait cycle

Walking is the process of locomotion where the erect body is supported first by one leg and then the other in a cyclic manner. As the body moves over the supporting leg, the opposite leg swings forward to prepare for the next step. One gait cycle consists of two phases; the stance and the swing phases (see Figure 1.7). The stance phase is when one foot is on contact with the ground, and the swing phase is the period when the foot is off the ground and moving forward in the direction of progression to begin the next step. When a gait cycle is described or recorded, it usually begins with the stance phase. The complete gait cycle for the right leg will now be described.

The gait cycle begins with the right foot contacting the ground at the start of stance, this is named 'heel strike'. Shortly after right heel strike the left leg will leave the ground and begin to swing forward for the next step. The period when both feet are supporting the body at the start of the cycle is called 'double support'. When the left toe loses contact with the ground, this is 'single support' and the body is supported by a one leg. A second period of double support occurs at the end of stance, when the left heel contacts the ground and begins the opposite stance phase. The right leg is now at the end of the stance phase, and at 'toe off' it begins its own swing phase. The right leg continues swing until it begins another complete gait cycle with the next heel strike (see Figure 1.7). As an individual walks at faster speeds, the period of double support becomes shorter and shorter, until double support disappears altogether when the individual starts to run.

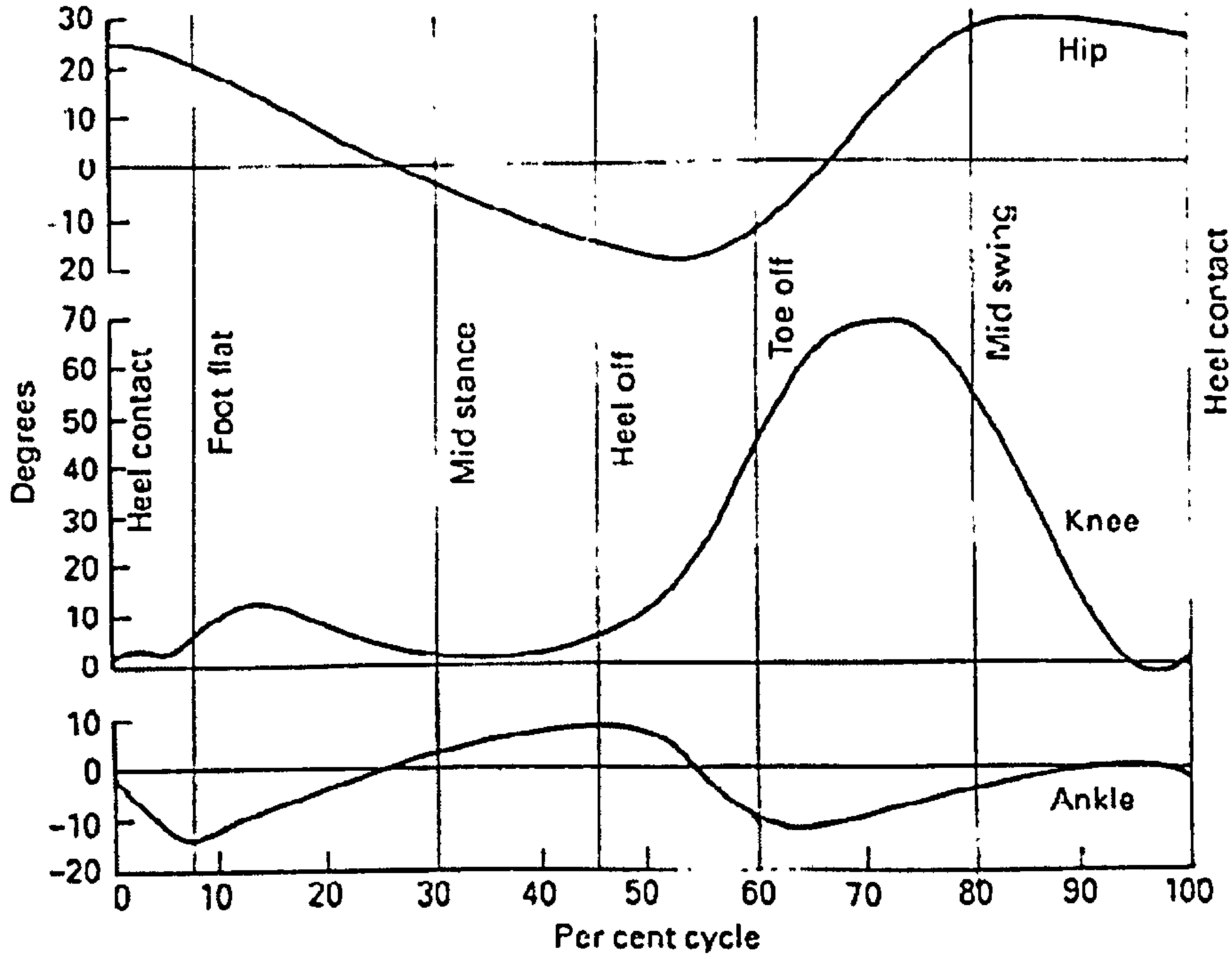


Figure 1.8 Hip, knee and ankle angles during the gait cycle. Flexion and dorsiflexion is positive. After Whittle (1991).

Joint angles (Flexion and extension)

All joint angles are measured from a specified zero point. This position is usually taken as the fully extended 'anatomical position' (Low and Reed, 1996). Flexion and extension in the sagittal plane are easy to record and are useful when describing muscle activity. The following description is adapted from Rose and Gamble (1994). Motion of the hip during the gait cycle is simple, and forms a sinusoidal curve (see Figure 1.8). Maximum hip flexion occurs during terminal swing, which is followed by extension, a short time before heel strike, to prepare the leg for supporting body weight. The hip extensor muscles act to decelerate the thigh previous to heel strike. Maximum extension occurs at the opposite limb heel strike, at the onset of the second double support phase.

The flexion-extension curve of the knee is not as simple as the hip, since it forms two distinct peaks. Knee flexion first occurs during the beginning of the stance phase, after heel strike, when the limb acts as a shock absorber during acceptance of the body weight. The quadriceps femoris, contracting eccentrically, acts as the principal shock absorber. By mid-stance the knee is in extension, with the eccentric contraction of the plantar flexors occurring at this point to restrain the leg from forward rotation. The knee begins to flex once more before toe off in order to clear the limb from the ground during early swing. Knee flexion starts before the foot leaves the floor, and precedes hip flexion. Maximum knee flexion occurs during the swing phase as the swinging limb passes the opposite supporting limb. The knee then undergoes swift extension reaching maximal extension just prior to heel strike. The quadriceps, hamstrings and gluteus maximus muscles aid this rapid extension.

The sagittal motion of the ankle is the most complex of the three lower limb joints. It can be broken down into four sections for simplification. First is the phase between heel strike of one foot and toe off in the opposite foot. At heel strike, the ankle is approximately at angle 0° at heel strike, then plantar flexion occurs until the foot is flat on the ground. The second phase occurs during single support in the stance phase, when there is dorsiflexion of the ankle as the body passes over the foot. Towards the end of single support the heel begins to rise as plantar flexion begins. The plantar flexor muscles to contract concentrically to bring about this movement, but fall silent after opposite heel strike. The third phase occurs between the opposite heel strike and toe off, and therefore corresponds to the second double support phase. Rapid plantar flexion occurs, and there is a maximum plantar flexion of about 20 to 25 degrees at toe off. The fourth and final segment occurs after toe off. There is rapid dorsiflexion of the ankle to aid foot clearance during the swing phase, coinciding with knee flexion. The foot is then held in an approximately neutral position (0°) until the subsequent heel strike.

Measuring joint angles

Goniometry is the most widely used technique for dynamic measurement of joint angles, and is recommended because of its simplicity (Gajdosik and Bohannon, 1987). Goniometers have been developed to record motion in two and three planes. A goniometer is simply a flexible steel strip (surrounded by a spring) fitted with strain gauges. The electrical output of the strain gauges is proportional to the angle between the two ends that are fixed to two adjacent body segments (see Figure 1.9). The output from a recording device thus gives a measure of the angle between the two body segments, and can also measure the change in angle against time. All joint movement is measured from a specific starting position, and usually the fully extended anatomical position is taken as 0°. The measured angle is very reliable as it is unaffected by the movements of the axes of the body segments or skin movements, and so goniometry is more precise than video recording for measuring joint angles (Winter, 1990).

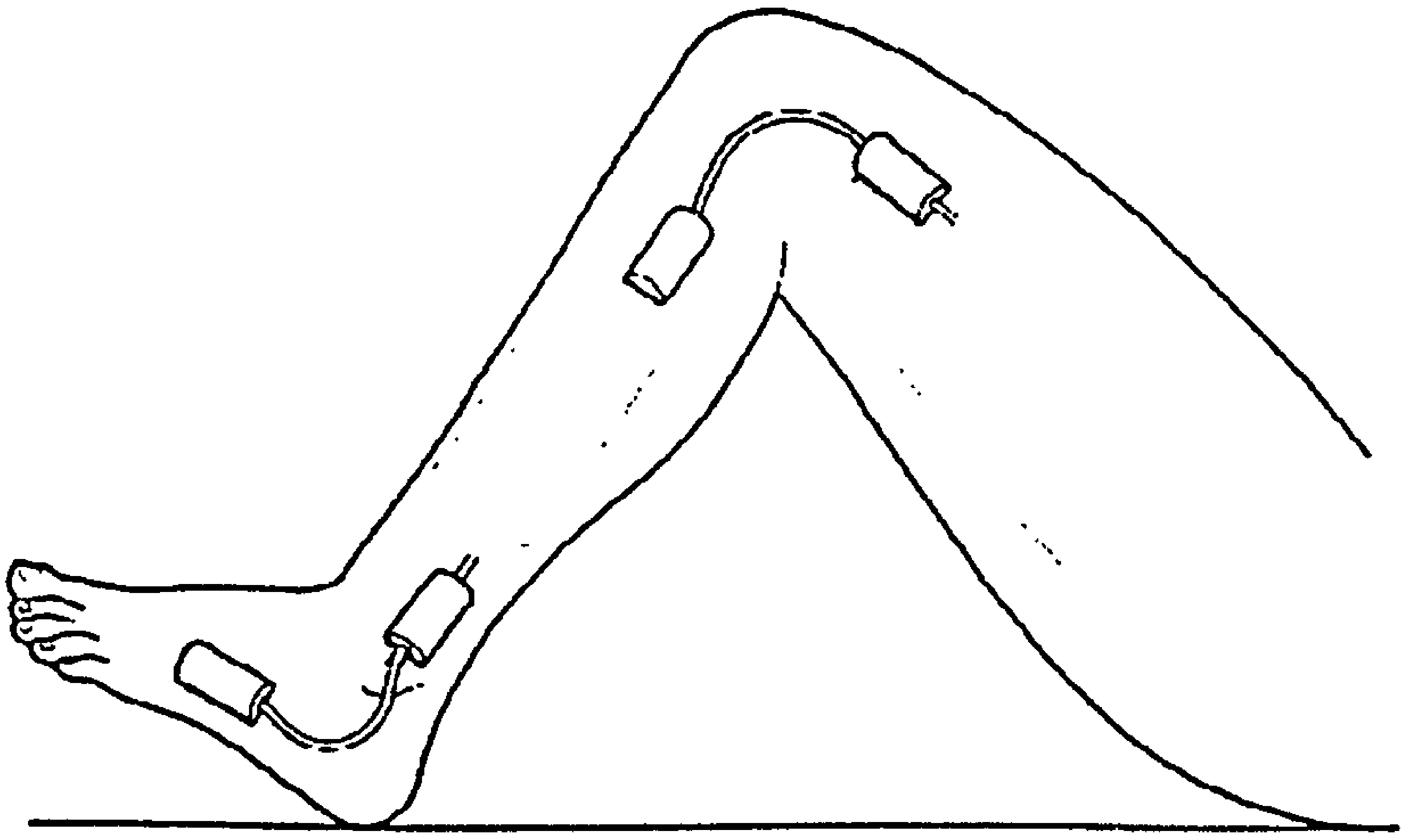


Figure 1.9 Goniometers for measuring knee and ankle angles. From Whittle (1991)

1.5.4 Force

According to Newton (Nelkon and Parker, 1977):

Force = mass x acceleration

Work = force x distance

Forces during locomotion can be estimated in a variety of ways. One simple way is to assess the turning force (moment, or torque) applied to each body segment, and infer the forces in corresponding muscles from this (Low and Reed, 1996). Isokinetic dynamometers are special devices that measure forces when a fixed velocity is applied to certain limb segments. An indirect approach is the use of electromyography (discussed in detail in section 1.8) which measures the electrical signals generated by muscular contraction. The electrical signals display a relationship to the degree of neuromuscular activity, and therefore degree of muscle contraction. However, this method actually measures muscle activity, and results do not directly represent muscle force. Muscle force is related to the physiological cross-sectional area (PCSA) of a muscle (see section 1.8.1, muscle structure and function). In some cases measurements of the limb circumference are used to assess muscle forces. The actual PCSA, however, is difficult to determine as direct measurement usually involves detailed dissection of the muscle (although approaches using MRI are currently being developed; see Thorpe et al., 1997). When assessing forces, both the force and the distance over which the force is applied must be taken into account. This is the moment of force (or moment arm), and is determined by multiplying the force by lever arm. The lever arm is the perpendicular distance between the line of action of force and the axis of rotation (Low and Reed, 1996). A simple example is in the use of a crow bar to lever objects open. The greater the length of the crow bar, the greater the force that is applied to open the object, as the lever arm and hence the moment arm has increased.

1.5.5 Energy, work and power

Energy

There are many forms of energy. Some examples are heat energy, mechanical energy, and chemical energy. Energy can neither be created nor destroyed, it can only change in form. The total amount of energy within a system always remains the same. This is the principle of the conservation of energy (Low and Reed, 1996).

Mechanical energy is measured in joules, or the amount of energy needed to apply a force of 1 Newton over a distance of 1 metre. In the body, mechanical energy is only generated within muscles. Muscles are also the major sites for absorption of energy. If a body possesses mechanical energy it has the ability to do work. Work (also measured in joules), is the transfer of energy from one body to another. Work can be positive or negative. Positive work is done when climbing stairs. Negative work is done when descending stairs, or if a force is applied to slow down or resist an objects motion (Kreighbaum and Barthels, 1996). The rate of energy expenditure can be measured in joules per second, which is otherwise known as a watt. A watt is a unit of power. Power, therefore, can be described as the rate of doing work (Winter, 1990). Power is force applied with a given velocity. Speed therefore does not affect work done, but affects the power output (Kreighbaum and Barthels, 1996).

Internal and external work

Work can be described as internal or external. Internal work is the only type of work that is done during walking, and is the work done on body segments.

External work is the work done on an external load (for example, lifting a box). External work can also be done on oneself, when lifting our own body weight through our arms, or when walking up a hill. External work can be positive or negative. Positive external work is done when moving an object away from you. Negative external work is done if an external force is applied to a body and the body gives way. Both positive and negative work require an input of metabolic energy.

Joint power

Joint power is the result of force multiplied by velocity. It is also described as the rate at which energy is generated or absorbed by joints and muscles. Power can be positive (power production), for example applying a force over a period of one second. Power can be zero, for example when a force is applied to resistance, and no movement occurs. Power can also be negative (power absorption), when the work done is negative. Positive joint power results during walking when the sign of the angular velocity or the direction of change in joint angle agrees with the sign of the moment in a given plane (Winter, 1990). Although power is the product of force times velocity, there is an inverse relationship between force and velocity in muscle. Force or velocity above a certain level results in a reduction in muscle power. Therefore muscle power is at a maximum when the force is applied at an optimal speed of muscle shortening (Kreighbaum and Barthels, 1996). Power production can vary between different muscle fibre types (see section 1.9.1). A peak in power production in joints during walking occurs around the push-off at the end of stance phase. Ankle plantarflexors generate approximately 500 W during this phase (Whittle, 1991). The knee joint generates three peaks of power absorption, and one peak of power generation (around 100-200 W). The hip joint shows more variation in power absorption and generation, but is generally below the 100 W level.

Energy transfer

Walking is a remarkably 'efficient' gait, mainly due to two forms of energy transfer and stabilisation during gait (Cavagna et al., 1976). Firstly, changes in the centre of gravity are kept to a minimum, while a system of energy transfer optimises the use of energy within each step. The simple type of energy transfer which takes place is an exchange between kinetic and potential energy. Kinetic energy, sometimes described as the energy of motion, is the energy possessed by a moving body. Potential energy is stored energy (Low and Reed, 1996), which is energy possessed by a body by virtue of its position, or state (Nelkon and Parker, 1977). There are two types of energy transfer that occur during gait. The second type is a transfer of energy between adjacent limb segments either through muscles or joints (discussed in section 1.8). The former is the simplest of the two types, and the clearest example is the vertical movements in the trunk during walking which cause fluctuations in kinetic and potential energy. When the trunk is at its highest point over the supporting leg, most of the energy is in the form of potential energy, having been converted from kinetic energy during the thrust forwards of the trunk by the supporting leg. As the trunk begins to drop down in front of the supporting leg, it picks up velocity, and the energy is converted back into kinetic energy. This form of energy transfer can be modelled by an inverted pendulum, where all of the energy is converted into potential energy at the highest point of the pendulum swing, and at the lowest point is then converted back into kinetic energy (Alexander, 1980). Other movements, such as the twisting in the pelvis and shoulder during walking, may also cause storage of potential energy in elastic-like tendons, which is converted back into kinetic energy when the trunk untwists.

Energy levels of limb segments in the sagittal plane have been studied in detail by Winter et al. (1976). They estimate that about a third of the energy in the thigh segment was conserved by exchange between potential and kinetic energy, but the shank conserved virtually no energy in this manner. Changes in energy of the individual segments were calculated to be greater than changes in total body energy, which indicates a transfer of energy from one segment to another.

1.5.6 Efficiency of human walking

It is necessary to distinguish between 'efficiency' and 'economy'. Efficiency refers to a ratio of work done to energy expended. If less energy is expended than work done, the process is deemed as efficient. Economy implies a reduced utilisation of resources. Larger animals are more efficient than smaller ones, as they expend less energy per kilogram to move a unit distance. However, smaller animals are more economical, as they utilise less resources to travel a unit distance.

There are a number of features of human walking, apart from energy transfer (see above), that make walking an efficient gait. Minimising both the vertical and horizontal movements of the centre of gravity reduces the amount of energy required to walk (Aiello and Dean, 1990). Movements in the pelvis that counteract the vertical oscillation of the centre of gravity are a primary example of this phenomenon. Firstly, the pelvis rotates around the supporting leg, producing a lateral movement in the swinging leg, rather than forward movement. Secondly, the pelvis drops below the horizontal on the swing side during mid-stance. Both of these actions aid to minimise the vertical displacement of the centre of gravity. Movements in other limb segments aid in the co-ordination of these actions (slight flexion in the knee during stance is one example).

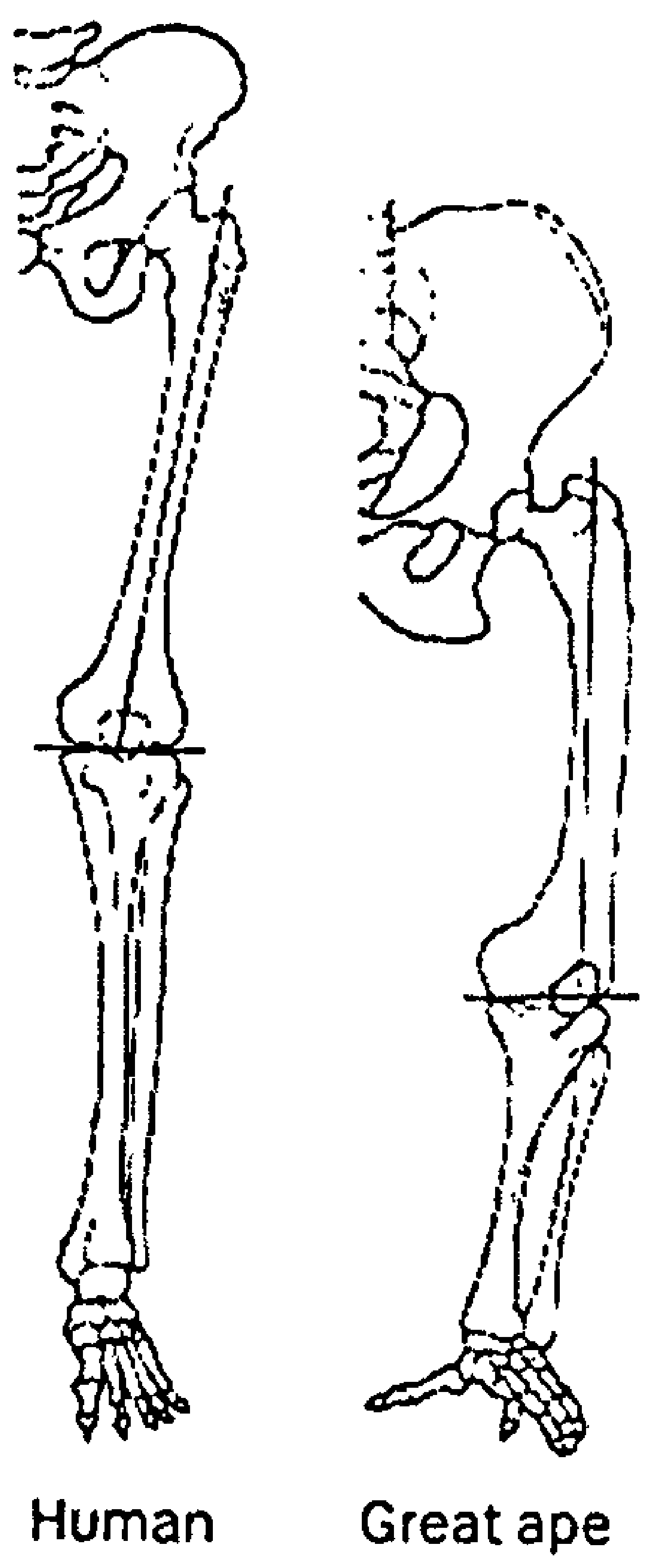


Figure 1.10

Human and chimpanzee lower limbs to illustrate differences. The angle from the femoral condyles along the axis of the femur is shown. The human femur is angled outwards from the knee, but in the chimp it is angled straight up. This ensures that in humans, the knee is brought well under the centre of gravity and is closer to the line of action of body weight (see text for more details, After Fleagle, 1992)

Horizontal displacement of the centre of gravity is minimised primarily by the shape of the femur and hip joint. The femur in humans is angled so that the knees are positioned as close to the mid-line of the body as possible. This phenomenon is due to the high bicondylar angle, which affects the angle between a line perpendicular to the femur shaft and a line running through the knee articulation, which is presumed to be horizontal (see Figure 1.10). The proximity of the knees to the mid-line minimises lateral movements in the centre of gravity as stance legs alternate during walking.

In human bipedal locomotion the lower limb functions as a pendulum. The lower limb acts as an inverted pendulum supporting the body mass, which pivots about the foot at the ground. The rise in potential energy gained during the rise in the centre of mass is roughly equal to the loss of kinetic energy during its descent (Carrier, 1984). Energy savings due to the transfer between kinetic and potential energy in this way are around 65-70% (Cavagna et al., 1976). A pendulum motion is also described by the swinging hindlimb rotating about the hip joint (Alexander, 1984).

In human walking, the direction of change in joint angle oscillates between positive and negative during one gait cycle. The angular velocities and joint moments also oscillate between positive and negative during one gait cycle. This characteristic cyclic motion of the limbs aids in the transfer of work and energy between muscles and joints. The joint angles of the hip and ankle oscillate in parallel, whereas the knee joint oscillates out of phase with the hip and ankle (see Figure 1.8). So, while the hip and ankle are extending, the knee is flexing and vice-versa. The phase patterns of the kinematics and moments of the three joints in the lower limb agree for part of the joint cycle, and disagree for other parts of the cycle. This, as described above, causes both positive and negative work to be done, and positive and negative power output will result.

1.5.7 Chimpanzee bipedalism

The locomotion of both common chimpanzees and bonobos differs from humans most strongly in one major feature, that their habitual gait is a 'knuckle-walking' form of quadrupedalism rather than striding bipedalism. However, both species occasionally use bipedal walking. Doran (1992) estimates that common chimpanzees spend 2.2% of all locomotion during travelling in a bipedal posture.

Bipedal locomotion during feeding accounts for 5.2% of the total locomotion during feeding. Estimates from bonobos reveal that bipedal walking accounts for 6% of total locomotion (Susman, 1984). Common chimpanzees use bipedal posture in a range of display behaviour including standing displays, a bipedal swagger and mock charges (Goodall, 1986). A study by Hunt (1994) observed adult chimpanzees in their natural habitat and established that the vast majority of bipedalism was postural, and related to feeding. Bipedal locomotion represents about four percent of all bipedal activity (Hunt, 1994). Bipedal behaviour observed as terrestrial locomotion usually involved movement between feeding sites at the same tree. Additional bipedal behaviour was observed during begging, playing, carrying an infant and scanning.

The occasional bipedal locomotion of chimpanzees differs from human bipedal locomotion in a number of features (Jenkins, 1972). During bipedal locomotion, the knee and the hip of the chimpanzee are not fully extended. Unlike in humans, the knee and ankle joints do not pass behind the hip joint during the stance phase. As a result, the propulsive forces produced during late stance are applied in front of the hip, resulting in shorter strides. As the chimpanzee lacks the bicondylar angle seen in humans, the chimpanzee knee is upright in morphology (see Figure 1.10), resulting in a greater lateral displacement of the centre of gravity during walking (see section 1.5.6). Other mechanisms for efficient walking seen in humans are lacking. In fact the pelvic tilt during stance phase in the chimpanzee is the direct opposite of that seen in humans, therefore not contributing to energy saving. The pelvis rises on the side of the swinging leg during stance (Aiello and Dean, 1990). Jenkins (1972) revealed that when walking bipedally, chimps reorient their pelvis to achieve an upright posture, but retain the same pattern of femoral flexion and extension as in quadrupedal walking. The lack of human characteristics in chimpanzee bipedal gait suggests that energy transfer between kinetic and potential energy may not take place. This mechanism is the chief method for saving energy in bipedal striding and is also apparent in quadrupedalism to a degree (see section 1.5.5). Bipedal walking in chimpanzees displays a characteristic pattern of kinetics as well as kinematics. Vertical ground reaction forces have a single peak or a plateau with two barely noticeable peaks, rather than the double peak usually seen in normal human bipedal walking (Yamazaki et al., 1979; Alexander, 1991).

As chimpanzees fail to extend their knees during stance, their bipedal locomotion requires a much higher degree of muscle activity in order to stabilise the bent-legged walk (for more details of muscle activity during chimp bipedalism see section 5.2.2.). Walking with bent knees generates large moments which tend to increase flexion in the knee, which in turn must be balanced by muscular tension (Alexander, 1991). In particular, increased activity in the extensors of the hip and knee contributes to the increased muscular activity (Tuttle et al., 1979a, b). However, despite these differences, the bipedal locomotion of primates (such as the chimpanzee) which use vertical climbing as a major part of their locomotor repertoire has been claimed to be more similar to human bipedalism than the bipedalism seen in more terrestrial species, such as Japanese macaques, in terms of kinematics and electromyography. It is thus suggested that vertical climbing may have been a precursor to terrestrial bipedalism (Fleagle et al., 1981).

1.5.8 Comparative energetics of human and primate locomotion

Several workers have hypothesised that bipedalism evolved as an efficient gait for travelling over long distances (see section 1.2). There has therefore been much endeavour to quantify differences in locomotor economy between bipedal and quadrupedal locomotion in various animals. The energetic requirement of each locomotor mode can be quantified using oxygen cost as an estimate of overall cost of locomotion (see section 1.7). As will be explained in a later section, energetic cost of locomotion is highly dependent on speed. Taylor et al. (1970) have shown that at maximum speed, human bipedalism incurs twice the energy cost per unit weight and distance as is predicted for a mammalian quadruped of similar size. However, Taylor and Rowntree (1973) measured the energy cost of quadrupedal and bipedal locomotion in chimpanzees, and could find no significant differences between the energy cost of quadrupedal and bipedal locomotion. They therefore conclude that efficiency of bipedal walking (versus quadrupedal locomotion) should not be used in arguments to account for the evolution of bipedalism. However, Ishida (1991) calculated that bipedal walking in chimpanzees was 5 times the energy cost of human bipedalism.

The reason for this apparent contradiction may be that the studies by Taylor et al.(1970) and Taylor and Rowntree (1973) based their conclusions on comparisons of human bipedal running compared to the running of other animals. Fedak et al. (1974) showed that human running is 75% less efficient than human walking. Further, Tucker (1975) studied the energy cost of locomotion (i.e. the mass-specific cost of moving a unit distance, see section 1.7.2) in both human walking and running. Their study supports the view that human walking is not energetically expensive when compared to true quadrupedal walking. Steudel (1996) calculated the cost of locomotion for human and chimpanzee walking and running, and compared these costs to expected costs for a mammal of similar size. The cost of locomotion for human running was consistently above expected values, but only by a small amount. Human walking, however, showed a decreased cost of locomotion when compared to generalised mammalian quadrupeds and chimpanzees, although non-primate quadrupeds also display the apparent efficiency seen in human bipedalism (Taylor et al., 1982). Rodman and McHenry (1980) found that not only are humans efficient during bipedal walking, but chimpanzees display a relative inefficiency during terrestrial quadrupedalism, compared to predicted costs from other, more cursorial quadrupedal mammals, and conclude that an increase in energetic efficiency was indeed important in the evolution of bipedalism.

The habitual locomotor mode of common chimpanzees is a form of specialised quadrupedalism. Since chimpanzees only use a bipedal posture occasionally (see above), it does not seem surprising that their morphology is not oriented towards efficient bipedalism. Indeed, some view chimpanzee morphology as a compromise between the demands of arboreal feeding and terrestrial travel, with a consequential inefficiency of both quadrupedal and bipedal walking (Rodman and McHenry, 1980). From the viewpoint of energy cost, chimpanzees could walk much longer distances if they adopted a fully upright bipedalism (Ishida, 1991). Even in the bipedal walking of Japanese macaques, 30% of energy expenditure can be saved by training, which leads to a small postural adjustment towards upright walking (Ishida, 1991).

1.6 Estimating Energy Cost

Estimating energy expenditure is important for many areas of research including human adaptation to environment and adaptability (Katzmarzyk, 1996). The most widely used technique for assessing total energy expenditure is the factorial method. This method uses observations of the amount of time spent in various activities during the day. The energetic cost of each activity (obtained by indirect calorimetry {see section 1.7.2} or from published sources) is then multiplied by the time spent in each activity to obtain a total energy expenditure for the entire day (e.g. Leonard and Robertson, 1997).

Although all data in the estimation of energy cost are expressed as a daily rate, all of the estimates given refer to a habitual level of energy expenditure. It is assumed that these values will vary from day to day, and also from week to week. The estimates calculated, therefore, represent the long term average.

Total energy expenditure can also be estimated using standard equations derived from studies on a variety of terrestrial mammals.

1.6.1 Estimating body size

The first step in estimating energy expenditure, especially of an extinct species, is obtaining a reliable estimate of body size, stature and body mass. The size of an organism has profound importance in many aspects of biology (Swartz, 1993). Terrestrial species tend to have a larger body size than arboreal species. This probably occurs because terrestriality removes pressures exerted by arboreal environments to keep body weight down, such as the necessity for increased mobility. Terrestrial species are also more likely to have more dispersed food resources and a higher predation rate, both of which select for increased body size (Clutton-Brock and Harvey, 1977b).

1.6.2 Estimating resting metabolic rate

A reliable estimate of resting or basal metabolic rate is important in any calculation of daily energy expenditure. Resting metabolic rate is the 'primary expression of energy requirement' (FAO/WHO/UNU, 1985). Resting energy requirements vary not only with absolute body weight, but also when expressed as metabolism per kilogram. Resting metabolism varies also with height and age.

1.6.3 Estimating daily living costs

The energy budgets of an animal are of great use in understanding its ecology. It is for this reason that knowledge of energy budgets in extant animals are important to evolution (Schmidt-Nielsen, 1983). Most estimates of daily living costs rely on knowledge of a number of variables including day range, home range and diet quality. Activity budgets are necessary in estimating activity costs, since time spent in various activities will affect total daily energy costs.

Estimating home range size

Home range is the total area used by a population group (Clutton-Brock and Harvey, 1977b). Home range size is positively related to body weight and negatively related to the proportion of foliage in the diet. Estimates of home range size predicted using body weight tend to be more reliable than those predicted by diet (Clutton-Brock and Harvey, 1979).

Estimating day range

Day range is defined as the daily path length (usually of a feeding group) within a species (Clutton-Brock and Harvey, 1977b). It is sometimes referred to as daily movement distance. Day range length is positively related to group weight (i.e. the total weight of the group of animals regularly associating together who share a home range, usually the feeding group), but negatively related to the proportion of foliage in the diet (Clutton-Brock and Harvey, 1977b). Other factors may be determinants in the distance that groups move in a day, but food dispersion is likely to be the most important factor.

Activity budgets

Activities of primate species are usually split up into time spent resting or inactive (including grooming); feeding or foraging; and moving or travelling. Activity partitioning for human societies is more complex, and therefore more activity categories are utilised. However, in using time budgets to model activity budgets for an extinct species, it makes sense to simplify the activity categories as far as possible.

1.6.4 Locomotion cost alone

It has been proposed in many studies (see section 1.2 and 1.5.8) that the energy cost of locomotion could be important to the evolution of bipedalism. Although costs of locomotion tend to account for only a small portion of total daily activity costs (Kasarov, 1992), differences in efficiency between postures within a single species can have important effects on the ecology of a species and its adaptation to habitat (Rodman and McHenry, 1980).

The energy cost of locomotion is also referred to as the cost of transport. Cost of locomotion is defined as energy expenditure per unit weight of an animal moving at a given speed on a level path for a unit distance (Tucker, 1975). Cost of locomotion varies markedly with speed. There is usually a particular speed for which the cost of locomotion is at a minimum, which determines the speed at which the animal can cover distance on the level with the least energy expenditure (Fedak, Pinshow and Schimdt-Nielsen, 1974). The cost of transport is highest for animals that walk or run, and lower for flying and swimming animals (Tucker, 1975).

1.7 Thermal Energy Budgets

Human heat balance occurs when the body is maintained at a constant 37°C (98.6 °F). Heat balance occurs when heat gain and heat loss from the body are equal, and no heat is stored within the body. When heat gain is greater then heat loss, body temperature will increase. When heat loss exceeds heat gain, body temperature will decrease. The thermoregulatory system thus involves a variety of mechanisms within the body to maintain a constant core temperature. During both rest and exercise the body strives to keep itself at 37°C. However, there exists a 'thermo-neutral zone', a range of environmental temperatures within which the body does not need to enforce thermoregulation (Nadel, 1977).

Heat exchange occurs due to four factors; convection, conduction, radiation and evaporation. Convection is defined as the transfer of heat from one place to another by motion of a fluid or gas. For example, a fan blowing cold air removes heat from the surface of the skin by "forced" convection. Convection also occurs when blood carries heat from muscles, through the core of the body, and ultimately to the skin (Fox, Bowers and Foss, 1993).

Conduction is the direct transfer of heat between two solid objects at different temperatures. Heat flows from the warmer object to the cooler object: for example if we touch a hot oven, heat is transferred from the oven to the skin.

Radiation is the transfer of heat by electromagnetic radiation. Radiation occurs when molecules within a body are constantly vibrating, and heat is given off as electromagnetic waves. About 60 percent of the heat loss from humans at rest is due to radiation. We gain heat from the environment on hot days through radiation, and conversely we can also lose heat from our bodies to the environment on a cold day.

Evaporation is a process which occurs when liquid is converted to a gas. Energy is required from the immediate surroundings for this change to take place. When we sweat, liquid sweat evaporates into a gas, and energy is extracted from the skin surrounding the sweat, therefore cooling it. For sweat evaporation to occur, the vapour pressure (humidity) of the environment must be less than that of the skin. For every kilogram of sweat evaporated, 580 kilocalories are released, so that sweat is an important mechanism of heat loss from the body. A kilocalorie (kcal) is the unit of heat energy most commonly used in physiology (1 kcal is defined as the amount of heat required to raise the temperature of 1 kilogram of water by 1 °C {Fox, Bowers and Foss, 1993}).

During rest, heat balance is usually maintained since heat produced from resting metabolism is easily dissipated through conduction, convection, radiation and evaporation. If no heat loss occurred, the body would gain 0.5 to 0.6 °C of heat every hour merely from normal metabolism. However, a person exercising, therefore producing more heat with the increase in metabolism, has more difficulty dissipating this heat. Activity affects the thermal energy budget because metabolic heat production is a significant component of heat gain in endotherms, and activity can affect evaporative and convective heat loss (Karasov, 1992; Wunder, 1970). An athlete exercising for about 1 hour produces about 580 kcal, which would result in an increase in temperature of 8.7 °C if no heat loss occurred (Fox, Bowers and Foss, 1993). During vigorous exercise, body temperature can rise by a degree or so, but at low environmental temperatures, rapid heat loss aided by vasodilation will suppress elevated core temperatures.

When exercising on a cool day, there is a large thermal gradient between the skin surface and the environment. This enables efficient heat loss from the body through the skin surface, as sweat evaporates quickly. On a hot day heat is gained by the body from the environment, increasing the need for heat loss from the body even when resting. During exercise on a hot day our body must cope with a large elevation in core temperature, and must therefore expend more energy in dissipating heat from the body. High environmental temperatures cause a reduction in the thermal gradient between the environment and the skin surface. A hot environment also causes skin temperature to rise. This has a consequence of reducing the thermal gradient between the skin surface and the body core. These alterations of thermal gradient impose a threat on the ability of the body to lose heat through convection and radiation. The barrier to heat loss causes core temperatures to remain at high levels, which severely limits an individual's capacity for work (Fox, Bowers and Foss, 1993). Overexposure to heat during exercise is dangerous, as it not only causes a decrease in work performance, but also can induce serious heat illness and in severe cases, can cause death (Fox, Bowers and Foss, 1993).

Metabolic energy cost at rest can be appreciably elevated by thermal stress. If a population is outside the thermoneutral zone for a substantial part of the day, estimations of resting metabolism taken in a temperate climate will not take thermal stress into account (Katzmarzyk, 1996). Deviations from predicted energy costs are substantial for temperatures above 25°C, and approximate to a 34% increase in resting metabolism (Katzmarzyk, 1996).

!Kung San from the Kalahari desert of Africa can expect highs of 35 to 45°C during the summer months. Since in these environments heat stress is defined as temperatures above 33°C, they can spend many hours in the day hunting and gathering under extreme conditions (Lee, 1979). On average 41% of days in a year have extreme temperatures (temperature increases above 33°C), indicating extreme sweat losses throughout the warmer months (Lee, 1979). A person walking in the sun at 38°C (100°F) sweats approximately 800 cc of water every hour, totalling over 3 litres of water for a typical working day (Lee and DeVore, 1976). As Newman (1970) points out, modern man, although possessing an efficient thermoregulatory system, cannot store large amounts of water within his body, as horses or camels do. The human thermoregulatory system therefore requires large amounts of water to be ingested for evaporative cooling.

Wheeler (1984; 1991a, b) modelled the costs of thermoregulation in early hominids. Assuming that they inhabited hot, dry, savannah environments, he calculated that quadrupeds would receive more incident radiation throughout the day than upright bipeds, since the surface area exposed to direct solar radiation is less for bipeds than quadrupeds. There are thus large savings in energy due to lowered thermal stress in bipeds, thus accruing selective advantages. Wheeler (1992a, b; 1993) went on to look at the consequences of the fact that early hominids were relatively large bodied, hairless creatures, and argues that they could gain maximum advantage from being bipedal in terms of heat dissipation while living in savannah environments. They were tall enough to take advantage of wind speeds that increase above the level of vegetation, which aids evaporative cooling. The studies showed that for the habitat and environmental temperatures typical of the savannah, bipeds could take advantage of longer periods during the day for foraging, because they need to spend less time in the shade for cooling off than similar sized quadrupeds. Wheeler also concluded that bipeds could travel longer distances compared to quadrupeds with the same water intake, due to the savings of decreased thermal stress, while taking advantage of higher wind speeds. The quadruped hominid water requirement was calculated at 2.5 litres compared with 1.5 litres per day for a bipedal hominid.

1.8 Measuring Energy Cost

Physiology is important to the study of bipedal evolution (Falk, 1991). Measuring the physiology and therefore energy cost of movement may help to answer some of the current issues in hominid locomotion. Following the recent advances in technology, measuring the energy cost of human walking has become a relatively easy task. The first problem, that of measuring the 'fuel consumption' of humans is overcome by measuring the oxygen used to oxidise food. Measurements of oxygen uptake are usually instantaneous and are used routinely in exercise physiology testing, to measure the metabolic response to different exercise regimes. The energy used by an individual exercising can be split into three sections. The first is the muscle work done to accelerate and decelerate the segments of the body in various directions. An increase in the energy expenditure by the muscles necessitates an increase in activity of the overall physiology; mainly involving the heart and lungs working harder during the exercise. There is also a small energy expenditure required in maintaining an upright posture. The third portion is the 'basal metabolism', or the energy costs of a person at rest. This comprises a substantial amount of energy used in the basic mechanisms needed to maintain health and growth. In many studies (e.g. Bhambhani and Singh, 1985) it has been usual to estimate the mechanical efficiency of locomotion by comparing oxygen cost at a given speed with the basal oxygen cost. This approach, however, neglects various overheads, (such as the energy required to maintain posture) and it has been suggested (Inman, 1993) that it may be more realistic to use the standing posture as a baseline for comparison with walking of various speeds.

Exercise Physiology

Exercise physiology is an aspect of kinesiology which involves the study of the human body and how it responds and adapts to exercise (Fox, Bowers and Foss, 1993).

The estimation of the energy cost of exercise requires measures of both aerobic and anaerobic exercise. Aerobic exercise occurs when energy for exercise can be obtained from the oxidation of glycogen stores in the liver, aided by oxygen inhaled during exercise. Anaerobic exercise occurs when energy requirements for exercise are increased above that which the aerobic system is able to cope with. The anaerobic system uses glycogen along with alternate stores of energy within the body. Anaerobic metabolism is usually brought into action at the start of exercise, and also during prolonged heavy exercise. Anaerobic metabolism involves the breakdown of glycogen without the presence of oxygen, causing a build up of lactic acid in the body (Fox, Bowers and Foss, 1993). Exercise rates are crudely divided into sub-maximal and maximal exercise rates. Sub-maximal exercise can be performed at a 'steady state', which indicates that all of the energy needed for exercise is provided by the aerobic system. As soon as steady state oxygen consumption is reached, anaerobic metabolism stops, and the level of lactic acid produced by anaerobic metabolism remains constant until the end of exercise. The cost of aerobic metabolism can simply be measured by oxygen consumption during exercise. Resting levels of oxygen consumption should be determined prior to the start of exercise, so these can be subtracted from exercise oxygen consumption, therefore estimating the oxygen cost of exercise alone. When measuring the energy cost of anaerobic metabolism, the measurement of resting, exercise and recovery levels of energy metabolism are necessary, since any lactic acid build up will only be metabolised after cessation of exercise (Fox, Bowers and Foss, 1993).

When studying the energetics of activity, it is necessary to be able to reproduce a particular work condition reliably. If physiological responses to a test condition differ between two testing sessions, it is necessary to be sure that the physiological change is a response to something other than the exercise test. This is especially true if responses to more than one work condition are being studied, for example if we wish to measure differences between a subject walking with and without shoes at the same speed. Motor driven treadmills are commonly used for this purpose, as they provide a means of controlling speed.

The prescription of an exercise protocol depends on the intensity of exercise, and the frequency and duration of each exercise intensity. A graded exercise test (see Figure 1.11) is commonly used in measuring the oxygen cost of a specific exercise.

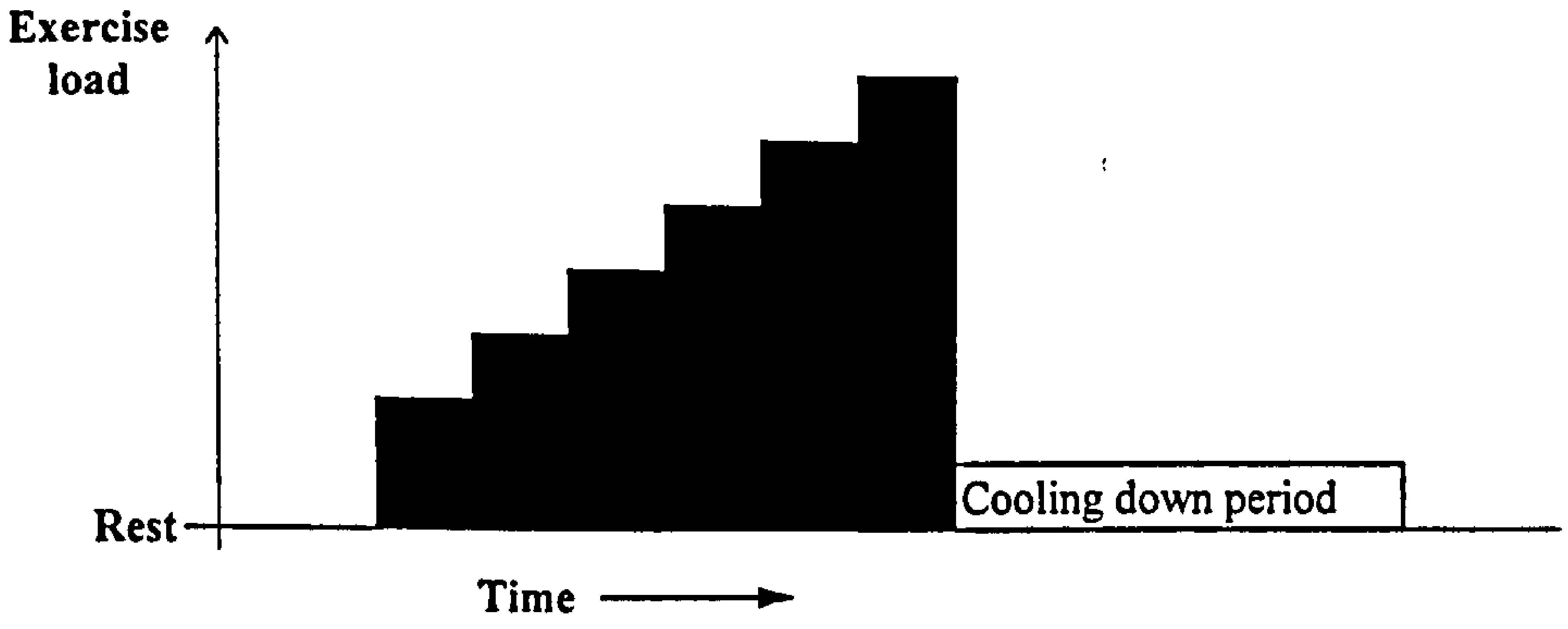


Figure 1.11 A graded exercise protocol, commonly used in exercise testing. This diagram demonstrates the continuous step increment loading method.

A graded exercise test first involves a period of rest, where resting metabolism can be calculated, followed by exercise at incremental levels. The increments can be a change in speed, or alternately, an alteration of grade (the angle of elevation of the treadmill). Exercise is performed at each level until a steady state is reached, before continuing to the next level of exercise. As previously mentioned, (see above) following cessation of exercise, a recovery period is necessary, in order to quantify demands upon the anaerobic system.

When a graded exercise test (GXT) is terminated prior to attaining maximal intensities, it is a submaximal test. Submaximal testing is normally terminated when a predetermined criterion is attained, usually an absolute oxygen consumption, heart rate, or rate of perceived exertion (see sections 1.8.2, 1.8.3, 1.8.4). In the current experiments (see chapter 4), maximal walking speed is used as the cut-off criteria for termination of the test.

1.8.1 Techniques for measuring energy cost

To calculate the total amount of energy used during an activity, the most exact method is 'whole body calorimetry'. This requires the subject being kept inside a closed, insulated chamber whilst carrying out the activity to be measured. The heat output from the body is measured to give the total energy cost (Whittle, 1991). This is very impractical, and the technique is not often used to measure energy cost in exercise physiology. Less direct techniques to measure energy cost are more often applied in research, which include measuring oxygen consumption, heart rate and other physiological measures. There are absolute and relative rates of energy cost. Absolute measures are kcal·min^{-1}, ml O_2·min^{-1} and L O_2·min^{-1}. All relative measures express oxygen cost as units per kilogram of body weight. Typical units include

$ml(O_2) \cdot kg^{-1} \cdot min^{-1}$, $kcal \cdot min^{-1}$, $kJ \cdot min^{-1}$ and METs. A MET is a multiple of the resting rate of oxygen consumption. One MET is equal to approximately 3.5 $ml(O_2) \cdot kg^{-1} \cdot min^{-1}$, which represents the oxygen consumption of an individual sitting at rest (American College of Sports Medicine, 1991). Values are usually given as STPD (standard temperature, pressure, dry). Gas volumes, such as oxygen consumption, should always be corrected to standard volumes such as STPD for comparison with data from the literature. Values measured in laboratories are usually in ATPS (ambient temperature, pressure, saturated), and will sometimes need to be converted into STPD using Charles and Boyles gas Laws (Montoye et al., 1996). Most automated gas analysers for measuring oxygen consumption in modern laboratories convert all data to STPD automatically.

1.8.2 Oxygen consumption

When energy is transformed from food to heat and muscular work in the body, oxygen is consumed. Oxygen consumption is defined as the oxygen that is taken into the body and used in the tissues. Measuring oxygen consumption is thus a reliable method with which to estimate the energy expenditure of an individual. VO_2 is the symbol used to express the volume of oxygen consumed, usually the rate of oxygen utilisation per minute. Sometimes rates of oxygen consumption are expressed as VO_2 per unit weight, which aids with comparisons between subjects of differing body weight. $\dot{V}O_2$ is the symbol used to express VO_2 per unit time (usually VO_2 per minute).

Methods of estimating energy expenditure from VO_2 and from VCO_2 (volume of carbon dioxide produced) are referred to as indirect calorimetry, as heat production is not measured directly. VCO_2 is usually measured simultaneously to VO_2, so the ratio of carbon dioxide produced to the volume of oxygen consumed can be calculated. This ratio, the respiratory quotient (RQ), gives a reasonable estimate of the type of food being metabolised, specifically the percentage of carbohydrate or fat. The calorific value of protein metabolism is very similar to carbohydrate, and is therefore ignored for simplicity (Montoye et al., 1996). The RQ value is 0.7 when pure fat is used as the only source of energy, and 1.00 when the source of energy is purely carbohydrate (Montoye et al., 1996). The RQ value is less for fat metabolism, since it requires more oxygen to release one calorie of energy (Fox, Bowers and Foss, 1993). RQ for a normal resting person is 0.82, which is equivalent to a metabolism of 66% fat and 33% carbohydrate. The RQ value is important in the conversion of energy cost of exercise to calorific values, since the calorific value of oxygen consumption depends on the type of energy metabolism. When measuring RQ, a "steady state" of exercise is assumed. This occurs when the oxygen uptake is equal to the oxygen demand from the tissues and there is no lactic acid production (Fox, Bowers and Foss, 1993). During steady state, the oxygen consumption as well as heart rate, ventilation rate and cardiac output remain constant, and therefore it is at this point during testing that all the variables are recorded.

Energy consumption expressed as energy cost per unit time (as in $\dot{V}O_2$), shows an approximate linear relationship with speed. Therefore minimal levels are recorded for slow walking and then the level increases with speed (Whittle, 1991).

The measurement of resting levels of VO_2 are necessary to determine the oxygen cost of the exercise alone. This value is determined by subtracting resting VO_2 from VO_2 measured during exercise. The oxygen cost of exercise alone is the net oxygen cost, whereas gross oxygen cost is the total oxygen cost, i.e. resting plus exercise oxygen cost (Fox, Bowers, and Foss, 1993).

During recovery from exercise, oxygen consumption continues at a relatively high level for a period of time, although energy demand has ceased as the subject is no longer exercising. This is the 'oxygen debt'. The extra oxygen is needed in order to restore the body back to the pre-exercise state. Oxygen consumed during recovery is used primarily in replacing energy stores depleted during exercise, and removing any build up of lactic acid in the blood and muscles (Fox, Bowers and Foss, 1993). To measure the oxygen debt, it is necessary to know the pre-exercise resting oxygen consumption and the total recovery time.

Energy cost of locomotion

Energy consumption (cost) can also be calculated as energy cost per unit distance. This is often referred to as energy cost of locomotion, or cost of transport. The energy cost of locomotion has a more perplexing relationship with speed than energy cost per unit time. At both very slow and very fast speeds, more energy is used per unit distance (Whittle, 1991). Minimum energy usage will occur at an intermediate walking speed, and this is sometimes described as the most 'efficient' walking speed. Energy cost of locomotion reflects a measure of cost effectiveness and is of great interest when considering whole animal energy budgets (Fedak, Pinshow and Schmidt-Nielsen, 1974).

1.8.3 Heart rate

The measurement of heart rate can give a surprisingly good substitute for oxygen consumption in the estimation of energy cost. Heart rate monitoring is easy to perform and usually very accurate. A simple ratio of resting heart rate to exercising heart rate shows a clear relationship with oxygen consumption (Whittle, 1991). Heart rate increases linearly with increasing work load or increasing oxygen consumption. Physical training has an important effect on heart rate. For highly trained individuals, heart rate is substantially lower (during rest or exercise) than the heart rate of untrained individuals. Even without the effect of training, the response of heart rate to exercise varies considerably from one person to another (Fox, Bowers and Foss, 1993). The relationship of heart rate to oxygen consumption, however, holds for both trained and untrained subjects (Fox, Bowers and Foss, 1993).

1.8.4 Perceived exertion

Ratings of perceived exertion are frequently used to supplement standard physiological responses during a graded exercise test. The RPE scale can be used to evaluate the effect of an experimental intervention (for example, a change in grade or a variation in posture). Rates of perceived exertion are often taken from the 'Borg' scale, a 15 level graded scale used to estimate the subjective response to an exercise test. The Borg scale is displayed in Figure 1.12.

6
7- Very, very light
8
9- Very light
10
11- Fairly light
12
13- Somewhat hard
14
15- Hard
16
17- Very hard
18
19- Very, very hard
20

Figure 1.12 The Borg RPE scale (15-graded rating scale)

RPE testing is usually applied as an adjunct to standard physiological measures, but it can also be used as a reliable single measure of physical fitness in the field. In the current exercise tests, RPE provides a subjective measure of exercise tolerance that complements objective physiological measures. An assumption basic to application of RPE in clinical testing is that perceptual and physiological responses are linearly related across a variety of exercise intensities or modes.

1.9 Muscle

1.9.1 Muscle properties and muscle mechanics

Muscle is a fundamental component of the mechanical system of the body. Key features in muscle cells allow fibres to shorten, generating forces that produce and control movement. In the following sections some of these key features of muscle, important to biomechanics, are described.

Muscle structure and function

Two types of muscle exist, smooth muscle and striated muscle (so called because of its characteristic banding pattern). This review only covers striated or skeletal muscle structure and function. The main function of skeletal muscle is contraction, resulting in movement. The basis for skeletal muscle function is the muscle motor unit, defined as a single motor nerve and the group of muscle fibres it innervates. There are many motor units within a single muscle. Within a motor unit are the individual muscle fibres. A single muscle may consist of only a few fibres, or may be composed of several thousands of fibres. The magnitude of force a muscle can generate depends of the number of fibres activated and also the line of action of the muscle. The number of fibres acting together within a muscle, which determines the total force a muscle can produce, is referred to as the physiological cross-sectional area (or PCSA).

Muscle fibres contain hundreds of myofibrils. Within these myofibrils are the contractile units, called sarcomeres. The contractile unit contain myofilaments consisting of protein units called myosin and actin. The myosin and actin proteins have a special arrangement, one myosin being surrounded by six or more actin filaments. Each myofibril has a complex structure (see Figure 1.13) consisting of I bands (light areas) and A bands (dark areas), which make the muscle appear 'striped'. In the middle of each I band is a dark line, the Z line. One sarcomere is defined as the myofibril between two Z lines. The Z lines adhere to the sarcolemma (muscle cell membrane), to give stability to the whole structure. The I band is composed almost entirely of actin filaments, which partly extend into the A band. The A band is therefore mainly composed of myosin filaments, with a small amount of actin extending into it. In the middle of the A band, there is a section with no actin filaments. This section is the H zone. Myosin filaments have small projections on each end, called cross-bridges, which extend towards the actin filaments. The cross-bridges play a very important role in muscle contraction. In each myosin molecule, there are two cross-bridge heads attached to the tail of myosin. The cross-bridge heads are where energy is converted (from chemical to mechanical) to produce muscle force.

Sliding filament theory

The sliding filament theory, originally proposed by Huxley (1969), describes how one set of filaments 'slides' over the other hence shortening the muscle and producing a muscle contraction. The length of the actin and myosin filaments do not change throughout contraction. The sliding of the filaments leads to a shortening of the I band, but not of the A band, ultimately leading to a loss of the H zone (see Figure 1.14). It is thought that the myosin cross-bridges form a chemical bond with sites on the actin filaments, forming a protein called acto-myosin (Fox et al., 1993). The theoretical model of contraction is divided into five phases: rest, excitation-coupling, contraction, recharging and relaxation.

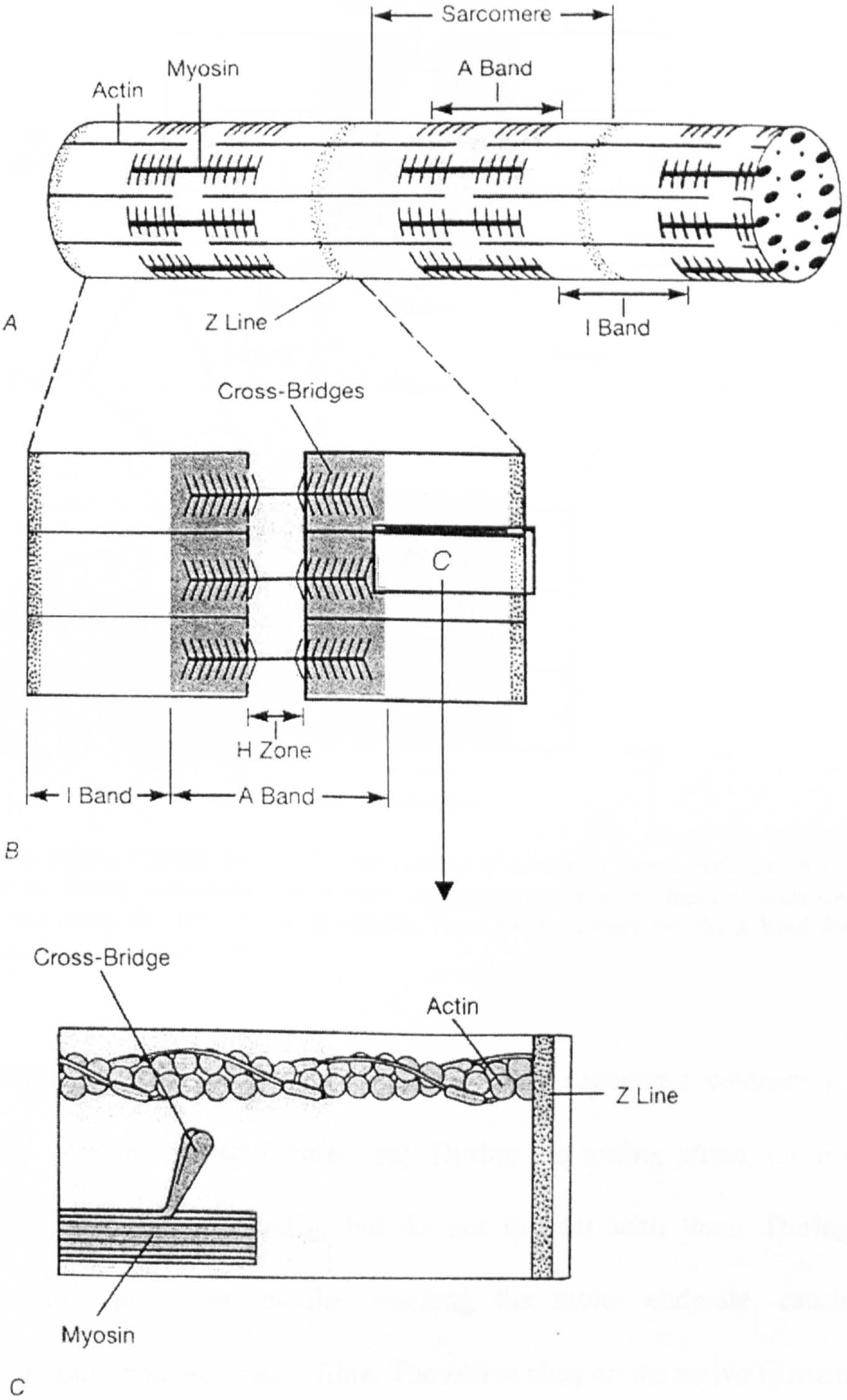


Figure 1.13 The structure of a myofibril, the contractile unit of a muscle.
A: Note that the A band is composed of two protein filaments (actin and myosin)
B: A closer look at the myosin filament, projecting in cross-bridging fashion towards the actin filament
C: A magnified view of a single myosin cross-bridge as it projects towards the single actin filament
(Adapted from Fox et al., 1993)

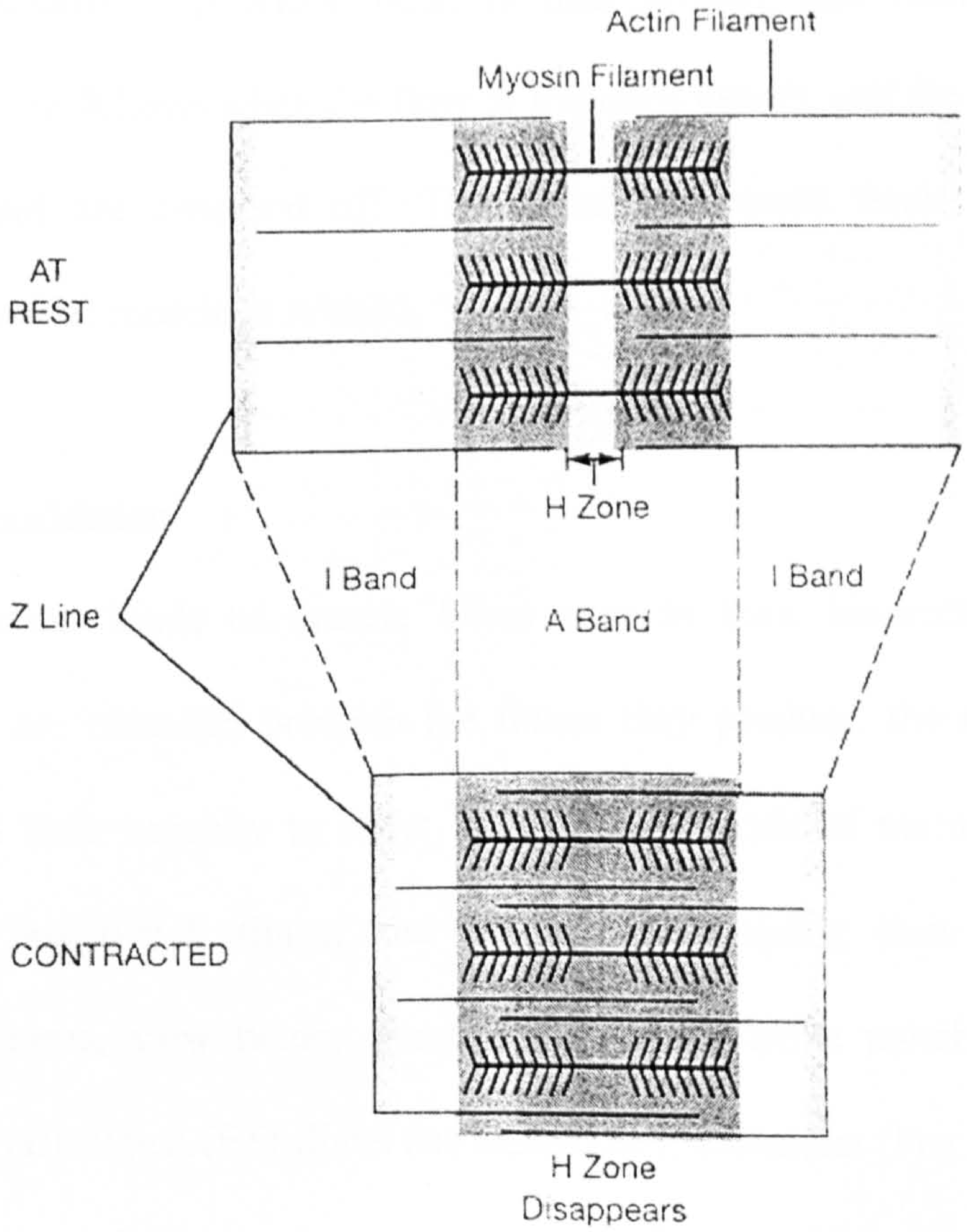


Figure 1.14 The sliding filament theory. The sarcomeres of a muscle shown both during rest and during contraction. During contraction, the H zone disappears as the actin filaments slide over the myosin filaments towards the centre of the sarcomere. The I bands shorten, but the A band does not change in length. (From Fox et al., 1993)

The sliding filament theory is briefly described for a concentric contraction (see section below- types of muscle contraction). During the resting phase, the myosin filaments projects towards the actin, but do not interact with them. During the excitation-coupling phase an impulse reaching the motor endplate, causing a generation of impulses in the muscle fibre. The active sites on the active filament are then 'switched on'. A chemical process results in the acto-myosin complex form, which activates a chemical (ATP) to be broken down, releasing energy. The release of energy influences the cross-bridge structure, which initiates the sliding of the actin over the myosin. In this manner muscle tension is developed and the muscle shortens.

The actin-myosin cross-bridge bond is then broken, and recharged with ATP. Relaxation then follows when the flow of impulses ceases, and the active sites on the actin filament are switched off. The muscle filaments return to their original positions, and the muscle is relaxed.

Muscle organisation

Different kinds of muscle fibres vary in their biomechanical properties. Differences are observed between the forces they produce, the rate at which they shorten and their capacity to resist fatigue. Two kinds of motor unit exist, those containing fast twitch fibres, and the other containing slow twitch fibres. In simplified terms, slow twitch fibres (ST) use oxidative metabolism to generate energy and fast twitch (FT) fibres use anaerobic metabolism (Fox et al., 1993). Slow twitch fibres are fatigue resistant. Fast twitch fibres can be either fast fatiguing or fatigue resistant. In general terms, locomotor muscles contain mostly fast twitch fibres, while postural muscles contain mostly slow twitch fibres (Swartz, 1993).

The deepest muscles in each group of extensors possess the highest proportion of ST fibres. More superficial extensor muscles have fewer ST fibres, but the antagonistic flexor muscles hold the least number of ST fibres. Fibres within a single muscle also show layering of fibre types, with slower fibres below the surface and fast fibres located superficially. This progression from deep to superficial muscles also reflects the order in which muscles are recruited during locomotion. Deep slow muscles are recruited first, through to more superficial fast muscles (Alexander and Goldspink, 1977).

Types of muscle contraction

There are two basic types of muscle contraction. Isometric contraction (same length) occurs when there is no change in the overall length of the muscle during contraction. Isotonic (same tension) contraction occurs if the muscle contracts with a constant force. Concentric contraction is the most familiar type of muscle contraction, and is used to describe a muscle undergoing isotonic shortening. Eccentric contraction is used to describe a muscle during isotonic lengthening. Isokinetic contraction occurs when tension develops in a muscle as it shortens at a constant speed.

In real life situations the limb segments interact with one another and with external forces. This results in a muscle being able to act on limbs segments to which it is not attached, and about joints which it does not cross.

During concentric contraction, a muscle does external work (see section 1.5.5), but during eccentric contraction it absorbs energy (Whittle, 1991). Muscles undergoing isometric contraction do no external work, but during isometric contraction a two-joint muscle can transfer power from one limb segment to another (see below).

Role of two-joint muscles

Under some circumstances, two-joint (biarticular) muscles can act to move limb segments in the opposite direction to their recognised anatomical actions, for example the gastrocnemius can act to extend the knee in upright standing, when usually it is known for flexing the knee.

Some two-joint muscles of the lower limb: sartorius, gracilis and semitendinosus, are remarkable for having long fibres and relatively small physiological cross-sectional areas (PCSAs). The characteristics suggest function through a large range, for example to stabilise the pelvis over the tibia. Other two-joint muscles, namely rectus femoris and gastrocnemius, have large PCSAs and are able to produce very large forces. Studies of jumping and locomotion have shown that there is a transfer of mechanical energy between joints by means of the two-joint muscles. This is also known as the 'tendon action' of muscles. This can be described for the example of rectus femoris as follows. If the hip joint is extending from the contraction of the gluteus maximus and the rectus femoris contracts isometrically (i.e. it does not shorten but prevents lengthening), then some of the force of the hip extension is used to bring about knee extension, so the rectus femoris is in effect acting as a tendon. Energy is transferred from the hip joint to the knee joint through the rectus femoris. The rectus femoris and gastrocnemius have been shown to transfer mechanical energy from proximal to distal and from distal to proximal joints (Prilutsky + Zatsiorsky, 1994), which enables force from the larger rectus femoris to contribute to generation and absorption of energy during toe-off and heel-strike in locomotion.

1.9.2 EMG and its uses

Electromyography or EMG is the measurement of the electrical activity in a contracting muscle. Since EMG measures the muscle action potential, which is electrical activity and not mechanical, it cannot differentiate between concentric, eccentric or isometric contractions. It is generally accepted that with an increase in muscular effort, more motor units (muscle fibres plus motor end plates) become activated. EMG measures an increase in the number of action potentials, and therefore the level of recruitment of muscle fibres (Platzer, 1986). It can therefore produce detailed data on the onset, duration and relative intensity of a muscle activity pattern with respect to any individual movement.

The importance of electromyography (EMG) to our understanding of human and primate locomotion has long been recognised, but it wasn't until 1968 that the use of these techniques in the study of non human primate muscle function was first reported, although EMG has since proved particularly valuable with reference to interpretations the of origin and evolution of human bipedalism (Ishida, Kumakura and Kondo, 1985).

Only partial agreement exists as to what is a 'normal' pattern of muscle activity during locomotion. This lack of agreement on muscle activity patterns is partly due to the variability within muscle anatomy from one individual to another, but also due to measuring technique. Muscle activity patterns not only vary between people (i.e. it is possible for two people to walk in an identical fashion while using different combinations of muscles), but can also vary within an individual with an increase in fatigue, or a change in walking speed (Whittle, 1991).

Although it is not generally possible to convert EMG directly into a measure of muscle force production, information on whether the muscle is simply inactive, is contracting slightly, or contracting strongly is very useful in the mechanical analysis of a body in motion (Whittle, 1991).

1.9.3 Human data

Human data will be fully discussed in Chapter 5, along with presentation of experimental data for EMG of the lower limb in human subjects. General patterns of data have been described by Whittle (1991).

1.9.4 Non-human primate data

The study by Ishida, Kumakura and Kondo (1985) concentrated on a comparison between quadrupedalism and bipedalism in six species of primate, including humans. Nine individuals from six species were tested for bipedal walking, and seven individuals from four species were tested for quadrupedalism. Three locomotor groups are represented in this group of primates, including habitual bipeds, quadrupeds and swinger-climbers. All non-human primates were trained for a period of two to six years to walk bipedally. Muscles tested while walking quadrupedally and bipedally included gluteus medius, vastus lateralis, long head of biceps femoris, tibialis anterior, and the lateral head of gastrocnemius.

The most important differences between the EMG of human and non human primate bipedal walking is the activity of the major muscles during the stance phase. In man, the muscles studied show activity for a short time during heel strike, and then generally fall silent during the rest of the stance phase. In non-human primates however, most muscles are simultaneously and highly active during most of the stance phase (tibialis anterior being an exception, with only slight activity). This high activity during the stance phase was explained by Ishida et al. (1985) in terms of the flexed joints of the non-human primate hindlimbs during the stance phase of bipedal walking. Data for chimpanzee bipedalism was said to differ markedly from the

Japanese macaque data, particularly during the stance phase. The chimpanzee data showed two peaks of calf muscle activity, one at the start of the stance phase and the other during the last half of the stance phase. The peak of activity during the stance phase was seen to correspond with propulsive forces in the foot, and it was therefore presumed that the calf muscles in chimpanzees were providing the propulsion for push-off prior to the swing phase. This was linked to the push-off mechanism needed for vertical climbing which the authors claimed was observed frequently during the natural behaviour of chimpanzees (but see Doran, 1992 for a contrasting view).

1.9.5 Limitations

The main limitation of EMG is that is only a semi-quantitative procedure, which will give an approximation of the strength of a contraction in an individual muscle. It is also quite difficult to obtain adequate recordings from a moving subject, as movement artifacts are quite common, causing a change in the electrical baseline of the recording. Satisfactory results can be obtained, however by a skilled operator who carefully selects the recording sites and minimises the skin resistance directly beneath the electrode. The equipment used also effects the outcome, and avoidance of electromagnetic interference from other electrical equipment is essential.

1.10 Aims and Objectives

The main aim of this project is to examine the likely cost of a BHBK gait (first proposed for 'Lucy' by Stern and Susman) to our early hominid ancestors. This study will examine the energy costs of locomotion in early hominids from a variety of perspectives. The energy costs of locomotion will first be estimated in Chapter 3, using both human and primate models based on an array of data taken from the literature. Estimates of energy costs will include costs of locomotion and total daily energy expenditure, calculated by a range of techniques. Data for energy costs will be converted to kilocalories wherever possible, for comparison with data from other sources. Actual energy expenditure and muscular activity during a BHBK gait will then be measured, using human subjects to simulate early hominid locomotion. A variety of techniques are employed in Chapters 4 and 5 to estimate the ability of humans to perform a BHBK gait. The methodology is adapted in order to obtain a direct comparison between humans walking in normal and BHBK postures. Previous biomechanical analysis of a bent-knee gait (Alexander, 1991) established that bent knees during stance produce a tendency towards further flexion in the knee, necessitating increased muscle activity in order to balance the gravitational forces. A straight knee during stance, which is typical of 'efficient' human walking, generates only minor activity in the knee extensors.

One main objective of this study is to provide real-world physiological tests of previous work reviewed in Chapter 2, in which a variety of biomechanical techniques and computer simulations (Crompton et al., 1998; Li et al., 1996) predicted that a bent-hip, bent-knee gait would be mechanically inefficient.

CHAPTER TWO

PREVIOUS WORK

"The designer of a bridge needs to know the strength of his steel or concrete and he needs to know how forces are transmitted through structures; he must draw on the expertise of materials science and structural engineering. A biologist studying an animal or plant structure cannot understand it fully without the same sort of knowledge"

R. McNeill Alexander (1981)

2.1 Computer Modelling and the Reconstruction of Hominid Gait

Attempting to resolve the debate between Stern and Susman (1983) and Lovejoy and colleagues as to how 'Lucy' and other early hominids walked (see section 1.1), Crompton et al. (1998) endeavoured to assess the mechanical effectiveness of AL 288-1 (Lucy) using predictive dynamic modelling, under two hypotheses. The first hypothesis is that the terrestrial bipedalism of Lucy was completely erect, with a bipedal locomotion resembling our own. The second hypothesis models the likelihood that her bipedal locomotion was "bent-hip, bent-knee", like the bipedalism of living chimpanzees. Mechanical effectiveness is assessed using mechanical joint power, simply the product of the angular velocity of a joint and the net joint moment (Winter, 1990).

Bent-hip, bent-knee walking in humans produces ground reaction force (GRF) curves intermediate in shape between normal human walking and chimpanzee bipedal walking (see section 1.5.7, p45). Normal human bipedalism is characterised by vertical GRF curves with two peaks, separated by a valley at mid-stance (Alexander 1984b, 1991). As speed increases, the GRF peaks increase. Previous studies (Li et al., 1996) have shown that during bent-hip, bent-knee walking, the second of the two GRF peaks is reduced, and a plateau-like curve results. These findings suggest that there is a functional connection between knee and hip kinematics and the shape of the vertical GRF curve (Li et al., 1996).

Dynamic models were constructed using ADAMS/Android software of a body with 9 segments (for more details about model construction, see Crompton et al., 1996). The rigid segments were given length, mass, and inertial properties and linked together. The stiffness and flexibility of joints were modified until models were capable of stable walking and there was confidence that the data resulting from the model consistently fell within the limits of real data for ground reaction forces. Data from the model was verified in every case by comparing with real data for humans. Once satisfactory results were obtained for real human data, the model was altered in order to simulate a bipedal gait in Lucy. The mass distribution characteristics and segmental inertial properties were obtained alternately from chimpanzee data and from human data (Crompton et al, 1996), and altered to match the current estimates of stature and body mass proportions in Lucy. Bipedal walking was simulated by applying motion data to each of the inertial models. These data consisted of real kinematic records for the sagittal plane, for normal human, chimpanzee and human "bent-hip, bent-knee" walking, previously obtained from video recordings (Crompton et al., 1996; Li et al., 1996). An inverse dynamics approach was then used to calculate the ground reaction force curves for each gait.

Segmental motion from common chimpanzees did not result in any successful simulations of bipedal walking, in terms of the criteria set out above. Common chimpanzee motion data is therefore assumed to be incompatible with the proportions of AL 288-1, whether human or chimpanzee mass distributions were implemented. The other combinations, simulating Lucy walking bipedally (i.e. with chimp or human inertial properties and human motion, or with chimp or human inertial properties and "bent-hip, bent-knee" motion) all produced successful simulations, producing ground reaction forces typical of previously recorded data (Crompton et al, 1998). Joint moments, mechanical joint power and angular accelerations of the joints were calculated. The "bent-hip, bent-knee" simulation produced substantial positive power at the hip joint (similar to human walking), but net negative power-output at the knee and ankle joints. Interesting differences were also seen in the comparison of kinematics between normal human walking and "bent-hip, bent-knee" walking. During "bent-hip, bent-knee" walking, hip and knee angles are sustained at increased levels, but showed smaller ranges of motion, when compared to normal walking. The motion at the ankle joint showed increased dorsiflexion, which progressively increased during the stance phase (Crompton et al., 1998).

At the hip, the direction of change of the joint angle was negative throughout stance, and the angular velocity, and joint moments remained negative. Thus, positive work was done at the hip throughout much of stance, and the power output therefore remained positive. This is the case in normal human walking (Winter, 1991). At the knee however, the direction of change of angle and angular velocity remain negative through about 50% of the gait cycle, but the joint moment remains positive throughout stance. As positive joint power only results when the sign of the angular velocity or the direction of change in joint angle agrees with the sign of the moment in a given plane (see section 1.5.5), no positive power output is produced by the knee during most of stance. When the signs (of direction of change in joint angle, angular velocity and joint moment) disagree, negative joint power results, and hence energy absorption at the joint (Winter, 1990a). Thus the knee joint produces very little positive work during "bent-hip, bent-knee" walking, resulting in net energy absorption by muscles. Similar results are found at the ankle joint, where the opposing signs of moments and joint angle/velocity during stance, produce predominantly negative power output at the ankle. The muscles around the knee and ankle joint therefore must be doing negative work, in other words they are absorbing energy. Since the knee shows little extension, and the ankle little plantarflexion during "bent-hip, bent-knee" walking, most of this energy which is absorbed cannot be released by the joint as work. Therefore, neither the knee or the ankle are contributing significantly to the propulsion of the body throughout the stance phase.

All external forces generated by simulations of normal human walking, and human "bent-hip, bent-knee" walking fall into the range possible for living humans walking normally and walking "bent-hip, bent-knee" respectively. Thus, the model takes into account differences in body proportions between modern humans and

AL 288-1. Crompton and colleagues (1998) predicted that bent-hip, bent-knee walking would have been mechanically ineffective for AL 288-1, assuming that the mass distribution of AL 288-1 falls somewhere between patterns seen in common chimpanzees and modern humans. According to the simulations, the greatest part of positive work done during bent-hip bent-knee walking must be done by the muscles of the hip, and energy absorbed at the knee and ankle will be absorbed by the muscles operating around those joints. The predominant outcome of the "bent-hip, bent-knee" gait is energy absorption at the knee and ankle (as negative joint power exceeds positive joint power for the whole gait cycle). There is little work done as the absorbed energy is not output as work, therefore energy must be released into the muscles as heat (Alexander, 1984b). The transfer of energy as heat to the muscles would ultimately be expected to induce an increase in core body temperature (see section 1.7).

Ground reaction forces predicted by the model of AL-288-1 performing normal and bent-hip, bent-knee walking fall well within the range of those actually measured from living humans performing these two gaits (see above). Thus we can therefore assume that the mechanical consequences of these two gaits for AL-288-1 will be similar to the consequences of a BHBK gait in humans.

Since much progress had been made toward predicting the biomechanical implications of the bent-hip, bent-knee gait for AL 288-1, the next step seemed to be to compare the predictions for the mechanical and energetic consequences of a BHBK gait in humans against real-world data. Measuring mechanical work, however, is not accurate, as it does not necessarily equal the actual work performed

(Saibene and Minetti, 1992). During both walking and running, the measurement of work done can be underestimated by as much as 15% (Saibene and Minetti, 1992). Muscular work done during contraction is not measurable in mechanical terms. Equally difficult to assess is the importance of transfer of energy between segments of the body, and possible storage of energy in muscles and tendons is hard to quantify. With insights provided by Cavanagh and Williams (1983), it seems rational to use physiology and energetics to verify conclusions made from biomechanical analysis of bipedal locomotion.

It has recently been shown by Wang (submitted paper) that bent-hip, bent-knee walking in humans (at a comfortable speed) results in less than half the 48-70% recovery of mechanical energy normally seen during erect walking.

This work intends to support data discussed in this section further by measuring the 'real' cost of a bent-hip, bent knee walking posture to humans, by assessing both the physiological and muscular costs of humans walking in this posture.

CHAPTER THREE

THE ESTIMATION OF ENERGY EXPENDITURE

"There is probably no single physiological characteristic, other than energy metabolism, which is a more sensitive measure of an animal's life style and particularly its function within an ecosystem"

Louw (1993)

3.1 Introduction

The quantification of daily energy requirements and energy balance can provide a useful insight into many behavioural and physiological responses to environment, food availability and other ecological parameters (Katzmarzyk, 1996). Clutton-Brock and Harvey (1979) suggest body size, diet and ranging behaviour are functionally related traits, and therefore will evolve as a complex. During evolution, therefore, permanent changes in food quality or distribution are likely to have an effect on body size.

Energy requirements are defined as the amount of energy needed to maintain health, growth and an "appropriate" level of physical activity (FAO/WHO/UNU technical report, 1985).

The major potential components of energy expenditure are

i) standard or basal metabolism,

ii) assimilation of nutrients (specific dynamic effect or calorigenic effect of food; Kleiber, 1975),

iii) thermoregulation,

iv) activity, and

v) production: growth, storage of energy, reproduction.

If we exclude from consideration those measurements based on production (i.e. energy expended during growth, storage of food, reproduction and repair) as well as those for mammals with significant thermoregulatory costs, it becomes relatively simple to calculate the daily cost of activity by subtraction. Cost of activity is the total energy expenditure used for activity (e.g. locomotion), and is normally recorded on a daily basis i.e. in kJ per day. Cost of activity is dependant on an animal's allocation of time to various activities and the rate of energy expenditure for each activity.

The cost of locomotion (the cost of moving a unit mass a unit distance) is of great importance in shaping the lifestyles of animals (Louw, 1993). Larger animals have a greater efficiency, since the cost of locomotion per unit distance is less than that for small animals. Since large animals are more efficient (see section 1.5.6), they are able to utilise larger home ranges, and move further every day in order to find sources of food or water (Louw, 1993).

Since the direct measurement of energy expenditure in early hominids is of course impossible, it is obligatory to rely on estimations of energy expenditure. A number of ways exist to estimate daily energy expenditure, cost of locomotion, and many other ecological variables. Mace and Harvey (1983) for example, determined that daily energy expenditure can be predicted directly from home range size in a number of birds and mammals. The exact relationship between the two, however, is dependant on diet type, since the density of food items predominantly influences home range size.

In the following sections body size in the best-known early hominid, *Australopithecus afarensis* AL 288 1, 'Lucy', will be discussed, and the use of body weight in calculating a number of ecological variables will also be considered. The environments and ecology (relevant to early hominids) in the Miocene, Pliocene and Pleistocene epochs will be evaluated, to assist in the assessment of early hominid habitats. Dietary requirements, home range size, day range and other variables will ultimately be used in the estimation of daily energy requirements in hominids.

3.2 Estimating Body Size for "Lucy"

Body weight is used to indicate overall size for a wide variety of allometric comparisons in the field of ecology (Hartwig-Scherer and Martin, 1992). Body weight is a good representation of the morphological and physiological requirements of an animal. Estimates of resting metabolism, for example, depend ultimately on a reliable estimate of body weight. Body weight is relatively easy to determine, and gives the best indication of the overall size of an individual (Hartwig-Scherer and Martin, 1992). However, for early hominids body weight must be predicted, since fossils consist only of bones. Body weight can be derived directly from the relationship between skeletal measurements and body weight, or from a previously predicted stature (Aiello and Dean, 1990). Stature is a useful variable for size comparisons between modern humans, extant great apes, and fossil hominids. Also, it is useful in a biomechanical context, as an understanding of height is necessary for the study of the kinematics of locomotion (Alexander, 1984 - also see section 1.5)

Stature

Body size or stature can be calculated primarily from measurements of fossil long bones. For estimation of hominid stature, it is necessary to know the correlation of long bone length and stature in living individuals. In modern humans, estimates using lower limbs are more reliable than those using upper limbs (Aiello and Dean, 1990), but obviously with fragmentary fossil material it is necessary to have estimates using a variety of bones/bone combinations. The accuracy of any stature prediction relies on the assumption that there is a close similarity in body proportions between the reference collection and the skeleton for which the stature is being predicted. Early hominids have body proportions that are very different from those of modern humans (see table 3.1). The most important difference between hominids and modern humans when estimating stature is in the dimensions of the femur. Early hominid femora are generally much shorter than in modern humans (Jungers, 1991), hence if we use modern human data for reference, the stature prediction will always be overestimated.

Species	Upper limb (% of total BW)	Lower limb (% of total BW)	Head + Trunk (% of total BW)
Modern humans	8	30	62
AL-288-1 (Lucy)	12	28	60
Pan paniscus	15.8	24.2	60
Pan troglodytes	15.8	18	66.2
Pongo pygmaeus	18	18	64

Table 3.1. Weight of major body segments as a percentage of total body weight (BW), to show the comparison between body proportions in 3 non-human primate species, modern humans and 'Lucy'. Adapted from Aiello and Dean (1990)

Using data for human pygmies can assist in overcoming the problem of short hominid femora. Human pygmy proportions are more similar to hominids such as AL 288-1 'Lucy', than to those of modern humans. However, Lucy's lower limbs are very short when compared to humans and are more ape-like in length (McHenry, 1991). When aspects of Lucy's anatomy are compared to samples of human pygmy data, and ape data (bonobos), her humerus length falls closer to that of human pygmy average. Her femur length, however, falls within the standard confidence limits of the bonobo mean. Therefore, in her body shape and lower limb design, she does not converge with even the smallest of modern humans (Jungers, 1991). Wolpoff (1983), however, contests this viewpoint and following his study of human pygmies, concludes that the proportions of Lucy's fore and hind limbs are within the human range. There are, therefore, certain limitations to the accuracy when predicting hominid body size.

Data derived from the Trotter and Gleser (1958) formulae, which were based on a sample of modern humans, result in statures between 126.1 and 128.4 cm for the small bodied hominids (including AL 288-1). Data derived from human pygmies, however, result in statures of between 103.9 and 108.9 cm (Jungers, 1988). Tuttle (1987) on the other hand used the Laetoli footprints to estimate stature, and obtained a higher estimate of 120 cm. The consensus holds that most individuals belonging to *Australopithecus afarensis* were well under 120 cm (Aiello and Dean, 1990). For comparison, an average stature for north European males is 172 cm, and 161 cm for females (Low and Reed, 1996).

In estimating body size, sexual dimorphism is also relevant and prediction of its likely influence in *A. afarensis* is necessary. *A. afarensis* is a highly dimorphic species, with body weight thought to average 29 kg in females and 45 kg in males (McHenry, 1992, 1994). Since there is such a large variability in body size, it is possible of course that *A. afarensis* represents two or more species, but most have argued against this theory (Boaz, 1988; McHenry, 1991; Lockwood et al., 1996). However, Häusler and Schmid (1995) do consider that the Hadar fossils represent two species of low sexual dimorphism. Assuming the Laetoli and Hadar groups of fossils represent a single species, it is predicted by Lockwood et al. (1996) and Richmond and Jungers (1995) that *A. afarensis* is more sexually dimorphic than both modern humans and chimpanzees, but no more than other extant hominoids (orang-utans and gorillas).

Body weight

Body weight estimates from predicted stature are based on two assumptions. Firstly, that the stature estimates are correct, and secondly, that the fossil species has the same relationship between stature and body weight as the reference population. Since it is very difficult to verify that both of these statements are correct, estimates of body weight from predicted stature cannot be completely reliable. Humans are usually used as the reference sample for prediction of body weight from stature. However, as hominids are assumed to be characterised by heavier upper limbs than are humans, predictions from humans tend to underestimate early hominid body weight, especially in australopithecines (Aiello and Dean, 1990). Stature-based weight predictions give estimates for *Australopithecus afarensis* of 35 kg (McHenry, 1974) using school children as the reference data; and 37.3 kg (Wolpoff, 1973) using human pygmies as the reference population.

Body weight predictions from measurements of fossil samples are subject to many errors, and results represent approximations to body weight. One major limitation of predicting body weight from fossil measurements is the assumption that the fossil sample represents an average for the species. Further, prediction equations for body weight are only accurate if the fossil species corresponds closely with the extant model. Since we do not know which extant species represents the best model for early hominids, prediction equations derived from a single extant species cannot be relied upon. Most predictions of body weight are not designed to be applicable to individual fossil specimens, but instead represent the mean for a species, since original allometric relationships were determined from the mean for a number of primate species over a broad taxonomic range (Hartwig-Scherer and Martin, 1992). It may thus be more appropriate to use an interspecific approach, using a combination of species to produce the prediction equations. For early hominids, the ideal combination would be a mixture of African apes and humans. However, a study by Hartwig-Scherer and Martin (1992) has shown that relationships between skeletal dimensions and body weight differ greatly between hominoids. An interspecific approach would therefore only disguise the scaling differences between primate species. An alternative approach is to use several intraspecific models, applied separately, to estimate the body weight of early hominids. This approach would yield a range of possible estimates for early hominid body weight, which could then be evaluated independently (Hartwig-Scherer and Martin, 1992). Jungers (1990, from Hartwig-Scherer, 1993) used a similar approach to produce a range of estimates of body weight for AL 288-1, using a variety of fossil measurements and relationships found in extant species. The mean estimate is shown in Table 3.2. Hartwig-Scherer and Martin (1991) also obtained an estimate for average body weight of AL 288-1, again shown in Table 3.2. McHenry (1992) estimated body weight in *A. afarensis* using hindlimb joint size, with a formula based on a sample of humans rather than of hominoids. The data (in Table 3.2) for the 95% confidence intervals reveal the variability in this sample. Finally, Hartwig-Scherer (1993) obtained a 'taxon-independent' estimate for body size in AL 288-1 from a variety of fossil bone measurements. As a number of estimates were given in this paper, the data presented in Table 3.2 indicates the mean and standard error of all the estimates given.

Male	Female	Species	Geological age (Ma)	Reference
-	-	31.0 ± 1.18 (SE)	2.6 - 2.9	Jungers (1990)
-	-	31.4 ± 1.33 (SE)	3.1	Hartwig-Scherer + Martin (1991)
44.6 ± 18.5	29.3 ± 15.7	37.0 ± 17.1	2.9 - 4.0	McHenry (1992)
-	-	31.6 ± 1.60 (SE)	2.6-2.9	Hartwig-Scherer (1993)

Table 3.2 Body weight estimates for *Australopithecus afarensis* in kg. Data is shown as means ± 95% confidence interval, or ± standard error (SE).

3.3 Resting Metabolic Rate

The largest component of energy expenditure is the basal metabolic rate (BMR). This consists of the energy needed to sustain everyday processes, such as respiration, circulation, muscle tone and growth. BMR can only be measured under standardised conditions, that is when the animal is in a post-absorptive state (is not currently digesting food), and is at rest at a comfortable temperature (Louw, 1993). For this reason, the resting metabolic rate (RMR) is more often referred to since RMR does not have to be measured under standardised conditions nor requires the individual to fast for a long period: RMR is usually measured 3-4 hours after an ordinary meal. RMR has been found to differ little from BMR (Rose and Gamble, 1994), and therefore as it is easier to measure, it is the usual parameter of choice.

In any individual the RMR is determined principally by body size, body composition and age. RMR is usually described as RMR per kg to standardise for weight. RMR per unit weight varies with age and height, but for most age-sex groups the relationship between weight and height (body mass index; BMI) is not an important determinant of the RMR (FAO/WHO/UNU technical report, 1985).

A number of studies have attempted to assess the differences between RMR values for different ethnic groups, but have failed to identify any significant differences that could not be related to nutritional state or climatic conditions (FAO/WHO/UNU technical report, 1985).

The equations given in the FAO/WHO/UNU technical report (1985) are regarded as the best estimates at present available for predicting RMR of healthy people in any population, but there is no substitute for direct measurement if it can be made. Equations are available (FAO/WHO/UNU, 1985, tables 5+6, p71) for 8 age-sex groups: men and women of age categories 10-18, 18-30, 30-60, and >60. The equation used is that which predicts RMR from weight (kg) and height (m) for women aged 18-30 as this is most likely to be appropriate to predictions for 'Lucy', as an adult female.

$$\text{RMR} = 13.3\text{W} + 334\text{H} + 35$$ **Equation 3.1**

where RMR is the resting metabolic rate ($\text{kcal}\cdot\text{day}^{-1}$)
W is body weight (kg) and H is height (m)

Kleiber (1975), supported by Feldman and McMahon (1983) has demonstrated that the interspecific relationship between RMR and body weight across diverse animal species is:

$$\text{RMR} = 70\,\text{W}^{0.75}$$ **Equation 3.2**

where RMR is the resting metabolic rate ($\text{kcal}\cdot\text{day}^{-1}$)
and W is body weight (kg)

Many exceptions exist to the use of this equation (equation 3.2), known as the Kleiber equation, to estimate resting metabolism, but on the whole it is a very useful unspecific equation, especially when actual measurements of RMR are not possible (Louw, 1993). Although no single equation adequately describes the relationship of body weight to RMR for mammals (Hayssen and Lacy, 1985), studies (such as

Leonard and Robertson, 1994, 1996) have shown that the Kleiber relationship holds for anthropoid primates. Resting metabolic rate, therefore, increases with increasing body weight, but not as rapidly. Thus large animals require a smaller energy intake per unit body weight than small animals. Substituting an average body weight of *A. afarensis* as 37 kg (McHenry, 1992) and a stature of 1.1 m (Jungers, 1988) into the appropriate FAO/WHO/UNU equation gives an estimate for RMR for *A. afarensis* of 895 kcal·day^{-1} (3744 kJ·day^{-1}), while the Kleiber equation gives an estimate for RMR of 1050 kcal·day^{-1} (4396 kJ·day^{-1}).

Research by Katzmarzyk (1996) on three human subsistence level populations found a discrepancy between measured and predicted resting metabolism for sitting, standing and lying postures. Energy expenditure was predicted using 1.2 x RMR for lying and sitting, and 1.4 x RMR for standing. Resting levels of energy expenditure were found to be 11% higher than predicted levels in females, and 16% higher in males. No differences were found, however, between measured and predicted levels of energy expenditure during exercise. This indicates that estimations of total energy costs using similar multiples of RMR are too low, since they rely on an underestimate of resting levels of metabolism (Katzmarzyk, 1996). Results from Katzmarzyk's study also point to a necessity for a correction in energy expenditure for traditionally living populations under thermal stress. The standard World Health Organisation (WHO) calculations for resting metabolism (Katzmarzyk, 1996) will substantially underestimate the energy expenditure of populations with higher thermal stress.

In summary, estimates shown above (from equation 3.1) for resting metabolism are likely to be too low, due to underestimation of nutritional or thermal stresses affecting a population. Since a large proportion of the day is spent at rest, even a small deviation in the estimation of energy expenditure at rest can produce a large reduction in the estimate of total energy expenditure. It therefore seems likely that the higher of the two estimates presented above (using the Kleiber equation) is likely to be the more representative of resting metabolic rate in early hominids.

3.4 Environmental and Ecological Evaluation

Understanding the nature of the available resources in the primary habitat of Miocene to Pleistocene environments is crucial for investigating hominid behaviour and adaptation (Sept, 1994). Since the hominoid fossil record is sparse, especially during the Miocene period, the issues of hominid origins cannot be answered using hominoid fossils alone (Vrba, 1985; Pickford, 1991). A knowledge of the evolving ecosystem surrounding hominid fossils is of benefit to our understanding of hominid evolution from the physiological and morphological perspectives.

Evidence exists that the earliest species in the hominid lineage (12-14 MYA) were associated with forested habitats (Andrews, 1992), possibly with decreasing percentages of arboreal species (Pickford, 1991). During the Miocene period, Europe had a tropical to sub-tropical environment. About 8 MYA, it is hypothesised (Pickford, 1991) that hominoids became extinct in Europe as the tropical and sub-tropical belts shifted towards the south. It is likely that hominoids moved into East Africa between 7 and 8 MYA as part of a general faunal movement (Pickford, 1991). A tectonic event, which altered the climate and therefore the ecology around 7.5 Ma could have created one pressure towards erect posture and bipedalism (Coppens, 1991; Vrba, 1995).

Attempts have been made to reconstruct the habitat of recently identified hominids (*A. anamensis, A. ramidus*) with the support of other fossil animals found close to the hominid site. It is likely that both species lived within or close to riparian habitats, possibly in a closed-canopy woodland (Leakey and Walker, 1997). Other data support the argument that early these early hominids were associated with closed woodland or forest environments, therefore probably retaining some arboreal adaptations (Andrews, 1995).

At the time of australopithecine species we find a fully bipedal hominid of which evidence is often discovered along lake shores (Isaac, 1984). The common view up until a few years ago assumed that hominids such as "Lucy" inhabited open savannah-like environments (Campbell, 1979; Wheeler 1984, 1991a, b).

A thorough investigation of australopithecine environments was recently carried out by Reed (1997). Reed's study uses primarily the morphological adaptations of other mammalian fossils to reconstruct hominid habitats. Palaeogeographic reconstructions are also used to support these data. The Laetoli region, where *A. afarensis* fossils and footprints have been recovered, is reconstructed as a closed to medium density woodland (Andrews, 1989; Reed 1997). Laetoli environments have previously been described as savannah vegetation, comprising diverse herbaceous plants with an abundance of grasses (e.g. Jolly, 1970). Boaz (1988) also identified them as open grassland, but with scattered trees.

The Tulu Bor and Usno foundations in Koobi Fora spanning, 3.36 to 3.0 Ma are associated with australopithecine species. Reed (1997) assessed these deposits as accumulating in scrub woodland or forests with extensive river systems. Hadar sites (3.4 to 3.18 Ma where *A. afarensis* was recovered) comprised medium to open woodland. The Denen Dora foundation (3.2 to 3.18 Ma), also in Hadar, was probably woodland, with some forest regions near to water and edaphic grasslands (i.e. floodplain grasslands, often waterlogged). This reconstruction is close to that made by Bonnefille (1983) on the basis of pollen analysis. Hadar environments are usually described as having greater amounts of water when compared to Laetoli habitats (Boaz, 1988). They seem to be more densely vegetated (possibly gallery forest, or wooded savannah). The absence of totally forest-adapted rodent species is an argument against the close proximity of extended forests. However, the abundance of woodland-living species of impala implies more closed habitats (Boaz, 1988). Turkana, Omo and Hadar environments were probably forested or savannah woodlands (Boaz, 1988; Williamson, 1985). It is unlikely that these environments were open, arid savannah habitats at any time (Reed, 1997). The Omo valley sites (3.6 to 1.0 Ma) comprise various members of the Shungura foundation (it is likely that australopithecines were associated with members B, C and D). Environments around 2.95 Ma were mostly closed woodlands with riverine forests and edaphic grasslands (Reed, 1997). By 2.85 Ma environments where australopithecine species are found consist of a range of woodlands and bushlands, and riverine forest (Reed, 1997). There is also an indication of fairly extensive grassland (Reed, 1997). At 2.52 Ma Reed (1997) reconstructs riverine forests within a woodland or bushland regime, which included edaphic grasslands.

The overall completeness of remains and the high percentage of skeletal parts-per-individual discovered at Hadar suggests to some (Johanson et al., 1982b) that the likely environmental reconstruction for this habitat is closed vegetation. However, there is evidence in the form of footprints (Laetoli footprints: Leakey and Hay, 1979; Tuttle, et al., 1991) that *A. afarensis* at least passed through open savannah and steppe areas (Boaz, 1990).

Therefore, aggregating the paleoenvironmental data, it is possible to construct a hypothesis that *A. afarensis* was capable of ranging from closed habitats to more open grasslands.

It is a possibility that during the evolution of hominids through australopithecine species to *Homo* there was a slow expansion from forested environments, through the forest fringe, and into more open habitats. The time scale of this expansion, though, is crucial, and is not yet resolved. The expansion could have been accompanied by a change from a predominantly vegetable and fruit diet to a more mixed diet (Campbell, 1979). A gradual decline in the percentage of arboreal species is apparent from 3.4 Ma to 1 Ma, possibly due to an increase in aridity or seasonality of environments (deMenocal, 1995; Reed, 1997). Arboreal, frugivorous species show a much reduced abundance after 1.8 Ma, coinciding with an increased percentage of grazing mammals in East Africa at this time (Reed, 1997).

From this data it is likely that early hominid inhabited a more closed habitat than was previously thought. The appearance of grasslands and a savannah-like environment is not apparent until about 2 Ma (around the emergence of *Homo erectus*) in sites containing fossil hominids (Reed, 1997, Spencer, 1997). This suggests that savannah environments are not linked to the origins of bipedality in the hominid lineage. It is hypothesised that the environment of chimpanzees would appear to be quite close to that postulated for the emergence of the first Hominidae (Campbell, 1979).

3.5 Energy Cost of Living

Estimates for the energetic cost of locomotion will be covered in section 3.6.

Diet quality

Diet quality has been shown to be connected with several energetic requirements, and has an effect on daily activity patterns of primates (Clutton-Brock and Harvey, 1977b; 1979). Diet quality shows a relationship with both day range and home range in primates (see section 1.6). In most environments, high quality food items such as fruit or insects are more dispersed than lower quality food items, such as foliage (Gaulin, 1979). This means that species which feed on foliage or other low quality food items will tend to have small ranges and lower activity budgets, and those exploiting the high quality food items will tend towards larger home ranges and higher activity budgets (Clutton-Brock and Harvey, 1977a, b; Leonard and Robertson, 1997).

Foraging (costs and strategies)

Foraging strategy depends primarily on diet preference, food patch density and habitat. Foraging strategy may differ between sexes in primates (Smuts et al., 1987), and also between seasons and habitat (Mitani, 1989; Yamakoshi and Sugiyama, 1995; Yamakoshi, 1998). For the purposes of this study (i.e. estimating living costs for early hominids), an average foraging strategy is assumed which therefore does not account for differences between sexes, season or habitat.

Day Range

Day range data, if not available, can be estimated from home range data.

$$\text{Home range area} = 2\,\pi\,r \qquad \textbf{Equation 3.3}$$

(where r is the radius, or maximal distance travelled away from home)

$$\therefore \qquad r = \frac{\text{Home range}}{2\,\pi} \qquad \textbf{Equation 3.4}$$

The radius is half of the average day range, since an individual has to travel away from home, and then travel home again,

$$\therefore \qquad \text{Day Range} = 2\,r = \frac{\text{Home range}}{\pi} \qquad \textbf{Equation 3.5}$$

Home Range

Home range size is a necessary factor in determining the energy cost of locomotion of any species. Home range size in hominids will also be related to daily travel distance. Home range size varies dramatically depending on the diet quality of the species, and also the density of food available. For example, hunting species (incl. insectivorous, frugivorous or carnivorous species) and granivores (i.e. grain-eaters) show a much wider home range than grazers or browsers, due to the low density of preferred food items (McNab, 1963). In addition, granivores consistently have larger home ranges than herbivores, once body weight is accounted for (Mace and Harvey, 1983). Other ecological factors also affect home range size, as terrestrial species tend to occupy larger home ranges than arboreal species, possibly because arboreal species are able to move within three dimensions within the home range (Clutton-Brock and Harvey, 1977b).

In mammalian species there is a predictable relationship between body size and the home range area. Body size is, amongst other things, an adaptation to the feeding niche of the species, and species which need to travel considerable distances when food is short tend to show increased body size. Therefore, home range size increases with body weight (Blumenburg, 1981; Clutton-Brock and Harvey, 1979). An allometric equation obtained for large bodied omnivore mammals by Harestad and Bunnell (1979) describes the relationship as:

$$H = 0.05W^{0.92} \qquad \textbf{Equation 3.6}$$

where H is home range in hectares, and W is the body weight in grams. It has been shown that primates specifically show a strong positive relationship between body weight and home range area (Milton and May, 1976).

If there is no home range data for a particular species, but day range data is available, it is possible to calculate a rough estimate for home range from day range by assuming the home range is roughly circular and day range approximates to maximal distance travelled away from home and back, and therefore is equal to twice the radius of that circle (adapted from Pennycuick, 1979):

$$\text{Home range area} = 2\,\pi\,r \qquad \text{(see equation 3.3 above)}$$

(where r is the radius, or maximal distance travelled away from home)

Since day range is equal to 2 r,

$$\begin{aligned}\text{Hrange} &= 2\,\pi\,(\tfrac{1}{2}\,\text{Day range})\\ &= \pi * \text{Maximal Day range} \qquad \textbf{Equation 3.7}\end{aligned}$$

Activity Budgets

Rates of total daily energy expenditure can be estimated by using the daily activity budget. A common method for determining activity budgets for an animal is through observing the time budget for that animal (Karasov, 1992; Louw, 1993; Leonard and Robertson, 1997). For each activity the length of activity is noted and the relative cost of that activity estimated. Data for activity costs of various activities have been gathered from the literature for use within this study (Table 3.4), and are based on the relative expenditure compared to the RMR. This data is often given as multiples of one MET, which is equal to RMR and approximates to 3.5 $ml(O_2)\cdot kg^{-1}\cdot min^{-1}$ (see section 1.7.1). Some data for the energy cost of various human activities is shown in Table AI.1 (Appendix I). The duration of each activity is multiplied by the rate of energy expenditure for that activity, then data for all activities are summed (see section 3.8 for more details). Activity budgets are presented as an average time spent in each activity, since activity budgets can vary with age, sex and season (Smuts, 1987; Mitani, 1989).

3.5.1 Human data

Average human data assembled from modern hunter-gatherer societies is shown in Table 3.5 (section 3.5.2) for comparison with other primate data.

Diet quality

The basic feeding pattern of modern humans is omnivory (Gaulin, 1979). Much stress, however, is put upon the fact that *Homo sapiens* are to some extent carnivorous (e.g. Blumenschine, 1994), although *Homo sapiens* are far from being specialised to this food source. For the great majority of human hunter-gatherer populations in tropical and sub-tropical regions, meat rarely constitutes more than 40% of the diet (Lee, 1968). For the !Kung San in the Kalahari desert, meat provides 20 - 50% of the diet by weight. Vegetable food usually provides the mainstay of their diet. Specifically in the diet of the ≠Kade San, vegetable food constitutes 81.3% of the total diet, and animal food constitutes 18.7%. However, if vegetable food consumed as a source of water is included in the vegetable food count, it increases to 96.4% of the total diet, indicating that animal foods do not provide an important food source for this group of modern hunter-gatherers (Lee and DeVore, 1976). The Hadza also rely mainly on vegetable matter for their food, since an estimated 80% of their diet consists of plant matter. In terms of calories, however, this estimate is too high, as meat and honey probably represent far more than 20% of the calorific intake (Woodburn, 1979).

Foraging (costs and strategies)

The hunter-gatherer societies in Africa (including Hadza, Dorobo, human Pygmies and San) all have gathering at the essence of their survival strategy, since they spend 60 to 80% of their time gathering (Lee and DeVore, 1976). Since plant foods are the primary food source of the vast majority of the worlds hunter-gatherers, they must spend a large part of their day searching for and gathering plants.

Day Range

During the dry winter months (May to October), the !Kung San rarely travel more than 10 km during a days trip (Lee and DeVore, 1976). Maximal day ranges are in the region of 15 km. Diurnal hunting trips in the Hadza people of Tanzania covered an average total distance of 14.9 km. The maximal distance for distance covered in one day is 28.3 km (Bunn, Bartram and Kroll, 1988), and an average day range for these populations is 12.5 km.

Home Range

The home range for hunter-gatherer societies in Africa, such as the !Kung San people from the Kalahari, is difficult to quantify since they are partly nomadic. However it is recognised that they have relatively large home ranges, bigger than expected for similar sized mammals or primates (McNab, 1963; Harestad and Bunnell, 1979). A hunter-gatherer group could utilise an small area of around 100 km^2 for about four or five years, but would then need access to a larger area (Lee, 1979). The total area that the !Kung population inhabits encompasses around 11,000 km^2 of land surrounding nine permanent water sources. Utilisation of the entire range is not possible, since the groups must stay within reasonable distance of a water source. Land use patterns differ from season to season, since it is their reliance on a supply of water that determines their foraging behaviour (Lee, 1979). Average home range area is also estimated from maximal day range data (see above).

$$\begin{aligned} \text{Home range} &= \pi * \text{Max. Day range} \qquad \text{(see equation 3.7 above)} \\ &= \pi * 15 \\ &= 47\ \text{km}^2 \end{aligned}$$

Activity Budgets

Activity budget data for modern human hunter-gatherer societies is difficult to obtain, and hence is rarely documented. Since hunter-gatherer activities vary very much from day to day, from season to season, and between sexes, data presented here for time budgets only represent approximations to the real time spent in each activity. Data is accumulated for use in this study from the few available sources (Lee, 1979; Lee and DeVore, 1976), and is presented as average hours per day spent engaged in each activity per adult (average of males and females). All the most reliable data came from the study of the !Kung San. Additional data revealed that the ≠Kade San spent approximately 4.5 hrs daily gathering food (Lee and DeVore, 1976).

Population	Hours per day						
	rest	gathering/ digging for food	tool making/ fixing	subsistence	housework	hunting	visiting
!Kung San	4.5	3.0	0.9	2.4	2.7	0.3	0.2

Table 3.3 Approximate time budgets for the !Kung San of the Kalahari, Africa. Data adapted from Lee (1979). Approximately 10 hours are spent sleeping (Lee and DeVore, 1976)

Energetic costs for certain activities:

Activity	ratio to RMR
Sleeping/Lying	1.0
Sitting	1.5
Walking moderate speed, not carrying	3.5
Walking moderate speed, carrying <24 lbs	4.5
Light work (e.g. Cooking)	2.5
Moderate work (e.g. Digging)	4.0
Heavy work (e.g. Hunting large game)	6.0

Table 3.4 Energetic cost of common activities for humans. From Montoye et al. (1996), for further details see Appendix I

3.5.2 Primate data

Data for primate body weight, home range size, day range, locomotor mode, and food preferences is shown in Table 3.5 Three species of baboon: the hamadryas baboon (*Papio hamadryas*), the olive baboon (*Papio anubis*) and the gelada baboon (*Theropithecus gelada*); three cercopithecine monkeys: the bonnet macaque (*Macaca radiata*), the patas monkey (*Erythrocebus patas*) and the graycheeked mangabey

(*Cercocebus albigena*); and five species of ape: the white-handed gibbon (*Hylobates lar*), the orang-utan (*Pongo pygmaeus*), the chimpanzee (*Pan troglodytes*), the gorilla (*Gorilla gorilla*, including sub-species) and the human (*Homo sapiens*) are accumulated for comparison. These species represent those for which data was available and includes examples of medium to large sized primates with varying habitats and food preferences. When data in alternate references were contradictory, the most recent data was noted.

Concerning the data for gorillas, the source (Garland, 1983) did not reveal which sub-species the data represent, therefore this data is taken to depict the average data for all sub-species. Home range size is given in both hectares and square kilometres for use in comparisons with other data. Habitat data is split into two broad categories; arboreal or terrestrial. This differentiation is only intended to represent the locomotor habitat the species are commonly utilising. Diet type is simply expressed as Frugivorous, Folivorous or Omnivorous. These are very general categories, and are intended to represent the most commonly eaten food. In the case of omnivory, this is only assigned for humans, although some primates (such as *Pan troglodytes*) are often referred to as omnivorous (Smuts et al., 1987), since they consume some meat and insects (Stahl, 1884).

Species	Male weight (kg)	Female weight (kg)	Body Weight (Average, kg)	Home range size (ha)	(km^2)	Day range (km)	Arboreal or Terrestrial	Diet	Source
Papio hamadryas	18.3	9.4	13.9	---		13.2	T	FR	Clutton-Brock + Harvey, 1977b
Papio hamadryas	---	---	20	---		9.5	T	FR	Siggs + Stolba, 1981
Papio anubis	21	12	17	2430	24.3	3.6	T	FR	Harvey + Clutton-Brock, 1981
Papio anubis	26	13	19.5	2430	24.3	3.6	T	FR	Clutton-Brock + Harvey, 1977a
Theropithecus gelada	---	---	14	---		0.63	T	FO	Mitani + Rodman, 1979
Theropithecus gelada	20.5	13.6	17.1	---		4.8	T	FO	Clutton-Brock + Harvey, 1977b
Hylobates lar	6.1	5.5	5.8	40	0.4	1.6	A	FR	Clutton-Brock + Harvey, 1977b
Hylobates lar	5.7	5.3	5.5	54	0.54	1.7	A	FR	Harvey + Clutton-Brock, 1981
Macaca radiata	7.3	3.7		230	2.3	0.88	T	FR	Clutton-Brock + Harvey, 1977b
Erythrocebus patas	10.0	5.6		5200	52	2.5	T	FR	Clutton-Brock + Harvey, 1977b
Cercocebus albigena	10.0	6.0		210	2.1	1.1	A	FR	Clutton-Brock + Harvey, 1977b
Pongo pygmaeus	69	37	53	300	3.0	0.4	A	FR	Clutton-Brock + Harvey, 1977b
Pongo pygmaeus	69	37	53	500	5.0	0.5	A	FR	Harvey + Clutton-Brock, 1981
Pan troglodytes	49	41	45	1200	12	3.9	T	FR	Clutton-Brock + Harvey, 1977b
Pan troglodytes	41.6	31.1	36.4	700	7	3.9	T	FR	Harvey + Clutton-Brock, 1981
Gorilla gorilla	---	---	127	---		0.5	T	FO	Garland, 1983
Gorilla gorilla (*beringei*)	160	93	126.5	620	6.2	0.4	T	FO	Harvey + Clutton-Brock, 1981
Gorilla gorilla (*beringei*)	160	93	126.5	800	8	0.47	T	FO	Clutton-Brock + Harvey, 1977b
Gorilla gorilla (*graueri*) - tropical forest	---	---	---	---		2.29	T	FO	Yamagiwa et. al., 1992
Gorilla gorilla (*graueri*) - montane forest	---	---	---	---		0.75	T	FO	Yamagiwa et. al., 1992
Homo sapiens (!Kung)	---	---	44 (Kalahari)	4700	47	10	T	OM	Lee + DeVore, 1976

Table 3.5 Data for body weight, home range size, day range, habitat, and food preference for 8 primate species. Diet is split into 3 groups, FR = Frugivorous; FO = Folivorous; OM = Omnivorous. Data for home range size are converted to hectares (ha) and square kilometres (km^2) for comparison with other data.

Diet quality

Most of the primates in the data set have relatively low quality diets. Since the primates selected were of intermediate to large body size, the data follow the prediction by Gaulin (1979) that larger bodied mammals are likely to favour a low quality diet. The gibbon and the gorilla are both folivorous species, the rest of the primates being frugivorous species. A gorilla diet consists of 90% leaves, stalks and other plant material (reviewed by Gaulin, 1979). The chimpanzee on the other hand, has a diet that consists mostly of fruit, and only 25% of its diet consists of very low quality food (Wrangham, 1977). Bonobo (*Pan paniscus*) diets are very similar to chimpanzee diets, however, they have a slightly higher incidence of invertebrates eaten in their diet (reviewed by Smuts et al., 1987).

Day Range

Day range lengths found in the literature are varied, even when estimated for the same species. Estimates for great apes range from 0.4 (*P. Pygmaeus*) to 2.29 km (*G. gorilla graueri* in tropical forest) per day. Day range exceeds 10 km for *Papio hamadryas* (see Table 3.5 for primate data). Estimates for day range tend to be lower for arboreal species than terrestrial species. Day range may change from season to season (Wrangham, 1977), so it is assumed that this data represents average day range.

Home Range

Exact estimates for primate home range size are sparse in the literature, coming mainly from only two sources (Clutton-Brock + Harvey, 1977b; Harvey + Clutton-Brock, 1981). Therefore, data may not be reliable. When estimates from these two sources were compared, however, they were very similar. Home range size estimates for great apes range from 3 (*P. pygmaeus*) to 12 km^2 (*P. troglodytes*) (see Table 3.5). Home range is about 0.5 km^2 for *Hylobates lar*, and exceeds 50 km^2 for *Erythrocebus patas*. Primates generally require smaller individual home ranges than solitary terrestrial mammals as they are social creatures. However the total home range for the social group will be much larger than individual solitary animals (Milton and May, 1976). Additional data describes chimpanzee home ranges as variable between habitats (Smuts, et al., 1987), from 5-38 km^2 in densely wooded areas, but between 25 and 560 km^2 in sparsely wooded areas.

Activity budgets

Great apes spend between 11 (*Pongo pygmaeus*) and 14 % (*Gorilla gorilla* and *Pan troglodytes*) of day length moving or travelling (see Table 3.6). Table 3.6 gives an idea of the general amount of time each species spends in the three major activities: feeding, resting or grooming and moving. Additional activities, such as mating, threatening or vocalising are fitted into the most appropriate category. This data, however is highly generalised and must represent the average between sexes, ages and seasons.

Species	% Day Spent		
	rest	feed	move
Papio hamadryas	40	30	26
Papio anubis	30.5	41	25.5
Theropithecus gelada	35	45	20
Hylobates lar	39	29	31
Pongo pygmaeus	39	46	11
Pan troglodytes	33	53	14
Gorilla gorilla beringei	54	25	14

Table 3.6 Data for activity budgets of some primates. Day length is estimated at approx. 12 hours.
Adapted from Clutton-Brock and Harvey (1977b)
rest = percentage of day length spent resting, inactive or grooming
feed = percentage of day length feeding or foraging
move = percentage of day length moving or travelling

Additional data from Wrangham (1977) provides estimates from a group of chimpanzees (*Pan troglodytes*). It is estimated that chimpanzees spend between 25-39% of the active day resting or grooming, 40-60% feeding and 8-20% travelling (Wrangham, 1977). Further data for orang-utans (*Pongo pygmaeus*) estimates that they spend 58% of the active day resting, 26% feeding and 16% travelling (Mackinnon, 1974). Another source gives data for a number of adult orang-utans, the average activity budget comprises 49% resting, 42% feeding and 9% travelling (Mitani, 1989). A very sparse data set was found for gorilla activity budgets. The only additional data was an estimate for time spent feeding as 45% of total active time (Smuts et al., 1987), which is a significantly higher figure than in the data set above (Table 3.6).

3.5.3 Estimation of living costs for "Lucy"

Studying the ecology and behaviour of extinct hominid species means reconstructing adaptations of our ancestors to their environment. Assessment of the environment of *A. afarensis* is covered in section 3.4, and therefore the conclusions made will hold for this section. It is assumed, therefore, that the hominids discussed were inhabiting environments similar to those surrounding chimpanzees today. Various models have been used as a primary basis for making inferences about the behaviour and ecology of early hominids, including amongst others a baboon model, a gelada model, and a chimpanzee model (Dunbar, 1989). However, since no living primate exists which will mimic the ecology and behaviour of *A. afarensis*, should we turn to extant non-human primates (such as our closest relatives, the chimpanzees and bonobos) for a model of hominid ecology? Or is it more realistic to use modern human hunter-gatherer societies as a model for gathering information about our ancestors? Since chimpanzees are a phylogenetically close species, often inhabiting dry semi-terrestrial habitats, and have a similar body size to hominids, it is often declared that this species should be used as the most appropriate model for early hominids (Foley, 1992).

Diet quality

Much controversy surrounds the question of the feeding adaptations of our hominid ancestors (see e.g. Isaac, 1978; Stahl, 1984; Stewart, 1994). A number of changes in dietary preference have been proposed during the course of hominid evolution. However, there is little evidence that any of the major dietary or diet-associated changes (shifts to carnivory, hunting and scavenging behaviours, use of fires) occurred before 2.0 Ma (Isaac, 1983; Stahl, 1984; Foley and Lee, 1991). The appearance of stone tools and large mammal bone processing around 2 Ma (Blumenschine, 1987, 1991) post dates "Lucy" by approximately 2 million years. Therefore, gleaning information of early hominid dietary habits from archaeological remains is at present impossible. Gaulin (1979) describes the large-bodied hominids as omnivores. Although this feeding strategy is attributed to hominids living in savannah environments, it is suggested that omnivory is also an adaptation to living on the fringe between open and forested environments. Kay (1975) compared australopithecine teeth to great ape teeth, and suggested a tendency towards omnivory in australopithecines since "all *Australopithecus* species may have had diets high in fibre and grit content" (Kay, 1975, p??). Walker (1981) described *A. afarensis* tooth morphology as characterised by relatively large incisors and slightly expanded molars, differing only slightly from the morphology of chimpanzees. This would indicate a largely frugivorous diet for early hominids. Dental morphology offers little evidence for carnivory in early hominids (Kurland and Beckerman, 1985), but it should be noted that the predatory episodes and omnivorous feeding strategies of chimpanzees cannot be deduced from their dental morphology. Therefore, it is certainly possible that the australopithecines functioned to some extent as omnivores, if they exhibited occasional, predatory episodes similar to chimpanzees or baboons (Teleki, 1975; Campbell, 1979). It has been hypothesised (Stewart, 1994) that early hominids may have included fish in their diet, as an alternative, seasonal resource. Although use of stone tools does not appear in the archaeological record until about 2 Ma, on the basis of modern hunter-gatherer activities (see section 3.5.1) it is thought that *Australopithecus* could have been using some tools, such as digging sticks or pestles, in acquiring food (Yamakoshi and Sugiyama; Yamakoshi, 1998), and it is likely that organic materials were used for tool making long before the advent of lithic technology.

Foraging (costs and strategies)

At about 2 Ma, it is thought that hominids were using 'home bases', a central place that hominids returned to after foraging (Isaac, 1978; Sept, 1992). At this time they were already using stone tools and co-operative foraging patterns (Isaac, 1978). However, there is little evidence for the foraging behaviour of early hominids pre 2 Ma, since an absence of stone tools found at the time of *A. afarensis* rules out the ability to infer foraging behaviour from archaeology. Lee and DeVore (1976) stated that the Pleistocene people in Africa were probably gatherer-hunters, whose subsistence mainly relied upon plants rather than the hunting of game. As the subsistence strategy of the ≠Kade San is very similar to that of the savanna-woodland living chimpanzee, it seems rational to state that early hominids were using similar foraging strategies. It is possible that early hominids could have taken part in scavenging from carcasses to some extent (Blumenschine et al., 1994; Blumenschine, 1995), but no evidence is yet known to indicate that this was a regular occurrence before 2 Ma.

Home range and day range

Using 37 kg as a likely estimate for mean body weight (from McHenry, 1992, see section 3.2), an equation from Harestad and Bunnell (1979) for omnivorous mammals predicts a home range of 941 ha (9.41 km^2) for *A. afarensis*. Using the same body weight, a general mammalian equation from Garland (1983, and see section 3.8) predicts home range as 744 ha (7.44 km^2). Many alternate equations are available, some of which force some decisions to be made about the diet of early hominids. Some sample equations for primate species and predictions of home range size for hominids (37 kg) are shown in Table 3.7

Equation	animal category	Estimate for H	Reference
$\log_{10} H = 0.83 \log_{10} BW - 2.17$ (1)	omnivorous primates	0.42 km^2	Milton + May (1976)
$\log_{10} H = 1.23 \log_{10} BW - 2.86$ (2)	all primates	5.74	Milton + May (1976)
$\log_e H = 1.37 \log_e BW - 2.95$ (3)	all primates	7.37	Blumenberg (1981)
$H = 0.0965\ BW - 0.0176$ (4)	primates	3.55	Blumenberg (1981)

Table 3.7 Estimating *A. afarensis* Home Range (H) in km^2 from body weight (BW) in primates

(1) H in hectares, BW in grams - conversion factor of 0.01 to give km^2
(2) same as (1)
(3) H in km^2, BW in kg - Blumenberg took data from Clutton-Brock and Harvey (1977a)
(4) H in km^2, BW in kg - Blumenberg took data from Clutton-Brock and Harvey (1980)

The equation giving the lowest value for home range is also the most specific, and assumes hominids are omnivorous primates. The more general equations which do not differentiate between feeding strategies of primates give intermediate values for home range. The highest value for home range uses a model for omnivorous mammals. This is not surprising since the model is based upon large species of North American mammals (Harestad and Bunnell, 1979).

The average estimate for the home range of *A. afarensis* is 5.7 km^2. Blumenberg (1981) used a variety of methods to estimate home range size. In this paper, the average home range for Plio-Pleistocene hominids is given as 4 km^2, in the absence of limited rainfall. These values are close to those supplied for pongids such as: 5 km^2 for *P. pygmaeus*; 6.2 for *G. gorilla* and 7 for *P. troglodytes* (Harvey and Clutton-Brock, 1981 - see section 3.5.2 for primate data). Foley (1992) states that hominid day and home ranges should be larger than those characterised by *P. troglodytes*, as more patchy resources in the likely hominid environment will have forced them to utilise a larger foraging area. No predictions are given, however, for home range size.

Using a general mammalian equation for non-carnivores (Garland, 1983; also see section 3.8) daily movement distance (i.e. the total distance walked) is estimated at 1.94 km·day^{-1}. Using the average home range area calculated above (5.7 km^2), day range can be estimated from the average home range area, using equation 3.5 above. The day range is estimated to 1.8 km. Day range and home range data can also be estimated using transport of stone material in Pleistocene hominids. Gowlett (1984) stated that hominids inhabiting the first well-known sites which contain evidence of stone tools (at Olduvai, Tanzania) were transporting stone materials at least a few kilometres. More recent evidence from the upper Pleistocene indicates that stone tools were transported over 150 km (Gowlett, 1984). Using such Plio-Pleistocene transport distances home range size can be estimated at between 12.46 and 50.2 km^2 (Foley, 1984).

Activity budgets

Activity budgets of hominids must be estimated from both human and primate data. Using chimpanzee data (from Clutton-Brock and Harvey, 1977b) for the primate model, it is estimated that *A. afarensis* spent 12 hours a day sleeping, 4.0 hours a day resting, 6.4 hours a day feeding and 1.7 hours a day moving. Using !Kung data (from Lee, 1979), it is estimated that *A. afarensis* spent 10 hours a day sleeping, 4.5 hours a day resting, 3 hours a day gathering food, 0.9 hours a day tool making, 2.4 hours a day in subsistence duties, 2.7 hours a day doing housework (including cooking), 0.2 hours a day visiting (moving) and 0.3 hours a day hunting.

3.6 Estimating Total Energy Cost of Locomotion

Daily Locomotion Costs

A previous study by Karasov (1992) calculated that locomotor costs account for less than half of the total daily activity cost in mammals, but this proportion appears to increase with an increase in body size (Garland, 1983). Baudinette (1991) determined that the energy cost of locomotion comprises between 1 and 6 % of the total daily energy budget. The assertion that locomotor costs only account for a small proportion of total energy expenditure has however been contested (Garland, 1983; Kenagy and Hoyt, 1989), as it is very likely that estimates of cost of locomotion are underestimated due to many factors. Firstly any vertical distances travelled by the animal are ignored, and it is likely that many animals move up and down hills during their daily foraging. Energy cost increases when an animal moves vertically as well as horizontally, and does work against gravity. If an animal is partially or fully arboreal, activity costs would increase even more. Secondly, most estimates of the energy cost of locomotion are made using treadmill walking or running. Treadmill based estimates sometimes underestimate the energetic cost of walking or running (Karasov, 1992), since energy cost of locomotion increases for soft or spongy surfaces when compared to hard surfaces (e.g. treadmills). Daily movement distances are also likely to be underestimated, especially if the animals are likely to move great distances, as do carnivores (Garland, 1983). Therefore, values for the cost of transport are likely to be larger (comprising 5 to 15 % of daily energy costs) than those calculated from Garland's equations (1983, see section 3.8; Table 3.11), if they involve larger species moving longer distances (Karasov, 1992).

Terrestrial species use a variety of mechanisms (including changes between gaits) to minimise locomotor costs. Animals usually have a 'preferred' speed within each gait where the locomotor cost is at a minimum. This is the speed at which the animal displays high economy of locomotion (Baudinette, 1991).

To approximate the percentage of total activity cost used during locomotion, the product of net cost of transport (in J/km) and daily movement distance (km/day) is calculated (Garland, 1983). Net cost of transport is calculated using measurements of energy expenditure (J/min) and velocity (m/s) during locomotion. By measuring energy expenditure and velocity simultaneously, the net cost of transport can be calculated from real data. However, in the absence of this data, net cost of transport can be estimated from equations using body weight. Rate of energy expenditure can be expressed as a linear function of velocity for most terrestrial mammals (Taylor et. al., 1982). The net cost of transport can in turn be calculated from a regression between rate of energy expenditure and velocity. The slope of the line between the two variables corresponds to the net cost of transport (in J/km), which is then independent of velocity (Karasov, 1992).

The cost for entire animal to run 1 km : (from Taylor et al., 1970)

$$M = 8.5\,W^{0.6} + \frac{6}{V}\left(W^{0.75}\right)$$ **Equation 3.8**

Where M is the metabolic cost of locomotion (ml $O_2 \cdot km^{-1}$)
W is the weight of the animal in grams
V is the velocity of travel

$$\text{Since } V = \frac{\text{Distance}}{\text{Time}}$$

and the distance is 1 km,

$$M = 8.5W^{0.6} + 6T\left(W^{0.75}\right) \qquad \textbf{Equation 3.9}$$

Where M is the metabolic cost of locomotion (ml $O_2 \cdot km^{-1}$)
T is the time taken to travel 1 kilometre (hrs)

Using the equation 3.9, estimates are made for the cost of locomotion using both a human and a primate model. Using data from the !Kung San (Lee and DeVore, 1976), time spent in locomotion is estimated at 3.5 hours per day and day range is 10 km. Time to travel 1 km is therefore 0.35 hr. Using the human model for early hominids such as *A. afarensis*, cost of locomotion is estimated at 10.7 L $O_2 \cdot km^{-1}$. For 10 km as an average day range, this totals 107 L O_2 per day. Data for chimpanzees (Clutton-Brock and Harvey, 1977a, b) gives the average time spent moving as 1.68 hours per day, and day range approximates to 3.9 km, therefore the time spent travelling 1 km is 0.43 hr. Using chimpanzees as a primate model gives an estimate of the cost of locomotion for *A. afarensis* at 11.6 L $O_2 \cdot km^{-1}$, if 3.9 km is an average day range, this totals 45.2 L O_2 per day.

Assuming an R-value of 0.82 (RQ gives an estimate of food type being metabolised and make it possible to estimate the calorific equivalent of oxygen consumption data; see section 1.8.2), these estimates for cost of locomotion for *A. afarensis* equates to 51.4 kcal·km^{-1} and 55.7 kcal·km^{-1} for the human and chimpanzee model respectively (since at resting RQ, kilocalories are roughly equal to 4.8 multiplied by VO_2; Montoye et al., 1996).

3.7 Foot Contact Time

Many studies have shown a connection between the time during a stride in which the foot is in contact with the ground and the energy cost of locomotion (McMahon et al., 1987; Kram and Taylor, 1990; Breit and Whalen, 1997). A variety of gait parameters such as gait speed and instantaneous rate of energy expenditure vary with foot-ground contact time (Cavanagh and LaFortune, 1980; Kram and Taylor, 1990). Data comparing weight-specific measurements of locomotor cost have been used to show that it is the stride frequency at equivalent speeds which is the major determinant of the cost of running at a given speed (Heglund and Taylor, 1988; Taylor, 1985). This implies that the time available for developing force during the stride is important in determining the energetic cost of locomotion. Since the period of time the foot is in contact with the ground is the period in which the muscles develop most of their force (Baudinette, 1991), it is not surprising that the contact period is an important determinant of the energetic cost of locomotion. The time that the foot is in contact with the ground is commonly referred to as 'foot contact time', or t_c. Walking and running gaits are easily distinguishable by t_c. Values for walking are in the range of 525-892 ms, whereas running displays lowers values of 183-367 ms (Breit and Whalen, 1997). An increase in walking speed usually results in an increase in vertical and horizontal ground reaction forces, but increasing speed results in a decrease in foot contact time. The inverse relationship observed between ground reaction force and foot contact time, may be used in the absence of reliable measurement systems to estimate various gait parameters. Ground reaction forces as well as loading rates and gait speed can be estimated with a single measurement of t_c (Breit and Whalen, 1997). The correlation of gait parameters with ground contact time is highly subject-specific, and there is a possible influence of body mass/leg length ratio on individual parameters (Breit and Whalen, 1997).

Temporal gait parameters, such as t_c, can be used to estimate rate of energy consumption during one gait cycle, total energy cost per exercise session, or daily energy costs. The mass-specific rate of energy expenditure is highly correlated with the reciprocal of t_c (Hoyt et al., 1994).

Using methodology from Hoyt et al.(1994), metabolic cost of locomotion was estimated using predicted foot contact time per stride from the previously discussed computer model (see section 2.1 and Crompton et al., 1998) of *A. afarensis* (Lucy) walking with flexed knees and hips. Minimum (at a comfortable speed) and maximum (at slow walking speeds) values were taken from the model to give a range of possible data for foot contact time.

$$M_{loco} = 3.702\left(\frac{W}{t_c}\right) - 149.6 \qquad \textbf{Equation 3.10}$$

where M_{loco} is the metabolic cost of locomotion,
W is body weight, and t_c is foot contact time
Average weight is taken as 37 kg (McHenry, 1992),
and t_c is 0.45 to 0.8 seconds (Y. Li, pers.comm.).

Assumptions made in using this model:

a) Most force exerted by muscles is done to oppose gravity
b) A unit volume of muscle exerts the same force on the ground irrespective of speed or size of animal
c) Muscles operate over similar ranges of the force-velocity relationship, regardless of speed and size

Using estimates of t_c derived from the computer model, rate of metabolic cost varies between 22 to 155 W. Data up to 200 W are defined as indicating a low rate of energy expenditure for humans (Spurr et al., 1988). These results indicate that when using simple gait parameters alone, estimates for the metabolic cost of locomotion in Lucy are relatively small. The small metabolic cost of locomotion calculated for Lucy walking with flexed joints implies that the gait parameters for this gait are within the normal diversity of upright walking humans.

Using methodology adapted from Breit and Whalen (1997) vertical ground reaction forces were estimated using the same data for foot contact time. Estimates were calculated as follows:

$$F_{Z1} = 0.795\left(\frac{1}{t_c}\right)+0.0289$$ **Equation 3.11**

$$F_{Z2} = 0.344\left(\frac{1}{t_c}\right)+0.616$$ **Equation 3.12**

Where F_{Z1} is the peak vertical force during heel strike,
F_{Z2} is the peak vertical force during push off and
t_c is foot contact time

Both vertical ground reaction forces are calculated for the minimum and maximum foot contact times, again derived from the computer model. Body mass was assumed to be 37 kg. Estimated ground reaction force data is shown in Table 3.8.

	minimum $t_c = 0.45$	maximum $t_c = 0.8$
F_{Z1}	1.80	1.02
F_{Z2}	1.38	1.05

Table 3.8 Estimates for ground reaction forces: F_{Z1} and F_{Z2} in bwt, derived from foot contact time. See text for calculations.

Peak ground reaction forces are measured in multiples of bodyweight or 'bodyweights' (bwt). Ground reaction forces for maximum foot contact time are similar to those for upright walking humans. For normal walking speeds F_{Z1} varies between 0.94 and 1.68 bwt and F_{Z2} varies between 0.94 and 1.46 bwt (Breit and Whalen, 1997). However, the minimum foot contact time derived from the computer model (Crompton et al., 1998) gives ground reaction forces more similar to those seen during running. Values for peak vertical ground reaction forces during running vary from 1.89 to 3.18 bwt.

Ground reaction forces, in particular the vertical ground reaction force, are a good discriminant of general daily activity level and lower limb musculoskeletal loading. These results, therefore, may suggest that if Lucy walked using a flexed hip, flexed knee gait, her daily activity levels and musculo-skeletal loading patterns would be higher than those seen during normal walking in humans. These data also confirm that during a flexed joint gait at a comfortable speed, the second peak in the vertical ground reaction force will be reduced as proposed by Li et al. (1996).

3.8 Total Energy Expenditure

3.8.1 Estimating total daily energy expenditure using activity budgets

Three common methods exist to estimate total daily energy expenditure. The first method (method A, see Table 3.9) requires a complete daily time-activity budget data for an animal. Data are obtained from field observations of daily activity budgets together with laboratory experiments to measure the energetic cost of each activity. Alternatively previously published data can be used for both the time and activity cost variables. The energy cost for each activity observed during the day is then multiplied by the length of each activity in hours. The results represent daily activity costs. Energy cost for resting metabolism is then added to daily activity costs, to provide an estimate of total daily energy expenditure.

Method B involves a similar process to method A. However, instead of using measured activity costs for individual activities (since this data is difficult and time consuming to obtain), average values for activity costs are implemented. These are usually obtained as a mean calculated from published data. Karasov (1992) calculated the mean activity cost for small terrestrial mammals as 4.1 multiplied by the standard metabolic rate. For the purposes of this research, it is assumed that the standard metabolic rate referred to by Karasov is equal to resting metabolic rate. The mean activity cost (4.1 x RMR) is then multiplied by total activity length during the day.

The mean activity cost seems high when compared to multiples of RMR that have been published for normal human activities (see section 3.5.1; Table 3.4). An overestimation of mean activity costs may have resulted from errors in the estimation of the period of activity in these mammals. Conversely, these high activity values may reflect the fact that activity costs are more usually underestimated when values are approximated using laboratory techniques (Karasov, 1992).

Method C assumes total daily expenditure equals a fixed multiple of resting metabolic rate, dependent on the animal and locomotor mode. Daily energy expenditure scales at 2.55 x RMR for wholly terrestrial mammals, assuming negligible thermoregulatory and productive costs (Karasov, 1992). If heat is produced during activity, or animals live in heat stressed habitats, this value for total daily energy expenditure would be an underestimate. The resting metabolic rate has already been estimated as 4400 kJ·day^{-1} for an early hominid such as Lucy (see section 3.3 for details).

Method	**Calculation**	**Total DEE (kJ·day^{-1})**	
		Pan Model	*Homo* model
A	Σ (activity cost × time in activity)	7268.8	9616.7
B	RMR + (total time spent active) * (4.1 × RMR·hr^{-1})	13399.6	14900.2
C	2.55 × RMR·day^{-1}	11209.8	

Table 3.9 Estimates for total daily energy expenditure (total DEE) using three methods. For model A and B, both a chimpanzee (*Pan*) and a modern human model (*Homo*) are used to estimate activity budgets (see section 1.4, and Appendix IV). Method B assumes chimps are active for 12 hours a day, while humans are active for 14 hours a day. Method C is a general model that estimates energy expenditure directly from RMR. RMR is assumed to be 4396 kJ·day^{-1} for early hominids (see section 3.3). RMR calculated per hour is 183 kJ·hr^{-1}. Adapted from Karasov (1992)

The results for estimation of total daily energy expenditure are shown in Table 3.9. For more details on these calculations, see Appendix IV. The estimate for daily energy expenditure using Method B is higher than when using both methods A and C, but as data was obtained for small mammals, this will tend to overestimate energy expenditure, as small animals expend more energy moving 1 kg than large animals (see section 3.1). For comparison, a human building worker has an average daily energy expenditure of 12600 kJ·day^{-1} (Louw, 1993). Published estimates for chimpanzees are approximately 5556 kJ·day^{-1}, for the !Kung San 8438 kJ·day^{-1}, and 11033 kJ·day^{-1} for the Ache (Leonard and Robertson, 1997). Data for Pima Indians and people in developing countries exhibited total daily energy expenditures of 11990 and 16160 kJ·day^{-1} respectively (Schulz and Schoeller, 1994)

3.8.2 Other methods used to predict total daily energy expenditure

Garland (1983) defines many ecological variables which scale with body mass. Regression equations similar to the ones usually used for predicting RMR can be used, with reasonable confidence of such variables, to estimate the cost of various life history processes (Louw, 1993).

Only equations most important to the calculation of total daily energy expenditure are displayed here; other useful equations are listed in the appendix (Appendix III, pA3).

Equation	**Units**	**Animal type**
$DMD = 0.875\ M^{0.22}$	(km/day)	Other mammals (not carnivores)
$ICL = 10{,}678\ M^{0.70}$	(J/km)	mammals from 0.01 to 260 kg
$BMR = 293\ M^{0.75}$	(kJ/day)	general equation for mammals
$DEE = 800\ M^{0.71}$	(kJ/day)	general equation for mammals
$Hrange = 14.9\ M^{1.083}$	(ha)	general equation for mammals
$ECT = 1.17\ M^{0.21}$	(% DEE)	Other mammals (not carnivores)

Table 3.10 Equations for estimation of energy expenditure using common ecological parameters. Data adapted from Garland (1983). For full details see appendix (Appendix III).

M = Body mass

DMD = Daily movement distance

ICL = Incremental cost of locomotion

BMR - Resting metabolism

DEE = Daily energy expenditure

Hrange = Home range area

ECT = Ecological cost of transport

Substituting data for

P. troglodytes (M = 45 kg, DMD = 3.9 km, Clutton-Brock and Harvey, 1977b)
H. sapiens (M = 44 kg, DMD = 10 km, Lee + DeVore, 1976, for Kalahari bushmen)
A. afarensis (M = 37 kg, DMD = 1.8 km, Using estimation from section 3.5.3)

Table 3.11 below gives mean data for *P. troglodytes* and *H. sapiens* (Kalahari bushmen), and *A. afarensis* from above equations (in Table 3.10):

Ecological variable		*P. troglodytes*	*H. sapiens*	*A. afarensis*
DMD	($km \cdot day^{-1}$)	2.02	2.01	1.94
ICL	($J \cdot km^{-1}$)	153,369	150,975	133,730
BMR	($kJ \cdot day^{-1}$)	5091	5005	4396
DEE	($kJ \cdot day^{-1}$)	11936	11747	10388
Hrange	(ha)	919.6	897.5	744.0
ECT	(% DEE)	2.60	2.59	2.50

Table 3.11 Predictions for daily energy expenditure and other common ecological variables. Data calculated using equations from Table 3.10 (after Garland, 1983).

Data from Table 3.11, using only allometric equations scaled to body weight generally do not agree with estimates for *A. afarensis* given in previous sections, and neither does most of this data represent accurate estimates for either *P. troglodytes* or *H. sapiens*, if we compare them to estimates in the literature. Therefore it seems that using this methodology for producing ecological data for a species is not satisfactory. Body weight alone cannot be relied upon to provide behavioural data for an extant species. For example, the daily movement distance calculated for *A. afarensis* is fairly similar to that estimated using average home range size in section 3.5. However, this figure was deemed an underestimate, and the figure above of 1.94 $km \cdot day^{-1}$ (Table 3.11) is also probably an underestimate, since the DMD for both *Pan* and *Homo* are small (compared to values from the literature of 3.9 and 10 km respectively, see section 3.5). Home range is underestimated for *Pan* and for *Homo*, therefore the low value estimated by this method for *A. afarensis* may be inappropriate. The estimate provided for total daily energy expenditure in Table 3.11 seems reasonable, since it agrees approximately with the average figure from Table 3.9.

3.9 Discussion and Conclusions

Body weight and RMR

An approximate body size estimate for *A. afarensis* is 37 kg (McHenry, 1992). This is a species average and is the value used in Chapter 3 for the estimation of many other ecological variables (see section 3.2 {Table 3.2} for other body weight estimates for *A. afarensis).* Since a stature estimate is not needed in further calculations, it was not so important to determine an accurate stature.

The estimate for body weight was in turn used to calculate an estimate for resting metabolic rate in *A. afarensis* derived from the Kleiber equation (see section 3.3). The approximate resting metabolic rate is 1050 kcal·day^{-1} (4396 kJ·day^{-1}). However, it should be noted that resting metabolic rate is often underestimated as it cannot take account of nutritional or thermal stresses affecting the individual, therefore the highest prediction for resting metabolism is used in subsequent calculations.

Hominid environments

Environmental evaluations seem to converge on the conclusion that *A. afarensis* lived within a medium to closed woodland, probably near to water and edaphic grasslands. Evidence supports a hypothesis therefore that *A. afarensis* was capable of ranging from closed habitats to more open grasslands.

Models for early hominids

The use of modern human hunter-gatherers as a model for early hominid research has come under close scrutiny (e.g. see Tooby and DeVore, 1986). Objections to the application of modern human behaviour to Plio-Pleistocene hominids include the inappropriate comparison with fully modern anatomy and possible technological sophistication (O'Connell et al., 1988).

If we cannot assume a direct similarity between modern human and early hominid ecology, on what other evidence can we base hominid models? Ecological variables such as home range and daily movement distance, peculiar to modern human hunter-gatherers, are used in the absence of more reliable data about the life and behaviour of early hominids. Many inferences can be made from fossil anatomy, and indeed fossils commonly form the basis for major conclusions concerning hominid lifestyles. However, simple analogies made between modern hunter-gatherer societies and hominids may still be useful in predicting the possibilities open to hominids inhabiting similar environments.

Estimating ecological variables from data for extant hominoids, such as the chimpanzee, is not precise either, since each species is specifically adapted to its own ecological niche. However, since environmental evaluations predicted that early hominid environments could have been similar to those of the chimpanzee today, studying chimpanzee lifestyles might give us some clues as to the ways in which early hominids utilised their habitat. Comparison of estimates for hominids with data for living primate species which possess varied diet types and habitat utilisation strategies is extremely useful.

Estimating early hominid diets

It seems likely that the diet of early hominids consisted mainly of fruit and vegetables (possibly up to 96%), high in fibre and similar to the diet seen in modern hunter-gatherers (Lee and DeVore, 1976). It is possible, however, that australopithecines might be better classed as omnivores, if indeed they exhibited occasional predatory episodes similar to chimpanzees or baboons (see sections 3.5.2 and 3.5.3). It is likely, though, that predatory episodes in chimpanzees have been overemphasised. Yamakoshi (1998) has recently supported previous suggestions (Stanford et al., 1994) that the amount of meat obtained by chimpanzees to supplement their diet is negligible. In conclusion it, seems quite likely that early hominids such as *A. afarensis*, were primarily ingesting a high fibre diet, consisting of fruit and vegetables, despite some leanings towards omnivory. Taking into account the environmental evaluation, omnivory could have served as an adaptation to diverse food types found on the fringe between two distinct habitats.

Day range estimate

Using equation 3.5 from section 3.5.3, day range was estimated at 1.8 km. This is likely to be a substantial underestimate, however, since using home range to calculate day range assumes a very simple relationship between the two, i.e. that day range approximates to the diameter of a circle, where the circle represents home range. Firstly, home range area is unlikely to be circular, and even if it was, day range is very unlikely to be walked in a straight line straight from the centre of the circle. The figure of 1.8 km may thus be more equivalent to 'foraging radius' (Pennycuick, 1979). However, the average day range for the great apes (shown in Table 3.5) using the mean data for *Pongo pygmaeus*, *Pan troglodytes*, and *Gorilla gorilla* is very similar to the predicted day range for hominids, at 1.7 km. The great ape average includes both terrestrial and arboreal primates, with various food preferences, and therefore represents a generalised great ape. The figure of 1.7 km thus represents day range for an average hominoid.

Data for stone transport distance in Plio-Pleistocene hominids, suggests however, that daily movement distances may have been much larger than 1.8 km, possibly a up to a few kilometres. However, it is important to note that these data may not necessarily reflect distances travelled during one foraging bout, or even during one day. With analogy to chimpanzees, which carry stones over short distances during nut-cracking activities (Günther and Boesch, 1993), stone tools could accumulate as an assemblage far away from the 'home base' if moved only a short distance each day (McGrew, 1992). A more reasonable assumption could be that early hominids of the Pliocene had larger day ranges than an average extant great ape, but not as large ranges as those estimated for hominids of the Pleistocene, or indeed those of modern human hunter-gatherers such as the !Kung San. Therefore, day range was likely to have been somewhere between 1.8 and 12.5 km.

Home range estimate

The average home range size estimated for early hominids is 5.7 km (see Section 3.5.3). This value is slightly larger than the home range given in the literature for *Pongo pygmaeus*, but smaller than both that for *Gorilla gorilla* and that for *Pan troglodytes* (Harvey and Clutton-Brock, 1981). Foley (1992) states that early hominid day and home ranges should have been larger than those of *P. troglodytes*, as more patchy resources in the hominid environment will have forced them to utilise a larger foraging area. However, no predictions for home range size were given in his paper. Estimates higher than the home range predicted here have generally been obtained using very general equations from mammals. The highest value, 9.41 km^2 uses an equation derived from large species of North American mammals (Harestad and Bunnell, 1979). Very similar estimates of 7.44 and 7.37 km^2 (Garland, 1983;

Blumenberg, 1981) were derived from allometric scaling in a large range of species (based upon 55 North American mammal species and 56 primate species, respectively). Blumenberg (1981) points out that this method may not prove accurate, and provides a second equation giving an estimate of 3.55 km^2. These three estimates are likely to be relatively generous, since the models are very general and include many small species with surprisingly large home ranges (e.g. *Erythrocebus patas*: average body weight 7.2 kg but home range 5.2 km^2) (Clutton-Brock and Harvey, 1977b). The smallest estimate for home range (0.42 km^2) comes from an equation for omnivorous primates (Milton and May, 1976). Folivorous or omnivorous primates will have a higher density of preferable food available than for frugivorous or carnivorous species, since low quality food items tend to be more widespread and higher in density than higher quality food items (Gaulin, 1979). If early hominids lived in a habitat similar to that of a chimpanzee, and they were relatively omnivorous, it is feasible that a home range of 5.7 km^2 is a reasonable estimate.

Activity budgets

Neither a chimpanzee nor human model can accurately represent the day-to-day activities of *A. afarensis*, but the use of models such as these can certainly aid in narrowing down the possibilities of behaviour and day to day activities in early hominids. It is surprising to discover a lack of available data for time-activity budgets in non-human primates. All conclusions are therefore tentative, since the accuracy of the data is questionable. Time budgets are more successfully applied to those species that can be kept under close observation at all times (Louw, 1993), which is undoubtedly difficult for non-human primates in the wild.

Estimates of brain size may also aid assessment of activity budgeting. For example the brain of *A. afarensis* is estimated at 384 cc, which is small when compared to *H. sapiens* (1250 cc), but more similar in size to the chimpanzee (*P. troglodytes* = 410 cc; McHenry, 1994). The large brain size of *H. sapiens* is greater than would be expected from an increase in body size alone (McHenry, 1994). Given that predicted brain size for *A. afarensis* is small and similar to that of extant hominoids, it seems more likely that behavioural patterns will follow ape data. This reveals that non-human primates concentrate more heavily on feeding (40 - 60 % of day) when compared to other activities (other than resting), especially when as for the gorilla their diet is dominated by foliage. It is hypothesised that *A. afarensis* activity budgets would have corresponded more closely to those of non-human primates rather than those of modern humans, and that they therefore spent a considerable amount of the day feeding.

Cost of locomotion

The general significance of the energetic cost of locomotion has previously been discussed in section 3.1; in addition locomotion costs can influence the benefits of specific foraging strategies (Steudel, 1994).

The cost of locomotion was estimated at 10.7 L $O_2 \cdot km^{-1}$ using modern human hunter-gatherers as a model. However using chimpanzee data, cost of locomotion was estimated at 11.6 L $O_2 \cdot km^{-1}$. The increased cost per distance when using the chimpanzee model supports conclusions that chimpanzee foraging is more costly per unit distance than is modern human foraging. As the average day range of a chimpanzee is less than half of the modern human, the total cost of locomotion for the chimpanzee is also much less. The estimated costs of locomotion for *A. afarensis* (see sections 3.6, 3.8 and 3.5 for estimated data, and appendix for calculations) correspond to about 8.8 and 17.5 % of the total energy expenditure for the chimpanzee and human models respectively. These data contradict assumptions (by Karasov, 1992) that the cost of locomotion contributes only a small percentage (below 6%) of the total daily energy expenditure. Since the methodology used here is known to underestimate the cost of locomotion (see section 3.6), the energy cost of locomotion may contribute even more to total daily energy requirements. There are limitations to the usefulness of this kind of data, but since these variables have never been calculated for *A. afarensis* they are of potential use in future studies.

Total energy expenditure

Methods relying on activity budgets to estimate total daily energy expenditure consistently produce lower values than those using average multiples of RMR. Since RMR is usually underestimated (due to a number of factors, see section 3.3), when multiples of RMR are used within estimates of the cost of each activity (in Method A), gross underestimation of TDEE results. Estimations using a multiple of 4.1 x RMR (Method B) seem to produce high estimates for TDEE. This may be due to the fact that mean activity costs were calculated for small terrestrial mammals, which spend a shorter amount of time active than larger mammals (as activity costs are high; they have an energy rich diet, and the amount of nutrients needed are comparatively small; Louw, 1993; Clutton-Brock and Harvey, 1977b). However, they spend most of that time engaged in highly energetic activities (reviewed by Karasov, 1992). Therefore, using means calculated from small animals will result in an overestimation of energy expenditure for larger primates, since their active period is prolonged for up to 14 hours of the day (Lee and DeVore, 1976).

The average total daily energy budget of early hominids such as *A. afarensis* was estimated at 11209 kJ·day^{-1} (Model C, section 3.8), since this estimate is closest to the average of all estimates in Table 3.9. Assuming this total energy budget, and after subtracting daily RMR (assuming no other activities were undertaken), a hominid with a body mass of 37 kg could be expected to walk up to 27 km a day (data modified from Low and Reed, 1996). This estimate assumes a 12 hour day; a speed of 1.4 m·s^{-1}; that a hominid is as efficient at walking as modern humans, and that it walks long distances at the most efficient speeds (see appendix X for calculations, p A19).

CHAPTER FOUR

THE MEASUREMENT OF ENERGY EXPENDITURE

"Walking is a very specific activity, allowing particularly economical locomotion. Thus, anything that interferes with the complex energy exchanges and predominantly isometric muscle activity of walking causes a faulty pathological gait and a considerable loss of function"

Low and Reed (1996)

4.1 Introduction

Estimates for daily energy cost for Lucy have been presented in Chapter 3. Measuring the actual energy cost of activity is the logical next step in studying energy cost of locomotion in early hominids. Here the energy cost of a BHBK gait in living individuals is measured to complement biomechanical approaches to the problem of bipedal locomotion in Lucy, already carried out in the laboratory. Since some previous effort has been devoted to analysing the oxygen cost of a bipedal gaits of chimpanzees (see section 1.5.8), human subjects are used in this study as a model for the BHBK gait proposed for Lucy (see section 1.1). The mass-specific rate of energy expenditure is a non-linear function of gait speed (Passmore and Durnin, 1955), therefore during the quantification of energy cost of a BHBK gait, it is useful to record energy expenditure during exercise at a range of speeds.

One principal problem with measuring the energy cost of a certain activity (or posture) is correction for the base-line value of the cost of no exercise. The cost of maintaining body posture can be used as a relative base-line, but in practice, this is hard to assess (Saibene and Minetti, 1992). The base line may deviate during exercise, as the rate of work increases, and also due to a rise in body temperature. It is therefore necessary to use 'normal' locomotion as a control with which to compare the alternative posture. Using a normal posture for comparison also aids in the statistical analysis of the physiological cost of a BHBK gait, since paired data can be collected (i.e. one subject performing both normal and BHBK walking for direct comparison).

4.2 Exercise Physiology

The energy cost of exercise reflects the interactions between the metabolic and biomechanical demands on the body. Alterations of the energy cost can be produced not only by physiological factors, but also by a modification in the pattern of gait (Brisswalter et al., 1996a).

The principal components for prescribing an exercise protocol are: a) intensity, b) duration, c) frequency, d) progression and e) activity mode (American College of Sports Medicine, 1991). The prescription of exercise intensity is based upon physiological and perceptual responses to a graded exercise. Physiological components are based principally on measurements of oxygen uptake ($\dot{V}O_2$), heart rate (HR) and ventilation rate ($\dot{V}_E$). Some researchers regard oxygen consumption, carbon dioxide production and ventilation rate as the most important physiological mediators for respiratory-metabolic signals of exertion (Noble and Robertson, 1996). During graded exercise, a 'sudden break' in $\dot{V}_E$ can usually be identified, which is often referred to as the anaerobic or ventilatory threshold. This occurs as a rapid non-linear increase occurs after the standard steady increase in $\dot{V}_E$ with level of activity. The ventilatory threshold (as described if determined by $\dot{V}_E$ data) is possibly synchronous with the onset of lactate accumulation in the blood. Anaerobic metabolism is deemed to have a lower efficiency than aerobic metabolism (see section 1.8), but the anaerobic contribution to exercise is however somewhat hard to quantify.

The ideal duration and frequency of increase in exercise intensity will depend on the length of time each subject takes to attain physiological steady state (see section 1.8.1 for details). If a subject is walking at a natural and constant pace so that the total time at each intensity exceeds three minutes, there should be sufficient time to establish a steady state (Noble and Robertson, 1996). Human adults normally walk at speeds between 0.8 and 1.7 $m \cdot s^{-1}$, but tend to run at speeds above 2.0 $m \cdot s^{-1}$ (Baudinette, 1991).

4.2.1 Oxygen cost

Various measurements are used in the estimation of the energy cost of exercise to a subject. Oxygen consumption is an accurate measure of the intensity of exercise, since it determines the use of oxygen during aerobic metabolism. Oxygen consumption data can also be used in quantifying numerous other variables useful in the study of exercise physiology. Maximal oxygen cost during exercise is usually referred to as $\dot{V}O_{2max}$, and is discussed in more detail in section 4.2.6. Oxygen consumption can further be correlated with other measures of exercise intensity (such as heart rate and perceived exertion) in order to study the complex physiological changes occurring during exercise.

4.2.2 Heart rate

Since heart rate and oxygen uptake show a positive, linear relationship with each other (see section 1.8.3), heart rate values can be used to verify oxygen cost data. Heart rate is also useful in the prediction of maximal volume of oxygen consumption ($\dot{V}O_{2max}$, section 4.2.6). As there is a possibility that anxiousness or anticipation may affect heart rate during a testing session (Wenos, et al., 1996), the use of a control is useful when measuring heart rate to study exercise intensity. Normal walking serves as such a control by allowing us to assess 'normal' heart rate levels in addition to testing in the BHBK gait.

4.2.3 Perceived exertion

Perceptual responses, usually described as rate of perceived exertion (RPE), are measured using a category rated scale (see section 1.8.4) which the subject uses to describe their feelings of exercise intensity, and sometimes pain intensity (Noble and Robertson, 1996). RPE increases linearly with exercise intensity, and is closely correlated with physiological responses such as heart rate and lactate production (Williams and Eston, 1996). RPE can be used both for the prescription and regulation of exercise intensity and RPE values alone are therefore sometimes deemed as sufficient for gauging exercise intensity (Williams and Eston, 1996). A perceptually regulated exercise prescription assumes that a certain aerobic rate of metabolism will be represented by the same RPE value during successive testing. The rate of perceived exertion (RPE) usually displays a linear relationship to heart rate, providing environmental temperature is kept constant (it is important to recognise that the perceptive response varies with an increase in ambient temperature). RPE will increase as ambient temperature increases, relative to thermoneutral conditions (24° to 27°C). Serial testing must be undertaken at the same ambient temperature, or differences in RPE may reflect only the change in ambient temperature {Noble and Robertson, 1996}). Correlation coefficients between heart rate and RPE range from r = 0.42 to r = 0.94 depending on the activity (Noble and Robertson, 1996). RPE multiplied by 10 approximates to heart rate for adults exercising at a comparatively high power output (Noble and Robertson, 1996).

4.2.4 Core temperature

During rest the core temperature is maintained by thermoregulation at a constant 37 °C. During exercise in a comfortable environment, core temperatures generally increase to a new level during the first 30 minutes of exercise. Core temperature reaches a plateau during steady state exercise between ambient temperatures of 10 and 30°C, and will usually remain elevated but at a 'steady-state' until exercise is stopped (Gisolfi and Wenger, 1984). Core temperature increases during exercise in proportion to the intensity of work (Fox, Bowers and Foss, 1993). As a result, the thermal gradient (see section 1.7) between the skin and the core increases, facilitating heat loss from the body. This is aided by a decrease of skin temperature brought about by sweating (see section 1.7).

Core temperatures are generally determined by measuring the rectal temperature of the individual. This is the most reliable method for measuring core temperature in athletes (Reilly and Cable, 1996). Rectal temperature data are best represented as a change from a base line, since a temperature gradient exists down the rectal tissues (Reilly and Cable, 1996). Data for core temperature increase during exercise can be useful in the prediction of thermal stress and other variables concerned with thermoregulation.

4.2.5 Blood lactate

Determination of lactate accumulation in the blood is a simple way to assess the contribution of anaerobic metabolism to exercise. As exercise intensity increases, and the supply of oxygen to the working muscles becomes insufficient, there is a build up of lactic acid. The lactate concentration in blood does not always reflect the total amount of lactate that has been produced. It is certain, though, that measures of lactate are an indication that anaerobic metabolism is taking place, although it is not yet clear how lactate concentrations can be used to give precise values for anaerobiosis (Winter, 1996). Blood lactate values should be given in addition to maximal oxygen uptake values for accurate prediction of endurance performance (Williams and Eston, 1996).

4.2.6 $\dot{V}O_{2max}$

$\dot{V}O_{2max}$ is the maximum oxygen uptake capacity of each individual. It can be measured directly using maximal exercise testing but it is also possible to calculate it from submaximal incremental testing. This is often preferable when using a range of subject ages and fitness levels. It is also difficult to find subjects willing to undergo maximal exercise testing, and those that are willing are usually athletes who are well outside the 'average fitness' category. Acquiring $\dot{V}O_{2max}$ data for subjects is useful as it is possible to determine at what percentage of maximum capacity each individual is working, during progressive stages of a protocol. It usually relates both to the percentage of maximum heart rate and also to RPE. $\dot{V}O_{2max}$ can be calculated by using both the plateau $\dot{V}O_2$ and heart rate from two stages of exercise testing.

It has been shown that there is a high correlation between $\dot{V}O_{2max}$ and distance running success, and therefore $\dot{V}O_{2max}$ is sometimes used as an indicator of fitness or athletic performance (Powers et al., 1983). Although the measurement of $\dot{V}O_{2max}$ is preferred (Cooke, 1996), this is physically challenging for the subject, and since predictions of $\dot{V}O_{2max}$ are considered almost as accurate, these are often substituted for actual measurements.

4.3 Relevant Work

4.3.1 Posture and energetics

A number of experimental studies have reported the specific effects of measured posture changes on some of the primary physiological factors, such as oxygen consumption and heart rate. Of these, most have dealt specifically with the changes observed between a number of different static postures such as standing, sitting, squatting and lying (e.g. Hellebrandt et al., 1940; Banerjee and Saha, 1970). Amongst these postural studies there are few records of the effect of flexing the hips and knees whilst standing. One study (Sato and Tanaka, 1973), however, reported the effect of three different 'crouched' postures on both oxygen consumption and heart rate. Some of the data reported by Sato and Tanaka is reproduced in Table 4.1; it shows that, for all of the crouched postures studied, both the oxygen consumption and the heart rate were significantly higher than for a normal standing posture ($p<0.05$; pg. 24, 25).

Posture and action	Oxygen consumption ($ml \cdot kg^{-1} \cdot min^{-1}$)	Heart Rate ($beats \cdot min^{-1}$)	Reference
Standing	3.2 ± 0.4	—	1
Standing at ease	3.84 ± 0.25	85.5 ± 2.98	2
Crouched standing	3.9 ± 0.3	—	1
Half-rising (180°)	5.03 ± 0.32	88.8 ± 2.63	2
Half-rising (120°)	6.41 ± 0.37	95.9 ± 2.67	2
Half-rising (90°)	7.46 ± 0.43	107.4 ± 2.09	2
Normal walking	6.0 ± 0.9	—	1
Crouched walking	13.7 ± 1.1	—	1

Table 4.1 Previously reported data for the effect of posture on oxygen consumption and heart rate
Ref 1: Abitbol, MM (1995) **Ref 2:** Sato, M & Tanaka, S (1973)

Very few studies have been designed to measure the effect of a postural change during locomotion. One such study, (Abitbol, 1995), reports the effect of a '*bent-head, bent-knee posture*' (BHdBK) on the energy (oxygen) consumption and blood flow in humans during locomotion. The posture was intended to simulate the posture of early hominids and to reveal features different from *Homo sapiens*. In the prescribed posture the subject puts his head and chest forward, and moves with hips and knees only slightly flexed at about 15°. An important feature of the study is that the subject was allowed to shift the body weight from side to side with each forward step. Baseline data were obtained for subjects at complete rest whilst lying supine or lateral. Subjects were then monitored whilst walking with the BHdBK posture at a constant 3.22 $km{\cdot}h^{-1}$ (approx. 0.9 $m{\cdot}s^{-1}$). Resulting data was compared with standing and walking with a normal posture. The significant outcome of the study is that a standing posture requires minimal oxygen consumption whilst a bent posture induces an increase of about 0.7 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ compared with normal. During locomotion the increase was more significant and increased by some 7.7 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ for the BHdBK walking compared with normal walking (see Table 4.1). The increase amounts to almost double the oxygen consumption during the bent walking posture. Data was also presented for blood flow changes (measured using sonography) that occur whilst standing and walking in the bent posture. Diminished blood flow to the brain was observed in BHdBK behaviours. Blood flow to the head and neck is lowest for standing and walking in the normal bipedal posture. The most noticeable change in blood flow occurs in the lower limbs, where a doubling in blood flow results from both standing and walking in the bent (BHdBK) posture. The study concludes that energy consumption is minimal for the normal human erect posture, both at rest and when walking. Energy consumption for the BHdBK behaviour tends to be greater than normal at all stages i.e. the bent posture is more energetically costly than normal posture and bent locomotion is relatively more energetically expensive than bent posture. Furthermore the energy cost of performing bent posture locomotion is almost double that for normal locomotion (walking). The change in blood flow is attributed to the increased activity in the muscles of the neck and the lower limbs during bent posture, necessitating an additional blood supply to these highly active areas (Abitbol; 1995, 1989).

A biomechanical analysis of knee flexion during walking was carried out by Winter (1983). The mechanical work cost was measured in joules per unit mass and distance walked and was assessed during walking with a range of knee flexion angles during midstance of between 6 and 33 degrees. A significant correlation was shown between maximum knee flexion and work cost, with an increase from 0.73 $J \cdot kg^{-1} \cdot m^{-1}$ to 1.65 $J \cdot kg^{-1} \cdot m^{-1}$ between minimum and maximum knee flexion angles. Walking with knee flexion is further described as an inefficient gait.

4.3.2 Groucho running

A study by McMahon, Valiant and Frederick (1986), focused on oxygen consumption during running in a 'crouched' posture. Running in this manner, with increased knee flexion, was described as 'Groucho running' (the subjects adopt a style of movement originally made famous by Groucho Marx). Angles of knee flexion were predicted by measuring decreasing thigh angle (the angle the femur makes with the horizontal, see Figure 4.1) as knee flexion increases. Thigh angle changes from the normal angle (≥70°) to a substantially flexed knee position, where the thigh angle is closer to 50°.

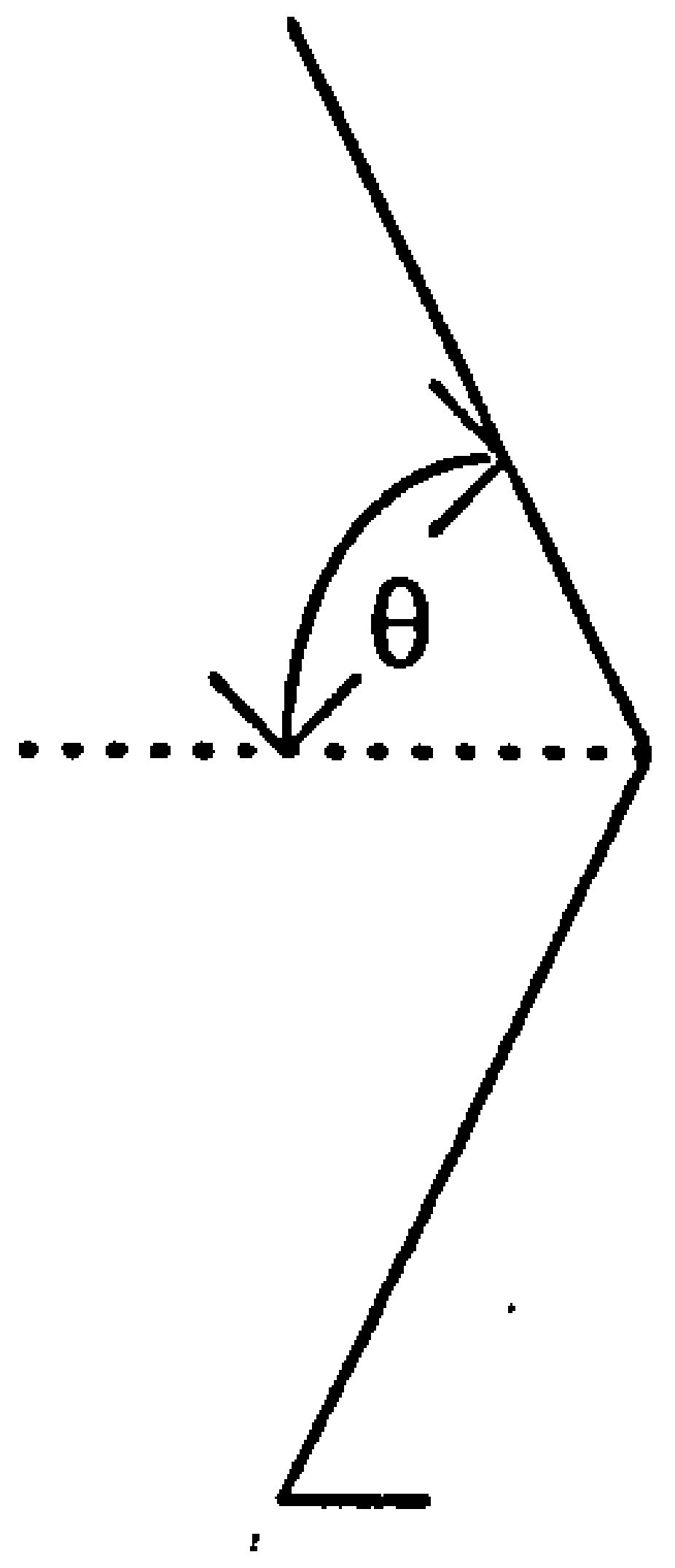


Figure 4.1 Diagram to show thigh angle (θ°) to the horizontal to determine the degree of knee flexion. Stick diagram shows the lower limb during midstance
From McMahon et al. (1986)

Subjects were required to run in both normal and flexed postures on a treadmill. All the subjects found the Groucho running to be considerably more tiring than normal running and one subject, running with increased knee flexion (thigh angle = 60°) was observed to increase his rate of oxygen consumption by 50% over normal. None of the subjects were able to run with thigh angles less than 60° for the six minute period necessary to achieve the oxygen consumption measurement. The increased energy requirement as measured by the steady state oxygen consumption of the flexed knee gait was attributed mainly to the increased force required in the knee extensor muscles due to increased work against gravity.

Each of these studies goes some way to assessing the effect of an alternate posture on human locomotion, however neither one is ideal for evaluating the current problem. Sato and Tanaka (1973) only measured the cost of a change in posture while standing. The study by Abitbol (1995) measured the effect of a slightly crouched posture on the oxygen cost of locomotion, but during a slightly crouched gait with side-to-side movements of the body weight. Abitbol failed to specify the reasons behind the use of a side-to-side gait in his subjects, but since he proposed that a balance mechanism similar to extant pongids was present in 'Lucy', it is supposed that he used extant pongid gait as a model for his study. Tardieu and colleagues (1993) firstly showed that the side-to-side gait, with low lateral and vertical displacements of the body centre of mass, is not applicable to the chimpanzee, as previously proposed by Jenkins (1972). Tardieu and colleagues, secondly, suggest that this type of gait is not indicative of a progressive bipedal gait, and therefore not attributable to *A. afarensis*. In agreement with Tardieu et al. (1993), I do not consider the posture (described above by Abitbol, 1995) to be characteristic of that presumably used by early hominids, with reference to subjects shifting their weight from side to side. McMahon et al.'s study (1986) of Groucho running was extremely thorough, but they did not study the effect of a flexed knee posture on walking. Running is mechanically very different from walking, and energy savings are generated by the elastic properties of tendons (rather than the pendulum motion of walking; Alexander, 1984b). Winter (1983) provided some preliminary data concerning knee flexion costs during walking, but in this and all other studies, however, there was no indication of the anaerobic contribution to this exercise. The effect of an alternate posture on core temperature has (to my knowledge) never been assessed.

4.4 Materials and Methods

4.4.1 Subjects and gaits used

Twelve normal, healthy volunteers gave their consent to perform in this study. Six men and six women with average fitness, encompassing a wide range of statures were used to give the best possible approximation to a cross-section from a normal population (for subject data see table 4.2). However, a group of willing subjects for a study such as this is usually comprised of young adults.

Measurement	Mean ± Standard deviation
Age	27.5 ± 4.5 yr.
Weight	67.6 ± 11.9 kg
Height	170.3 ± 11.6 cm
$\dot{V}O_{2max}$	42.2 ± 16.5 ml $\cdot kg^{-1} \cdot min^{-1}$

Table 4.2 Subject data. Averages and standard deviations of age, weight, height and $\dot{V}O_{2max}$ for 12 subjects

The personal details of each subject were obtained using a prepared questionnaire. Their age, height, weight (before and after exercise), shoe size, exercise rate, and some anthropometric measurements were noted. Shoe size was measured in order to estimate foot length. The anthropometric measurements included upper leg length (H→K, estimated by taking measurements from the greater trochanter to the lateral femoral epicondyle), and the lower leg length (K→A, estimated by taking measurements from the lateral femoral epicondyle to the lateral malleolus). Exercise rate (the number of exercise bouts per week) was used to ascertain the current activity level of each subject, which ranged from low activity to highly active (see section 4.5.1 for full details of the subject data). Levels of habitual activity are considered to be a good indication of fitness level (American College of Sports Medicine, 1991).

The selected protocol measured the metabolic cost of exercise whilst the subject walked on a treadmill. It has been shown that an initial four minutes of treadmill walking is sufficient to attain the 'normal gait' condition (Taylor, Evans and Goldie, 1996). The protocol developed for testing therefore involved four minutes walking at each new (increased) speed to ensure complete familiarisation. This requirement also tended to produce a relatively natural walk for each subject, and further, achieved a plateau in the subject's energy consumption. Walking in two postures, with an identical protocol, made it possible to develop a direct comparison between the metabolic cost of each posture for the range of subjects.

Stage	Time for next stage (mins)	Time spent in stage (mins)	Speed
1	0:00	5:00	0 m/s - Resting Metabolism
2	5:00	4:00	1.0 m/s
3	9:00	4:00	1.2 m/s
4	13:00	4:00	1.4 m/s
5	17:00	4:00	1.6 m/s
6	21:00	4:00	1.8 m/s
7	25:00	4:00	2.0 m/s
8	29:00	20:00	0 m/s - Recovery

Table 4.3 Exercise protocol for each subject, performed at both postures.

Each subject was given the same instructions on how to perform the BHBK gait (see below for explanation of BHBK gait) so as to reduce any inter-subject differences between the BHBK gait parameters. The subjects were asked to perform identical protocols (see table 4.3) for each posture on different days, but the 'time of day' was retained from day to day to account for possible diurnal changes in physiological variables (such as core temperature). The study was conducted in a large room where the temperature, relative humidity, and ventilation were kept constant. Ambient temperature was measured both before, during and after testing to assure steady temperatures. It was possible to either heat or and cool the room if conditions altered significantly. Data were collected for each subject (see table 4.4 for the intervals at which data was collected) while walking on a treadmill (Woodway Instruments, Cranlea, UK). The protocol consisted of a baseline measurement of energy consumption with the subject at rest in a standing posture, followed by subsequent measurements with the subject walking at increasing, incremental speeds. The walking measurements were immediately followed by a twenty minute recovery period after the exercise had ceased. The 'recovery from exercise' period involved the subject sitting comfortably on a chair, in a posture that incurs very little energy consumption, thus emulating the resting metabolism as closely as possible. All data measurement continued throughout the resting period to investigate any effects of the alternative gaits on recovery from exercise. Twenty minutes was determined to be the appropriate time for the increased metabolism to return to a normal resting level.

Measure	**Formula**	**Units**	**Time in experiment**
Oxygen consumption	$\dot{V}O_2$	ml·min $^{-1}$	every 20 secs.
Carbon dioxide production	$\dot{V}CO_2$	ml·min $^{-1}$	every 20 secs.
Ventilation Rate	$\dot{V}_E$	L·min $^{-1}$	every 20 secs.
Heart Rate	HR	bt·min $^{-1}$	every 2 mins (in 2nd + 4th min.of each stage)
Rate of perceived exertion	RPE	6-20	every 4 mins (in the 3rd min. of each stage)
Core Temperature	T_R	°C	every 2 mins (in 2nd + 4th min.of each stage)
Blood Lactate	LA	mMol·ml $^{-1}$	in the 3rd minute of recovery

Table 4.4 Data obtained during the walking protocol.

Subjects were always required to acclimatise to treadmill walking prior to the testing session and all test walking was undertaken barefoot, with light clothing. The speeds selected were:- very slow walking (1.0 $m \cdot s^{-1}$), very fast walking (2.0 $m \cdot s^{-1}$), with four intermediate speeds between the two speed extremes (1.2, 1.4, 1.6 and 1.8 $m \cdot s^{-1}$). Each subject was weighed and measured both before and after each testing session and differences noted. Subjects were required to walk with the two distinct postures:- normal upright walking and bent-hip, bent-knee walking, using the BHBK gait.

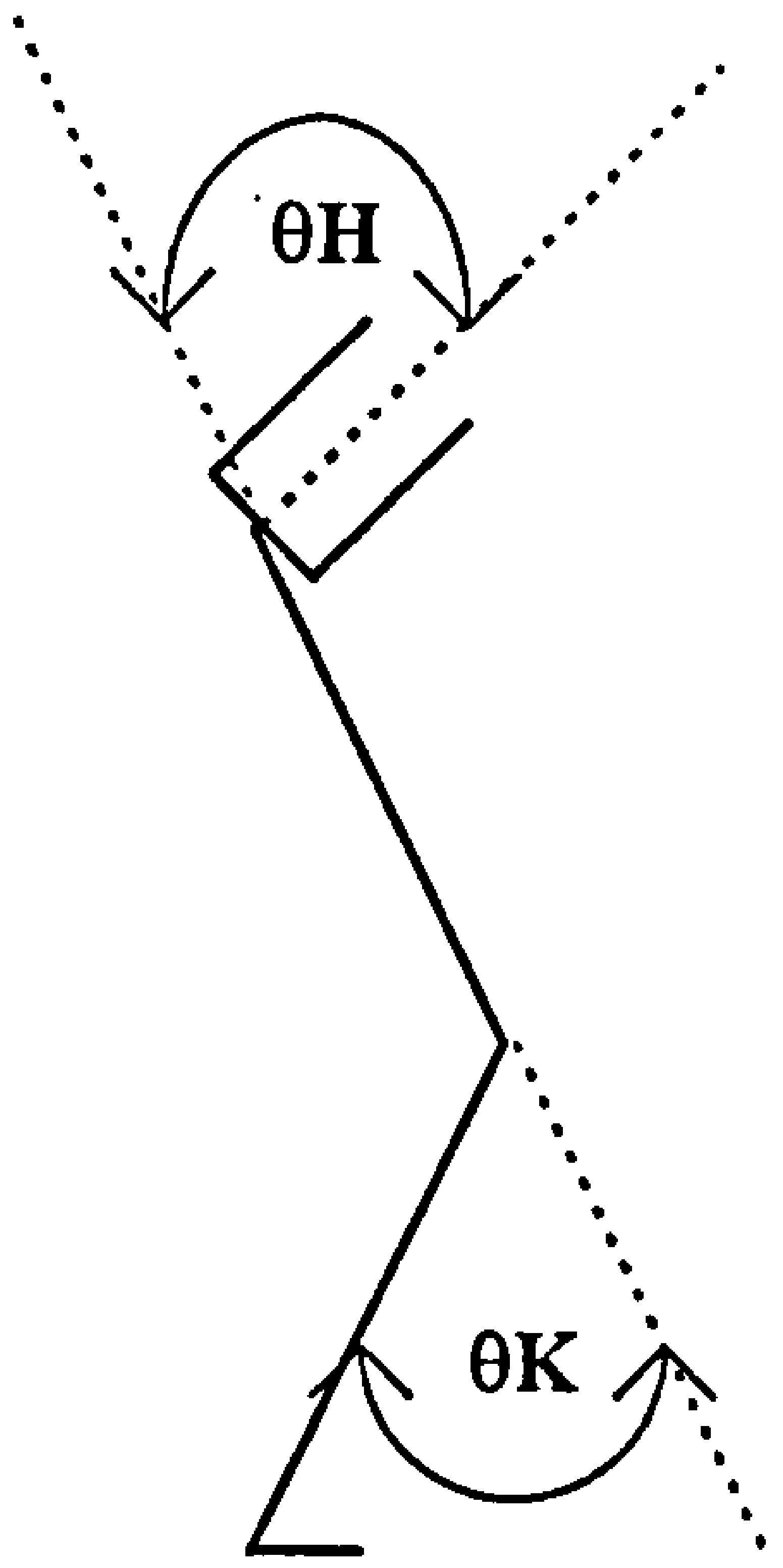


Figure 4.2 Diagram to show approximate hip and knee angles during BHBK walking. θH is the hip angle, and θK is the knee angle.

The "BHBK gait"

In order to use humans as an acceptable model for Lucy, it becomes necessary for the human subjects to perform the posture suggested for Lucy (Stern and Susman, 1983). This, as previously mentioned (see section 1.1), is a posture requiring both flexed knees and flexed hips. When subjects are asked to perform this posture, they are instructed to bend the knees (at approximately 50°) and the hips (at approximately 30°) while attempting to walk as normally as possible (see Figure 4.2).

When asked to flex the hips and knees, subjects will also tend to bend the trunk forward slightly and, since this is observed in chimpanzee bipedalism, it is permitted. When performing the BHBK posture at higher speeds, during testing, some subjects were inclined to run. This practice was always discouraged since the study required walking gait; moreover the mechanics of the running gait are quite different from those of walking.

4.4.2 Oxygen consumption

The twelve human (volunteer) subjects were again used to provide measurements of the oxygen cost of exercise. Subjects were asked to walk using the two postures:- upright walking and BHBK walking. The volume of absolute oxygen consumption per minute ($\dot{V}O_2$) was measured using a gas analyser (Sensor Medics Metabolic Cart 2900). Before each testing session the equipment was calibrated (volumes of oxygen/carbon dioxide to standard mixtures of gases, and all volumes calibrated against a known volume of air at STPD - see section 1.8.1). Recordings were made in millilitres per minute ($ml \cdot min^{-1}$) and data recorded (and calculated) every 20 seconds during the test period.

Carbon dioxide production, in $ml \cdot min^{-1}$ ($\dot{V}CO_2$), was measured at the same time as the measurement of oxygen consumption, at 20 seconds intervals during the test, so that the respiratory exchange ratio can be calculated. The ventilation rate, ($\dot{V}_E$ in $l \cdot min^{-1}$) was also measured and recorded during testing. $\dot{V}_E$ operates as a mediator between the respiratory and metabolic cues for level of exertion. However, $\dot{V}CO_2$ and $\dot{V}_E$ are not, in themselves, good indicators of energy cost, economy or efficiency and are regarded simply as further indicators of exercise intensity (Noble and Robertson, 1996).

4.4.3 Heart rate

The subject's heart rate was also measured simultaneously with measurement of oxygen consumption while the subjects walked the treadmill. Heart rate (HR) was measured using a portable heart rate monitor (Polar Electro Favour, Kemple, Finland) strapped to the subject's chest and fitted so as not to impede breathing. The heart rate was recorded every two minutes, in beats per minute (bpm/bt·min^{-1}) and readings were made at the start, in the middle and at the end of each stage of the protocol. The data taken towards the end of each stage provide a measure of heart rate during the exercise plateau (steady-state) at each speed.

4.4.4 Perceived exertion

Rate of perceived exertion or RPE is a useful indicator of the perceptual response to a graded exercise test and is used as a measure of the subject's reaction to the exercise intensity. This is sometimes valuable when comparing subjects of varying fitness using an identical protocol. At 3 minutes into each stage (ie: at the exercise plateau), a card showing the 15-grade Borg scale for measuring RPE, described earlier, was held up so that the subject could indicate the level of exercise intensity he/she was experiencing. RPE is useful in determining perceptual responses between modes of exercise that require different levels of muscle mass (i.e. the RPE will increase although other physiological variables may not; Noble and Robertson, 1996).

4.4.5 Core temperature

Temperature changes during exercise give an indication of thermal stress to the subject (see section 1.7.4). Core temperature is the most effective way of measuring the temperature of a subject. The rectal probe is more efficacious than the throat probe since there is very little time lag in the measurement, and if inserted past the anal sphincter it is very close to the body core. The rectal probe was inserted to a depth of 8 cm beyond the anal sphincter, which allows reliable data to be collected (Reilly and Cable, 1996). Core temperature was recorded in this way every two minutes during rest, in the 2nd and 4th minutes during the exercise, and again at two minute intervals during the recovery period.

4.4.6 Blood lactate

Blood lactate was measured using blood samples (100μλ) taken from an arterialized fingertip during the third minute of recovery for every case. The samples were collected in heparinized capillary tubes and were analysed for their lactate content within minutes. The analysis was made with Analox (GM7, Analox, UK) lactate equipment. Unfortunately it was not possible to take lactate measurements during the treadmill walking. Lactate values were therefore measured only once during each protocol and, in each case, three readings were taken to obtain an average for each subject. One subject objected to this procedure so that blood lactate values were obtained for 11 of the 12 subjects; this however provided more than sufficient data for statistical analysis.

4.4.7 Method for determining $\dot{V}O_{2max}$

$\dot{V}O_{2max}$ is the maximal oxygen uptake capacity of each individual. It is estimated using the submaximal incremental test in the present protocol. Data is derived from any two stages of an incremental exercise test. The subject's age, along with heart rate and oxygen uptake data from two points during testing, are used to calculate $\dot{V}O_{2max}$. The measured data is analysed using the equations (from Williams and Eston, 1996) :-

$$\dot{V}O_{2max} = \dot{V}O_2\, st2 + b((220 - \text{age}) - \text{HR}\, st2) \qquad \textbf{Equation 4.1}$$

where ....

$$b = \frac{(\dot{V}O_2\, st2 - \dot{V}O_2\, st1)}{(\text{HR}\, st2 - \text{HR}\, st1)} \qquad \textbf{Equation 4.2}$$

and

$\dot{V}O_2\, st1$	is the oxygen cost of stage 1
$\dot{V}O_2\, st2$	is the oxygen cost of stage 2
HR *st1*	is the heart rate during stage 1
HR *st2*	is to the heart rate during stage 2
age	is the subject's age

Stages 1 and 2 are any stages of an incremental exercise test where stage 1 is at a lower exercise intensity than stage 2

This method is subject to some errors as a true heart rate maximum has not been calculated, but these predictions use a multi-stage test, which is considered to show acceptable levels of accuracy (American College of Sports Medicine, 1991).

4.4.8 Training effect

At the outset it seemed essential to assess the effect of previous training in the BHBK posture. Regular subject training in the BHBK posture over a number of weeks is the only effective way to approach this problem. Unfortunately this method proved impossible to establish since willing volunteers with the time required to carry out the required training were unavailable.

However, some popular sports utilise the crouched posture of 'bent-hip, bent-knee' walking routinely, for example, sword-fencing, table-tennis and skiing. One willing subject, recently returned from 3 weeks continuous skiing in the Swiss mountains volunteered to be tested. His previous daily skiing was considered to provide a significant training in the crouched posture and he was thus requested to undertake the same testing protocol as the earlier twelve subjects who had received no previous training in the BHBK gait. The results obtained with this volunteer were compared with data obtained from the 'normal' subjects.

4.5 Results

4.5.1 Statistics

Commonly used and reliable statistical tests were performed on all of the appropriate data. T-tests were used for comparing means and variances within a sample. Correlated t-tests for paired data were judged more appropriate than independent t-tests, since problems can occur with independent t-tests if the subjects differ dramatically in their response to a task, so that the differences between subjects tend to obscure the experimental effect (Parker, 1979). A correlated samples type of experimental design (i.e.: each subject performs one experimental design, in two dissimilar postures, so that direct comparisons can be made between postures for each discrete subject) overcomes the problems of large variations between subjects. This is accomplished by using a repeated measures design, where the same subject performs both experimental situations (e.g. 2 separate postures, as here). The two most frequently used tests to investigate correlated sample experimental designs are paired t-tests for correlated samples and the Wilcoxon tests for correlated samples (Nevill, 1996). The paired samples t-test was used (SPSS Statistical Package for Windows) on all paired data. Statistics were reported as probabilities, where statistical significance was taken at the $p<0.05$ level, common for physiological testing (Nevill, 1996). Statistics reported as significant to the $p<0.01$ level were considered to be very significant.

4.5.2 Summary of subject data

Preliminary subject data was provided voluntarily by the selected subjects on the first day of the exercise test protocol. A summary of the data is shown in Table 4.5.

Subject No.	Age (yrs)	Height (m)	Weight (kg)	Weekly exercise [A]	$\dot{V}O_{2max}$ (ml·kg^{-1}·min^{-1})[B]	Shoe size	H→K (cm)	K→A (cm)
1	25	1.86	79	2	48.10	11	47	45
2	27	1.6	53.5	5	84.60	5	50	38
3	26	1.74	71.2	1	34.51	8.5	42	43
4	38	1.75	78.1	1	38.24	8.5	40	43
5	26	1.83	89.3	6	65.17	9	49	41
6	24	1.57	62.9	2	31.16	5.5	44	37
7	35	1.55	53.6	0	31.60	4.5	40	38
8	28	1.69	71.6	3	34.83	7.5	38	40
9	25	1.84	79.5	3	34.52	8	43	45
10	28	1.79	68.4	7	39.77	9	43	44
11	25	1.55	58.9	0	30.00	5	37	37
12	23	1.62	52.9	1	33.95	6.5	42	40

Table 4.5 Summary of subject data.

[A] Weekly exercise in bouts·week^{-1}

[B] See section 4.4.7 for determination of $\dot{V}O_{2max}$ and 4.5.7 for explanation of data

Weekly exercise taken (only bouts of exercise longer than twenty minutes were recorded) averaged 2.6 ± 0.67 (mean ± SE). Shoe size averaged 7 ± 0.58. The anthropometric measurements are recorded as H→K (hip to knee) for the upper leg length, and K→A (knee to ankle) for the lower leg length. The averages for leg length are 42.0 cm (± 1.18) for H→K, and 40.9 cm (± 0.87) for K→A.

Weight was measured both before and after exercise to provide an indication of the fluid loss (perspiration) during normal exercise. Data were taken during both normal and BHBK walking, and are presented in Table 4.6. In most cases there was some weight loss during normal walking, but this was not significant: the mean mass loss was 0.18 ± 0.11 kg (mean ± SE). The mass change during BHBK walking, however, was significantly different ($p<0.05$) from that during normal walking, with a mean mass loss of 0.37 ± 0.05 kg.

Subject No.	Weight loss (Normal) kg	Weight loss (BHBK) kg
1	0.2	0.4
2	0.5	0
3	0.1	0.1
4	0.3	0.5
5	1.2	0.7
6	0	0.5
7	0.2	0.3
8	0	0.4
9	0	0.4
10	0.4	0.4
11	0	0.4
12	0.2	0.3

Table 4.6

Weight loss in kilograms during exercise in two postures. Weights are measured both before start of exercise and immediately post recovery. Weight loss gives an indication of fluid loss during exercise.

4.5.3 Oxygen cost

Figures 4.3 and 4.4 show the mean gross oxygen cost (see section 1.7.2) at each stage of the protocol for normal walking. The averaged data shows the plateau effect after subjects exercised for three minutes. At the start of each increase in speed there is a noticeable increase in oxygen consumption; the oxygen consumption then levels off into a steady state as the plateau for each speed is reached. Data for the whole exercise test (Figure 4.3) were recorded in millilitres per kilogram, per minute to increase data uniformity between subjects of different weights.

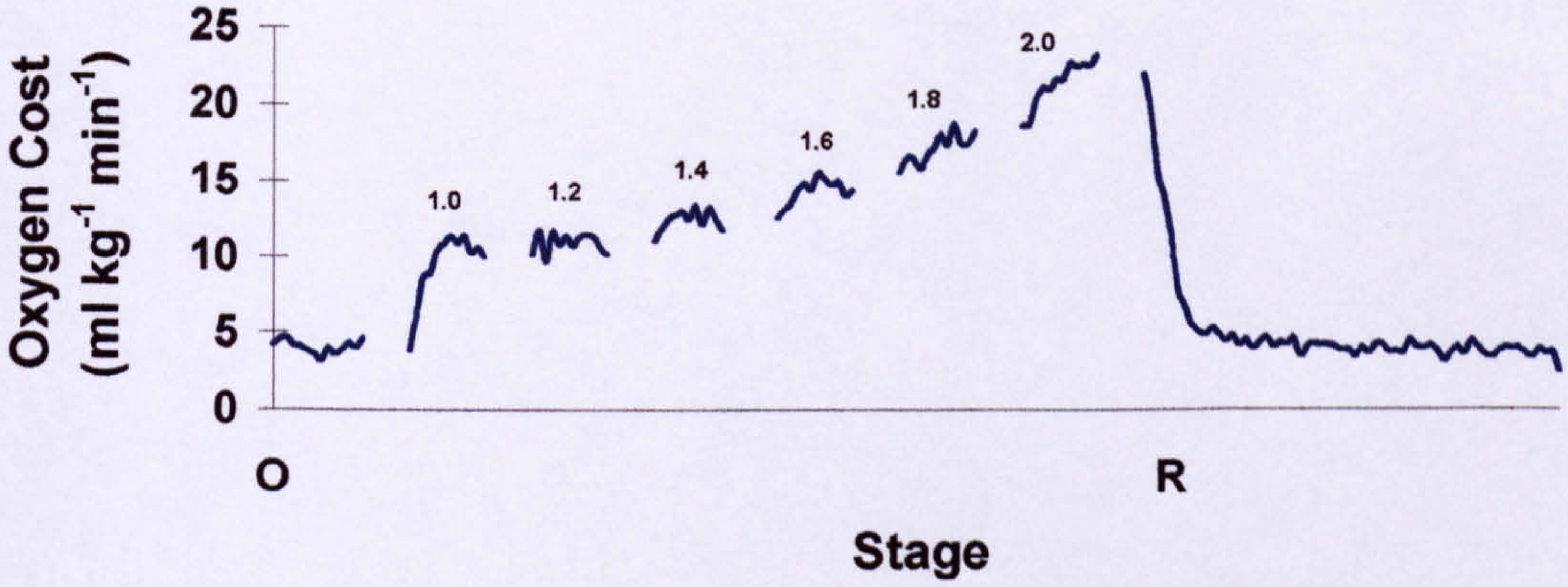


Figure 4.3 Average oxygen cost (for 12 subjects; ml·kg $^{-1}$ · min $^{-1}$) during normal walking showing a gradual increase in oxygen cost with each increase in speed. Gaps in the data are intended to separate distinct exercise rates. Stage O denotes resting levels and stage R is the recovery period (20 minutes) after exercise is complete. After resting levels the walking speed increases incrementally, and the walking speed of each section is displayed above.

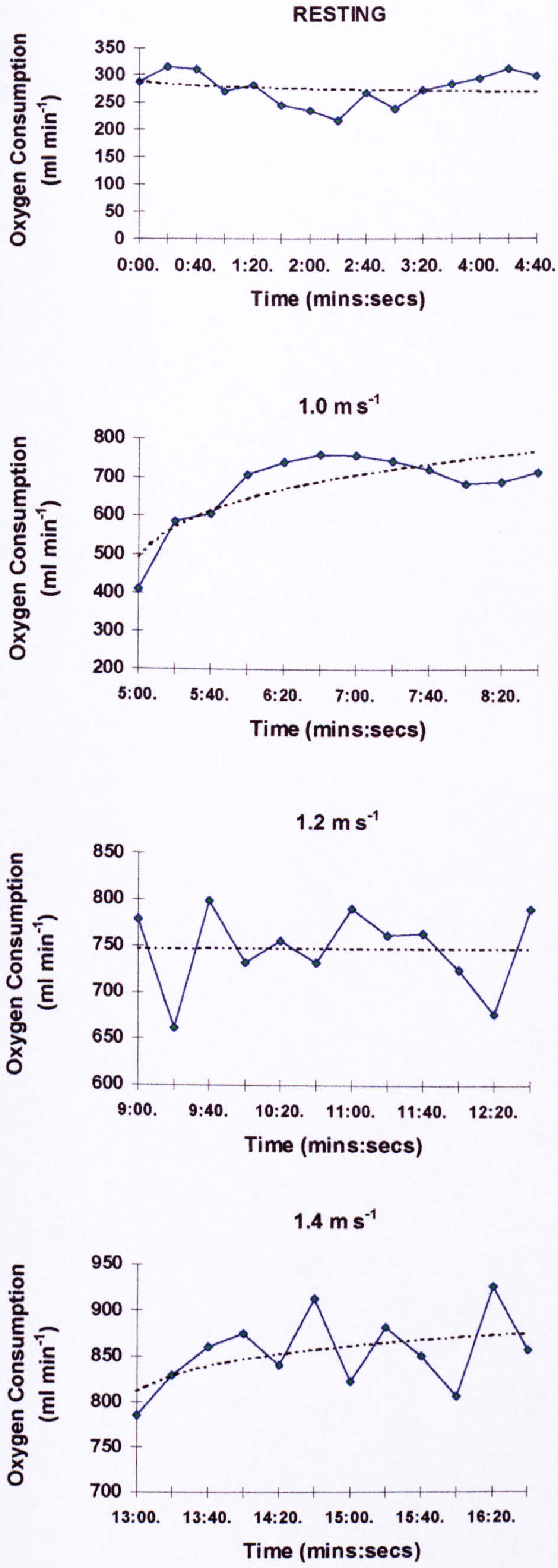
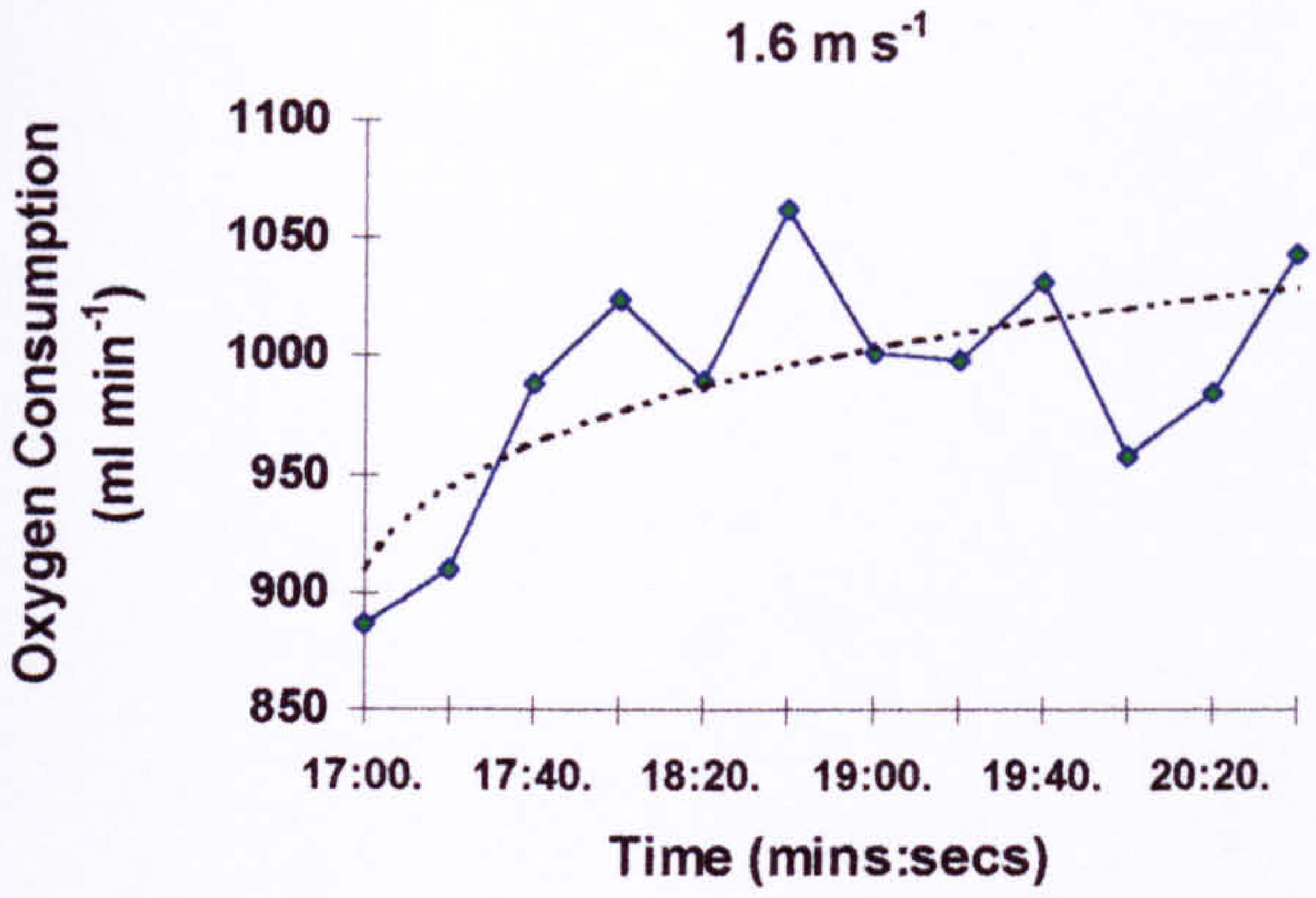


Figure 4.4 (a-h) The eight sections of the protocol, shown in more detail to display the plateau effect after the steady state is reached (approximately 3 minutes exercise at each speed). Dashed lines are a representation of the trends in the data, and depict an 'eye-balled' best-fit line.

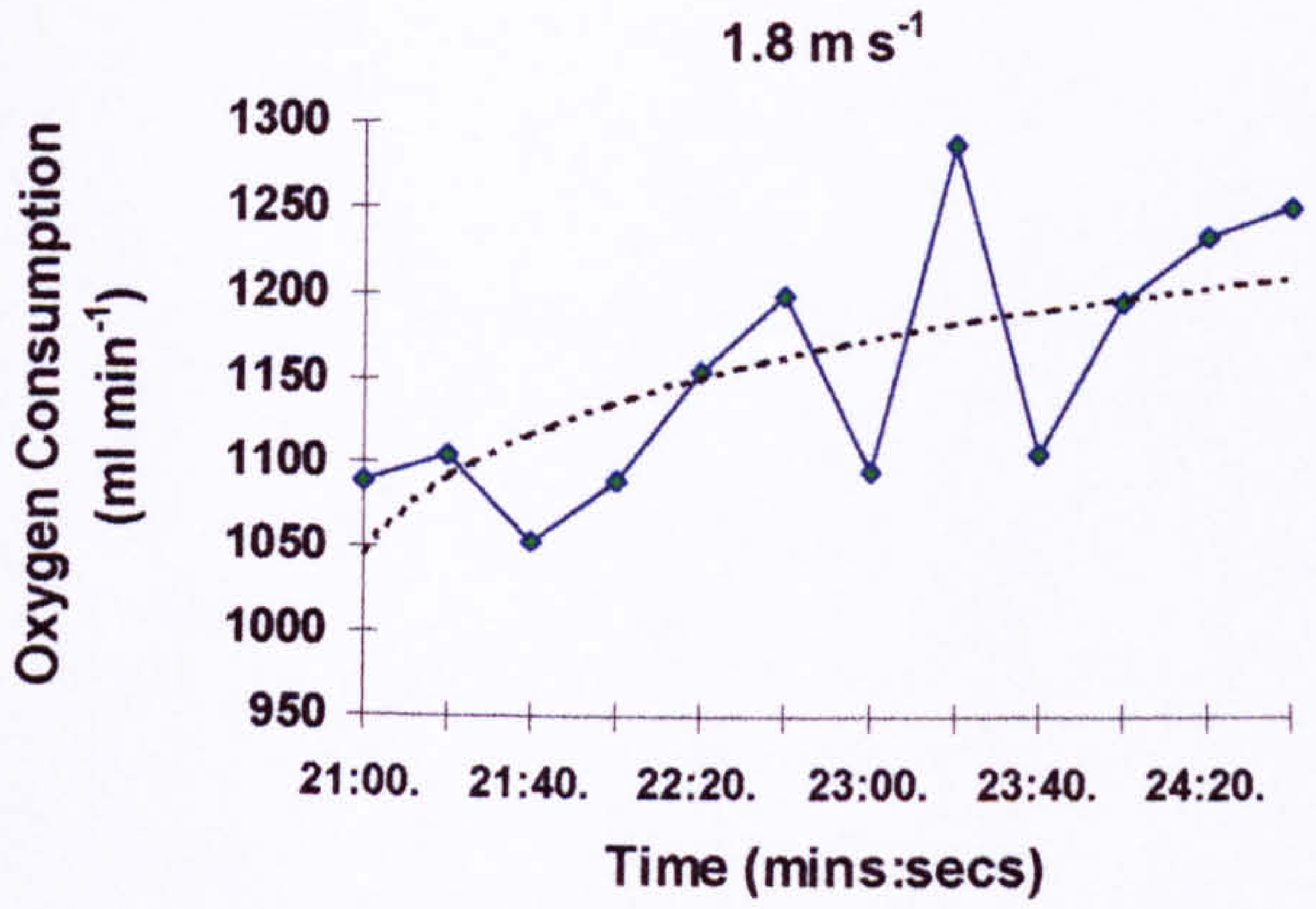
(b)

(c)

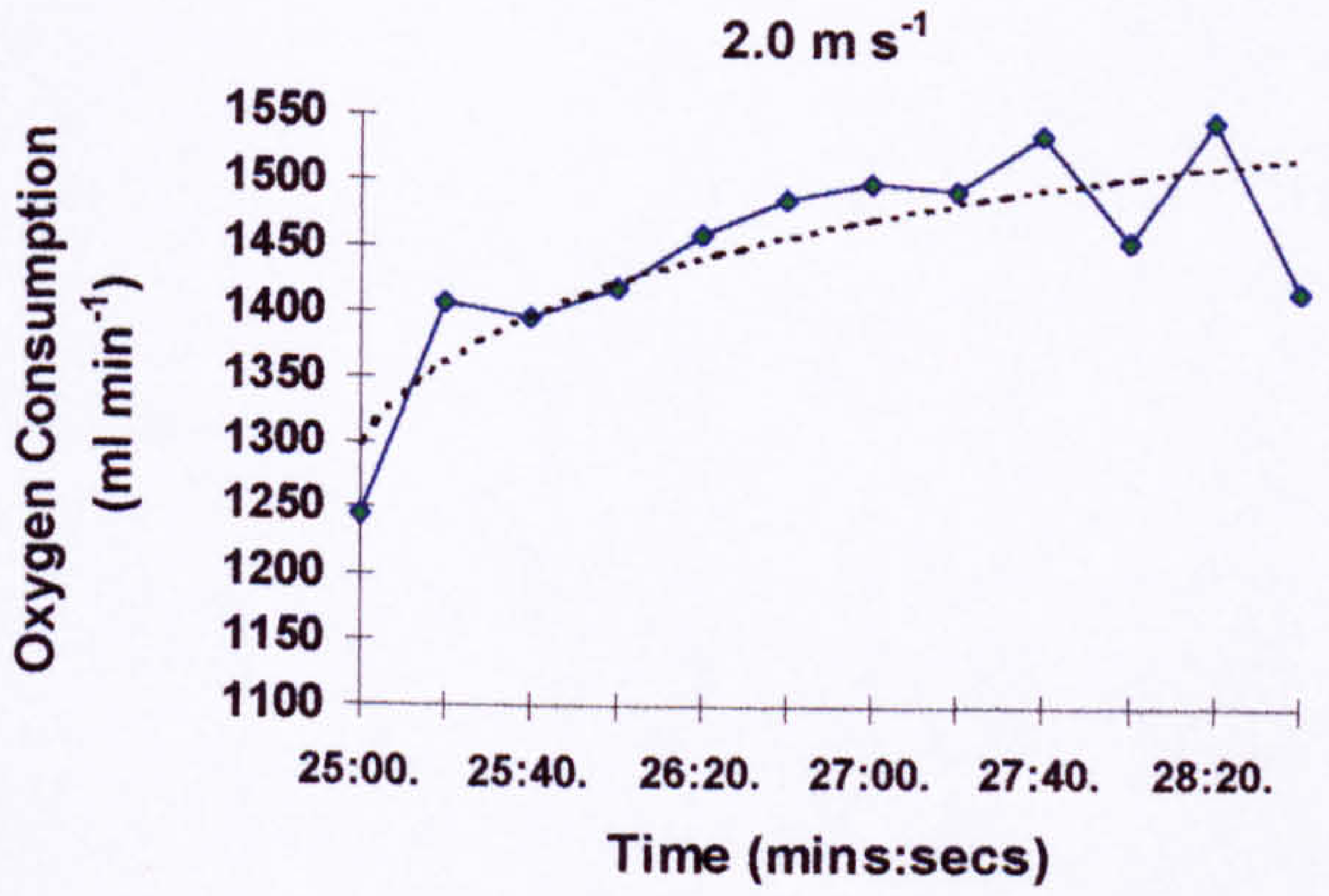
(d)


1.6 m s^{-1}

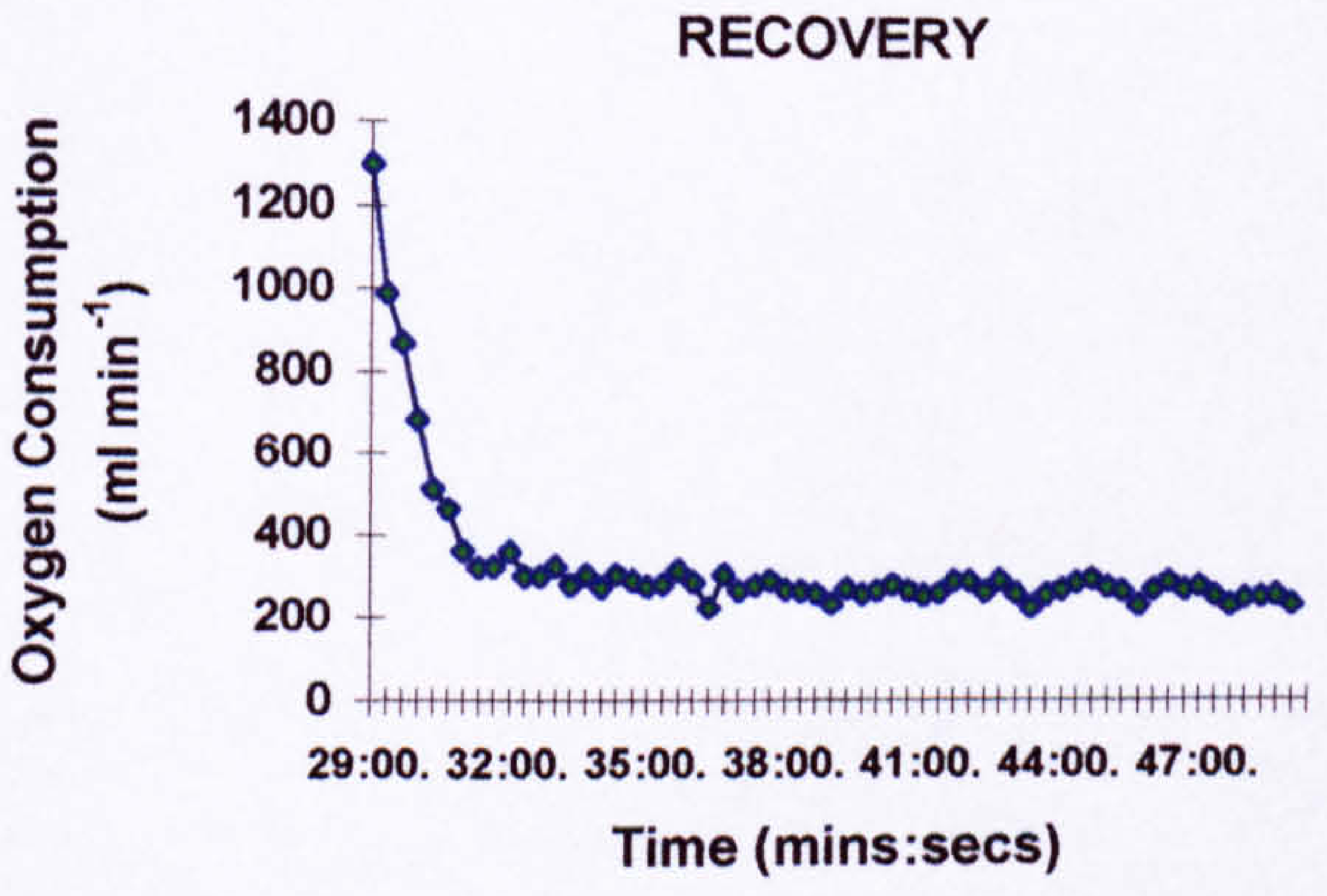
(e)


1.8 m s^{-1}

(f)


2.0 m s^{-1}

(g)


RECOVERY

(h)

Figure 4.5 shows the effect of the BHBK gait on the gross oxygen cost of exercise. In this case data is shown in litres per minute for direct comparison with other available data in this field. Exercise in the BHBK posture causes a significant increase ($p<0.05$) in the oxygen consumption during exercise when compared with that for normal walking. This is the case for all the speeds observed and the data indicates an average of 52% increase in oxygen consumption for BHBK walking compared with normal walking. The standard error for the BHBK posture is very slightly greater, at all speeds, than that for normal walking: i.e. there is more variation in the effect of BHBK exercise between subjects than between subjects walking normally.

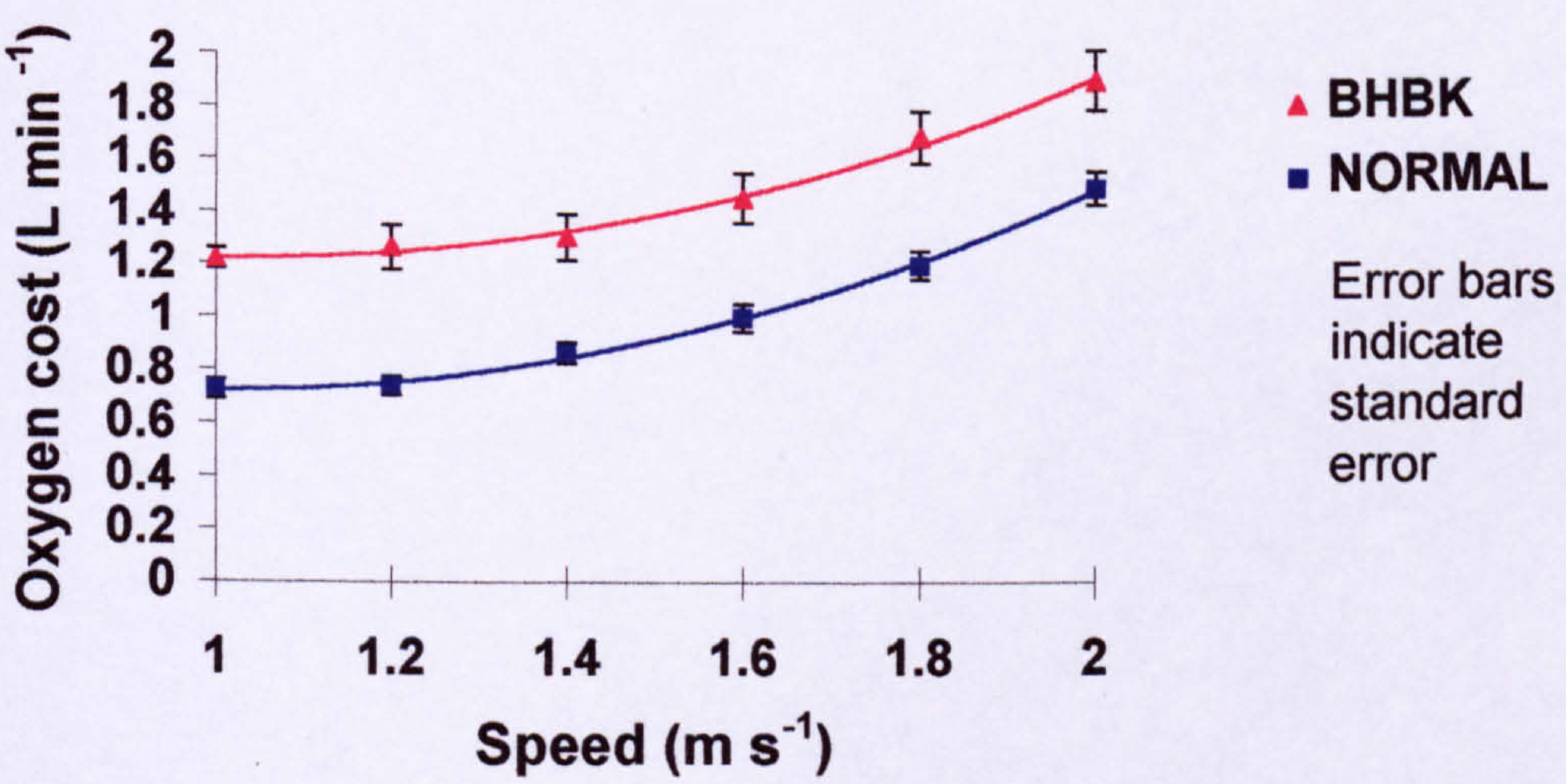


Figure 4.5 Oxygen cost of two postures in l·min $^{-1}$ (means and standard errors for 12 subjects) Speeds of exercise range from 1.0 to 2.0 metres per second.

Back extrapolation to zero on the y-axis of the oxygen cost data provides an estimate of the oxygen required purely to maintain postural equilibrium during locomotion (see Appendix XIII). The energy required to maintain posture is estimated at 0 L·min^{-1} in a normal upright stance and 0.45 L·min^{-1} for the BHBK posture.

The results obtained for $\dot{V}CO_2$ and $\dot{V}_E$ are detailed in the Appendix (see appendix VI). Both $\dot{V}CO_2$ and $\dot{V}_E$ show a positive linear relationship with speed, and increase as speed increases. Both $\dot{V}CO_2$ and $\dot{V}_E$ are elevated above normal levels during exercise in the BHBK gait.

Oxygen debt is the oxygen consumed during recovery from exercise. It was calculated as an average for each five minutes of recovery across all 12 subjects, as an indicator of when the oxygen consumption returned to normal levels. Figure 4.6 represents average values for all 12 subjects. Total oxygen debt is calculated by summing the oxygen cost for each stage of recovery. Data for zero minutes is taken from the last data to be recorded during exercise, and therefore corresponds to oxygen cost at 2.0 m·s^{-1}.

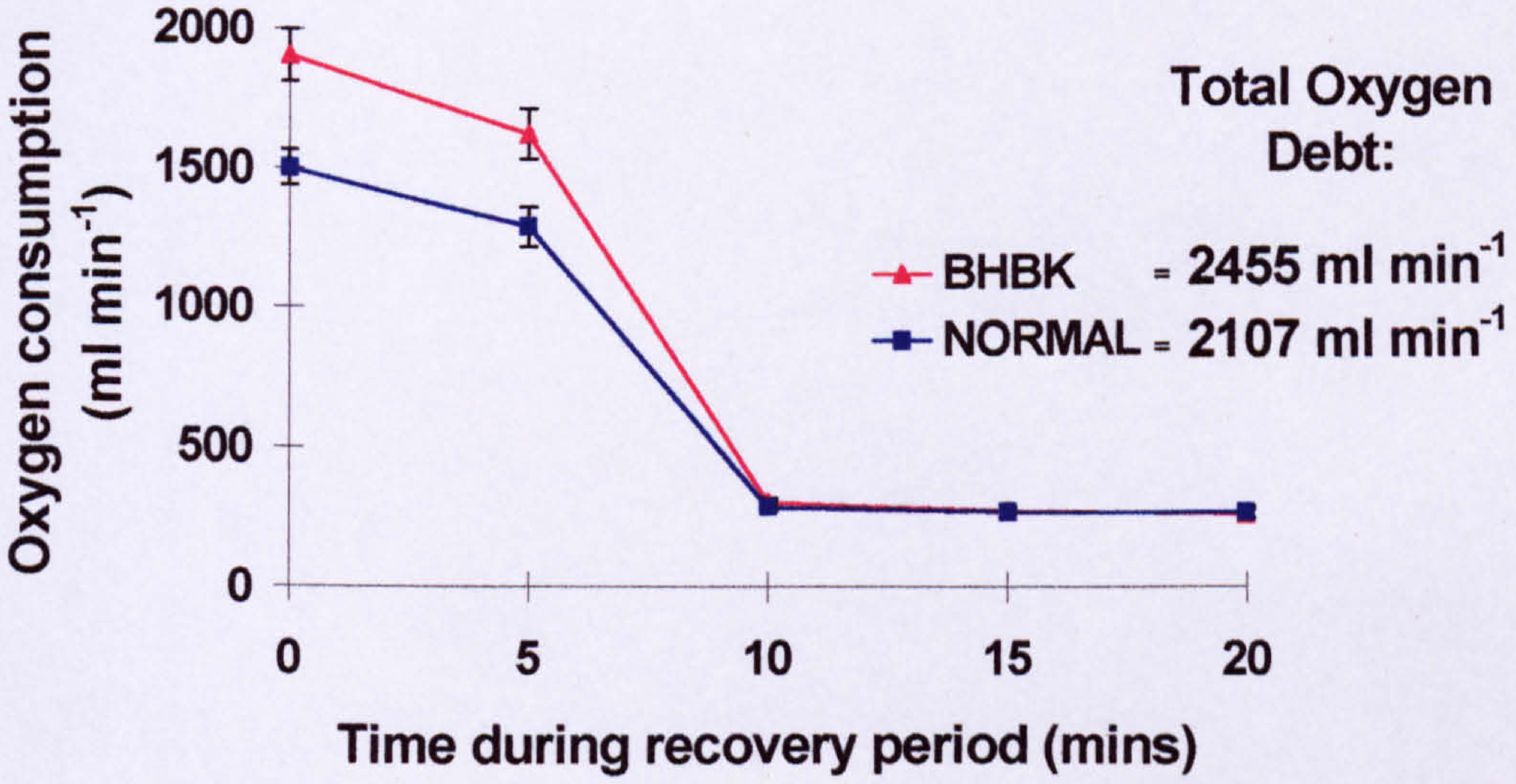


Figure 4.6 Oxygen debt (mean ± SE), displayed as oxygen cost for each stage of recovery (ml·min^{-1}). Total oxygen debt is also displayed.

Note that the oxygen cost at 5 minutes into recovery is higher for BHBK walking than it is for normal walking, but returns to normal levels by 10 minutes into recovery in both postures. Total oxygen debt is, however, clearly increased for BHBK walking over levels for normal walking.

Energy cost of locomotion (E_L)

To establish the energy cost of locomotion, E_L (see section 1.8.2) in the BHBK posture data are calculated as energy cost of exercise per kilogram, per unit distance. These data are shown in Figure 4.7. The results provide an indication of efficiency, since the efficiency of gait is high when E_L is a minimum. It is clear from this figure that E_L in the BHBK posture is greater than that during normal walking, at all speeds, although the results also indicate that the minimum E_L occurs at 1.2 $m \cdot s^{-1}$ for normal walking and at 1.4 $m \cdot s^{-1}$ for BHBK walking.

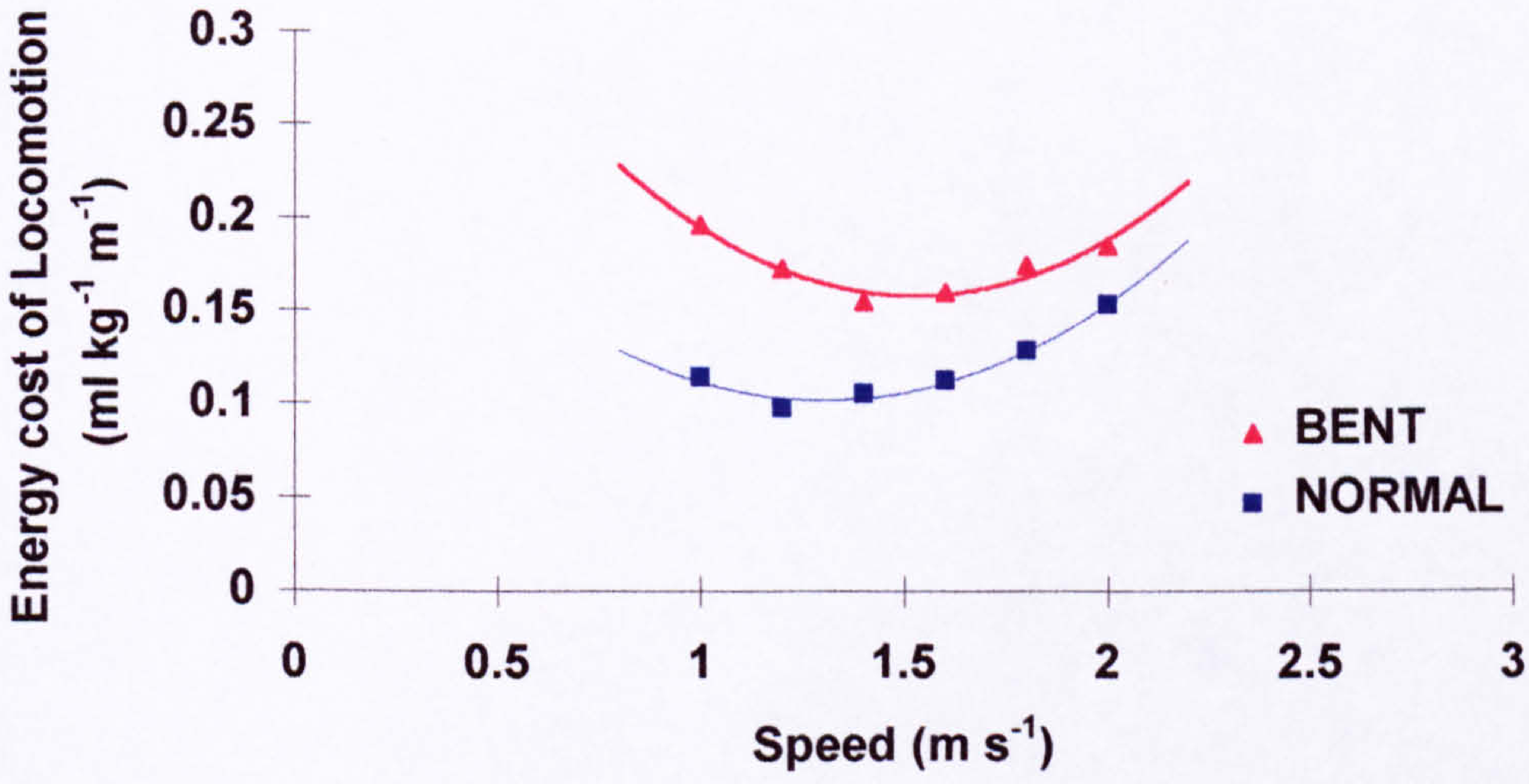


Figure 4.7 Energy cost of locomotion (ml O_2 {above resting levels}$\cdot kg^{-1} \cdot m^{-1}$) as a function of speed ($m \cdot s^{-1}$). Extrapolation to zero motion is used to estimate the energy needed to maintain the posture.

4.5.4 Heart rate

Figure 4.8 shows the effect of BHBK gait on the heart rate. Heart rate is seen to be consistently higher during BHBK walking at an average 30 percent difference, significantly higher ($p<0.05$) than during normal walking. The one exception is during BHBK walking at 2.0 m·s^{-1}, where a substantial increase in heart rate is noticed, but results are not statistically significant ($p>0.05$) at this speed. Heart rate shows a linear increase with speed during normal walking, and a similar relationship is seen for BHBK walking. However the relationship between HR and speed differs in the intercept of the line on the y-axis, which indicates the difference between normal and BHBK postures on HR.

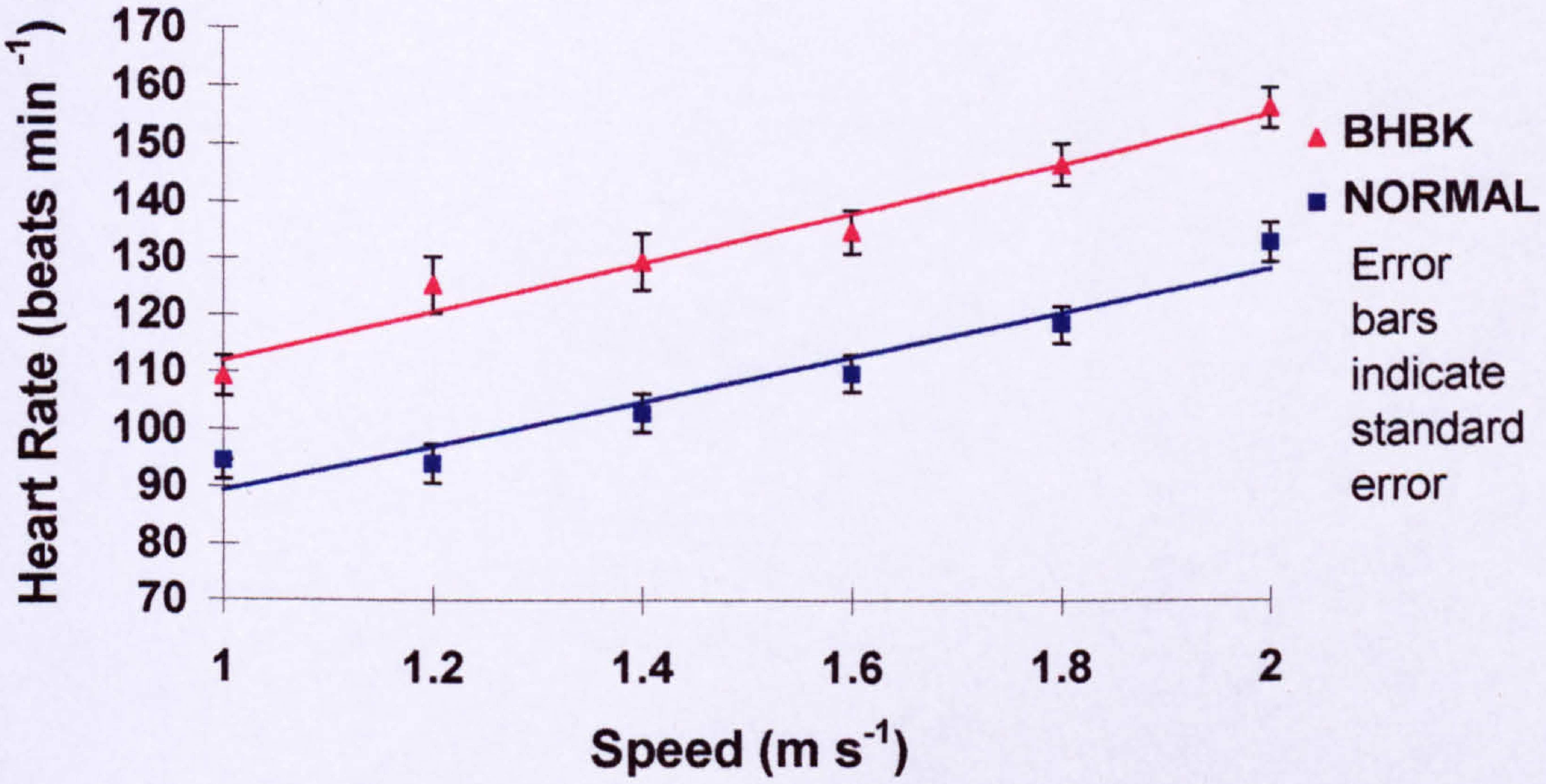


Figure 4.8 Heart rate against speed for normal and BHBK walking. Data is shown as values plus and minus the standard error of the sample together with the linear trendline. Heart rate is recorded in beats·min^{-1} and speed in m·s^{-1}.

Speed, heart rate during rest and heart rate during exercise can be combined to calculate a Physiological Cost Index (PCI), another indicator of locomotor efficiency (Butler et al., 1984). According to Butler and colleagues (1984):

$$\mathrm{PCI} = \frac{\mathrm{HR_E} - \mathrm{HR_R}}{\mathrm{speed}}$$

where $\mathrm{HR_E}$ = Heart rate at rest
$\mathrm{HR_R}$ = Heart rate during exercise at a specific speed

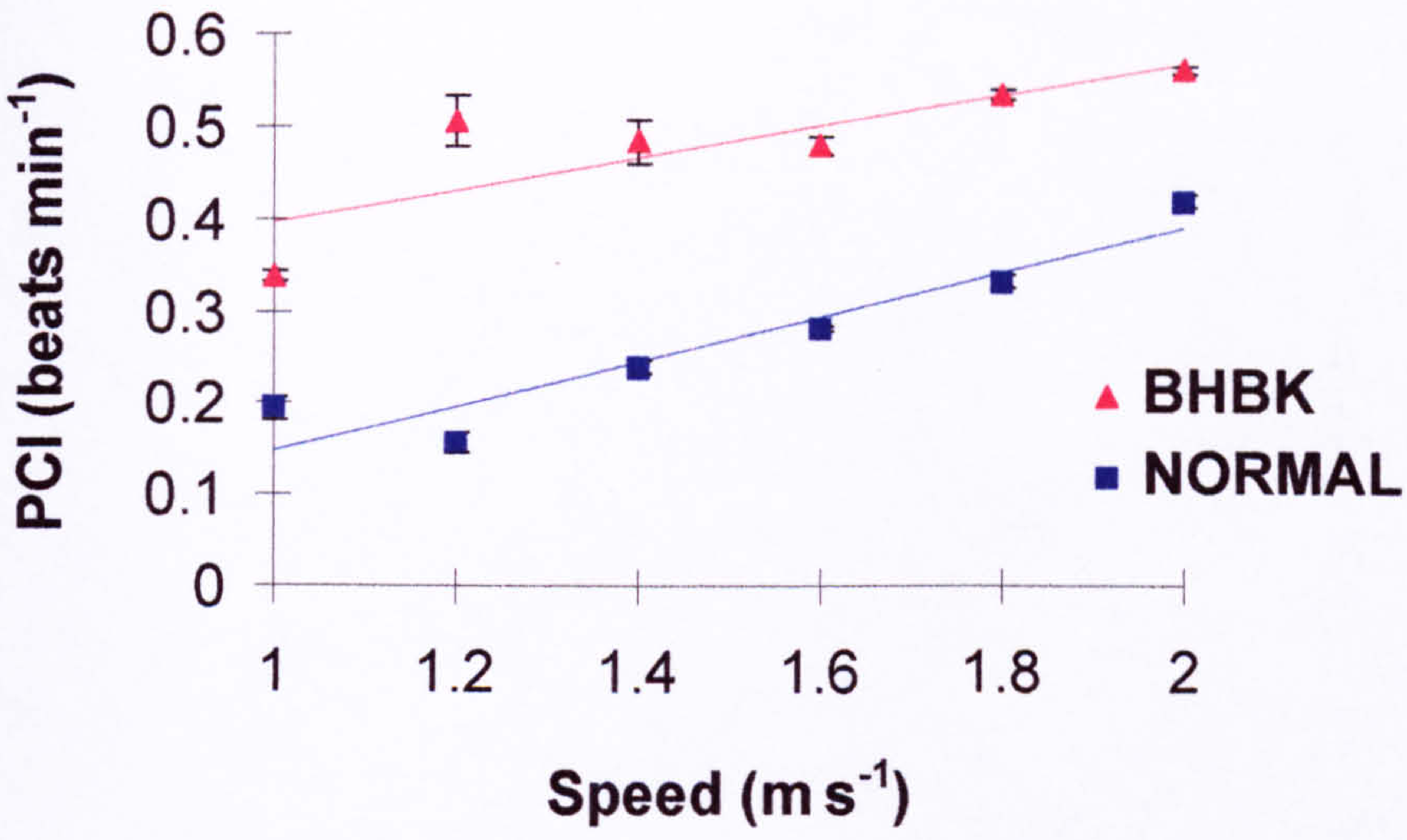


Figure 4.9 Physiological Cost Index. PCI (beats·min^{-1}) against speed (m·s^{-1}) for normal and BHBK walking

PCI is plotted against speed in Figure 4.9. PCI is displayed against speed for a wider range of speeds in Appendix VI (Figure AVI.7).

4.5.5 Perceived exertion

The perceived exertion of subjects at each speed is shown in Figure 4.10. The rate of perceived exertion (RPE) increases linearly with speed and is significantly higher ($p<0.01$) during the BHBK gait than during normal walking. Perceived levels of energy cost are generally 2 levels higher during BHBK exercise than for normal walking. Figures 4.11 and 4.12 show the relationship of heart rate to RPE for walking in both postures, and it is evident from this figure that there is a close relationship between heart rate and RPE for both postures.

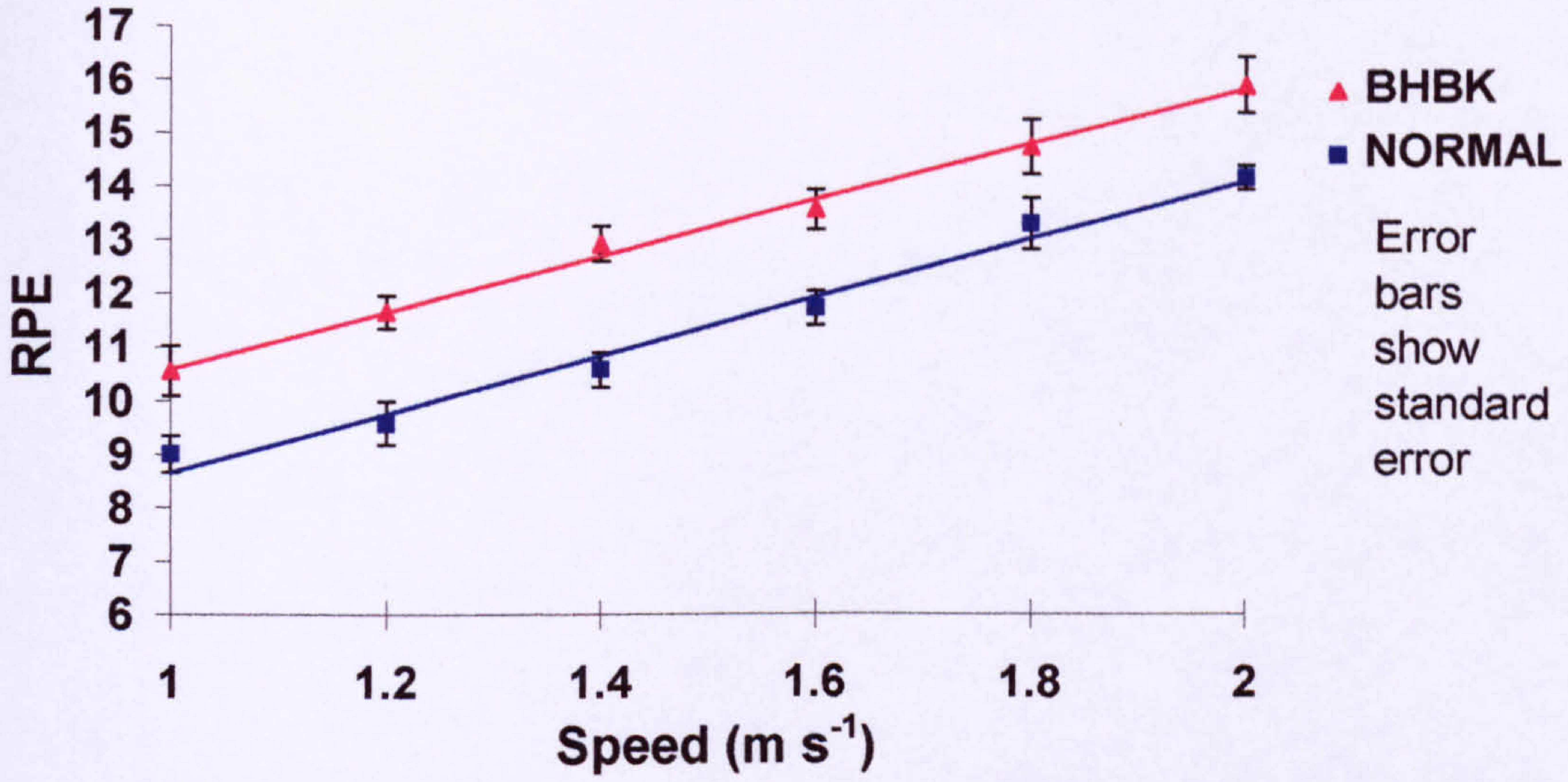


Figure 4.10 Rate of perceived exertion (RPE) for exercise in the two gaits. Data is given as a number from 6-20. Values of RPE are shown with standard error bars against speed (in m·s^{-1}) for normal and BHBK gait (for more information on RPE see section 4.4.4).

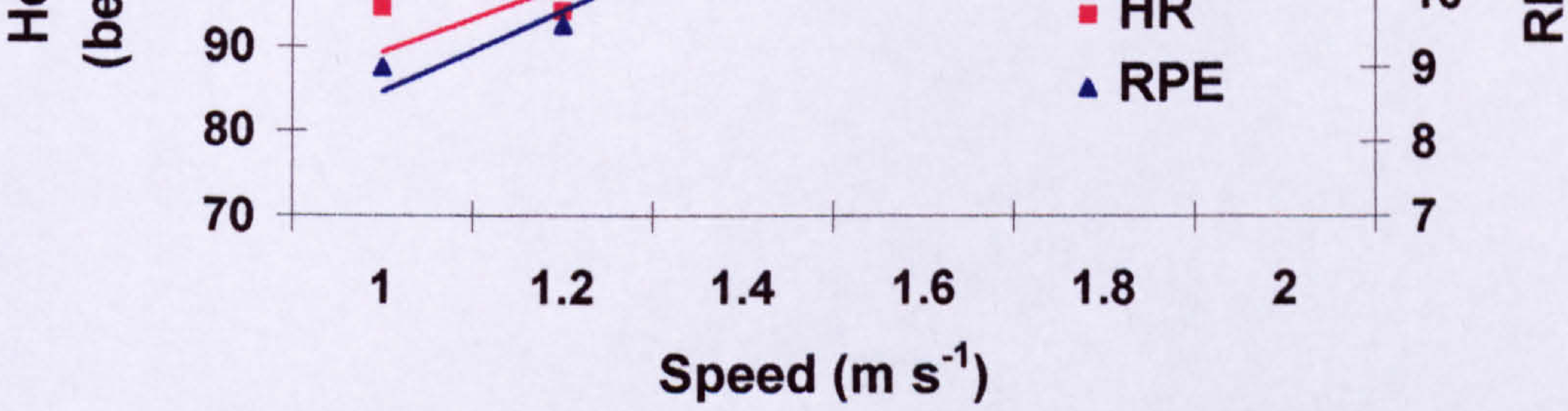


Figure 4.11 Relationship between heart rate and RPE for normal walking

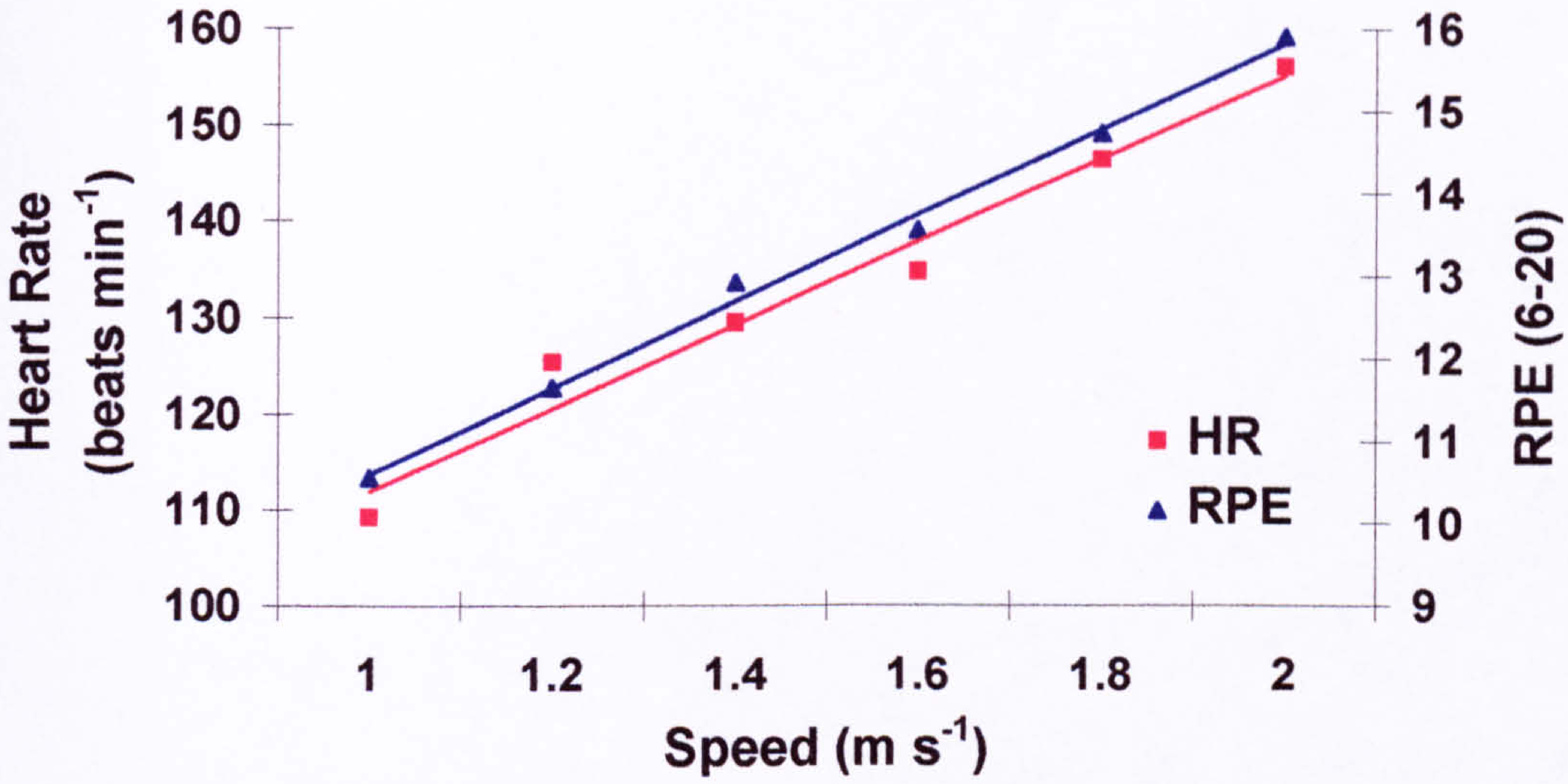


Figure 4.12 Relationship between heart rate and RPE for BHBK walking

4.5.6 Core temperature

Although core temperatures were recorded in full (Appendix VI, Figure AVI.6) during the exercise protocol, only the change in core temperature as a function of time is presented in this section in Figure 4.13.

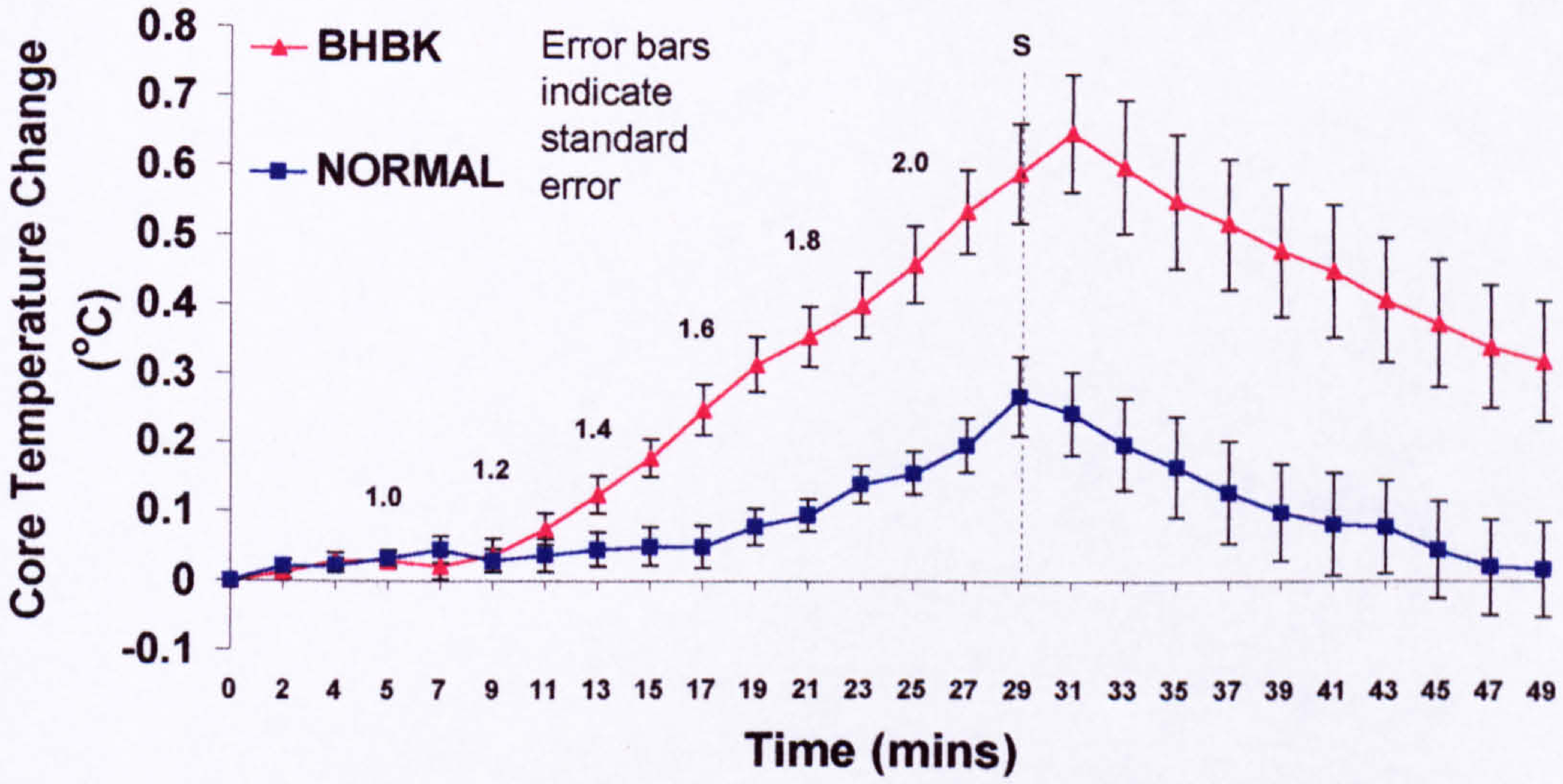


Figure 4.13 Core temperature (°C) change during the exercise protocol. Average data (means and standard errors) are given for 12 subjects. Measurements were taken for an initial resting period of five minutes. Exercise began at 5 mins, and speed increased every 2 minutes until 29 mins. S (at the dotted line) denotes where exercise stopped and the start of the 20 minute recovery period. Each speed is shown above the moment at which it began.

The plot also shows temperature changes during the initial five minutes of resting metabolism, to give a baseline for temperature change, together with further measurements of temperature changes during the 20 minute recovery period. Core temperature shows an increase of approximately 0.3°C during thirty minutes of exercise at three incremental speeds of normal walking and returns to the initial level after twenty minutes of recovery. Changes in core temperature during BHBK walking are significantly different from those during normal walking (P<0.01). During BHBK walking, the core temperature increases immediately the exercise commences, and continues to rise as the speed is increased. The total change in core temperature is approximately 0.7°C, i.e. more than twice that for normal walking, and core temperature continues to rise for two or three minutes after the walking exercise has stopped. After the twenty minutes recovery period the core temperature was still not back to the initial level.

Since 20 minutes of recovery in the BHBK posture served to reduce the core temperature by approximately 0.3°C, it is estimated that to reduce the core temperature back down to normal levels (i.e. a further reduction of 0.4°C), another 27 minutes of recovery time would be required.

4.5.7 Lactate production

Blood lactate production was measured only once during the protocol. The data is presented in Figure 4.14 as total lactate production for each gait. Lactate production is significantly higher (p<0.01) during BHBK walking when compared to normal walking.

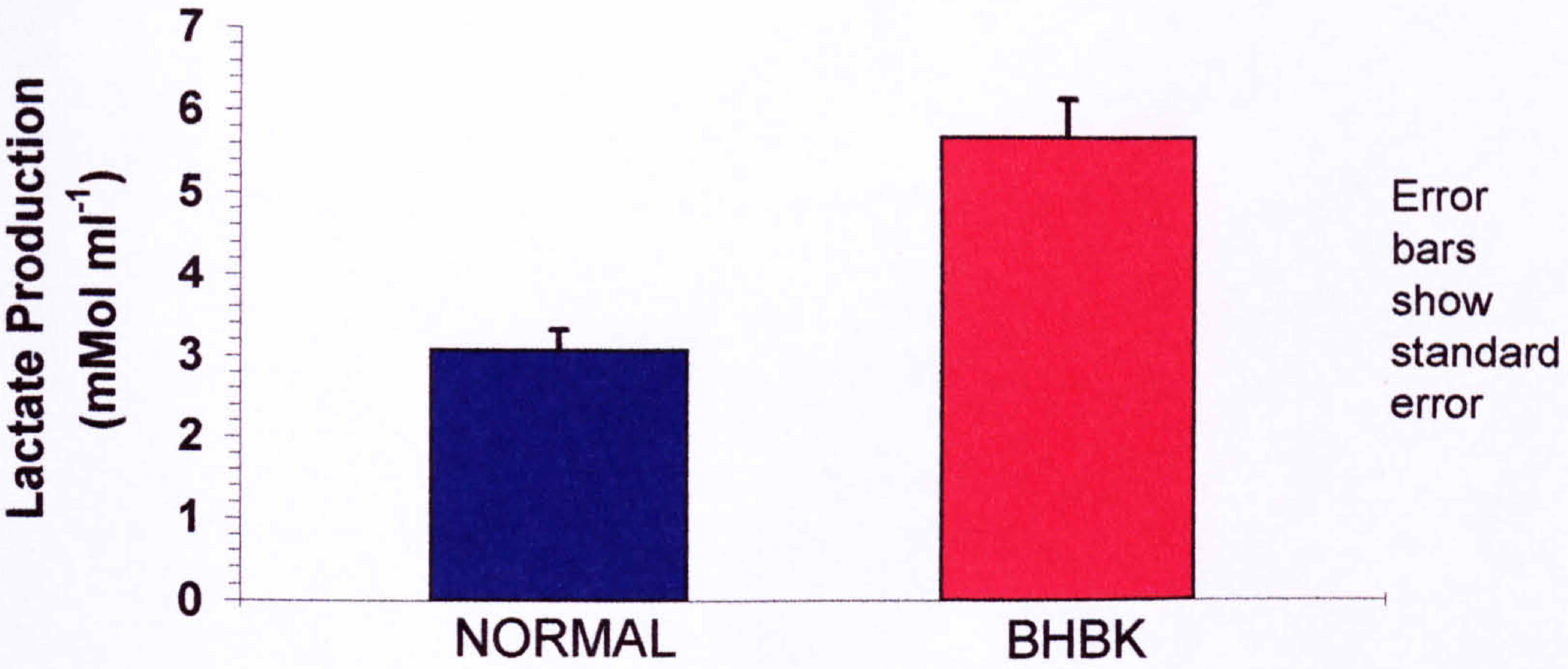


Figure 4.14 Blood lactate production measured at cessation of exercise. Lactate production is measured in mMol·ml^{-1}, and the standard error of the sample of 11 subjects is shown.

Blood lactate production for normal walking is 3.07 (± 0.25) mMol·ml^{-1}. Walking BHBK produces an average increase of 92 (± 22.0) % in lactate production to a level of 5.66 (±0.46) mMol·ml^{-1}.

4.5.8 $\dot{V}O_{2max}$

Describing the oxygen cost as the percentage of $\dot{V}O_{2max}$ is an ideal way to ascertain the proportion of maximal exercise each subject has attained (Winter, 1996). The results of the calculations to determine $\dot{V}O_{2max}$ for each subject are shown in Table 4.5, and the oxygen cost expressed as % of $\dot{V}O_{2max}$ is displayed in Figure 4.15. Data show averages for all twelve subjects. The standard error was minimal (maximum standard error ≅ 0.06), and therefore is not included on the graph.

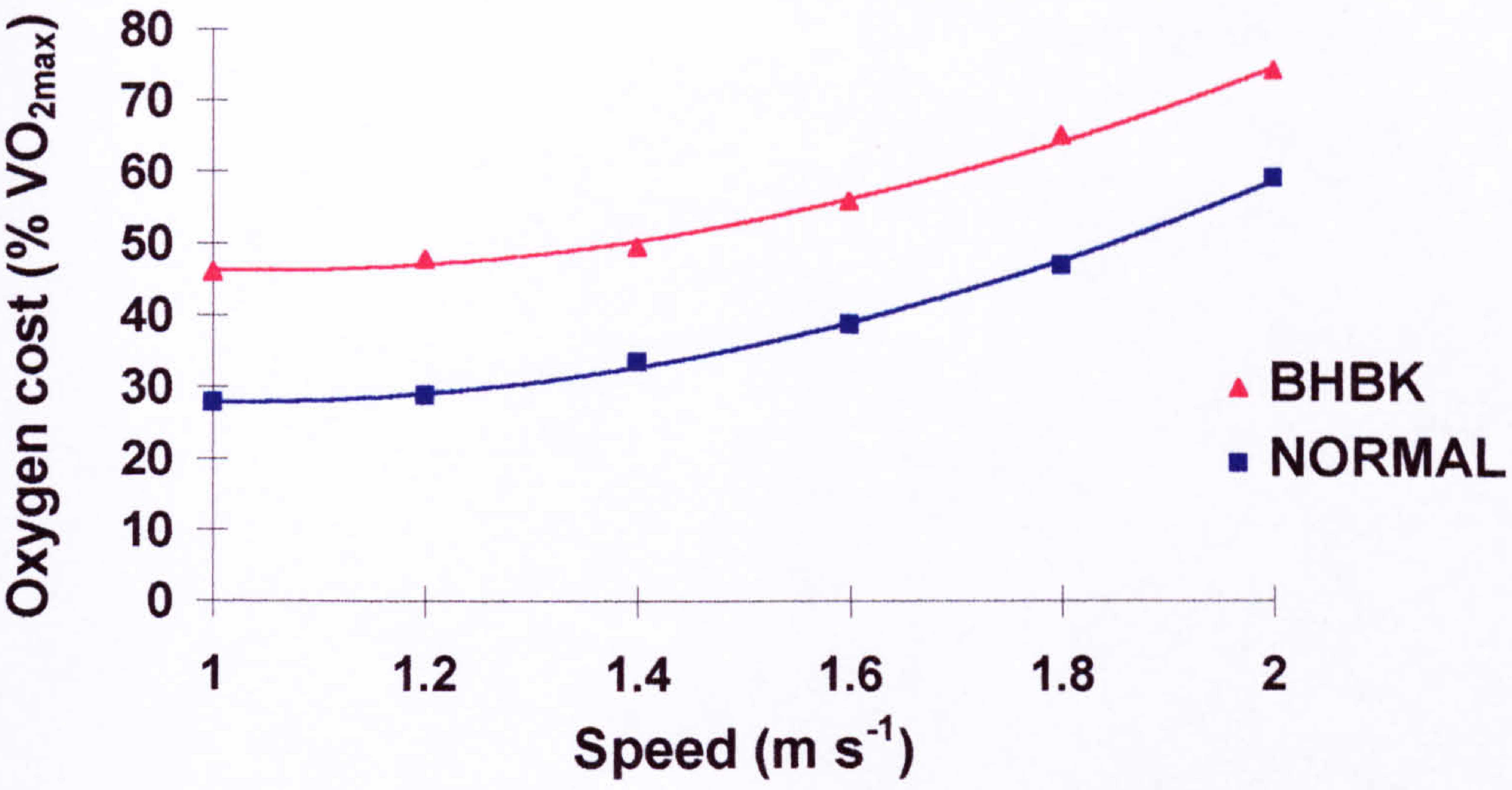


Figure 4.15 Oxygen cost expressed as % of $\dot{V}O_{2max}$ against speed.

The % of $\dot{V}O_{2max}$ ranges between approximately 30% to 60% for normal walking, and 45% to 75% for BHBK walking during the exercise protocol.

4.5.9 Training effect

Preliminary data on the effect of training on BHBK walking is described in this section. Further data would be needed to substantiate conclusions concerning the effect of training on the energy cost of a BHBK gait. In estimating the effects of training in a BHBK posture, a skier was tested using exactly the same protocol as the former 12 untrained subjects (N.B. Training in this section is defined as specific training in the BHBK posture, and does not indicate general fitness training). Figures 4.16 and 4.17 display the effect of training on oxygen cost during normal and BHBK postures.

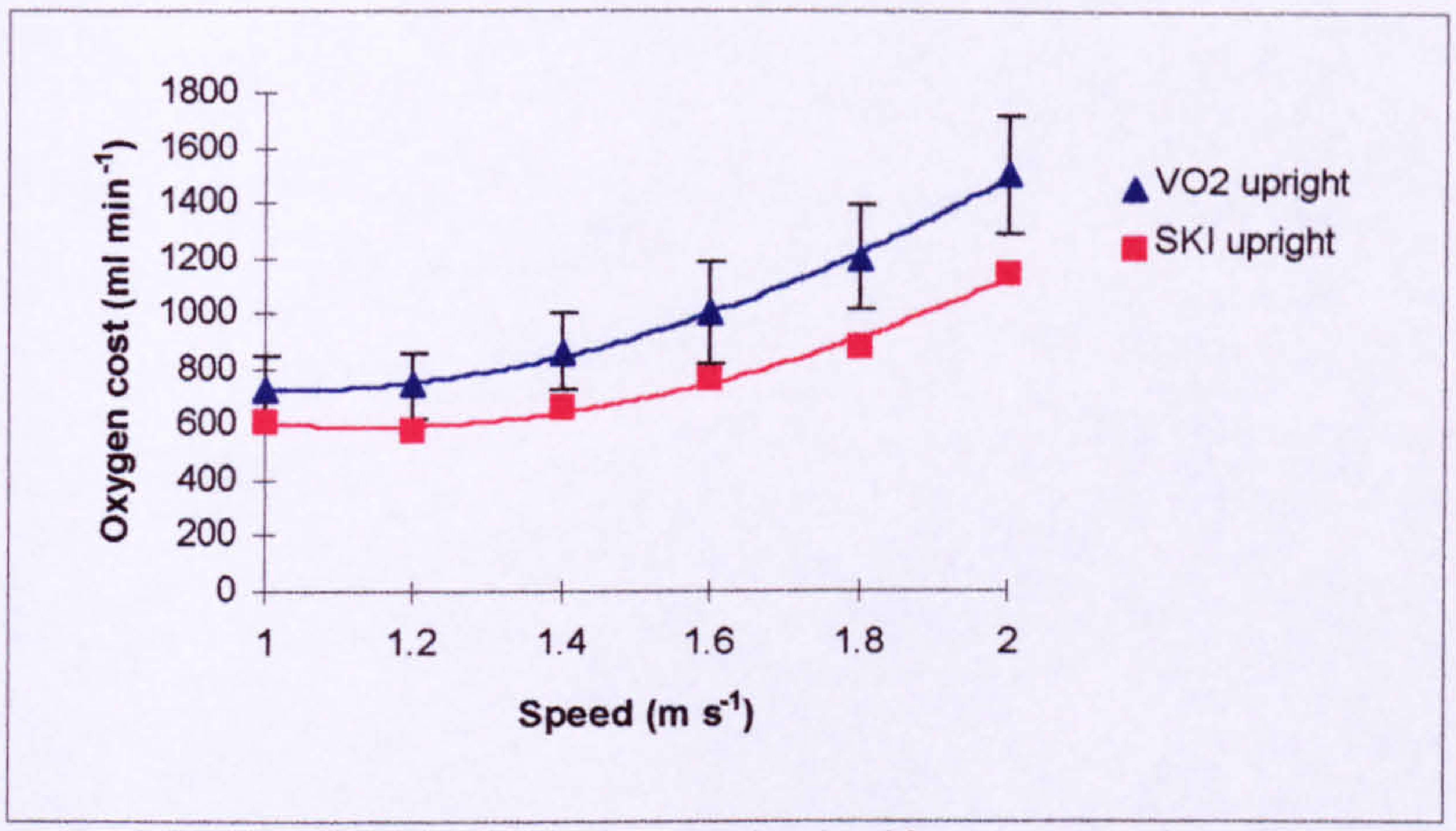


Figure 4.16 Oxygen cost of normal walking. Trained subject compared to 12 untrained subjects (average ± SD)

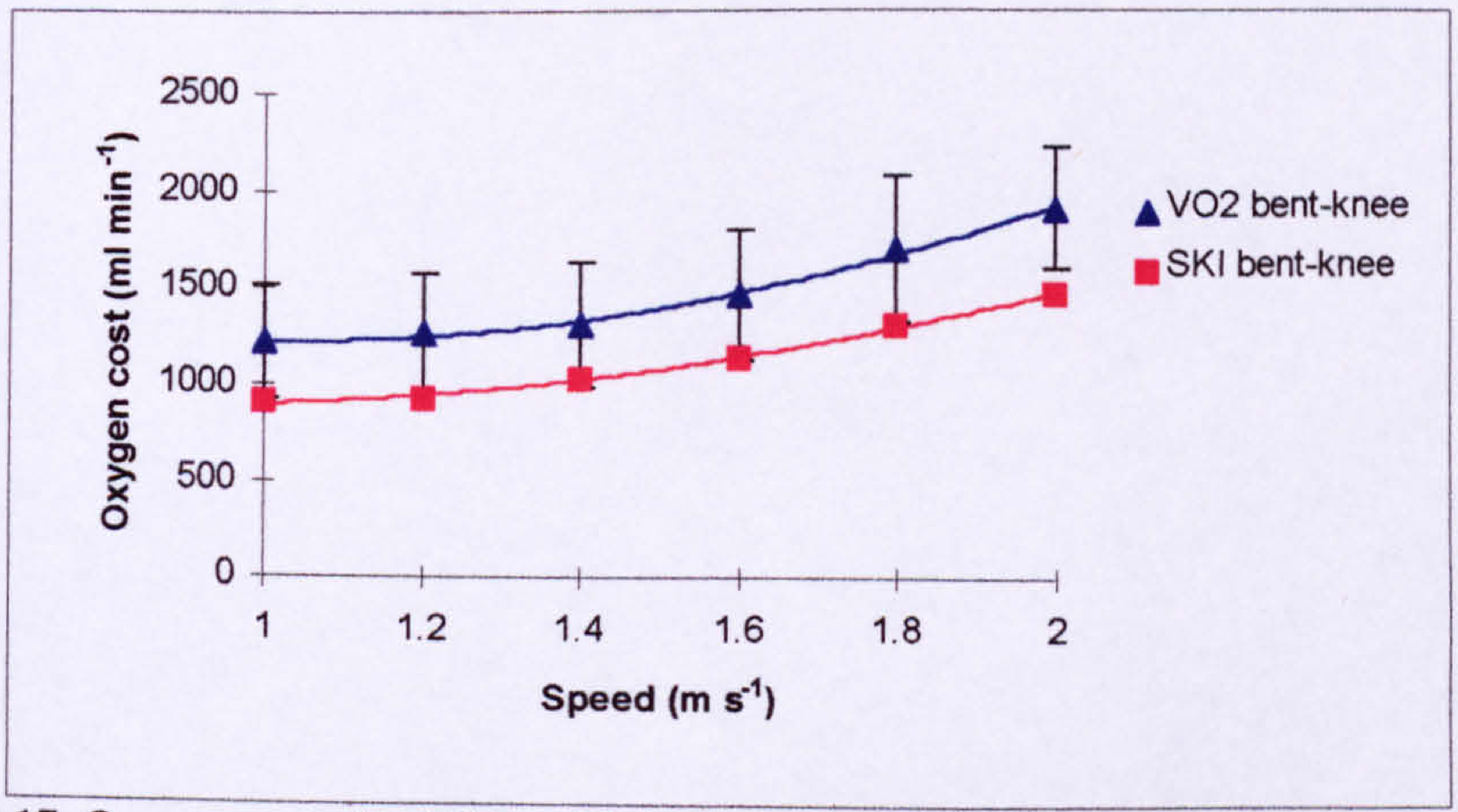


Figure 4.17 Oxygen cost of BHBK walking. Trained subject compared to 12 untrained subjects (average ± SD)

The oxygen cost during BHBK walking to the skier was lower than that for the untrained average, a difference that was statistically significant ($p<0.05$). However normal walking in the skier produced oxygen consumption data (Figure 4.16) which was also significantly lower ($p<0.05$) than the mean for untrained subjects. Other physiological variables measured during exercise for the trained subject are shown in the Appendix (Appendix IX, Figures AIX.1, 2). Heart rate increased substantially from normal exercising levels during exercise in the BHBK gait for the trained subject. Core temperature change was doubled during exercise in the BHBK posture when compared to normal walking in the trained subject (from a 0.2°C increase to a 0.4°C increase).

4.5.10 RQ values

RQ (the respiratory quotient) is the ratio of VO_2 to VCO_2, which is important in the conversion of energy cost to calorific value (see section 1.7.2), and can be used in the calculation of calories that subjects are using during exercise in each gait. Average data for RQ values are shown in the Appendix (Appendix VI, Figure VI.5). RQ values are higher in the BHBK posture, indicating a slightly different ratio of carbohydrate to fat during metabolism, but average RQ values are not significantly different between normal and BHBK walking. Values for normal walking range from 0.83 to 0.92 (average 0.87), while values for BHBK walking range from 0.82 to 0.94 (average 0.89). An RQ value of 0.82 is normal for a resting person metabolising a mixture of carbohydrate and fat. RQ values approaching 1.00 indicate a tendency towards anaerobic metabolism, but as values shown here are averaged between subjects and over three minutes at each speed, they will not reflect short periods of anaerobic metabolism.

4.5.11 Measured daily energy cost of locomotion

Using an equation from Montoye et al. (1996), kilocalories can be calculated from oxygen consumption data. Using the minimum energy cost of locomotion data from section 4.5.3, normal and BHBK energy costs (0.1 and 0.15 $L \cdot kg^{-1} \cdot km^{-1}$, respectively) can be converted to kilocalories using equation 4.3.

Heat production in kilocalories = VO_2 (3.9 + 1.1 RQ) **Equation 4.3**

∴ Normal walking = 0.1 (3.9 + (1.1 x 0.87))

= 0.49 $kcal\cdot kg^{-1}\cdot km^{-1}$

∴ BHBK walking = 0.15 (3.9 + (1.1 x 0.89))

= 0.73 $kcal\cdot kg^{-1}\cdot km^{-1}$

To work out the difference in energy cost for 'Lucy' walking distances similar to those published for distances walked by chimpanzees, it is necessary to multiply the value in kilocalories by predicted weight and distance walked. Values will represent minimum cost of walking since energy cost data were taken at minimum values. Assuming an average body weight of 37 kg (McHenry, 1992), and a daily walking distance of 3.9 km (Clutton-Brock and Harvey, 1977b), minimum total cost of daily walking in each posture is:

Normal walking = 0.49 x 37 x 3.9

= 70.7 kcal (296 kJ)

BHBK walking = 0.73 x 37 x 3.9

= 105.3 kcal (441 kJ)

It is evident that if a BHBK posture is used, estimated minimum costs of locomotion in 'Lucy' are 49% higher than normal walking.

4.5.12 Heat balance during exercise

Using data collected during normal and BHBK walking, thermal loads and heat exchange can be estimated.

According to the heat balance equation (Reilly and Cable, 1996):

$$HS = M \pm (R \pm Cv \pm Co) - E - W \qquad \textbf{Equation 4.4}$$

where HS is heat stored, M is metabolism, R is radiation, Cv is convection, Co is conduction, E is evaporation and W is Work. (all variables are in units $kJ \cdot m^{2} \cdot h^{-1}$)

Rearranging the main equation:

$$(R \pm Cv \pm Co) = HS - M + E + W \qquad \textbf{Equation 4.5}$$

where

$$HS = \frac{(\text{post } T_B - \text{pre } T_B) \text{x } 3.47 \text{ (kJ kg}^{-1} \text{ h}^{-1} \text{ x mass)}}{\text{Time (h) x BSA}} \qquad \textbf{Equation 4.6}$$

$$M = \frac{\dot{V}O_2 \text{ (l min}^{-1}\text{) x calorific equivalent x 60}}{\text{BSA}} \qquad \textbf{Equation 4.7}$$

$$E = \frac{\text{(pre-mass - post-mass) (kg) x 2430 (kJ L}^{-1} \text{ sweat loss)}}{\text{Time x BSA}} \qquad \textbf{Equation 4.8}$$

$$W = \frac{\text{work rate (kJ min}^{-1} \text{ x 60)}}{\text{BSA}} \qquad \textbf{Equation 4.9}$$

T_B = body temperature (T_B = 0.65x rectal temp. + 0.35 x skin temp.)
BSA = body surface area (BSA = $M^{0.425}$ x $H^{0.725}$ x 71.84 x 10^{-4})
Time = hours spent in exercise (0.48 hr)

All variables were calculated for each subject from data collected (see Appendix VIII). Since work rate cannot be quantified for level walking and was the same for each posture, a reference value of 600 kJ·hr^{-1}·m^{-1} was added (from level walking, in Fanger, 1970, p. 24). Data are shown with and without work, since accuracy of defined work is questionable. Average data are shown in Table 4.7.

Variable	Normal (mean ± SE)	BHBK (mean ± SE)
total VO_2	39.9 ± 1.8	55.4 ± 3.3
HS	4 ± 44.5	174 ± 50.8
M	516.6 ± 9.7	718.9 ± 27.7
E	588.4 ± 208.8	2001.6 ± 325.3
R ± Cv ± Co (-W)	75.83 ± 190.3	1456.8 ± 313.3
R ± Cv ± Co	675.83 ± 190.3	2056.8 ± 313.3

Table 4.7 Thermal balance during normal and BHBK walking. See Appendix VIII for full data. Variable names are as those in text equations 4.4 - 4.9

Statistically significant differences were found at the $p<0.01$ level, for all variables in the heat equation. BHBK walking therefore causes a significant increase in heat storage, metabolism and evaporation. The heat equation predicts that during normal walking the body gains an average 76 kJ·m^2·hr^{-1} of heat from the combined processes of radiation, convection and conduction. During BHBK walking, this is increased to 1457 kJ·m^2·hr^{-1} of heat gained during exercise. During BHBK walking all values for heat storage were positive, compared to normal walking where the majority of subjects lost heat rather than storing it during exercise.

4.6 Discussion and Conclusions

4.6.1 Energy cost of BHBK walking

Since the aerobic requirement of treadmill running has been shown not to differ significantly from that recorded during overland running (at approx. 4 $m \cdot s^{-1}$), it is assumed that the data presented in this chapter equates to normal overground walking on hard surfaces (Powers et al., 1983).

Oxygen cost

Common values in the literature for resting oxygen consumption are around 250 to 300 $ml \cdot min^{-1}$, or 3.5 to 4.5 $ml \cdot kg^{-1} \cdot min^{-1}$ (Fox, Bowers and Foss, 1993). Data for resting VE are in the region of 6 to 8 $L \cdot min^{-1}$.

Maximal values of oxygen consumption during normal walking in this study are in the region of 1.5 $L \cdot min^{-1}$, which corresponds to a moderate work rate as defined by Fox, Bowers and Foss (1993). During BHBK walking oxygen consumption increases to nearly 2.0 $L \cdot min^{-1}$, corresponding to a heavy work rate. Maximal values for VE during normal walking in this study are about 42 $L \cdot min^{-1}$, and about 60 $L \cdot min^{-1}$ for BHBK walking. According to data accumulated by Fox, Bowers and Foss (1993), the work rate obtained during normal walking in this study (determined from VE and lactate accumulation) would be classed as 'seasonal work'. A work rate such as this could be sustained for approximately eight hours daily for a few weeks. However, the work rate during BHBK walking, being much higher, could only be sustained for four hours, two or three times a week. This level of work rate is classified as 'special physical training' (Fox, Bowers and Foss, 1993).

'Economical' walking or running is defined by Cooke (1996b) as oxygen uptake per kilogram per minute for exercise on a treadmill at a given speed and slope. The higher the oxygen uptake, the lower the economy. According to this definition, BHBK walking is far more uneconomical than normal walking. Efficiency during BHBK walking cannot be determined precisely from this study, since it is necessary to have estimates of work done during exercise for the calculation (walking on the level without pulling a weight, for example, results in zero work being done {Cooke, 1996b}). However see Heart Rate (below) for an indication of efficiency from the Physiological Cost Index (PCI).

The standard error of the oxygen cost of exercise is slightly greater at all speeds in the BHBK posture (see section 4.5.3) than observed during normal walking. This is only to be expected since the 'new' alternate gait is very unfamiliar to the subjects, thus increasing diversity in the way subjects walk.

It is likely that the oxygen cost of BHBK walking is greater than during normal walking because the flexed joint postures increase muscle activity, and therefore metabolism during exercise (this is covered in more detail within Chapter Five). BHBK gait tends to increase the proportion of the stance phase in the gait cycle. Therefore, the BHBK gait becomes consequently more difficult when walking at higher speeds. The cost of the BHBK gait to humans does not, however seem to be as costly per unit weight as bipedal walking in chimpanzees (see Appendix II and section 1.5.8).

Extrapolation of the trend line to zero speed gives a rough estimate of the energy required to maintain a particular posture. The estimate normal, upright posture is 0 L·min-1, therefore revealing that this posture requires minimal energy. The estimate for the BHBK posture is 4.5 L·min-1, which is very high and approximately equal to the energy cost of very slow walking in normal posture (see Appendix XIII). It seems therefore that the BHBK standing posture is very energetically costly to humans.

Energy cost of locomotion

The data for the energy cost of locomotion (E_L) describe the cost per unit distance of both types of gait for all speeds tested. E_L is a good indicator of ability for long distance locomotion (Brisswalter, et al. 1996). Data collected from other sources (Low and Reed, 1996; Steudel, 1996) agree with the present data for normal walking, and indicate that the most economical speed for walking is between 1.2 and 1.45 $m\cdot s^{-1}$. During normal walking, the minimum cost of locomotion (per kilogram body weight, per kilometre) is around 0.1 $ml\cdot kg^{-1}\cdot km^{-1}$. This agrees with the predicted energy costs for a mammal the size of man (Taylor et al., 1970). E_L is higher during BHBK walking than in normal walking, with a minimum of 0.15 $ml\cdot kg^{-1}\cdot km^{-1}$.

An estimate of efficiency is also available from the E_L data. The speed where the minimum E_L occurs is the most efficient speed for that posture, and this occurs at a different speed for normal and BHBK walking. The more efficient speed is greater for BHBK walking. However, remembering that the data plotted are averaged over twelve subjects, the linear trend of the data may better indicate the general form of the results. The best fit straight lines through the averaged points converge at about 2.7 $m\cdot s^{-1}$, a speed that is not possible whilst walking; i.e. the energy cost of the different postures might be expected to converge in the running gait.

It has been revealed by Saibene and Minetti (1992) that metabolic factors are not the sole determinant for the speed at which the walking gait changes to a running gait. The speed at which costs for walking and running converge (about 1.9 m·s^{-1}) is not the speed at which the change in gait occurs. In fact the change of gait occurs at around 2.2 to 2.5 m·s^{-1}, and increase of 14 to 29 % in speed (Saibene and Minetti, 1992). We can assume from this that the speed at which BHBK walking will switch to BHBK running will be higher than that at which the cost is the same. The physiological cost index (PCI) might provide a clearer estimate of the speed at which a BHBK gait is equal in efficiency to normal walking.

It should be noted that running is not merely a simple progression of walking, it is an entirely different gait with very different mechanical characteristics (Low and Reed, 1996)

Measured daily energy cost of locomotion

Daily energy cost of locomotion was calculated at 0.49 kcal·kg^{-1}·km^{-1} for normal walking, and 0.73 kcal·kg^{-1}·km^{-1} for BHBK walking. This corresponds to an increase of 49% in the energy cost of locomotion if a BHBK posture was adopted. Real daily energy expenditure for locomotion is likely to be substantially higher than these estimates, since a hominid could not be assumed to walk at the optimum (most efficient) speed at all times.

Lactate

Lactate concentration in the blood in this study was measured at around 3.0 mMol·L^{-1} for normal walking and 6.0 mMol·L^{-1} for BHBK walking. Resting lactate levels (Noble and Robertson, 1996) are generally around 1.0 mMol·L^{-1}. It seems reasonable to assume therefore that normal levels will increase about threefold during normal submaximal exercise and nearer six-fold when a subject undertakes BHBK exercise.

The ability to produce high lactate levels in the blood is probably acquired through training and has been shown not to be sex related. Therefore, it is preferable to discuss blood lactate change as a percentage increase of lactate concentration in the blood, as the total muscle mass of individuals will affect the amount of lactate production during maximal effort (Avlonitou, 1996). The latter is evident in the current data, as there is a large variation (SE ≅ 20) in the percentage increase in lactate concentration between normal and BHBK walking after exercise. However, since lactate concentrations were not measured in resting subjects, a percentage increase from resting levels cannot legitimately be deduced. Using the resting lactate concentration provided by Noble and Robertson (1996), normal submaximal exercise produces three times resting lactate production, and BHBK walking produces six times the lactate production at resting levels. BHBK walking therefore caused a doubling in lactate production during this protocol.

Peak blood lactate concentrations for a given event tend to be an indicator of effort, as was shown in a swimming study by Avlonitou (1996). It is evident from the data that BHBK walking necessitates a substantially higher effort then normal walking. Blood lactate levels of around 4.0 mMol·L^{-1} are generally associated with high intensities of exercise. Levels of lactic acid production below 4.0 mMol·L^{-1} at elevated exercise intensities indicate the possibility for exercise endurance in the individual (Williams and Eston, 1996). From lactate concentrations recorded in the present study, it is evident that endurance walking would be possible in normal gait, but not in BHBK gait, since the latter produces lactate concentrations far in excess of 4.0 mMol·L^{-1} for high exercise intensities.

The results indicate that there is a greater participation of muscle fibres during BHBK walking, resulting in a higher production of lactate during exercise. Factors other than muscle activity, such as thermoregulation, blood flow changes or body position may be responsible for the production or removal of lactate (Tesch and Lindeburg, 1984). It is unwise, therefore, to discuss results from lactate production in isolation, and preferable to consider the data in combination with other physiological evidence. However, since we find a substantially greater energy cost associated with the increase in lactate production, it is reasonable to conclude that an increase in anaerobic metabolism is indeed taking place. Even if the anaerobic contribution to total energy requirement is small, the large difference in lactate production indicates that the BHBK walking requires either a higher contribution of isometric effort in the active muscles, or a larger muscle mass engaged in activity (Veicsteinas et al., 1992). Both of these events will lead to an earlier onset of fatigue in the muscle groups involved.

Data given in Low and Reed (1996) report that in maximal exercise for half an hour under normal conditions the body obtains 97 percent of its energy from aerobic sources, and the remaining 3 percent from anaerobic sources. If we assume that the current protocol produces similar results, then the doubling in lactate production might indicate that anaerobic contribution to exercise will rise to around 6-7 percent of the total energy required.

Heart Rate, RPE and PCI

The present study found that while normal exercise produced average maximal heart rates of around 125 beats·min^{-1}, BHBK walking produced an increase of about 25% in heart rate, so that average maximal heart rates during BHBK walking were around 150 beats·min^{-1}. Generally, resting heart rates are in the region of 70 to 80 beats·min^{-1} (Fox, Bowers and Foss, 1993)..

The standard error of the sample gives an indication of the variability in heart rate between individuals. Any difference due to variability in resting heart rates, or variability in individual responses to exercise will be apparent in the standard error of heart rate during normal walking. In this case, the standard error was only slightly greater during BHBK walking than normal walking. Therefore the variability in the response of a group of subjects with varying sex, age, height and weight is about the same in both postures. Females tend to show higher heart rates (and therefore RPE) than males for the same exercise rate (Noble and Robertson, 1996). This is apparent in data from the current study (see Appendix VI, Figure AVI.8, 9). It is important therefore to stress that physiological responses to BHBK posture are shown as an average of all subjects (including 6 males and 6 females).

It is evident from Figures 4.11 and 4.12 (in section 4.5.5) that there is a close relationship between heart rate and RPE for both postures (the slopes of the best fit lines are very similar). Estimation of heart rate from RPE thus seems possible from the current data, since an RPE of 10 corresponds to a heart rate of 100 beats·min^{-1} in both Figures 4.11 and 4.12. Since we can show a genuine relationship between heart rate and RPE, this validates the RPE data even if it was considered in isolation.

An increase of RPE by 2 values for every 1.7 $km{\cdot}h^{-1}$ (approx. 0.5 $m{\cdot}s^{-1}$) has been reported in the literature (Noble and Robertson, 1996). This effect also holds for the current data, during normal walking. RPE increases slightly more than 2 values every 0.5 $m{\cdot}s^{-1}$ for BHBK walking, confirming that with each increase in speed the subjects find BHBK walking comparably more difficult than normal walking.

It is interesting that heart rate during BHBK walking was significantly higher than normal walking in all speeds except for the fastest speed. It is likely that as normal walking becomes less 'efficient' at higher speeds, the fall in efficiency is reflected in heart rate and BHBK heart rate therefore begins to converge with normal levels. Indeed, the physiological cost index, which is a sensitive indicator of locomotor performance (Butler et al., 1984) reveals that normal and BHBK walking converge in efficiency at about 4.5 $m{\cdot}s^{-1}$. The efficiency of BHBK waking is therefore likely to be greater than normal walking at those speeds normally associated with running.

$\dot{V}O_{2max}$

Aerobic exercise programs are usually set at between 50 and 70% of maximal heart rate or $\dot{V}O_{2max}$. Similarly, BHBK walking induces oxygen consumption at 50 to 70% of $\dot{V}O_{2max}$ (Figure 4.15), but evidence from lactate concentration indicates that the exercise is not being fuelled exclusively by aerobic metabolism.

Training effect

The use of skiing as a training exercise for BHBK walking seemed to cause a reduction in the overall energy cost of exercise. The cost of BHBK to the trained subject was lower than for the untrained subjects, but it seems that this difference is simply due to the general training that skiing induces, therefore also reducing the energy cost of normal walking in the skier, compared to the untrained mean. Therefore this reduction in overall energy cost is seen as an individual effect, rather than an effect due to training BHBK. Tentative conclusions from this preliminary data regarding the effect of training on the cost of BHBK posture are that training does not reduce the energy cost of BHBK walking more than would be expected from general exercise training effects alone. More experiments to assess the effects of training on the cost of a BHBK posture would be desirable. Training which involves walking in the BHBK posture itself would provide more accurate data on the effect of training on the energy cost of BHBK walking.

4.6.2 Thermal cost of BHBK walking

Core temperatures increase by 0.7°C during BHBK walking, compared to an increase of only 0.3°C during normal submaximal exercise. The core temperature increase during exercise is thus 2.3 times (130%) higher during BHBK walking than the increase during normal walking. Oxygen cost indicates a 52% increase in metabolism, a substantially lower figure than the changes occurring in the core temperature data. This indicates that the increase in core temperature is higher than would be expected from the increase in metabolism alone. This could indicate that some locomotory muscles were performing eccentric contractions, therefore absorbing energy and resulting in excess heat storage within the body core. Core temperature remained elevated long after exercise ceased, indicating that a large amount of heat was stored during exercise in BHBK posture. It was estimated that a further 27 minutes of recovery time in addition to the 20 minutes already given would be needed for restoration of normal body temperature. Thus a total of 47 minutes is necessary for the body to restore normal body temperature after exercising in the BHBK posture for approximately 30 minutes.

Water balance

A decrease in body mass during exercise suggests that thermoregulation processes are leading to dehydration. A possible effect of dehydration on the energy cost of exercise must be assumed, but cannot be precisely evaluated without an actual measure of dehydration. During submaximal exercise in a normal upright posture the average fluid loss was 180 grams, but during BHBK walking, the fluid loss increases to 370 grams.

Heat balance

According to the heat balance equation (see equation 4.5), any discrepancy between heat gain and heat loss is reflected in heat storage. If the balance of the equation is positive, there is positive heat storage, and therefore an increase in core temperature (Stitt, 1993). Heat gain or loss by conduction can be ignored in most cases, unless the subject is in contact with warm or cold surfaces. Heat storage, estimated in section 4.5.12, indicates that the body stores approximately 4 $kJ \cdot m^2 \cdot h^{-1}$ during normal walking. This is increased to approximately 174 $kJ \cdot m^2 \cdot h^{-1}$ during BHBK walking. Total heat balance equations seem to suggest that the body gains an average 76 $kJ \cdot m^2 \cdot hr^{-1}$ of heat from the combined processes of radiation, convection and conduction, during normal walking (if work done is not taken into account, since it cannot be quantified). During BHBK walking, this is increased to 1457 $kJ \cdot m^2 \cdot hr^{-1}$ of heat gained during exercise.

Under normal circumstances exercise is the condition which imposes maximal strain on the thermoregulatory system (Nadel, 1977). In order to maintain thermal balance, an exercising subject has to cope with the double challenge of heat loads from metabolism and from the environment (Werner, 1993). Evaporation of sweat from the skin surface is a major avenue of heat of heat loss in an exercising subject (Mitchell, 1977). Once the core temperature reaches a critical level, the sweating response is stimulated. This critical level is dependant on many factors, including environmental temperature, wind speed, solar radiation and clothing. At higher ambient temperatures, conduction, convection and radiation become less important and evaporative sweating becomes more important in loss of heat from an exercising body (Werner, 1993). At high humidities, however, evaporation of sweat from the skin becomes more difficult, and therefore reduces one of the major avenues of heat dissipation from the body. Exercising in high ambient temperatures with high humidity will cause intense thermal stress to the individual. When high ambient temperatures and high humidity prevent the dissipation of heat during exercise, even highly trained and heat acclimatised individuals risk heat injury when exercising for only a short time (Werner, 1993).

This study confirms that BHBK walking causes a significant increase in energy cost and serious thermal stress, across a wide range of subjects, when compared to normal walking. The combined effect of locomotion in a BHBK posture along with high ambient temperatures will be discussed in more detail in Chapter 6, with reference to the evolution of bipedalism in early hominids.

CHAPTER FIVE

ELECTROMYOGRAPHY

"It is not possible to forecast the exact phase of activity in a muscle during walking by only examining it through artificial tests of prime movers"

(Basmajian, 1978)

5.1 Introduction

The cost of a BHBK posture has so far been evaluated mainly from the aspect of energy consumption. Since the posture causes an increase in energy costs compared to normal walking, and cost of exercise may depend on the relative number of muscle fibres that are recruited (see section 1.9), attention will now be paid to the pattern of force production in some of the muscles concerned with walking. In particular it tests whether the duration and intensity of muscles increases during BHBK walking and whether co-contraction of biarticular muscles support energy transfer between joints, which may to some extent offset the mechanical problems of BHBK walking.

Electromyography or EMG is the study of muscular function through the measurement of electrical signals produced in association with muscle contraction. Studies in locomotor activity commonly require information describing the timing and magnitude of muscle contractions during anatomical movements: EMG provides this data. EMG is used increasingly in diverse fields such as neurology, neurophysiology, neurosurgery, bioengineering, functional electrical stimulation, orthopaedics, rehabilitation, ergonomics and occupational biomechanics, zoology, physical therapy, sports medicine and sports science (Clarys, J.P. 1993). A specialised area of EMG has been developed, which aims to analyse the function and co-ordination of muscles during selected movements and postures. This is usually called 'kinesiological EMG'. The areas of most relevance to this study are the evaluation of functional anatomical muscle activity, synchronisation studies of antagonistic muscles and normal muscle function during different postures. Surface and needle electrodes are the two major types of electrode used but surface electrodes are more often used in kinesiological EMG studies (see section below - recording the EMG).

The neuromuscular system

Electromyography records the changes in electrical potential occurring in a muscle when it contracts, after stimulation by a motor nerve impulse. It is the only method of assessing when a muscle is active, and is often used to detect the activity and timing of the major muscle groups during a specific activity. Nerve impulses cause all the muscle fibres of a motor unit to contract. Stimulation of a muscle fibre at the motor end-plate results in a reduction in electrical potential of the cell followed by the spread of the action potential through the muscle fibre. The depolarisation wave which spreads across the muscle fibre is the motor action potential (MAP). The MAP radiates along the muscle fibre from the motor end-plate and generates and electrical field around the muscle fibres. A recording electrode detects this potential or voltage on activation of the muscle fibres.

Muscle fibres never contract alone, but in small groups called motor units. The muscle fibres within the motor unit innervated by the same axon contract almost simultaneously. Therefore, in surface EMG, the signal is a representation of the action potentials coming from multiple motor units at one time.

Recording the EMG

There are several different types of recording electrode: indwelling needle (or fine wire) electrodes, active surface electrodes and passive surface electrodes. Needle electrodes are not commonly used in kinesiological studies although they are necessary for recording activity of deep muscles. They consist of a pair of alloy wires, the diameter of a human hair, which are inserted directly into the muscle of interest. They tend to be more accurate than surface electrodes when data from one particular muscle is required, but they are invasive and have many limitations to their usage.

Surface electrodes are mainly used for large groups of muscles and are not suitable for deep muscles. 'Cross-talk' can be a problem, caused by interference of EMG signals from neighbouring muscles but is only usually a serious problem at low activation levels. 'Cross-talk' can be minimised by careful electrode placement. A smaller separation distance between the two electrodes increases the probability of recording from the correct muscle. Active surface electrodes have only recently been available commercially and therefore are not yet used commonly. Bipolar active electrodes can overcome some electrical problems (such as high input impedance) seen in passive electrodes and also have the advantage that there is no need for skin preparation (Burden and Bartlett, 1997). However they have some disadvantages: in the need for a power supply to the electrodes; possible health and safety problems, and an increase in overall noise in the EMG signal. Passive surface electrodes overall are safer, easier to use, more acceptable to the subject and provide a good degree of quantitative repeatability in comparison with needle electrodes (Burden and Bartlett, 1997).

Passive surface electrodes, usually composed of silver-silver chloride, are placed upon the skin in conjunction with conducting gels. They are easy to apply, give little discomfort to the subject, are readily available and require only a brief training period for the user.

Before researchers begin work with EMG, according to Clarys and Cabri (1993), they must possess a basic understanding of both fundamental electrophysiology and anatomical kinesiology. Therefore the next section is devoted to accumulated knowledge concerning the functions of the major muscle groups in the lower limb, with a brief description of the major phases of activity in those muscle groups (mostly drawn from the classic work by Basmajian [1978] and Whittle's text [1991]).

The hamstring group is known to contract at the end of flexion and during early extension of the thigh, preventing flexion of the thigh before the heel touches the ground. The hamstrings also contract a second time in the gait cycle, during the end of support, to assist in the movement of the body over the supporting limb, and possibly to prevent hip flexion. They also act to decelerate the leg prior to heel strike and act simultaneously with the quadriceps to stabilise the knee during the stance phase (Lange et al., 1996).

The quadriceps femoris group contracts as extension of the knee is being completed. The quadriceps continues to act during the early part of the supporting phase, (when the knee is flexed and the centre of gravity falls behind it). Quadriceps activity also occurs at the end of the supporting phase to fix the knee in extension, probably counteracting the tendency towards flexion initiated by the gastrocnemius.

The calf muscles (triceps surae) display peak activity when the knee, in extending, stretches the gastrocnemius across the back of the joint, thereby helping the calf muscles (as a group) lift the heel (plantar flexion). Plantar flexion has been defined as the most essential action for producing push-off and thrust within the normal walking cycle (Basmajian, 1978).

Muscle activity within a selected group of muscles was recorded in this study, in an attempt to illustrate where the increased energy cost of BHBK locomotion arises. The muscles tested were restricted to the relatively large superficial muscles of the lower limb, comprising: rectus femoris, biceps femoris, tibialis anterior and gastrocnemius. The major functions of these large surface muscles are discussed below, with reference to their points of origin and insertion.

Rectus femoris (Figure 5.1) is one of the two-joint (biarticular) muscles in the lower limb. It is a flexor of the hip and extensor of the knee joint. The whole muscle is believed to contract even during isolated movements of the knee or hip. Rectus femoris (RF) is not active in hip flexion accompanied by knee flexion (due to antagonistic inhibition of reciprocal innervation). It also functions as a lateral (but not a medial) rotator and aids in abduction of the thigh. RF shows slight biphasic activity during moderate walking (and sometimes triphasic activity, depending on cadence {step frequency}). RF arises from the anterior inferior iliac spine and the adjacent part of the acetabulum. It inserts (via a tendon) into the patella, and is anchored to the tibial tuberosity by the patellar ligament. RF is the only muscle of the quadriceps group that originates on the pelvis, and therefore is able to flex the thigh at the hip.

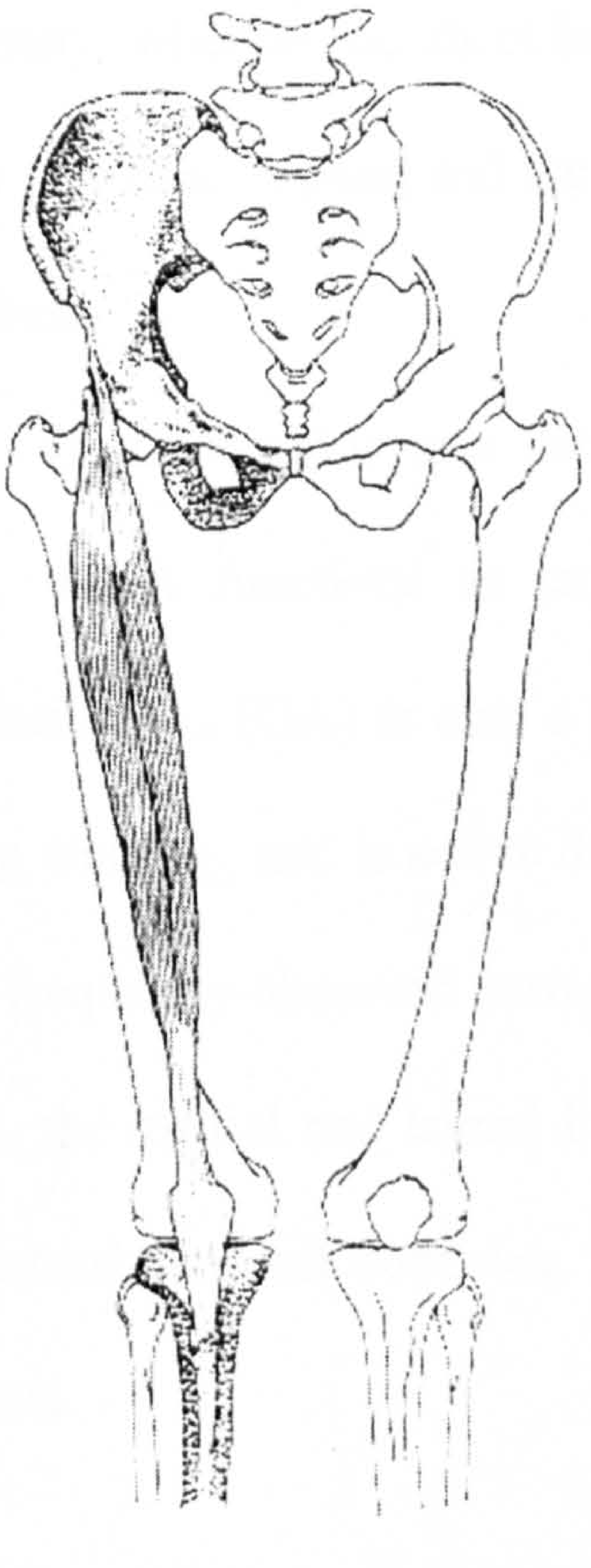


Figure 5.1 Anterior view of the hip, thigh and leg showing Rectus Femoris (RF) of the quadriceps group.

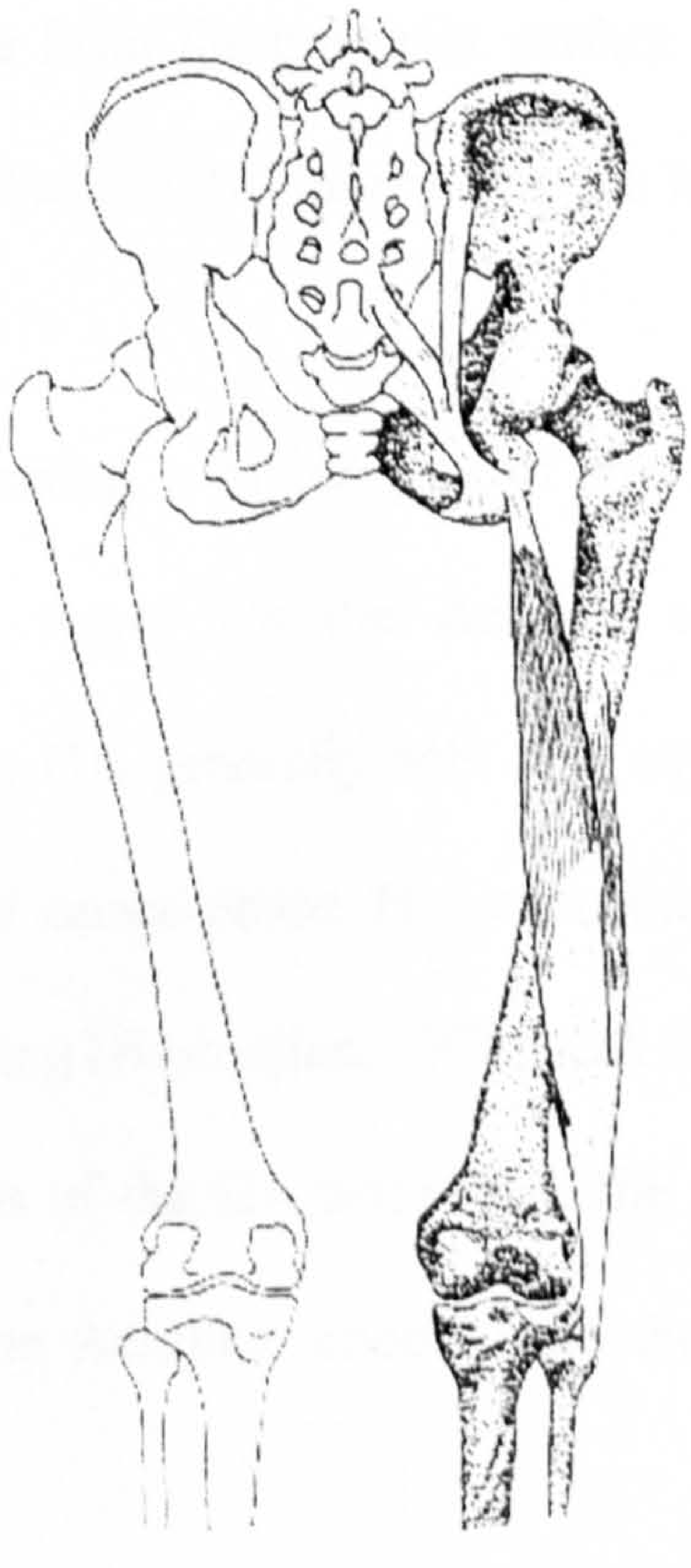


Figure 5.2 Posterior view of the hip and thigh, showing Biceps Femoris (BF) of the hamstrings group.

Biceps femoris (Figure 5.2) is also a two joint muscle. It is active in extension of the hip joint, and in flexion and lateral rotation of the knee. Biceps femoris (BF) is also active in lateral extension of the extended hip, and in adduction of the abducted hip against resistance. BF has two heads, the short and the long head. Although both heads act synchronously during flexion, the short head acts during the swing phase of walking, while the long head acts as a stabiliser when the foot is on the ground. Basmajian (1978) found that in the long head a biphasic pattern changes to a triphasic one with an increase in walking speed. The BF long head (LH) arises on the ischial tuberosity, whereas the short head (SH) originates from the posterior surface of the femur (the linea aspera) and the lateral supracondylar line. BF inserts into the head of the fibula.

Gastrocnemius is a two-joint muscle, forming a major part of the triceps surae, which functions as an auxiliary plantar flexor via the Achilles tendon. Gastrocnemius (GA) is also a flexor of the knee. GA generally acts as a stabiliser during walking, and is active during the middle of stance phase. However, there is a burst frequently observed during the middle of swing (Basmajian, 1978). GA has two heads, the medial and lateral head. The two heads of the GA arise from the medial and lateral femoral condyles. GA inserts (via the Achilles tendon) into the tuber calcanei.

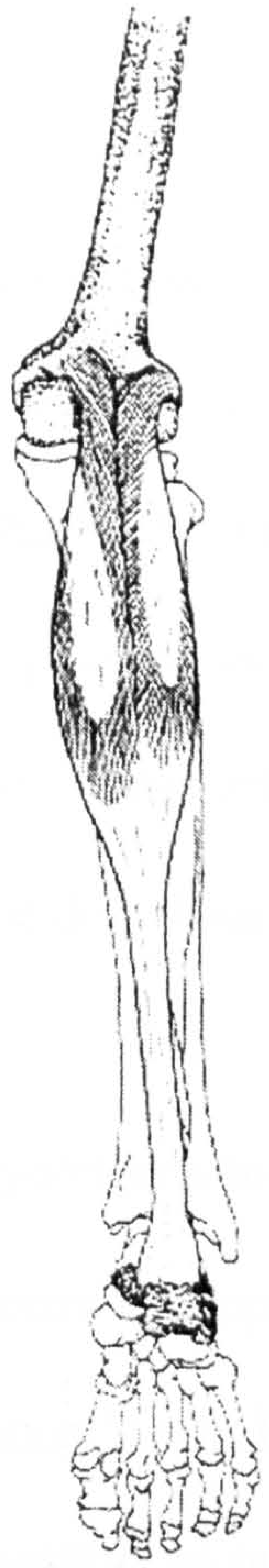


Figure 5.3 Posterior view of the leg showing Gastrocnemius (GA) of the calf group

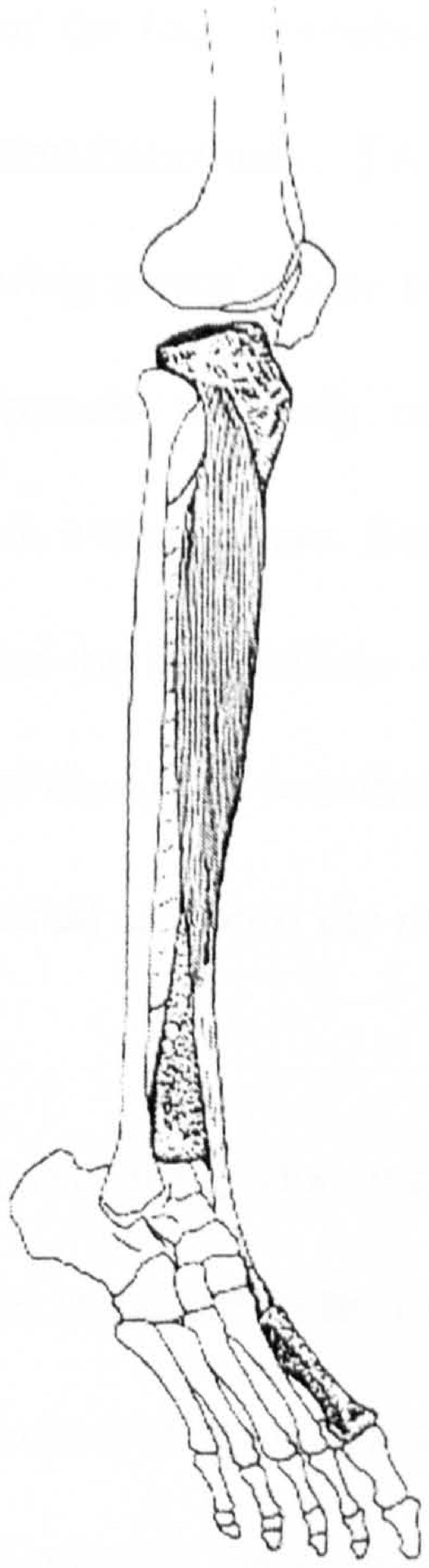


Figure 5.4 Anterolateral view of leg showing Tibialis Anterior (TA)

Tibialis anterior (TA) is a dorsiflexor of the foot. Variable activity is noticed during inversion when dorsiflexion occurs simultaneously. TA is strongly active during forced eversion. It is mainly active during swing phase to provide adequate clearance of foot from the ground. TA represents the only one of the muscles involved in this study that contracts strongly in swing phase. Early in stance phase TA shows a peak of activity, therefore it acts as a stabiliser during stance. TA originates from a large area on the lateral side of the upper two-thirds of the tibia, and inserts onto the dorsal surface of the first metatarsal and onto the medial cuneiform.

The hypothesis tested in the following section is that walking in a posture with flexed knees and hips (BHBK) will require intensive muscular activity. Since a change to a flexed hip or knee posture evokes increased muscle activity even in order to maintain equilibrium in a standing posture (Kummer, 1991), muscle activity levels should rise, and a general increase in muscle stress should be apparent while walking BHBK.

5.2 Relevant Work

General patterns of muscle activity in humans

General patterns of activity in the major muscle groups have been described by Whittle (1991). Figure 5.5 shows the typical muscle activity patterns of some major muscle groups during normal walking. Although this shows a typical pattern it is not the only possible pattern, and 'normal' patterns of gait differ between individuals.

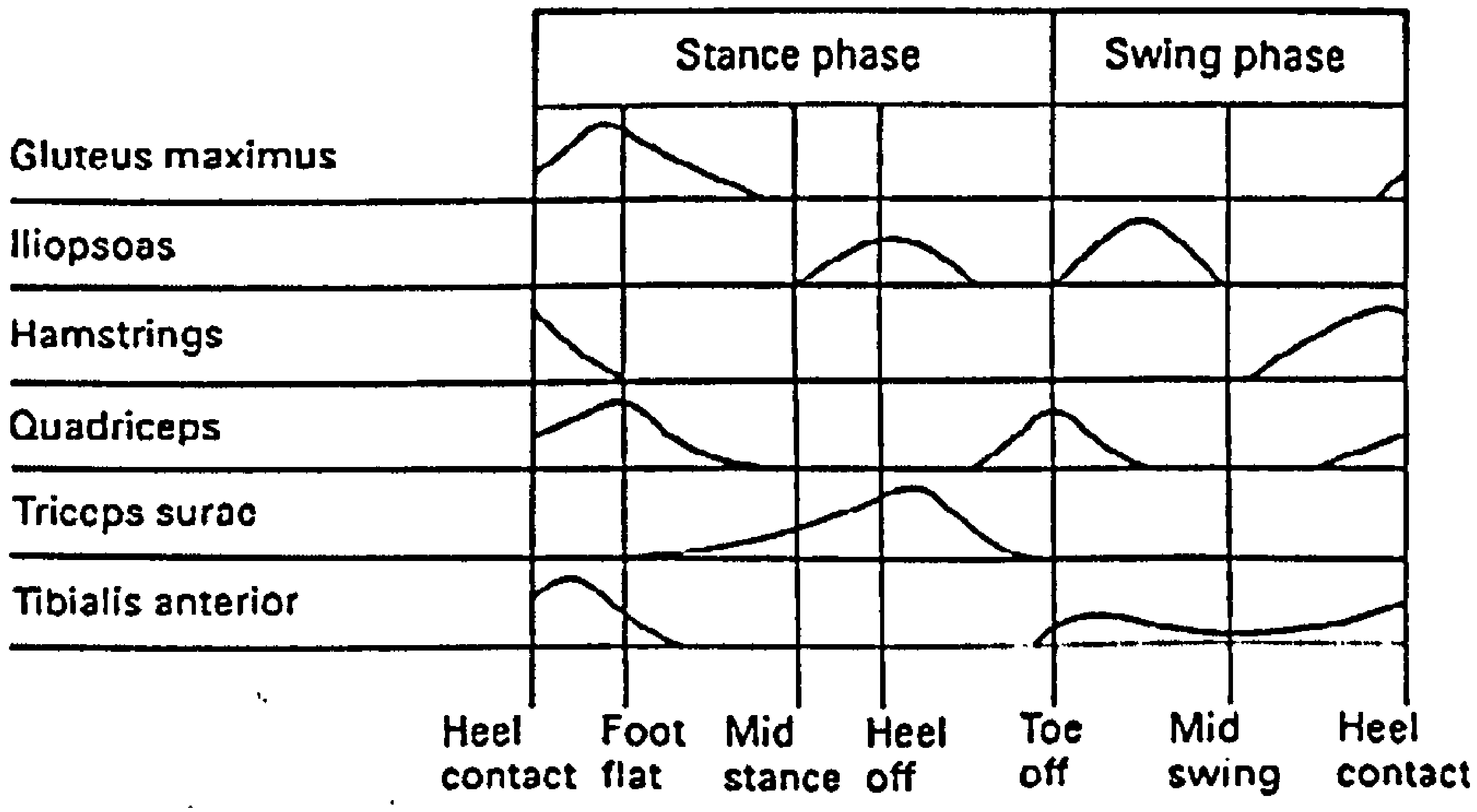


Figure 5.5 Typical activity patterns of some major muscle groups during the gait cycle. From Whittle (1991)

5.2.1 Postural standing

Very few studies have been specially designed to demonstrate the effect a particular posture has on muscle activity. One such study, (Okada, 1972), measured the effect of standing, half-rising and sitting postures on the electromyographic activity of various muscles of the trunk and lower limb in humans. Five adult males served as subjects, each of whom assumed all postures. The results of specific interest to this study are the activity differences between normal and half-rising postures. Two half-rising postures were maintained, a moderate half-rise and a deep half-rise, both of which had two variations;

a) straight with flexed knees and hips, and
b) forward bending with flexed knees and hips.

The posture closest to the one used in the present experimental study is the straight deep half-rise. Normal posture (i.e. standing upright, or at ease) elicited only negligible activity in all muscles. Muscle activity in the leg muscles and the trunk was found to be above a moderate level in both the straight and forward bending postures. Activity in the quadriceps was markedly higher than in normal posture, i.e. 15 - 30% of maximal contraction during moderate to deep half-rise postures. Activity in the biceps femoris (BF) was similar to that for the quadriceps. Tibialis anterior (TA) displayed high levels of activity (50%) during deep half-rise, but diminished (to 25%) on forward bending. Activity in the gastrocnemius (GA) increased from 2-3% for moderate half-rise to above 5% for deep half-rise. Forward bending increased this activity to 10% and above for GA in moderate half-rise and deep half-rise. The vasti muscles (vastus medialis and vastus lateralis) also displayed an increase in activity during half rise especially during deep half-rise, in which the activity of vastus lateralis increased to 45%. On forward bending activity in vastus lateralis disappeared, but stayed consistent in vastus medialis. Soleus (SL) activity was reduced during moderate half-rise and deep half-rise, but increased to normal levels with forward bending. Other activity increases were observed particularly in erector spinae (ES) during deep half-rise.

5.2.2 Bipedal walking

Ishida (1991) represents the only study located in the literature concerning estimated muscle forces and power for humans walking in flexed joint postures. Ishida's study used computer and biomechanical modelling to estimate the effect of a flexed joint posture on the energy expenditure of human walking. It also went on to compare costs to those in bipedal walking in some non-human primates. Muscle forces in the hip joint extensors (gluteus maximus) and knee joint extensors (vastus group) modelled in Ishida's study were higher than in normal walking. Muscle power in flexed joint walking was three times that of normal walking during the first quarter of stance phase. Flexed joint walking accrued an average of 216% increase in energy expenditure over that during normal walking.

EMG in bipedal walking non-human primates

Electromyographic data for bipedal walking generally differs between humans and other primates (Ishida et al., 1974). Humans exhibit very little muscular activity during one stride, whereas in bipedal walking non-human primates, there is strong activity in most muscles during the stance phase. Human bipedalism is characterised by a brief contraction of the hip and thigh muscles followed by a delayed action of the gastrocnemius. Chimpanzees, however, display sustained simultaneous contraction of hip and thigh muscles with a delayed activity in the gastrocnemius (Ishida et al., 1974).

A study by Ishida et al. (1985) compared primate bipedalism to human bipedalism. The number of human subjects who participated in this study was not reported, and it was not clear at what speed the human subjects were required to walk at, or indeed if the speed was constant for all subjects. Non-human primates tested in this study were trained for bipedal walking prior to testing for 2 to 6 years. Ishida et al. (1985) showed that training a Japanese monkey in bipedal walking prior to testing (and therefore producing a much more upright posture during gait) results in a 68% reduction in energy expenditure.

Data for EMG were presented in the raw form in the study by Ishida and colleagues (1985), and therefore it is difficult to use these data for comparison with other studies. Reference to this work is therefore only made for the specific muscle studies that provide results which are directly comparable with the present data. Bipedal walking observed in trained non-human primates was divided into three categories in this study: chimpanzee type, gibbon-spider monkey type and Japanese macaque-hamadryas baboon type. The chimpanzee-type is characterised by peaks in the activity of the calf muscles during the first and the last parts of the stance phase. The Japanese macaque-hamadryas group were characterised by a peak in calf muscle activity in the middle of the stance phase. The major differences seen in the calf muscle activities were attributed to the varying natural locomotor modes in each group, and the function of the calf muscles in aiding different propulsive mechanisms in the different groups. Specifically for the chimpanzee, Ishida et al. (1985) report that biceps femoris contracts strongly before heel contact. Tibialis anterior and gastrocnemius lateralis showed some slight and simultaneous activity before heel strike. Just after heel contact, gluteus maximus became highly active, simultaneous to activity of biceps femoris. At the middle of stance, vastus lateralis and gastrocnemius became simultaneously active at high levels of activity. Gluteus medius was active throughout stance. During the swing phase, only tibialis anterior was active.

5.3 Materials and Methods

5.3.1 Subjects, muscles and gait

Four normal, healthy volunteers gave their consent to perform in this study. Two males and two females of about average stature (≈ 1.60 m for females, and ≈ 1.8 m for males), and of average fitness, were used to represent a normal population. Each subject was given time to acclimatise to treadmill walking prior to the start of testing, which always amounted to more than three minutes (see section 4.4.1).

Subjects walked at 3 speeds on a motorised treadmill (Powerjog G200, Sports Engineering Ltd) in both normal and BHBK postures. Speeds were determined by asking both subjects of each sex to each select slow, medium and fast speeds from the whole range of normal walking speeds. The average speed for each sex was then used in testing with EMG. It was necessary to check that BHBK walking was still possible at the highest speed before the speeds were finalised. The speeds obtained were 4, 5 and 6 $km \cdot h^{-1}$ for females and 4, 6 and 7 $km \cdot h^{-1}$ for males. It was deemed necessary to have a different range of speeds for males and females, as the females (with a smaller stride length) found it almost impossible to walk at 7 $km \cdot h^{-1}$, however males (with larger stride lengths than females) selected 6 $km \cdot h^{-1}$ as a medium speed. The correlation between speed in $m \cdot s^{-1}$ and $km \cdot h^{-1}$ is shown in Table AV.1 (see Appendix V) for comparison with data from the Chapter 4.

Muscle activity was tested using bipolar silver-silver-chloride electrodes filled with electrode gel. Areas for attachment of electrodes were prepared (as recommended by Clarys and Cabri, 1993) by shaving the skin, roughing the surface with sandpaper, and finally applying alcohol wipes. The sandpaper serves to reduce the resistance of the skin, and the alcohol removes any traces of grease to ensure a good connection between the electrode and the surface of the skin. A study by Dawson (1996), confirmed that there are no significant asymmetries between the left and right leg during walking and running, barefoot or shod. A bilateral symmetry of gait was therefore assumed and so muscle activity data was taken for the right leg only.

EMG data was collected using an 8 channel biomedical telemetry receiver system (MTR8, MIE Medical Research Ltd). The use of a telemetry system allowed the subject to walk as naturally as possible without interference of trailing wires. 2000 samples were recorded at a frequency of 1000 hertz, at 0.4 volts, which produced 2 seconds of data. For both postures and all speeds of walking this amount of time was sufficient to record one full stride. Three strides were recorded as soon as the subject was comfortable in that walking speed on the treadmill. Arsenault et al. (1986) reported that three strides of EMG data provides as much information as twelve strides, therefore three strides of data are deemed sufficient for averaging and analysis in the current study. See Figure 5.6 for a summary of EMG methodology.

Goniometry was used to measure the joint angles in order to gauge where the gait cycle begins and ends (see section 1.5.3). The beginning of the gait cycle is determined as heel strike. This point can be estimated by measuring knee angle, and determining the point of maximal extension (after that for maximal flexion) which occurred just prior to heel strike. In this study the goniometer was set up to measure movement in the sagittal plane only. The axis of the goniometer was placed over the axis of the joint, in this case, the knee joint. The arms of the goniometer are placed parallel to the mid-line of the limb segment (see Figure 1.9, p37). The placement of the goniometer was reproduced as exactly as possible for each subject in order to achieve maximum reliability of results. The goniometer was calibrated both before and after each testing session to ensure reliability of measurements, as the alignment of the goniometer can vary over time (Winter, 1990). Knee angles of 0° and 90° were used in calibration of the goniometer.

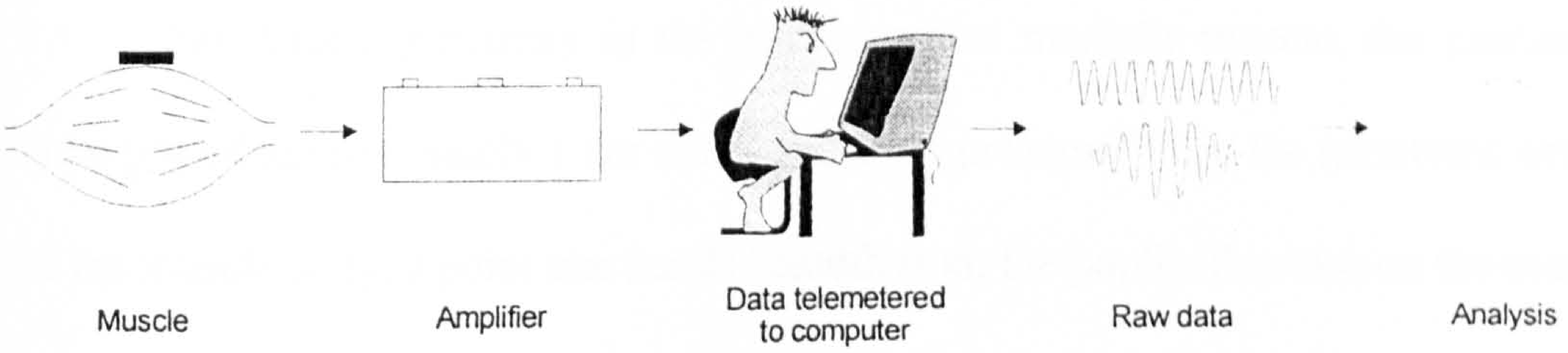


Figure 5.6 Methodology of EMG data collection. Muscle activity is collected by electrodes, and passed through an amplifier before being telemetered to a computer. The raw data was then analysed to produce full-wave rectified waveforms.

Muscles tested

As indicated in Section 5.1, so as to avoid cross-talk from neighbouring muscles as far as possible, the muscles tested were restricted to the relatively large superficial muscles of the lower limb: rectus femoris; biceps femoris (long head); tibialis anterior; gastrocnemius (medial head). See section 5.1 for details of the anatomy and function of each muscle tested.

5.3.2 Data collection

For recording activity in each muscle, a pair of electrodes were placed superficial to each muscle about 2 cm apart on the geometric centre of each muscle belly, with the detection surface acting along the length of the corresponding muscle fibres (as recommended by Basmajian, 1978). A third, grounding electrode was placed on any convenient bony point. The third electrode is necessary for the recording of an inactive site for comparison with the two recording electrodes. Bony projections situated close to the site of testing but as far away from the recording electrodes as the connecting wire would allow were selected for grounding sites (Electrodes were usually placed on the condyles of the femora and tibia around the knee, or the medial and lateral malleoli around the ankle). These were prepared in exactly the same way as the skin over the muscles.

For detecting activity in the gastrocnemius medialis muscle, the electrodes were placed approximately 1 cm distal and 1 cm proximal from the geometric centre of the muscle belly, a point one hands breadth from the popliteal crease on the medial mass of the calf. The third earth electrode was placed on a bony point at the proximal end of the gastrocnemius

For tibialis anterior, the electrodes were placed approximately 1 cm distal and proximal to the geometric centre of the muscle belly, a point four fingers width distal from the tibial tuberosity and one fingers breadth lateral to the tibial crest.

For biceps femoris, the electrodes were placed approximately 1 cm distal and proximal from the geometric centre of the muscle belly, at the midpoint of a line between the head of the fibula and the ischial tuberosity.

For rectus femoris, the electrodes were placed approximately 1 cm distal and proximal from the geometric centre of the muscle belly, a point on the anterior aspect of the thigh, midway between the superior border of the patella and the anterior superior iliac spine.

All electrodes and their connecting wires were securely fastened to the subjects leg with electrical tape. To reduce excess movement in the cables and to reduce low frequency noise, specially made wraparound cuffs were used to hold all the wires still.

Maximum voluntary contractions

Maximal voluntary contractions (MVCs) were used to estimate the relative muscular activity of individual muscles. This was necessary to compare data between subjects, and separate testing days, as individual data for muscle activity levels varies widely. The maximal level of postural isometric activity was used as the maximum to which all EMG data are compared. The average EMG output could then be converted to a percentage ratio to compare between subjects.

Each muscle was tested during isometric contraction, while exerting the muscle maximally. The methods employed are commonly used in electromyography testing to produce maximal contractions in the muscles involved (Yang and Winter; 1983, 1984). The isometric contraction with maximal effort was made for every muscle tested, at the end of each experimental session. MVCs were measured during the following procedures (all performed whilst sitting on a chair, with the knee flexed, femur at right angles to tibia):

RF - extending the knee joint against resistance (a wall)

BF - flexing the knee joint against resistance (chair leg)

GA - plantar flexion of the ankle joint against resistance

TA - dorsiflexion of the ankle joint against resistance

In each case the maximum exertion was produced for about 5 seconds against a fixed resistance with the appropriate position for each contraction held constant. EMG measurements were made three times so that an average could be calculated, and each isometric contraction was separated by at least three minutes to allow for recovery from possible fatigue in the muscle. Each subject was given verbal encouragement during the contraction in order to attain a maximal value. Since both normal and BHBK walking were undertaken during the same experimental session, one average MVC is used for both normal and BHBK walking, allowing direct comparison of activity levels between the alternate gaits. Data for average MVC is given in Table 5.1.

5.3.3 Initial processing and analysis of EMG data

The raw data is produced in the form of sets of positive and negative voltage spikes plotted against time. The signal was processed before analysis to produce a relatively smooth trace of entirely positive data, in which the height represents the amount of muscle activity occurring. The following stages of processing were applied to the data before analysis:

i) Filtering with a high-pass filter to remove low frequency signals including movement artifacts
ii) Full-wave rectification, so that positive and negative waves do not cancel each other out, but instead produce a simple curve increasing only in one direction
iii) Filtering using a low-pass filter to smooth out the data, removing spikes to produce a moving average of the data points. This is usually called 'enveloping' the data.

iv) High pass filtering and smoothing of goniometer data.

v) Splitting the data into single strides, from heel strike to subsequent heel strike.

vi) Normalising the time data to give a percentage of gait cycle for comparison

vii) Normalising the voltage data to give a percentage of MVC for comparison

Appropriate filtering is essential especially at the first stage, as the use of a cut-off frequency that is too high can lead to the loss of valid EMG data, by erasing low frequency data as if it were 'noise'.

5.4 Results

5.4.1 MVC

Data obtained for maximal voluntary contraction is displayed in Table 5.1. The data is presented as the average of three recordings taken for each muscle. As differences of electrode placement between subjects and between tests cannot be avoided completely, variability between tests is high. For this reason data was calculated to percent MVC for each individual test, therefore minimising inaccuracy of the data. Percent of maximal voluntary contraction is therefore used as the parameter for comparison to data from other sources, and for comparisons between muscles. The EMG data on its own is not directly comparable.

Subject	Tibialis anterior	Rectus femoris	Biceps femoris	Gastrocnemius
1	0.4	0.4	0.25	0.25
2	0.2	0.3	0.4	0.1
3	0.18	0.13	0.27	0.4
4	0.6	0.45	0.6	0.35

Table 5.1 Data obtained for maximal voluntary contractions for each subject (volts).

The goniometer data was used to estimate phases of the gait cycle. Goniometer data shows the knee angle against percentage of gait cycle (Figures AVII.1, 2). For an example of hip, knee and ankle angles during normal walking, see Figure 1.8 (p35), and for an example of hip, knee and ankle angles during BHBK walking, see Figure AVII.3 (Appendix VII). During BHBK walking the knee angles shows some distinguishing features when compared to normal walking. As the hips and knees are significantly flexed during BHBK walking, the knee angle is greater than during normal walking over a large percentage of the gait cycle.

5.4.2 EMG during normal walking

Data obtained during telemetered electromyography of normal walking is shown in Figure 5.7(a-c). Raw data was high pass filtered, full-wave rectified and enveloped (see methods, section 5.3.3). The whole gait cycle is represented, as the raw data is selected from one heel strike to the next, of the right foot. Data was normalised by calculating it as a percentage of maximal voluntary contraction (percent MVC). EMG data is presented as the average for four subjects ± standard deviation to give an idea of variation between subjects.

The muscle activity patterns can be seen to be relatively consistent between subjects. In some cases a high standard deviation caused the data to deviate below the zero on the y-axis (% of MVC). Data is presented for each muscle individually, at three speeds. In the data description below, the activity levels are split up into three categories: low, moderate and high activity, defined on the basis of the whole data set. Low activity is defined as 10 to 20 percent of maximal voluntary contraction, moderate activity as 20 to 40% MVC, and high activity as 40 to 60% MVC.

Slow speed

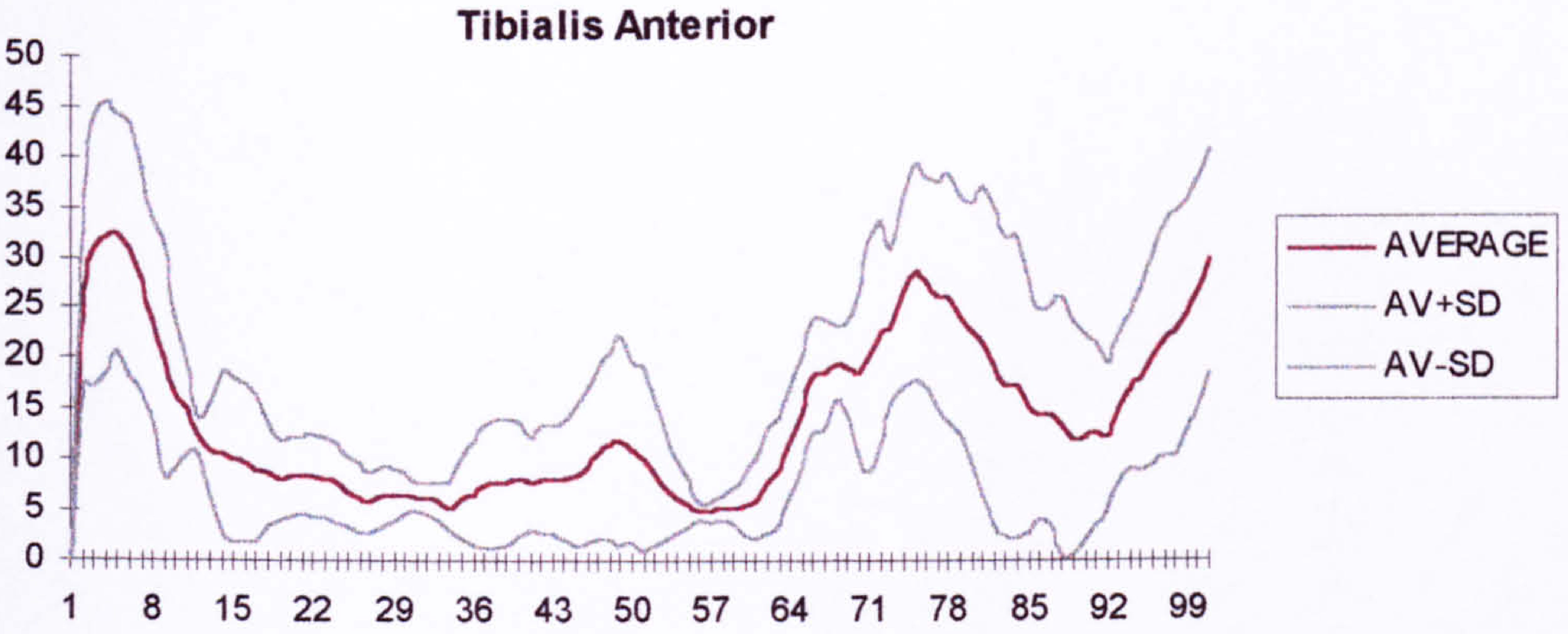
Before heel contact, tibialis anterior (TA) and biceps femoris (BF) showed moderate activity, while rectus femoris (RF) displayed low activity and gastrocnemius (GA) was not active (see Figure 5.7a for details). During the beginning of stance, tibialis anterior showed increased activity for a short time and then fell inactive. RF and BF also showed increased activity for a short time during the beginning of stance, simultaneous to TA activity. GA was moderately active during mid stance to about the end of stance. TA, along with RF and BF showed slight activity at the end of stance, just before toe-off. RF, BF and GA fell silent from the end of the stance phase into the swing phase. TA, however, increased activity into the swing phase, and continued moderate to high activity throughout the swing phase. BF became moderately active during the end of stance, and continued activity through to the next heel strike.

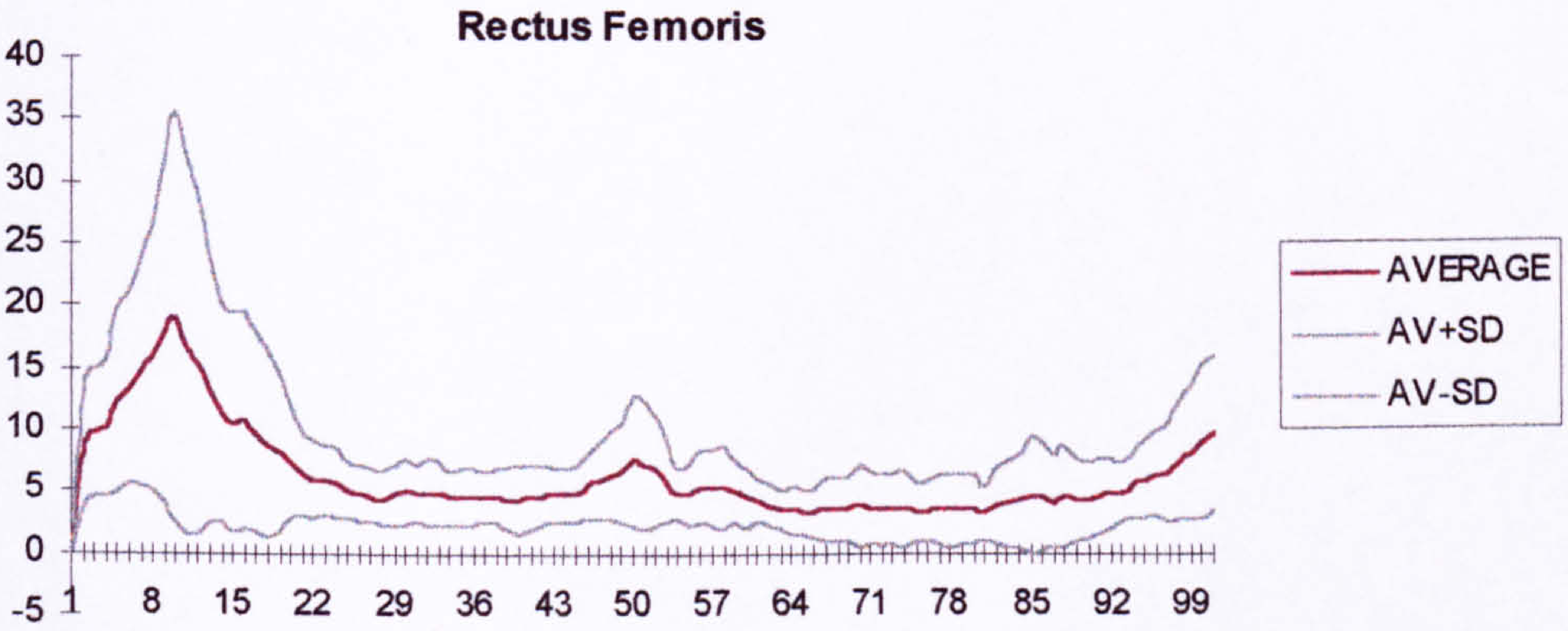
Medium Speed

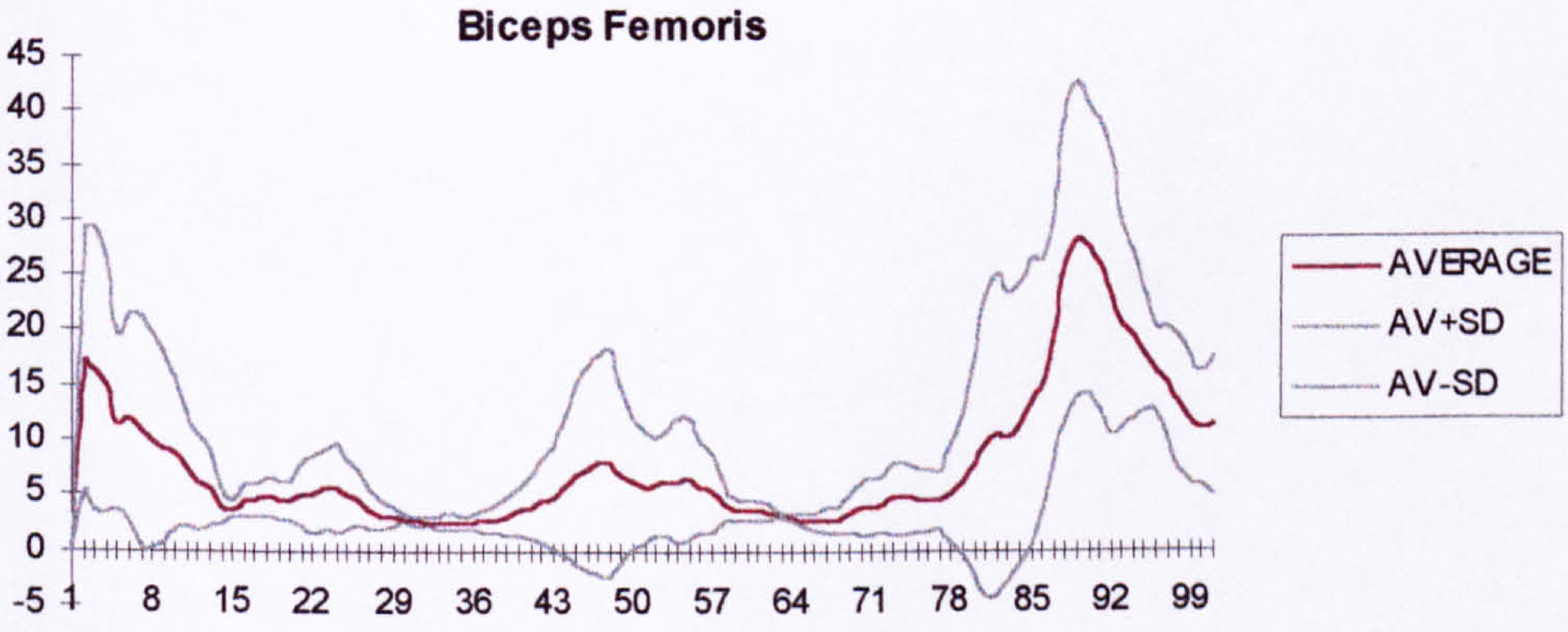
Overall the activity of TA followed that during slow walking except that where the peaks of activity occur (in early stance and end of swing), the level increased from 30-35% to 40-45% MVC (see Figure 5.7b for details). Activity of TA occurred during the same phases as in slow walking. RF, BF and GA also showed very similar activity patterns compared to slow walking. Peak activity in RF (during the first part of the stance phase), however, increased from 25% to 35% MVC. Peaks of activity in BF occur at the heel strike and at the end of swing, and, when compared to slow walking, the peaks increased from 20% to 30% MVC. GA was active at increased levels during the peaks of activity, while resting levels stay the same. The peak of activity in GA, occurring at the end of the stance phase, increased to 50% MVC, from 40% during slow walking.

Fast Speed

Overall activity patterns of TA remain the same. Peak levels, at the end of the stance phase were increased to around 60% MVC, higher than in both slow and medium speeds (see Figure 5.7c for details). RF showed patterns of activity only slightly different from those in slow and medium walking, but the major phase of activity occurred earlier, during middle to late stance. Low levels of activity were detected before toe off during slow and medium walking, but during fast walking activity increased to a moderate level, forming another substantial peak of activity during late stance. The largest peak of RF during early stance was larger than in slow and medium speeds, at 40% MVC. No activity was apparent in RF during the swing phase. BF showed similar activity patterns to other speeds during fast walking. However, an activity trough during late stance occurred slightly earlier during fast walking, and the muscle was active for a shorter period of time. Further, peaks of activity in BF were slightly increased over levels at other speeds, to 35% MVC. Peak activity in GA increased to 60% MVC during fast walking. Activity patterns remained similar except around the middle of the stance phase, when the point of moderate level of activity in GA seemed to occur at a slightly later stage during mid-stance (at about 35% gait cycle, compared to 20% gait cycle at other speeds), and the point of high activity occurred at an earlier stage (at 35% gait cycle compared to 45% gait cycle at other speeds).







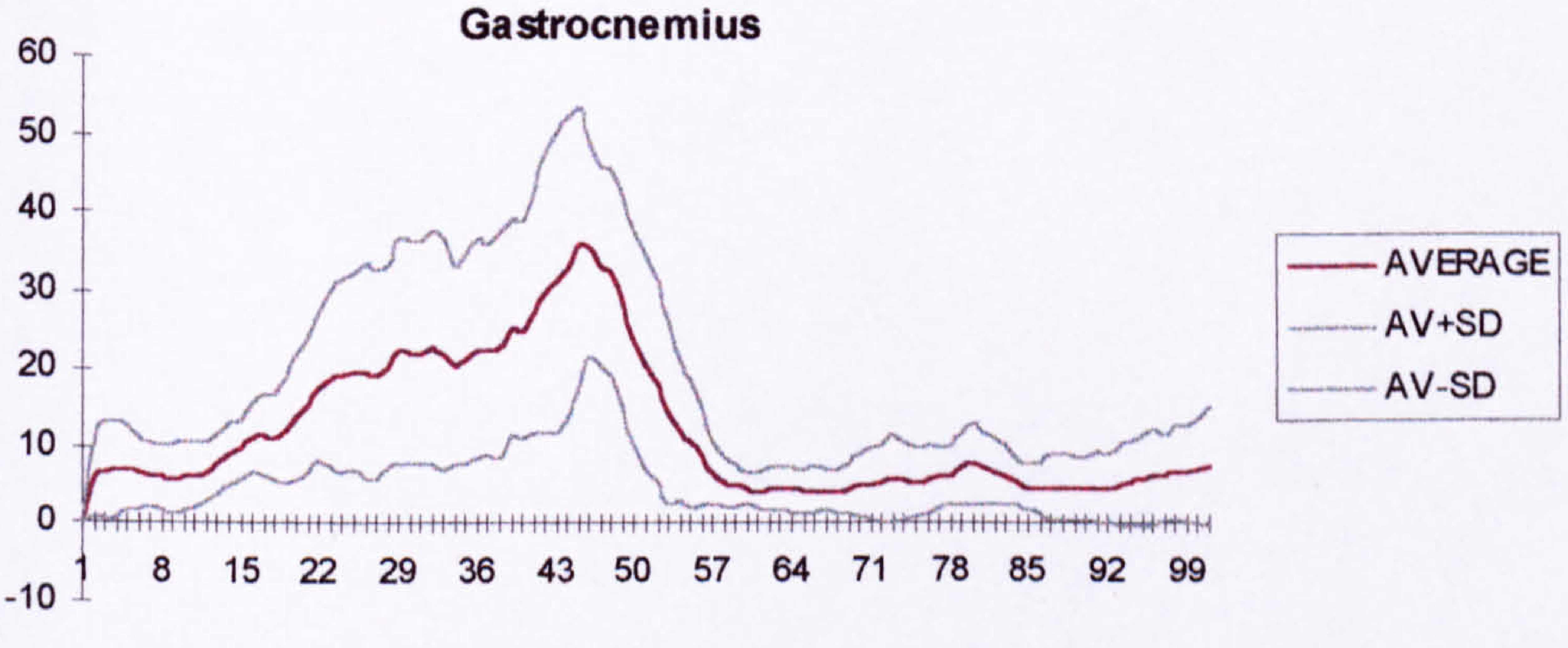


Figure 5.7a Telemetered EMG data for '**NORMAL SLOW**' walking. Data shows the average for four subjects ± the standard deviation. Data is presented as percentage of MVC (y-axis) against percentage of gait cycle (x-axis). Both 0 and 100 % of gait cycle represent right heel strike.

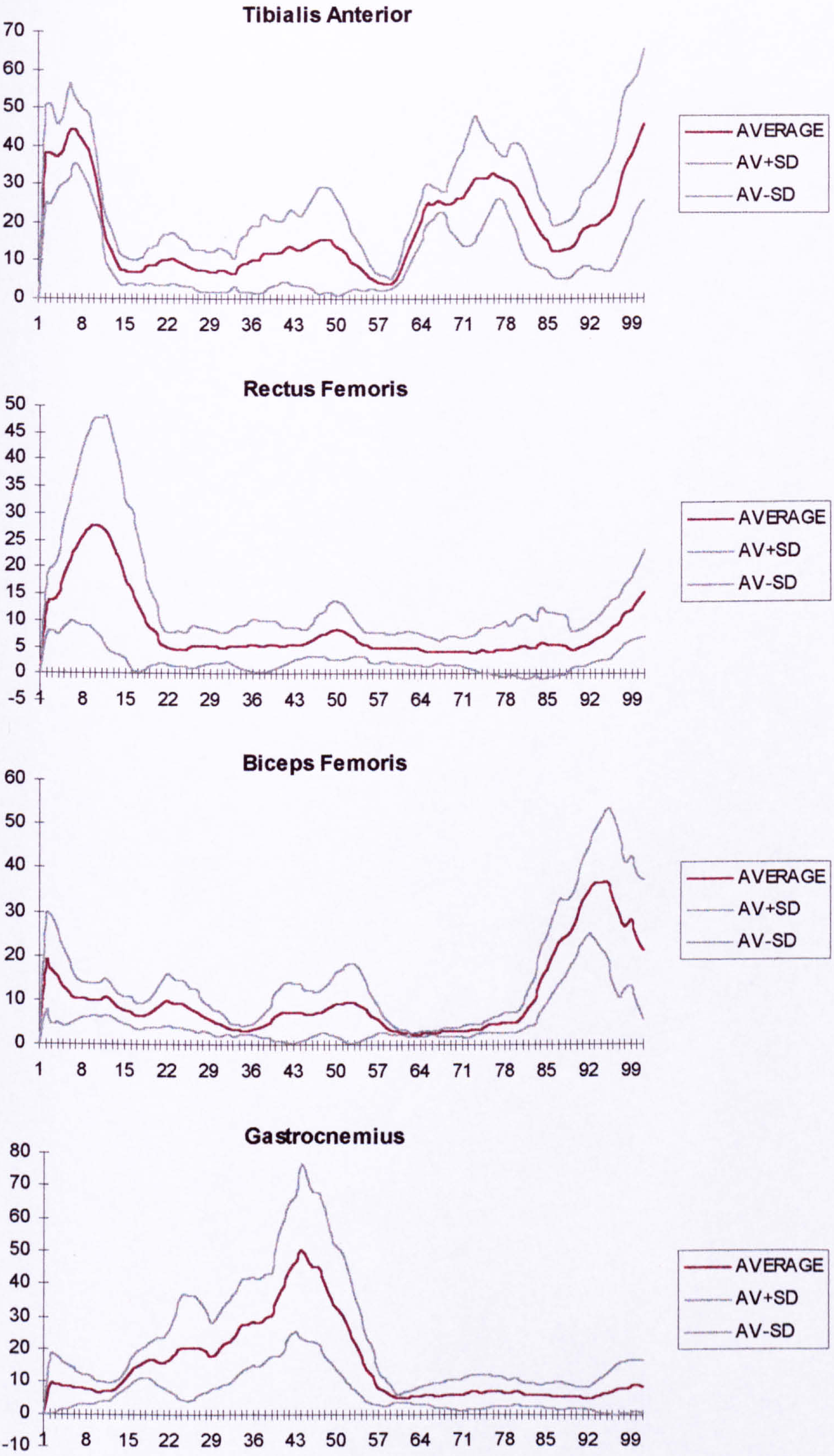


Figure 5.7b Telemetered EMG data for '**NORMAL MEDIUM**' walking. Data shows the average for four subjects ± the standard deviation. Data is presented as percentage of MVC (y-axis) against percentage of gait cycle (x-axis). Both 0 and 100 % gait cycle represent right heel strike.

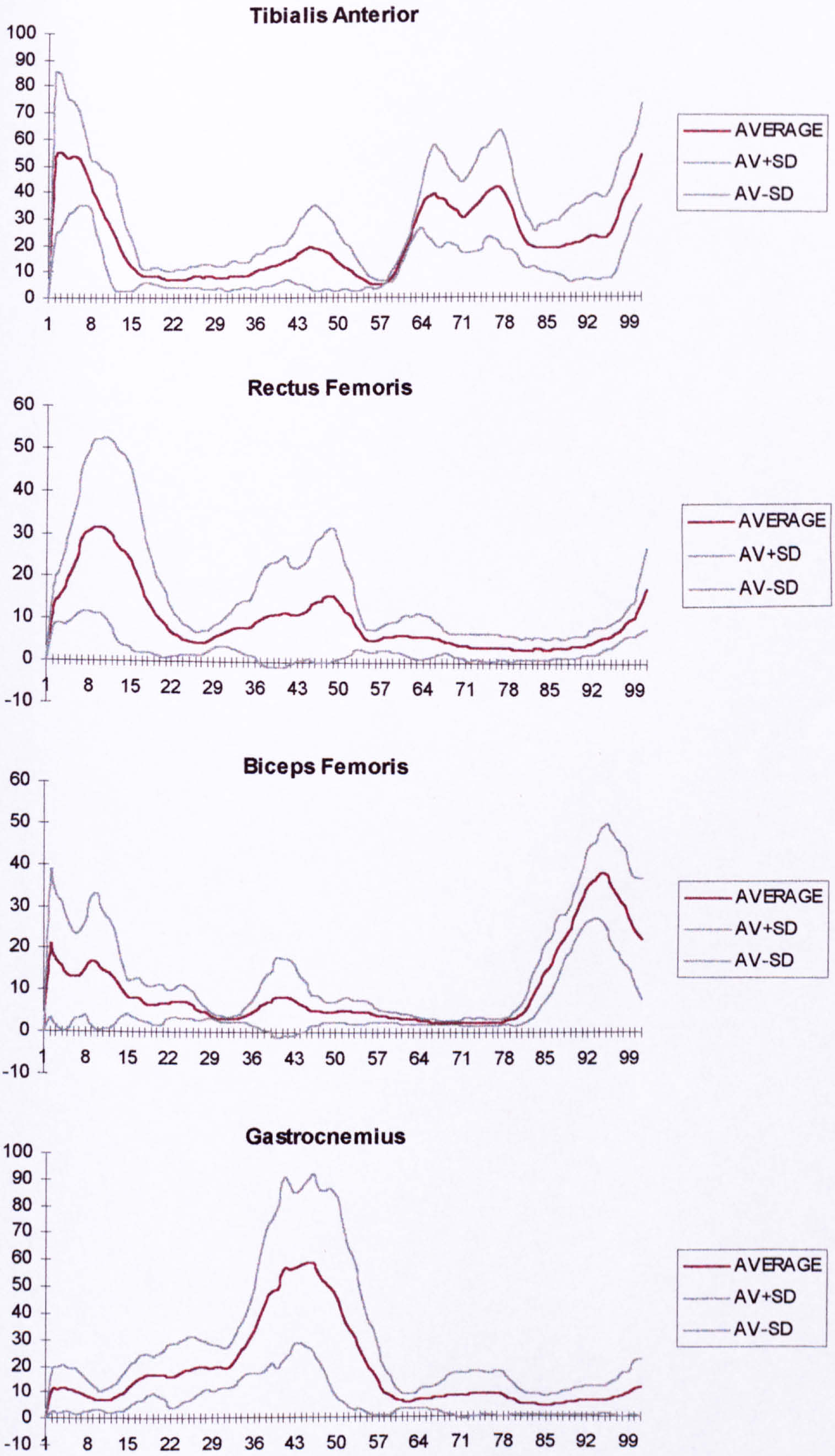


Figure 5.7c Telemetered EMG data for '**NORMAL FAST**' walking. Data shows the average for four subjects ± the standard deviation. Data is presented as percentage of MVC (y-axis) against percentage of gait cycle (x-axis). Both 0 and 100 % gait cycle represent right heel strike.

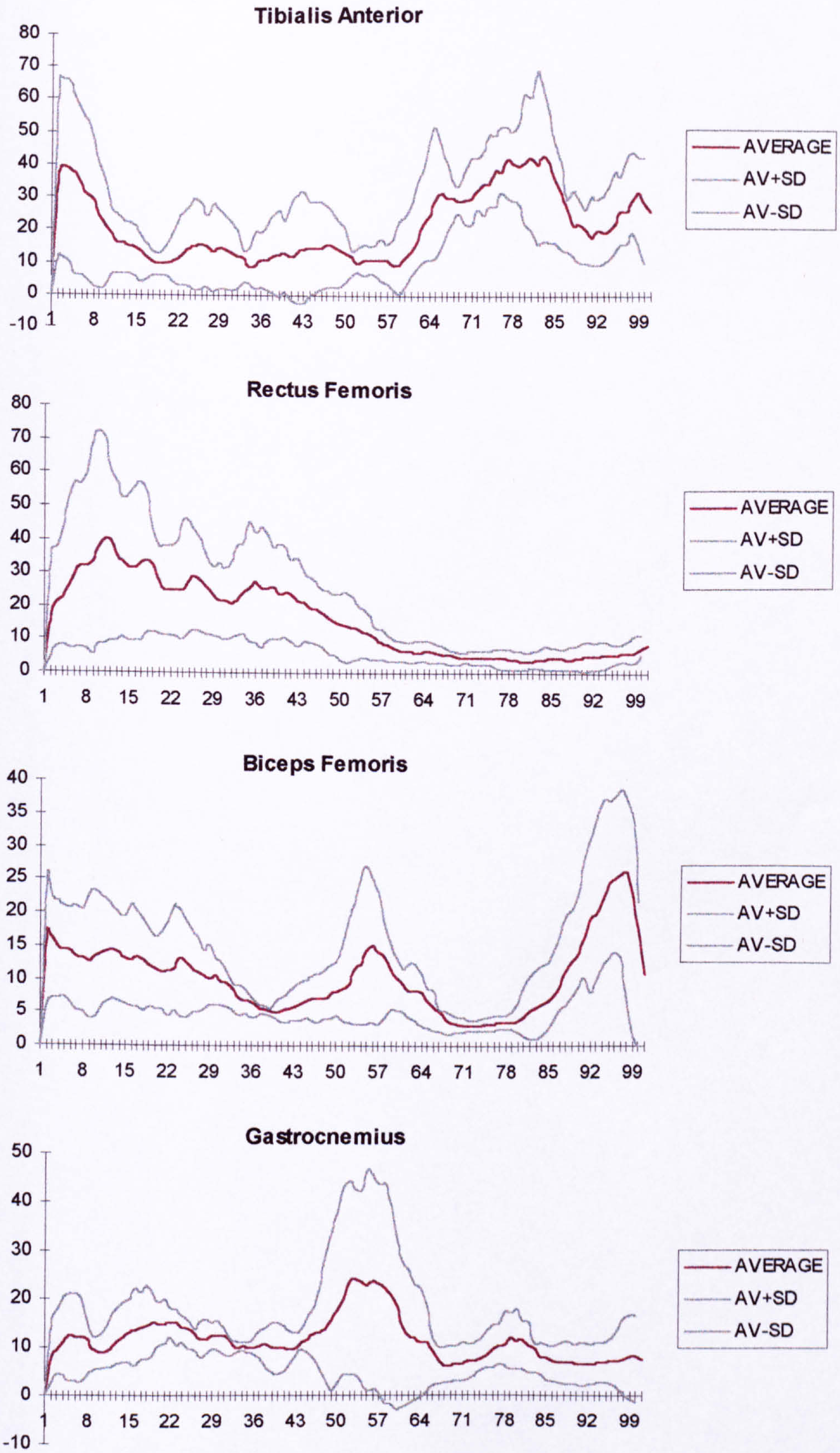


Figure 5.8a Telemetered EMG data for **'BHBK SLOW'** walking. Data shows the average for four subjects ± the standard deviation. Data is presented as percentage of MVC (y-axis) against percentage of gait cycle (x-axis). Both 0 and 100 % gait cycle represent right heel strike.

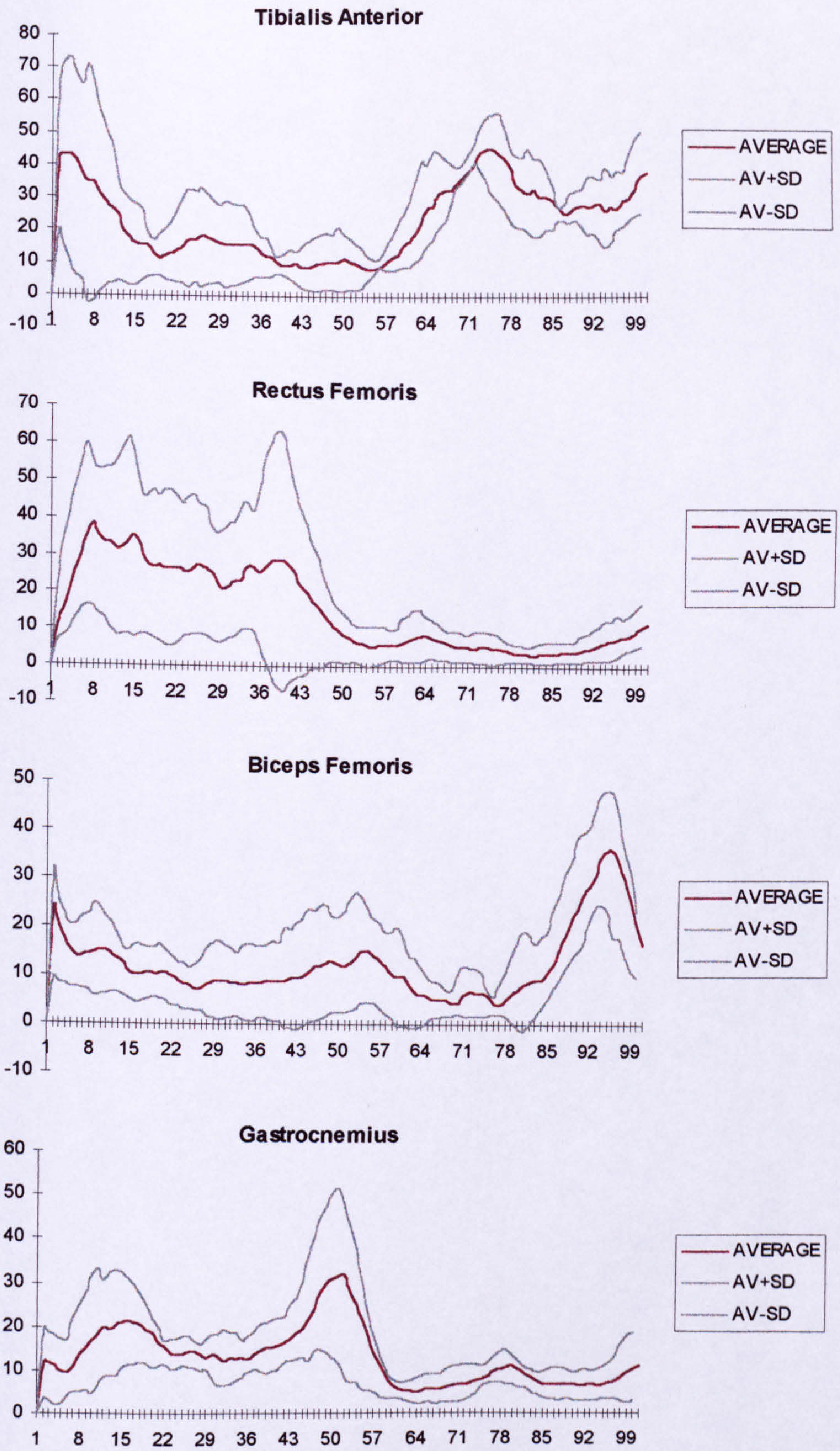


Figure 5.8b Telemetered EMG data for '**BHBK MEDIUM**' walking. Data shows the average for four subjects ± the standard deviation. Data is presented as percentage of MVC (y-axis) against percentage of gait cycle (x-axis). Both 0 and 100 % gait cycle represent right heel strike.

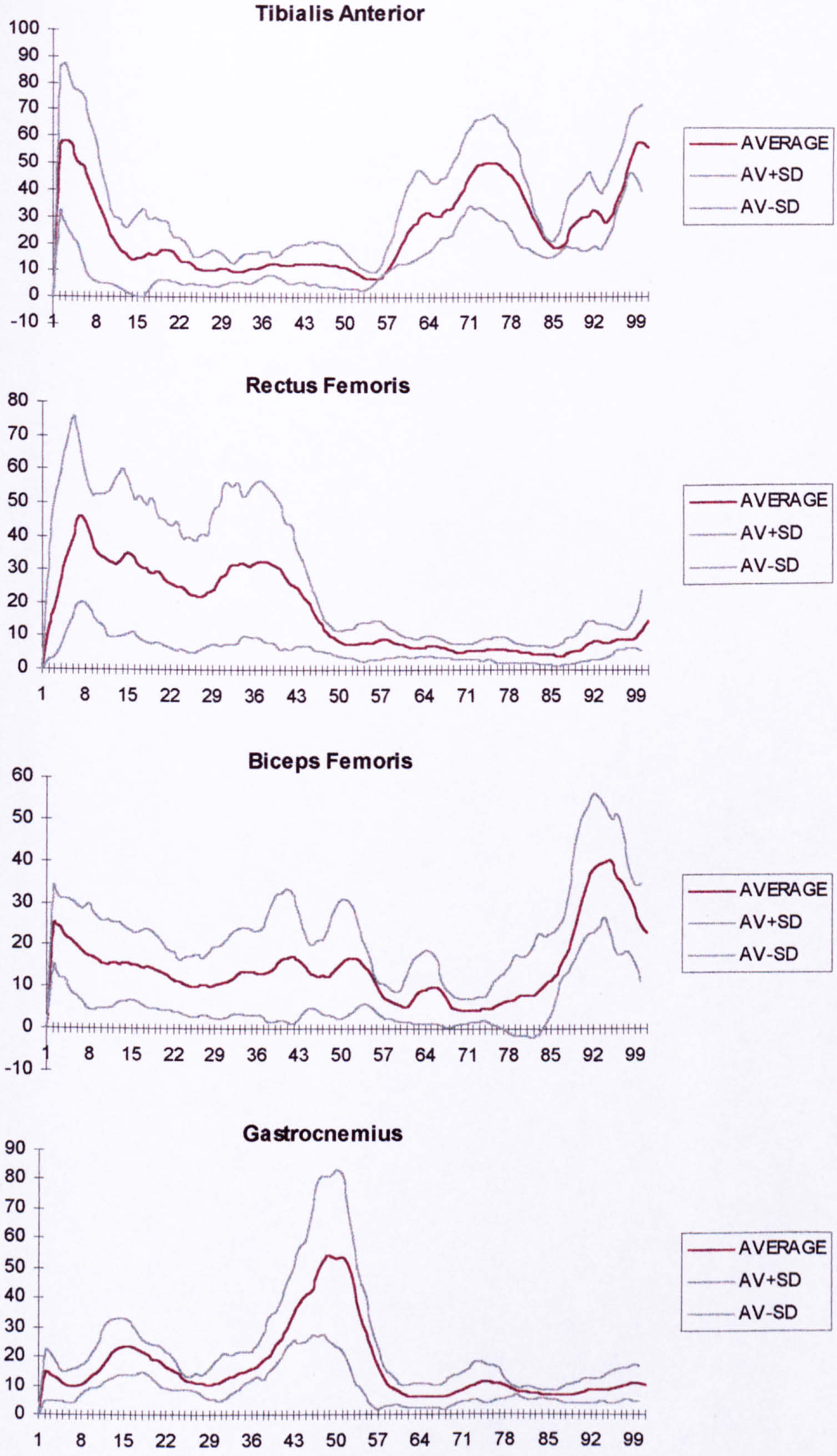


Figure 5.9c Telemetered EMG data for '**BHBK FAST**' walking. Data shows the average for four subjects ± the standard deviation. Data is presented as percentage of MVC (y-axis) against percentage of gait cycle (x-axis). Both 0 and 100 % gait cycle represent right heel strike.

5.4.3 EMG during BHBK walking

Data obtained during telemetered electromyography during BHBK walking is shown in Figure 5.8(a-c).

Slow speed

Before heel contact, tibialis anterior (TA) and biceps femoris (BF) showed moderate to high activity, while gastrocnemius (GA) displayed low activity and rectus femoris (RF) was inactive (see Figure 5.8a for details). At heel strike, a peak of activity occurred in TA, which fell to low activity shortly after. RF showed low activity at heel strike, increasing to relatively high activity in early stance, followed by moderate activity which continued throughout the stance phase. BF was active at a low level throughout the stance phase, with another peak of moderate activity occurring at the end of the stance phase. GA also showed low activity throughout the stance phase, with a short peak occurring prior to toe-off. Once into the stance phase TA increased activity to high levels, and activity continued throughout swing. RF was silent during swing. BF was inactive at the beginning of the swing phase, but increased levels of activity around mid-swing to a peak of moderate activity, which continued until just before the following heel strike. GA was active at a low level during the swing phase.

Medium Speed

TA displayed very similar activity patterns during medium speed walking. Levels of activity were the same in all phases, except for a slight rise (20 to 30% MVC in one short period) during late swing phase (see Figure 5.8b for details). RF also showed very similar levels of activity during the same phases, compared to slow walking. A small decrease in duration of activity towards the end of stance phase was detected, where the muscle activity reached minimal activity earlier during the gait cycle (at 50% gait cycle) in medium walking than during slow walking (at about 58% gait cycle). Higher activity levels were sustained in BF throughout the stance phase compared to levels during slow walking, increasing from 5 - 15% MVC to 10 - 20% MVC. Higher activity levels were also found in BF during swing, increasing from 25% to around 40% MVC. GA showed increased levels of activity during medium speed walking. During stance, activity levels were at around 15% with a peak of 30% MVC compared to 15% MVC generally in slow walking increasing to 20% at the peak. Activity levels in GA during swing phase were similar to those during slow walking.

Fast Speed

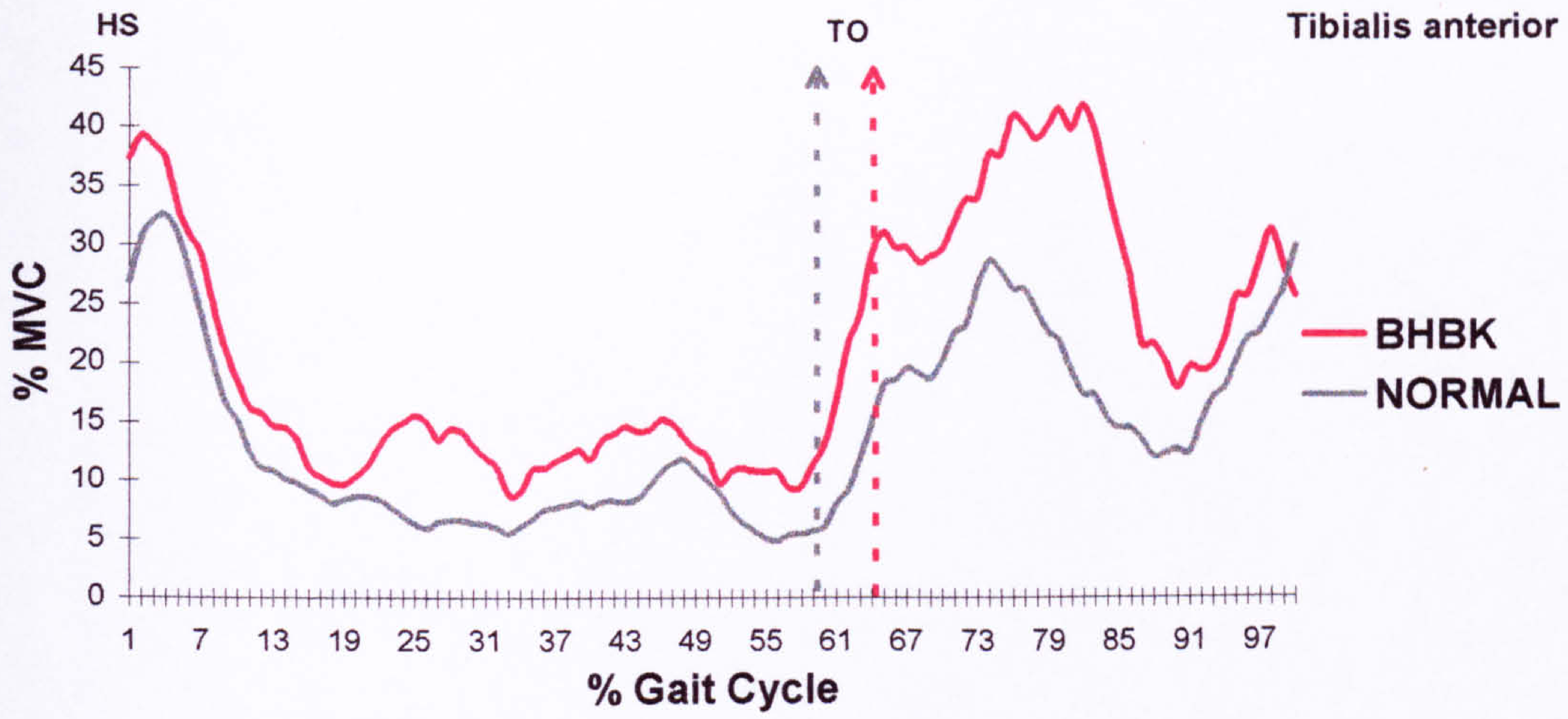
During fast walking TA showed higher peaks of activity than at the other two speeds. Peaks (during early stance and at mid-swing) increased from 40% to 60% MVC (see Figure 5.8c for details). General activity levels were similar to those during walking at other speeds. RF activity increased during stance from around 30% to around 40% MVC. During fast walking, a decrease to low levels of activity occurred earlier again (at 48% gait cycle) when compared to other walking speeds. Activity patterns in BF were very similar to those during medium speed walking, except the muscle displayed a higher peak of activity at 40% MVC. GA displayed a marked increase in activity level at the end of stance, rising to 50% MVC, higher than at both slow and medium walking speeds. All other activity remained similar to that displayed during medium walking.

5.4.4 Comparison between normal and BHBK walking

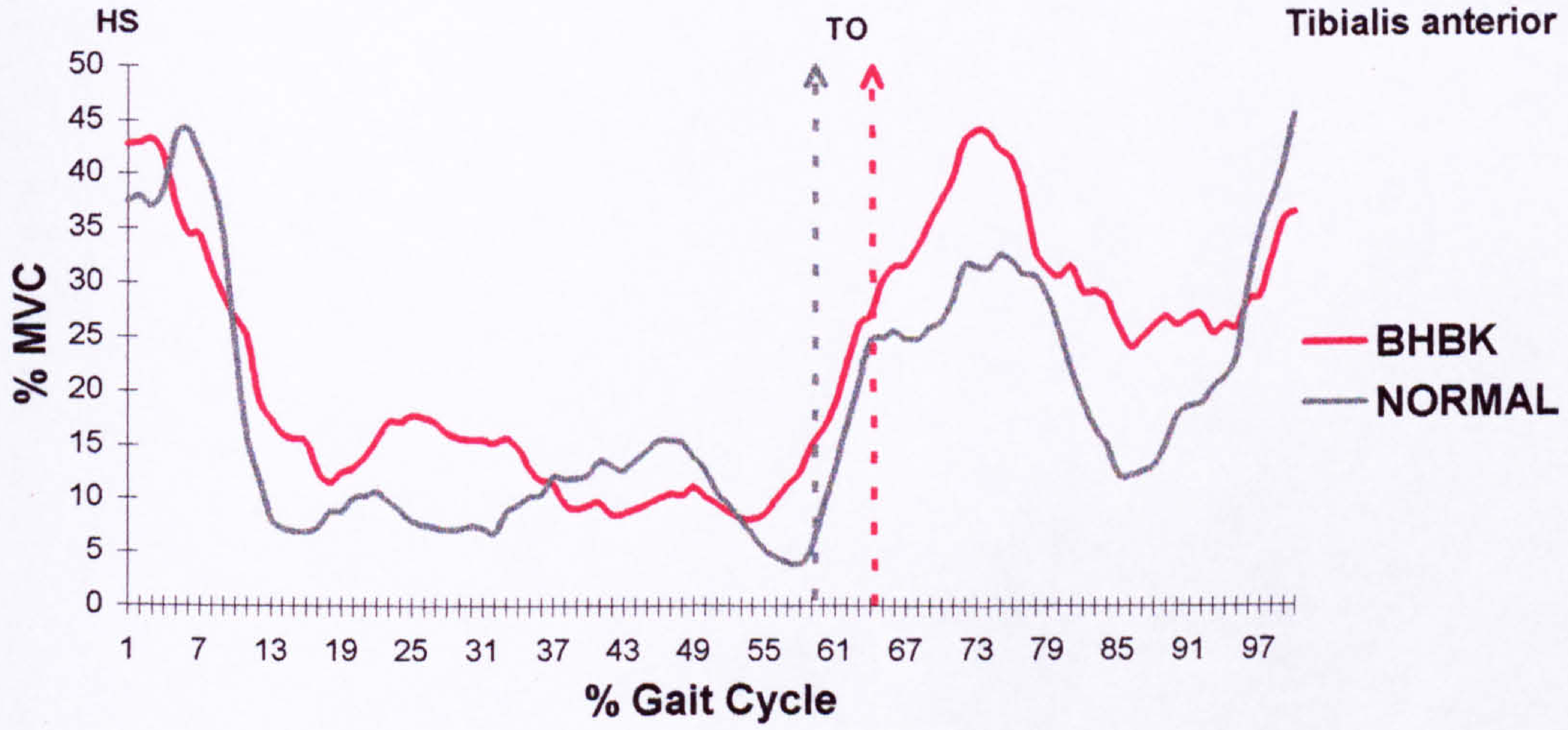
Data for comparison between normal and BHBK walking is shown in Figures 5.9 to 5.12. Data is shown as % MVC (averaged over four subjects) against percentage gait cycle. Heel strike and toe off are shown, but two lines are shown on each graph for toe off, since toe off occurs at a different position in the gait cycle for each posture.

The most noticeable differences in EMG between normal and BHBK walking, at any speed, are the activity levels in the rectus femoris and gastrocnemius. Rectus femoris (RF) shows an increase in activity during BHBK walking compared to normal walking at all speeds. During slow walking, peak activity is over twice that during normal walking, while at medium and fast speeds, the peak of activity is about 50% higher than that during normal walking. For gastrocnemius (GA), however, the peak of activity is actually higher in normal walking than that during BHBK walking. During slow and medium speed BHBK walking peak activity in GA reduces by about 40% to 60%. However at fast speed, the difference between normal and BHBK walking in peak activity of GA is smaller than at slower speeds. There is only a 15% difference between peak activity in BHBK and normal walking during the stance phase.

SLOW



MEDIUM



FAST

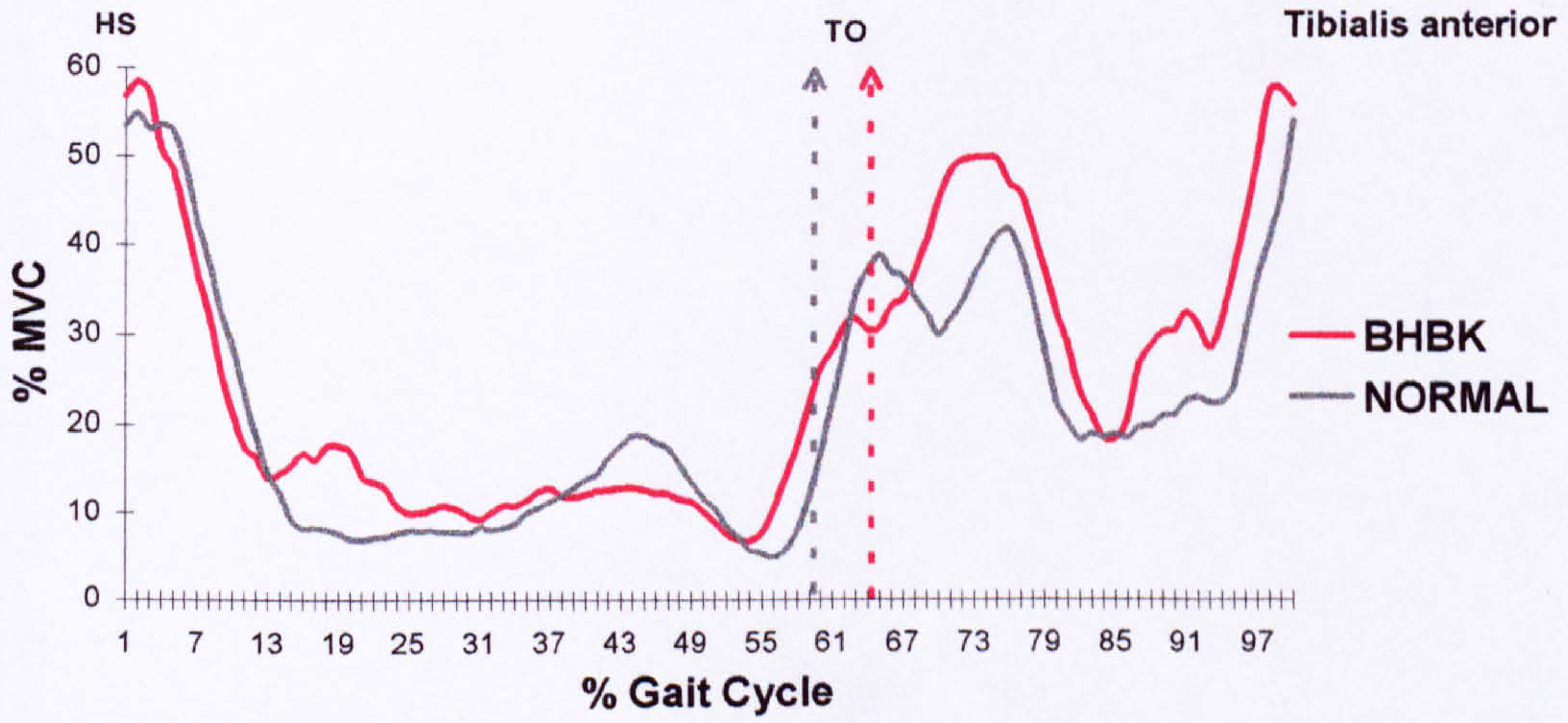
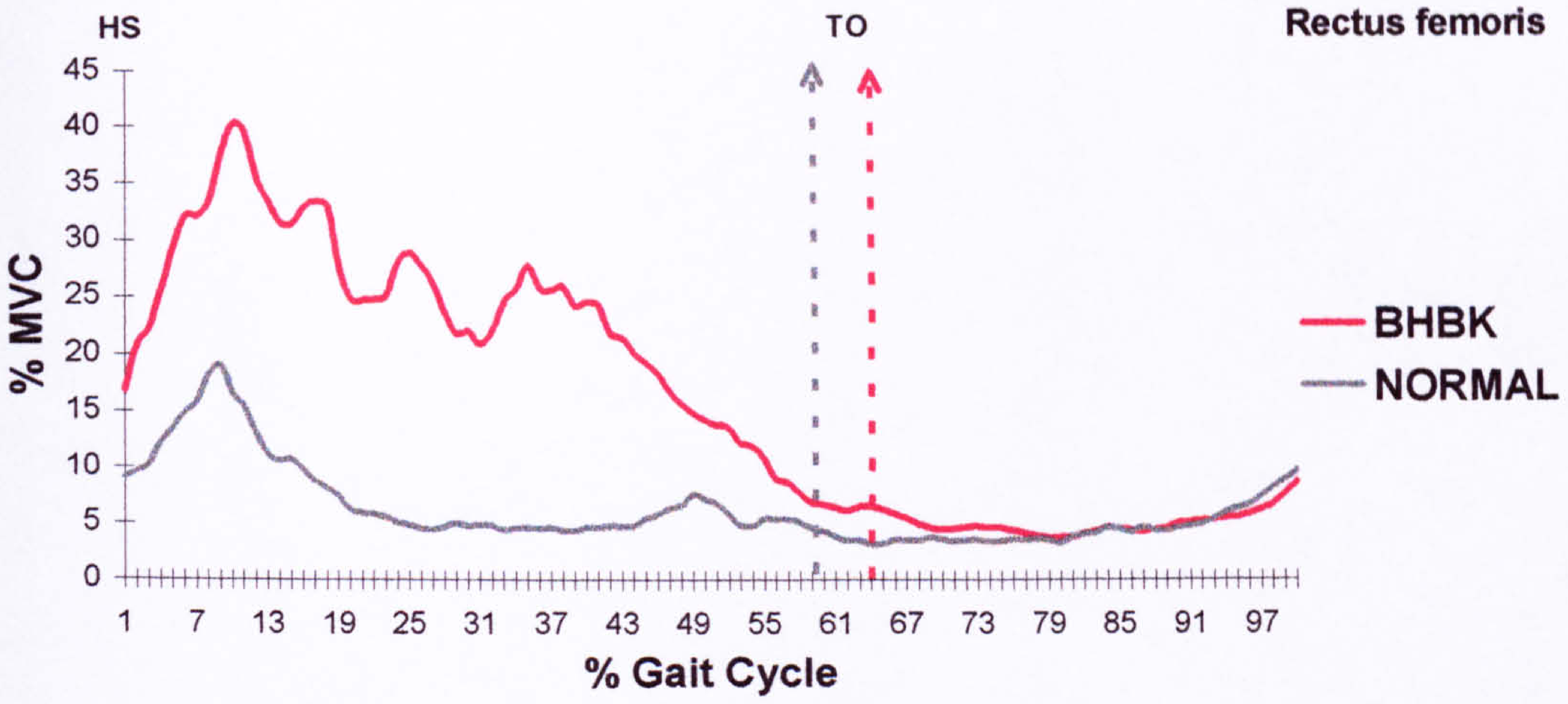
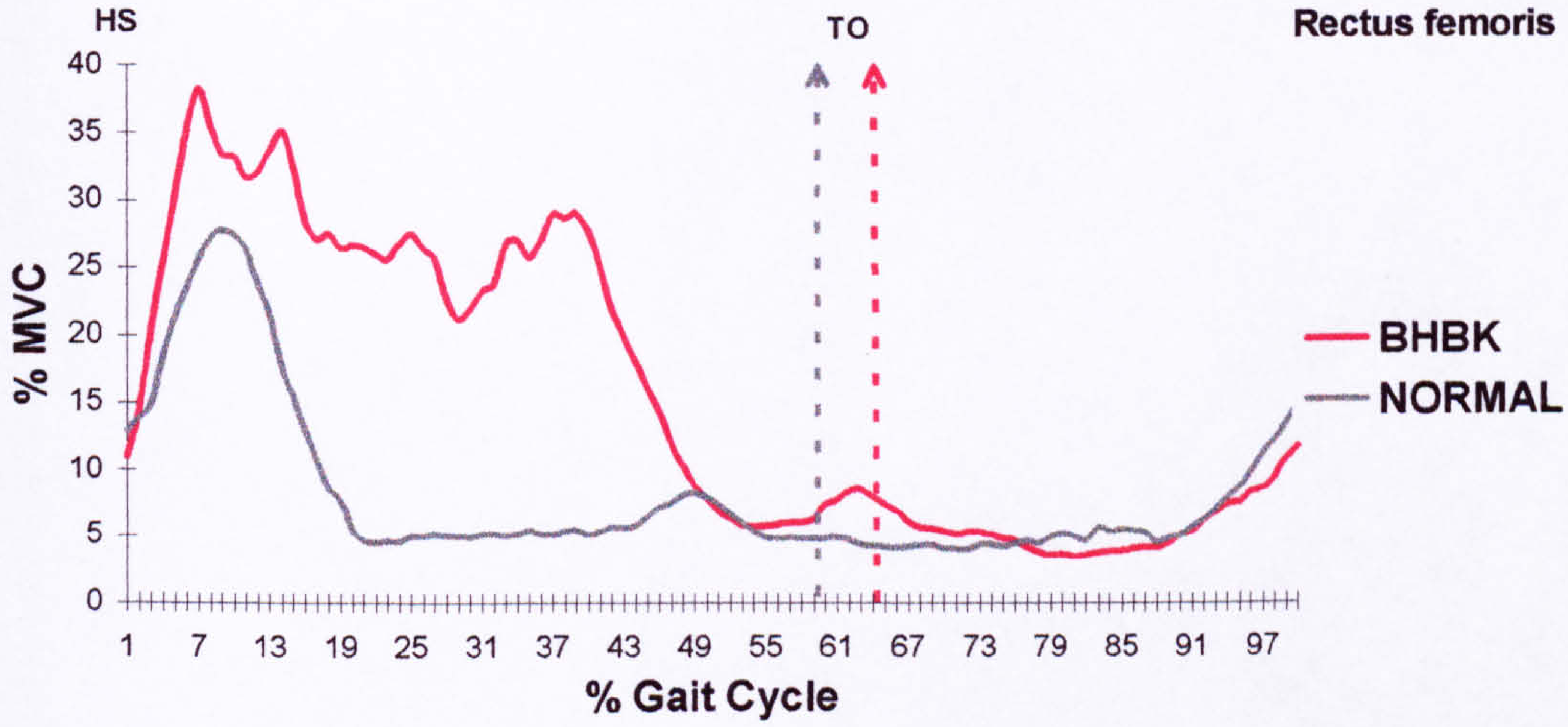


Figure 5.9 EMG data for **Tibialis anterior** during normal and BHBK walking. Three graphs display data for three different speeds.

SLOW



MEDIUM



FAST

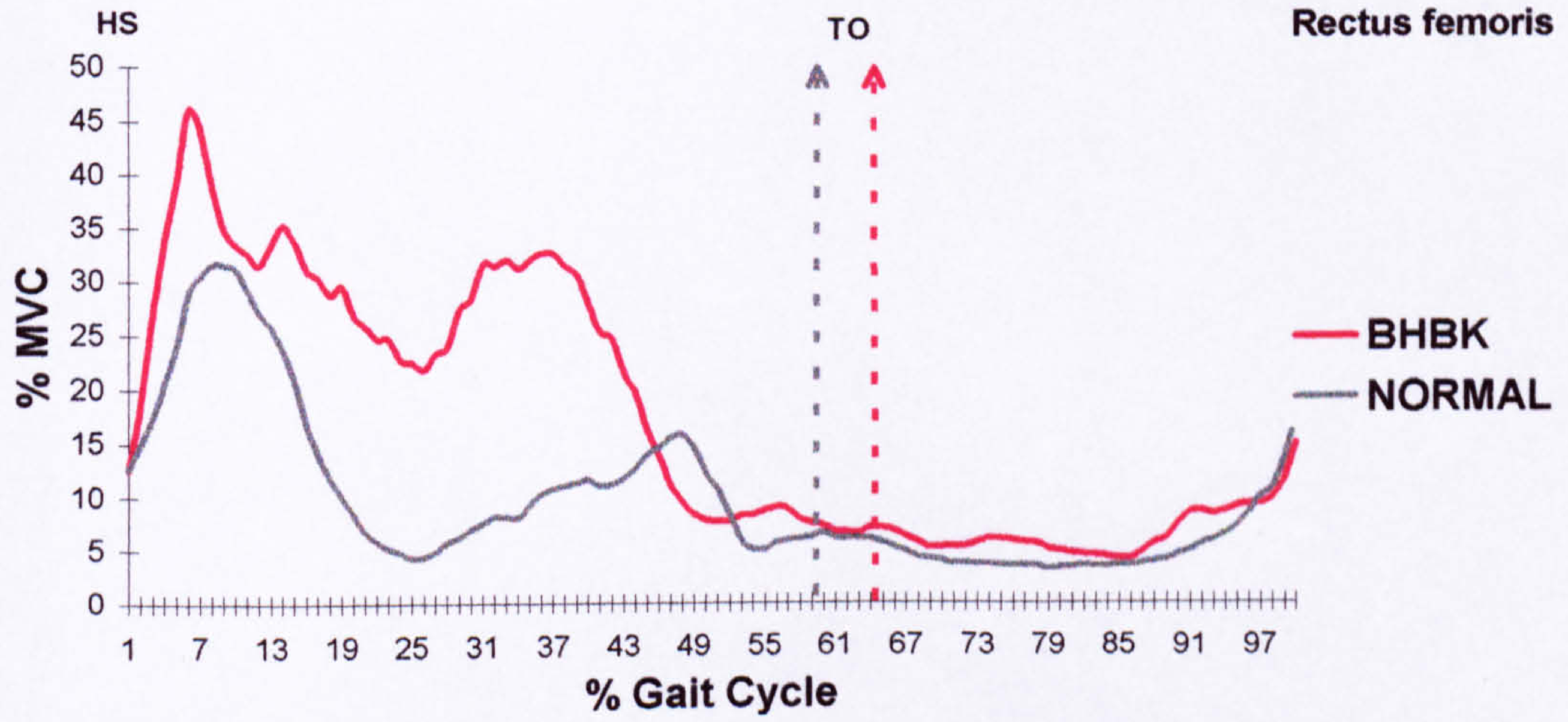
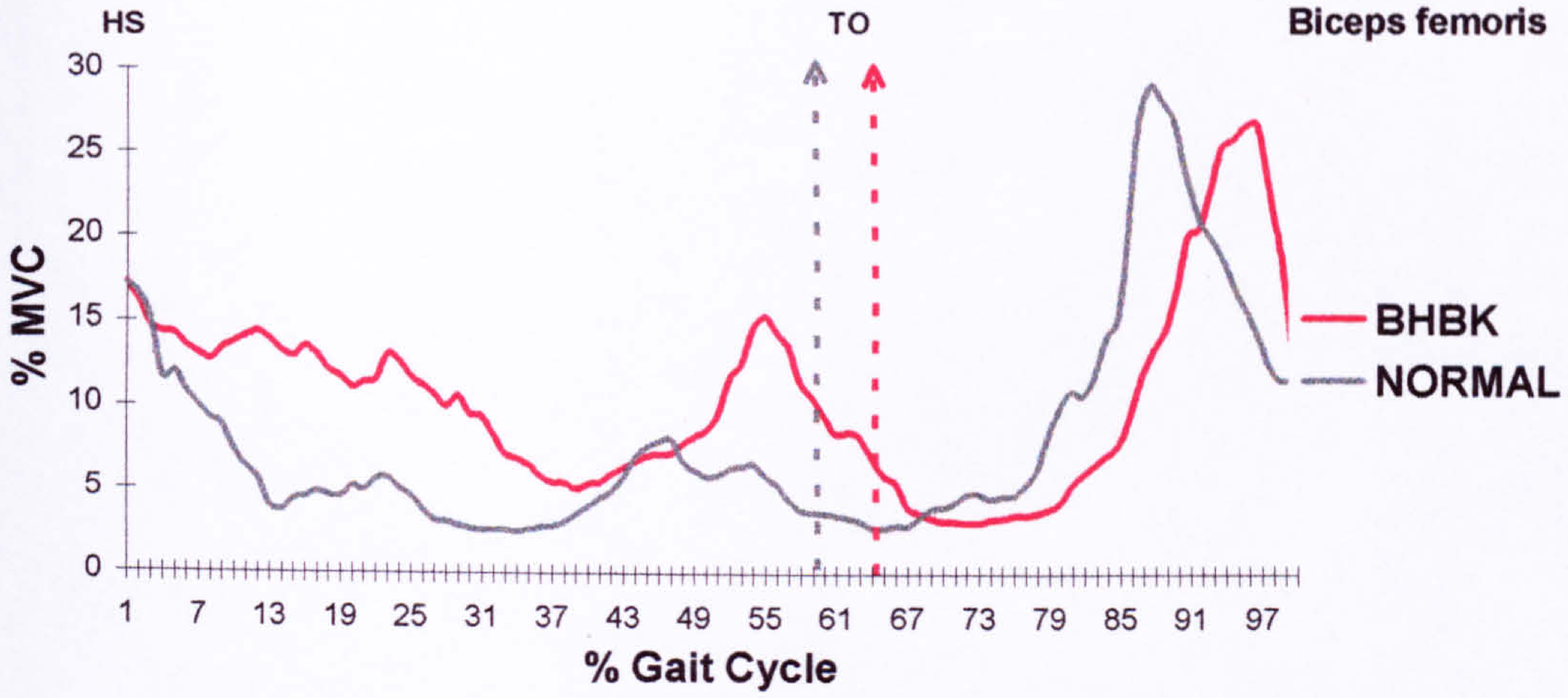
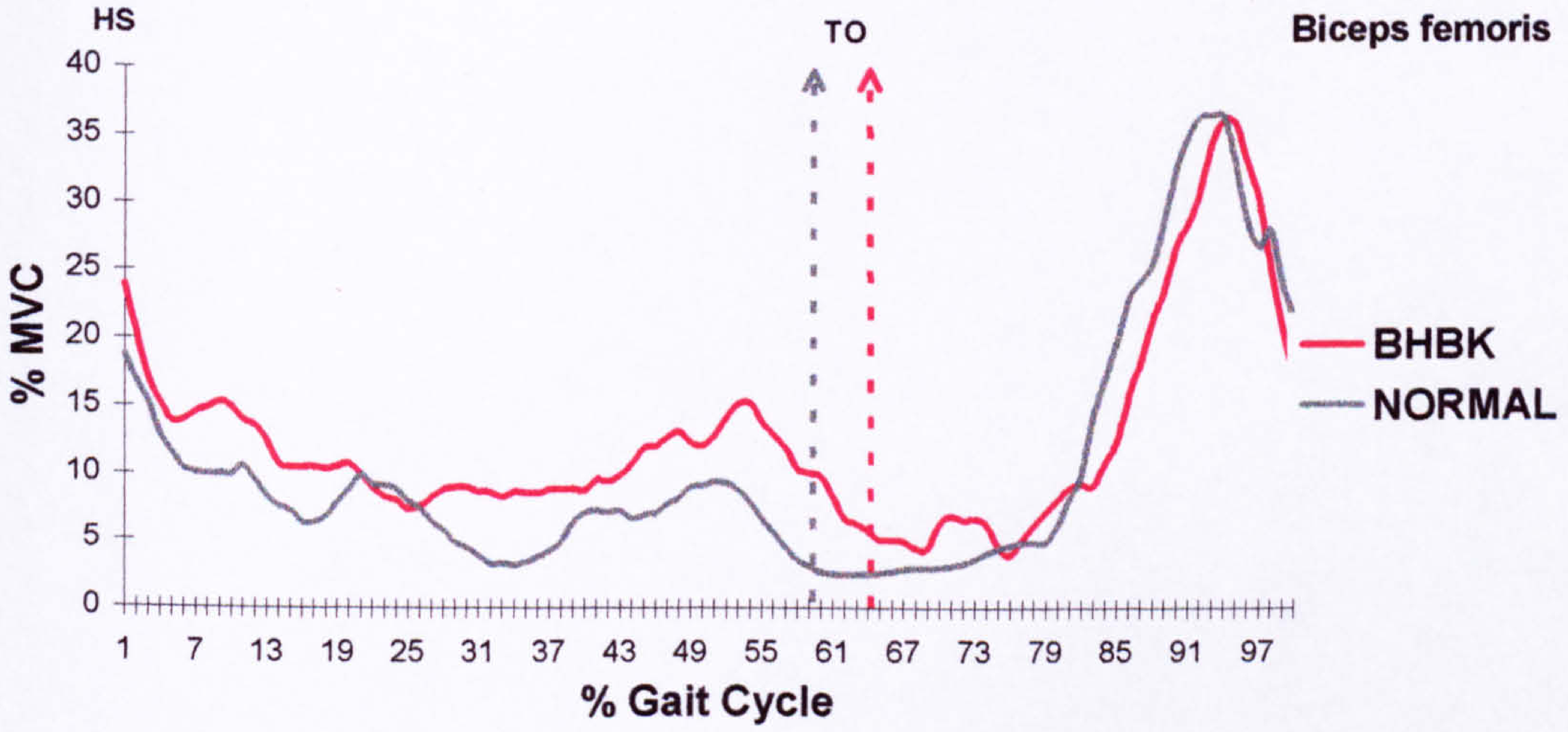


Figure 5.10 EMG data for **Rectus femoris** during normal and BHBK walking. Three graphs display data for three different speeds.

SLOW



MEDIUM



FAST

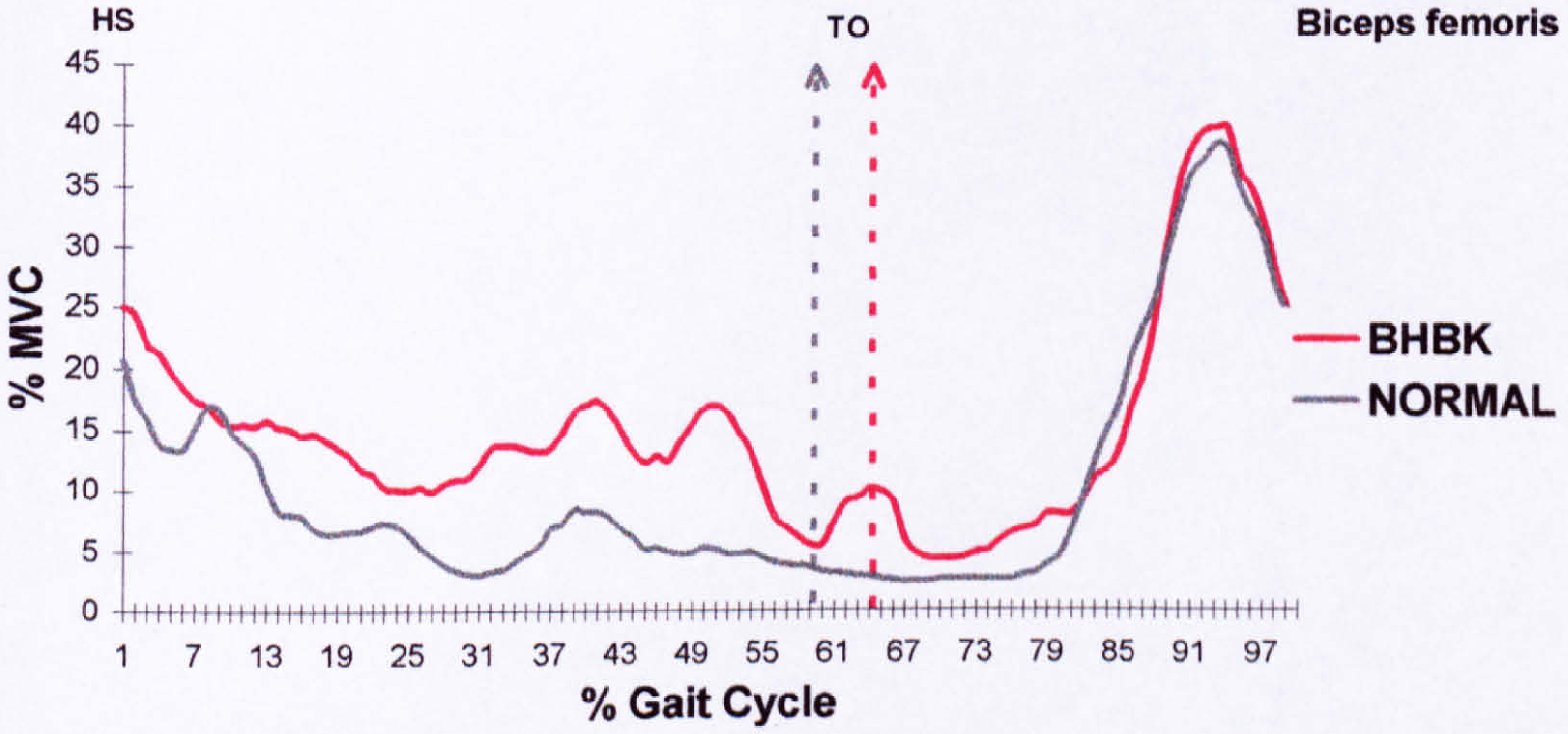
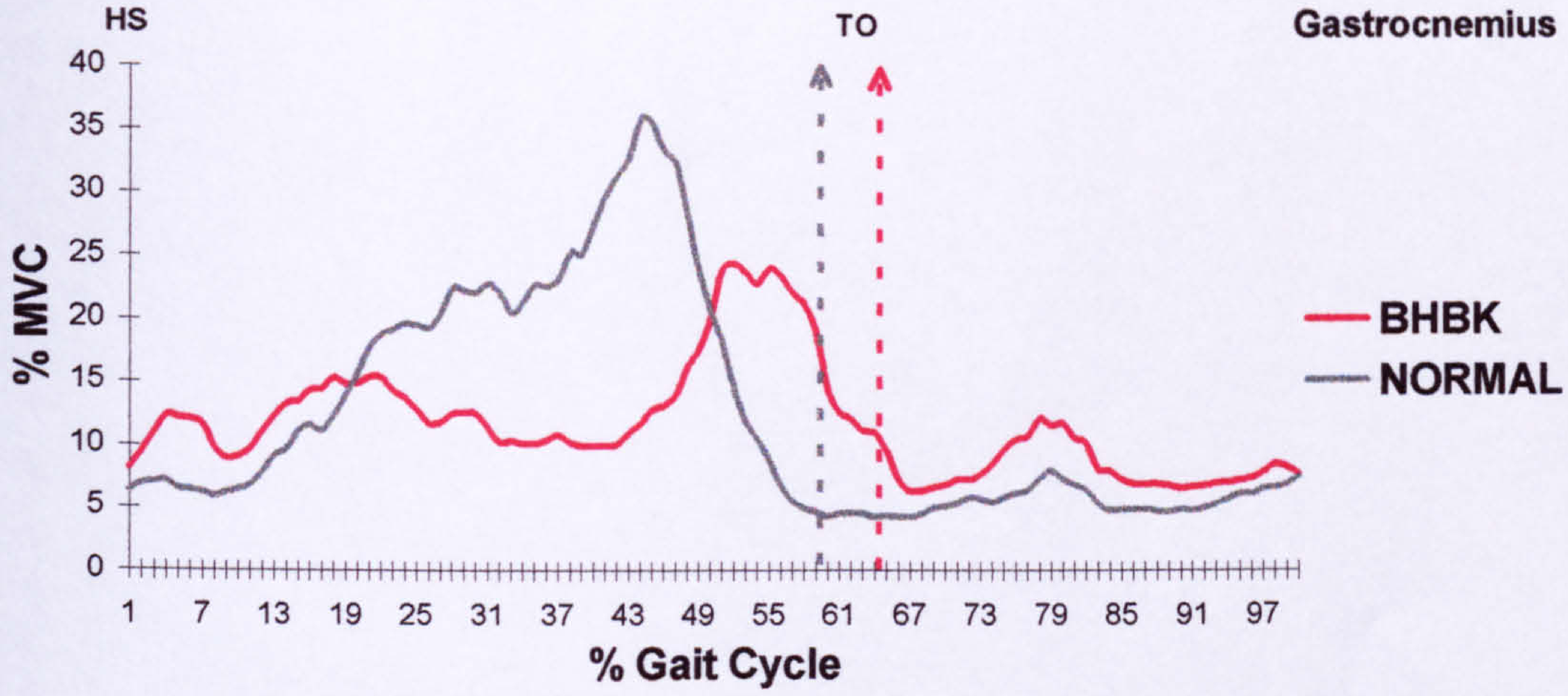
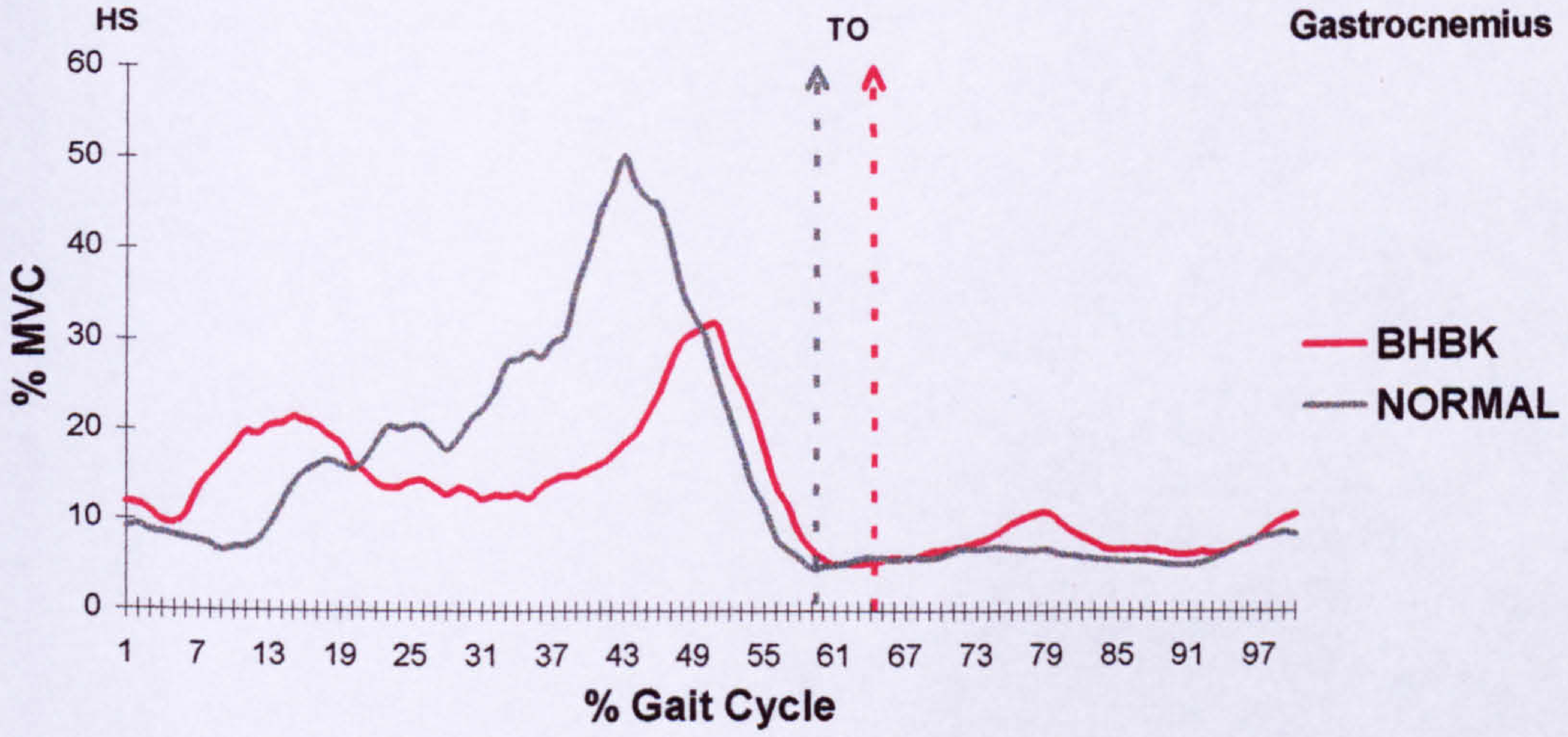


Figure 5.11 EMG data for **Biceps femoris** during normal and BHBK walking. Three graphs display data for three different speeds.

SLOW



MEDIUM



FAST

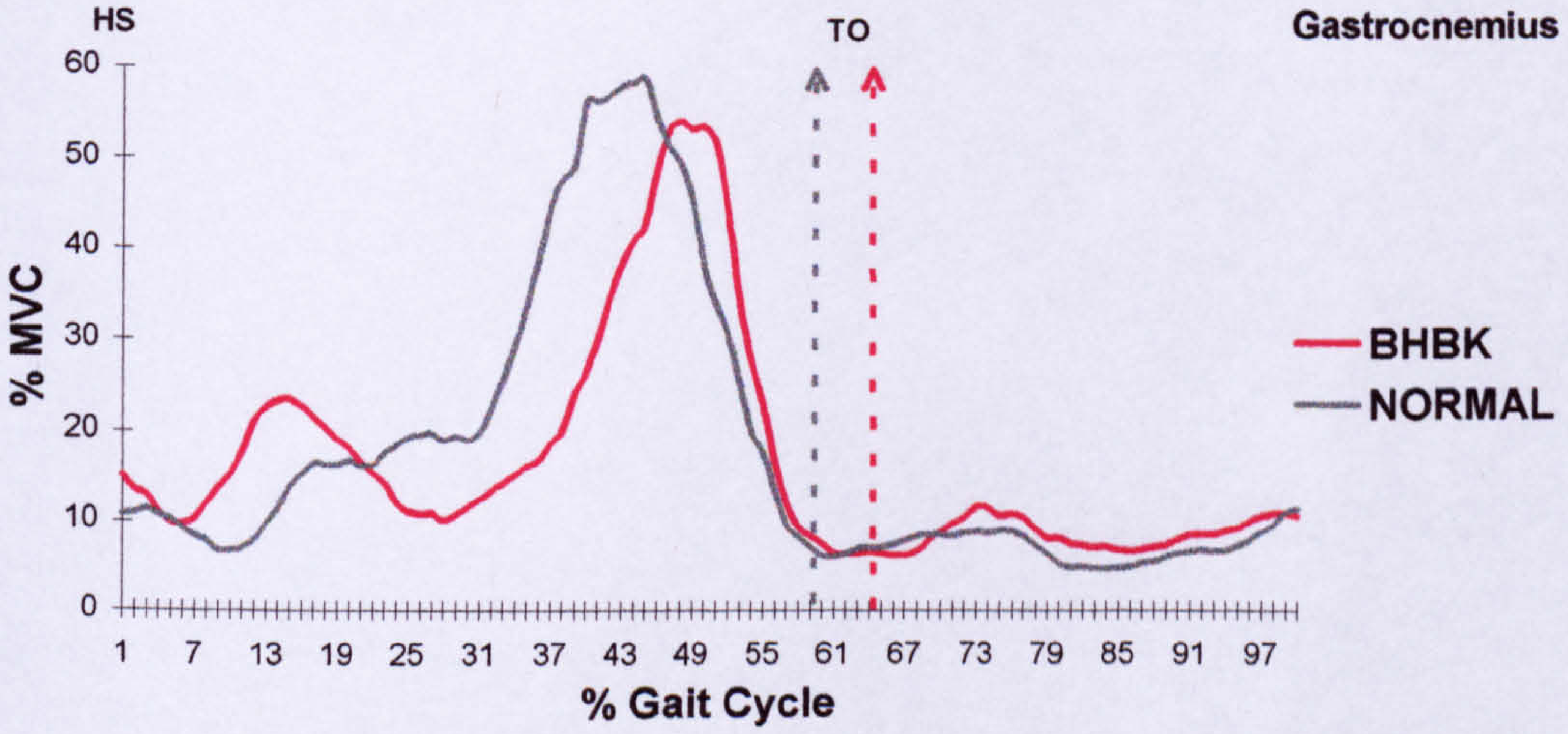


Figure 5.12 EMG data for **Gastrocnemius** during normal and BHBK walking. Three graphs display data for three different speeds.

5.4.5 Further analysis

According to Prilutsky et al. (1996) an individual muscle can be assumed to be producing force once above 20% MVC. In the study by Prilutsky and colleagues, this fact was used to estimate at which phases during the gait cycle each muscle was producing force, and therefore to predict the phases in which two-joint muscles could possibly be transferring energy across joints. This approach assumes an electromechanical delay of 40 ms between the EMG data increasing above the 20% threshold, and a production of muscle force (see Figure 5.13). Data in the literature estimating the electromechanical delay are inconsistent, but this value represents a reasonable average of electromechanical delay (Prilutsky et al., 1996). The end of force production is estimated at 140 ms after the EMG data falls below the 20% threshold (Prilutsky et al., 1996).

Using EMG collected in this study, force production is now predicted using the methodology set out above for each muscle during both normal and BHBK walking using EMG collected in this study. Likely force production phases are shown in Figures 5.14 to 5.16 (a + b).

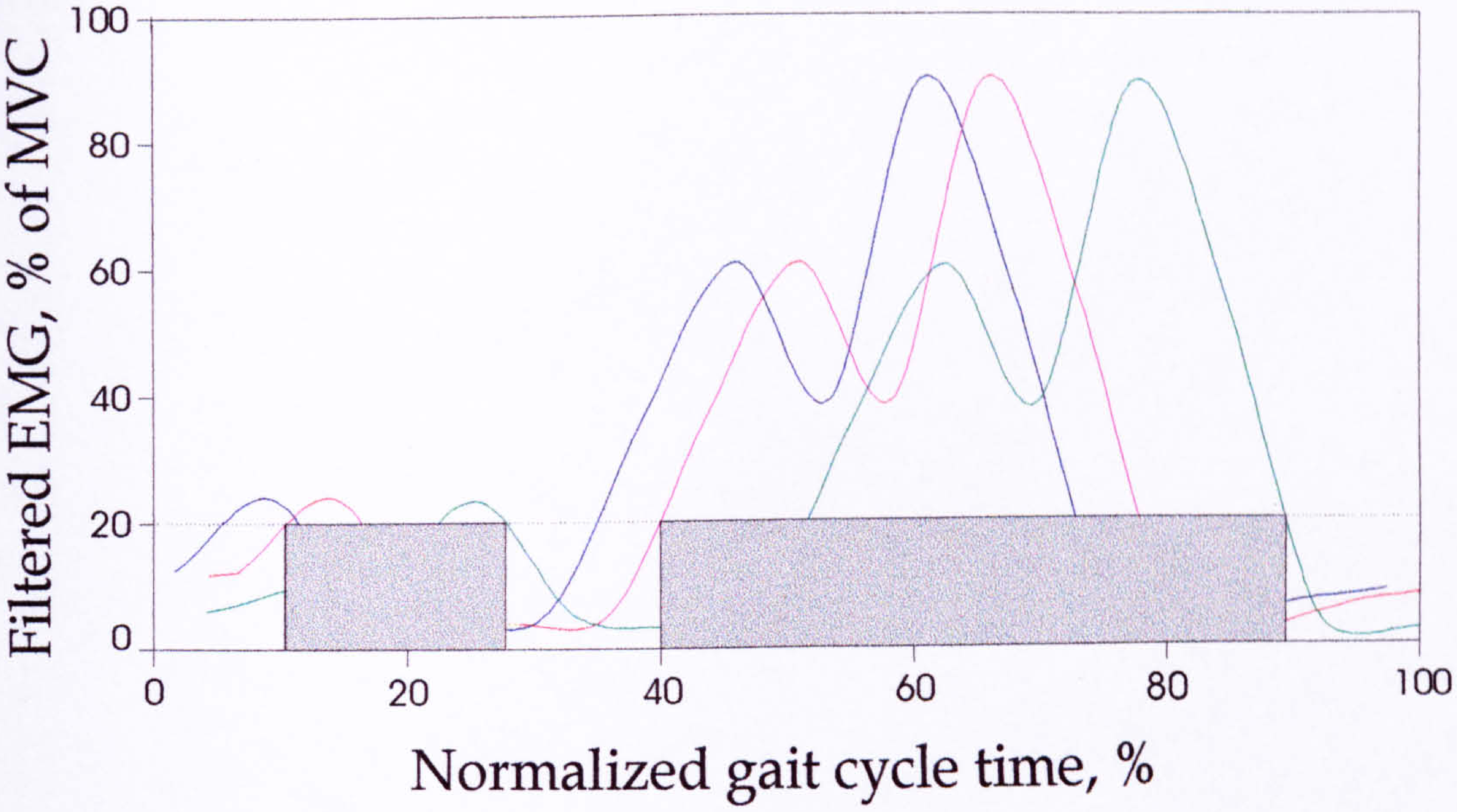


Figure 5.13 Estimating the phases where the muscle produces force from filtered EMG data. The blue line is the linear envelope containing full-wave rectified EMG data. The muscle is assumed to be producing force when the data exceeds 20% of the MVC value, therefore the threshold value for force production is at 20%. To allow for the electromechanical delay (EMD), the EMG data is shifted by 40 ms, after which the muscle is assumed to be producing force. To estimate the instant when force production ceases, the EMG data is shifted by a further 100 ms. Force production ceases when this curve falls below 20%. The red line represents the EMG data shifted by 40 ms., while the green line represents the EMG data shifted by 100 ms. The shaded areas thus represent the approximate phases where the muscle is producing force. Adapted from Prilutsky et al. (1996)

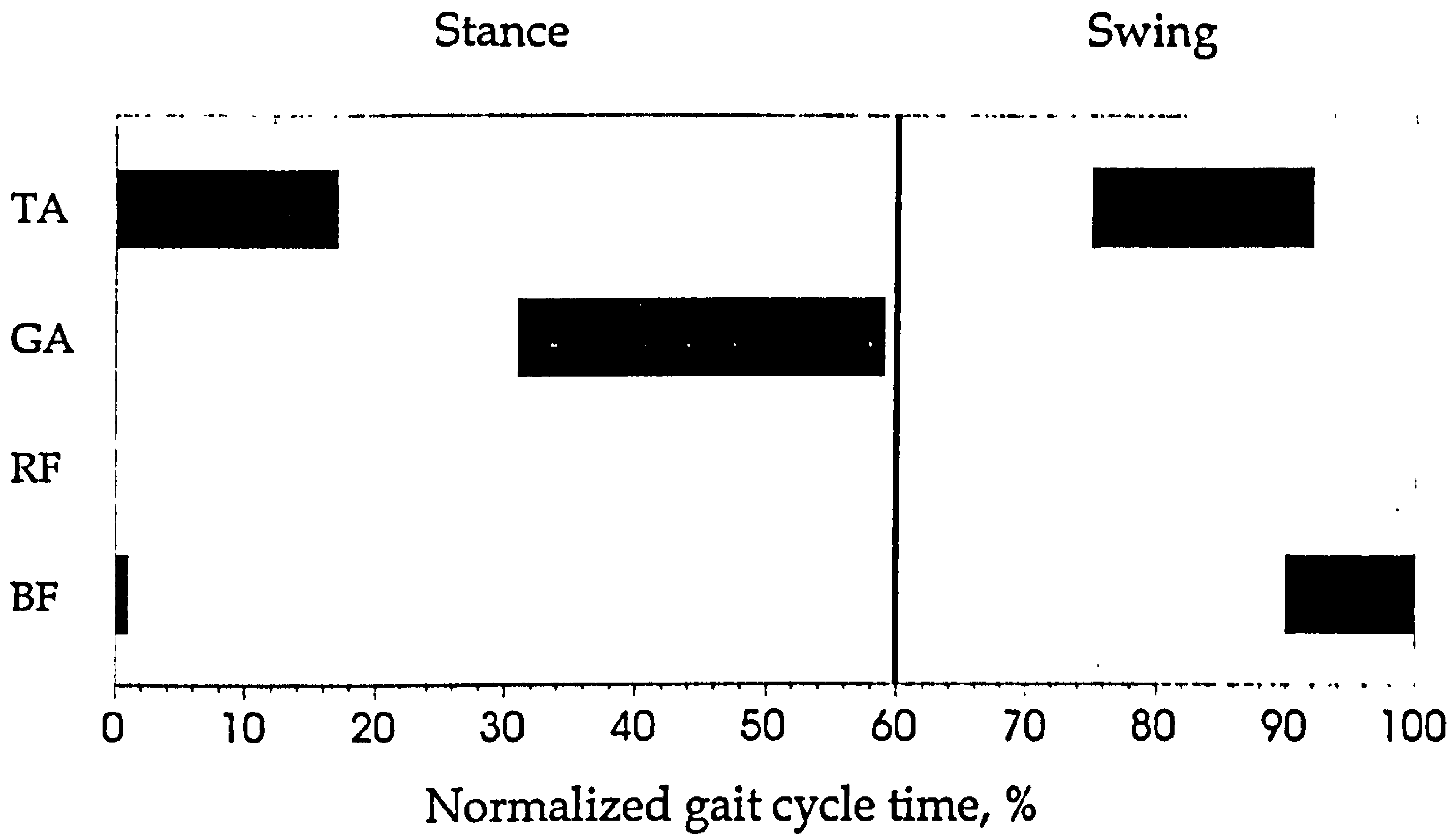


Figure 5.14a Normal walking, slow speed. This diagram represents the phases of the gait cycle where the four major surface muscles in the lower leg are producing force.

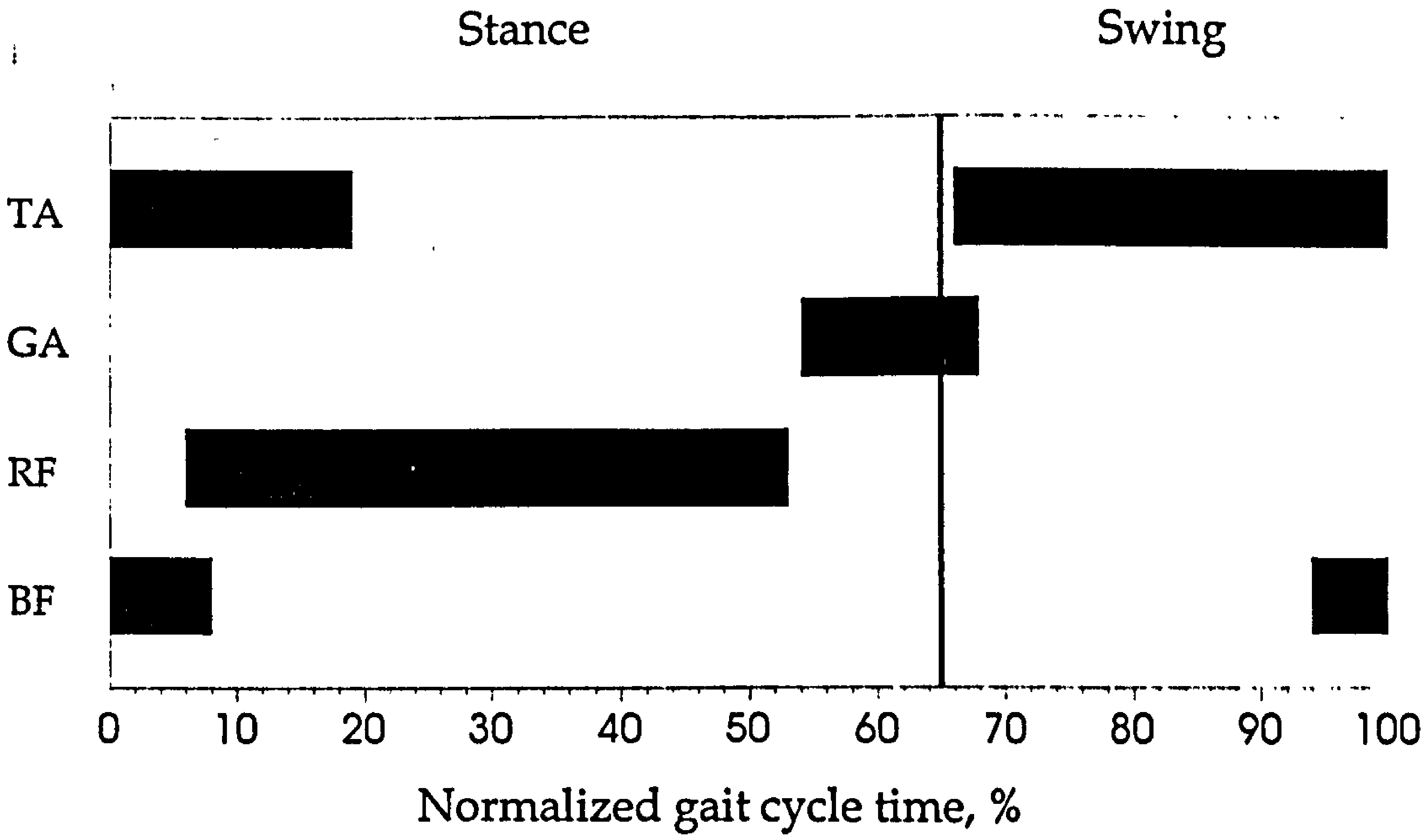


Figure 5.14b BHBK walking, slow speed. This diagram represents the phases of the gait cycle where the four major surface muscles in the lower leg are producing force.

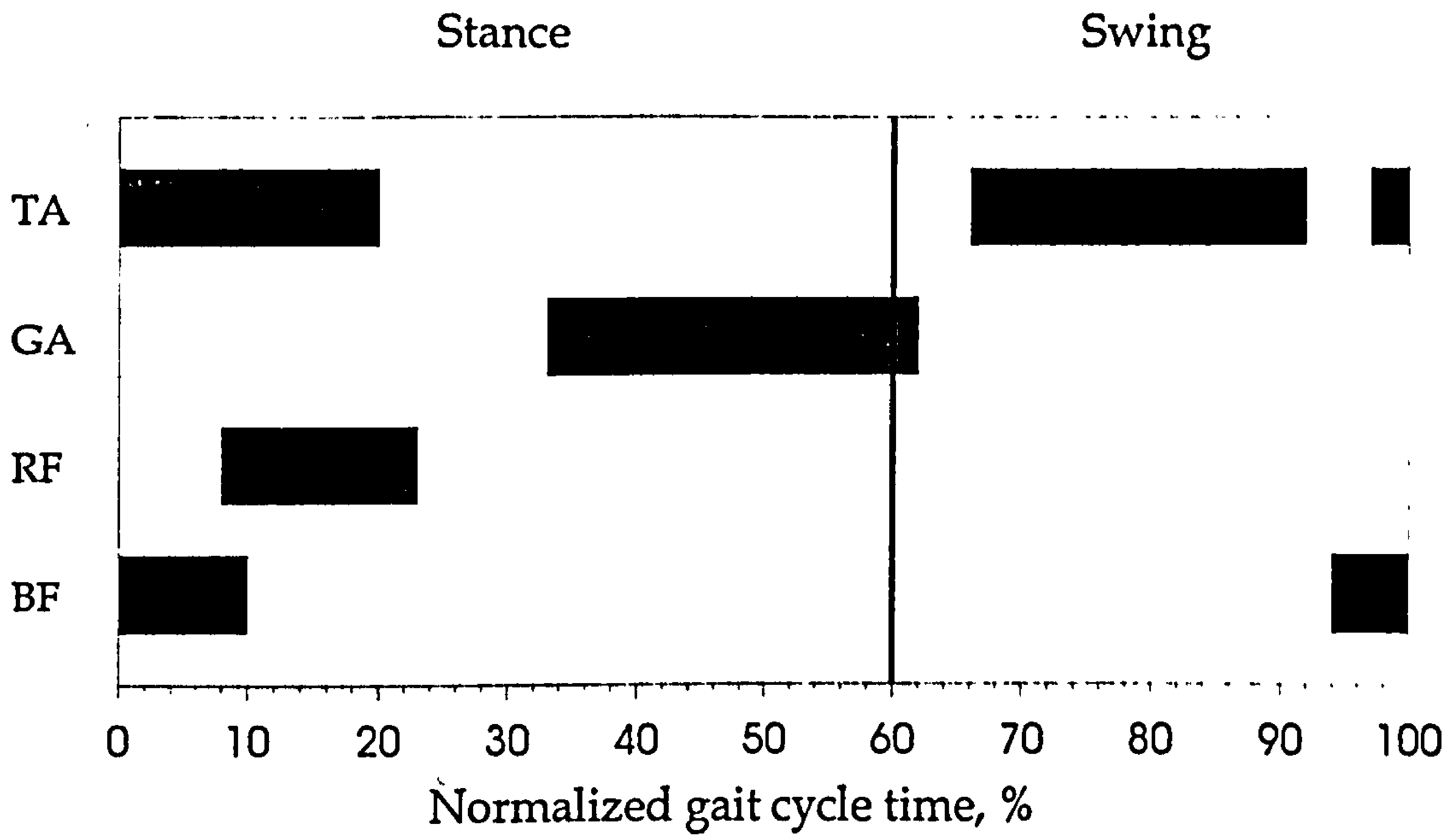


Figure 5.15a Normal walking, medium speed. This diagram represents the phases of the gait cycle where the four major surface muscles in the lower leg are producing force.

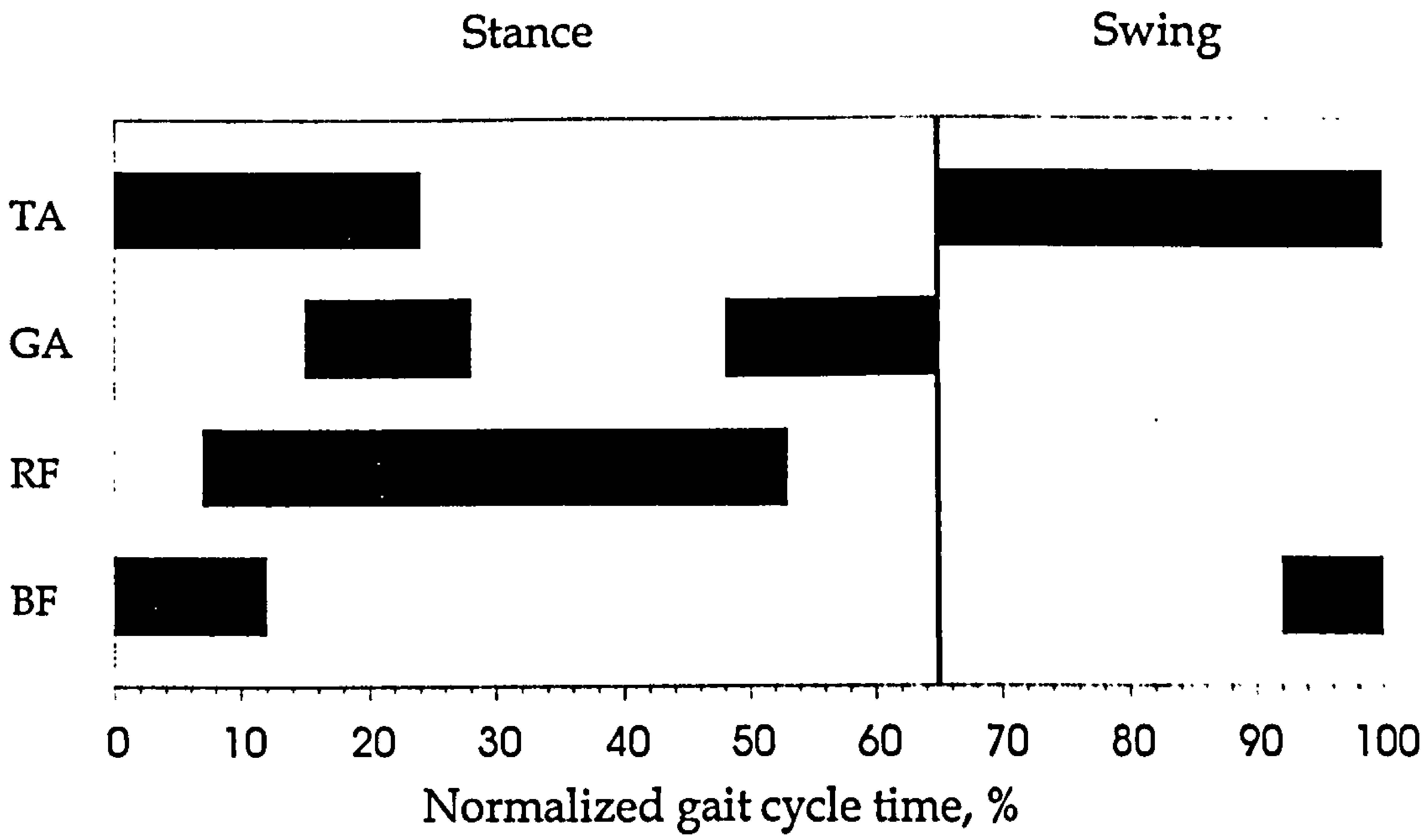


Figure 5.15b BHBK walking, medium speed. This diagram represents the phases of the gait cycle where the four major surface muscles in the lower leg are producing force.

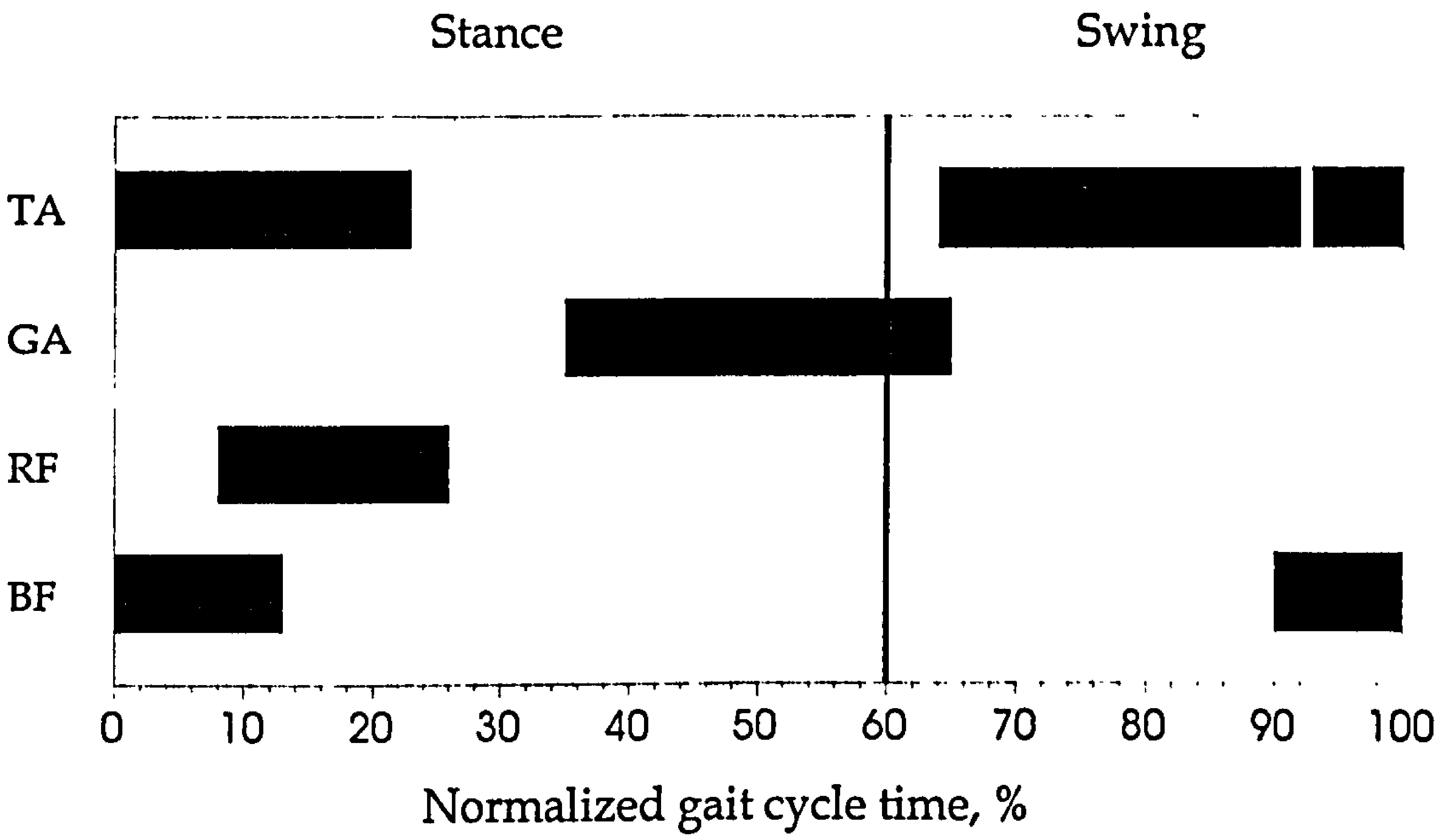


Figure 5.16a Normal walking, fast speed. This diagram represents the phases of the gait cycle where the four major surface muscles in the lower leg are producing force.

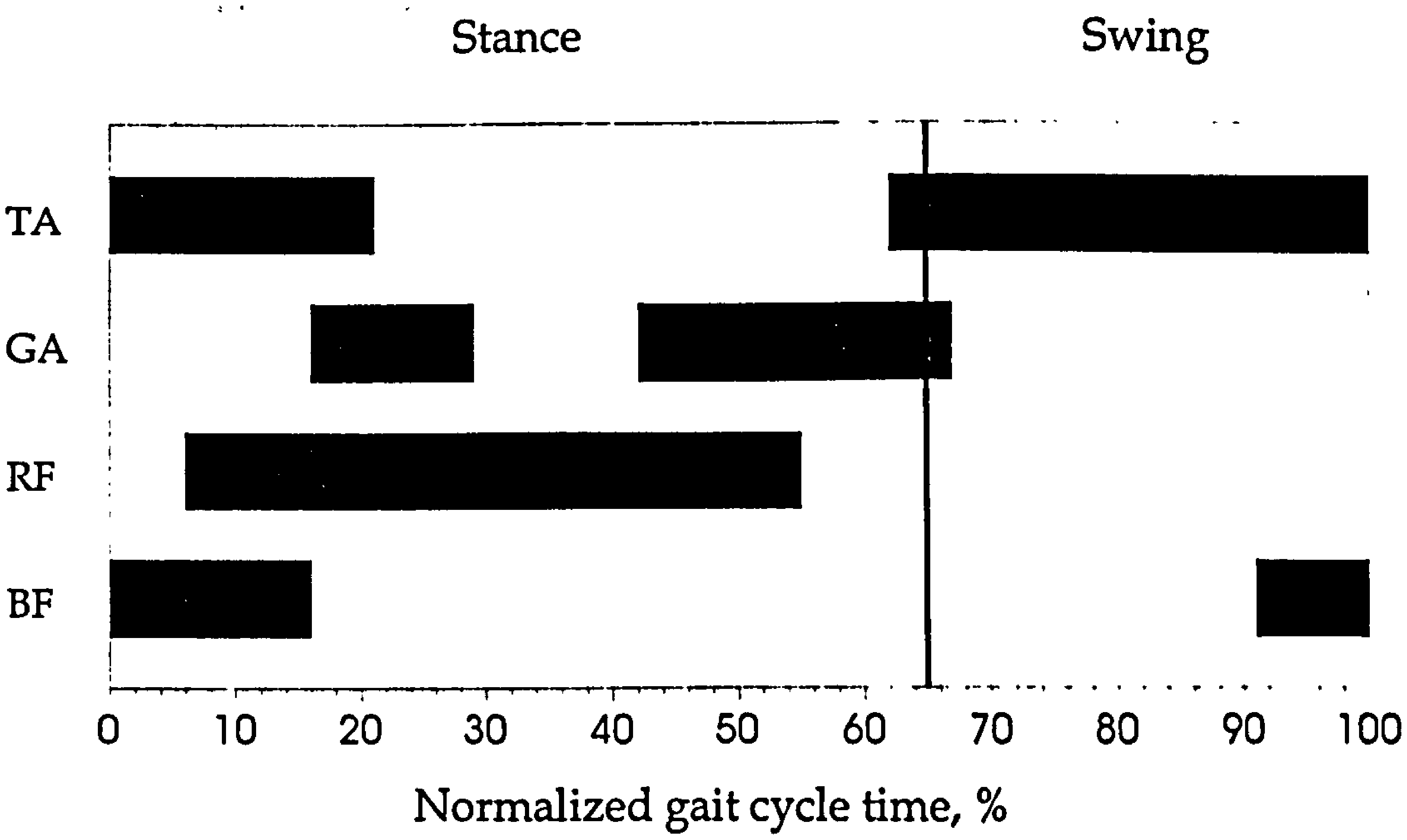


Figure 5.16b BHBK walking, fast speed. This diagram represents the phases of the gait cycle where the four major surface muscles in the lower leg are producing force.

From Figures 5.14 to 5.16 (a and b) it seems that rectus femoris (RF) in particular is producing force for a greater part of the gait cycle during BHBK walking. Using Prilutsky and colleague's methodology, RF produces force throughout 40 to 50% of the gait cycle at all speeds during BHBK walking. During normal walking, for comparison, RF only produces force during medium and fast walking for about 10 to 15% of the gait cycle. During stance in medium and fast BHBK walking, gastrocnemius (GA) produces force throughout 25 to 35% of the gait cycle, similar to the force production during normal walking. However, simultaneous force production for RF and GA is apparent during BHBK walking at medium and fast speeds. According to Prilutsky and colleagues (Prilutsky et al., 1996; Prilutsky and Zatsiorsky, 1994), co-activation of two-joint muscles located on adjacent segments and crossing the same joint from opposite sides (i.e. antagonistic muscles), can result in the transfer of mechanical energy between joints. Simultaneous activation in the current study occurs between RF and GA at 15 to 25% and 45 to 50% of the gait cycle during medium speed BHBK walking. During BHBK fast walking simultaneous activation occurs at 15 to 25% and 42 to 54% of gait cycle time. In contrast, no simultaneous force production in RF and GA can be identified from EMG during normal walking at any speed. Simultaneous force production of opposing muscles also occurs for tibialis anterior and gastrocnemius during medium and fast BHBK walking; and in RF and BF at all speeds during BHBK walking. Note, however, that co-activation of rectus femoris and biceps femoris occurs during medium and fast normal walking. Co-activation of antagonistic two-joint muscles thus accounts for about 2% of the total gait cycle during normal walking (medium speed), but 23% of the total gait cycle during BHBK walking (medium speed).

Muscle	NORMAL WALKING			BHBK WALKING		
	Slow	Medium	Fast	Slow	Medium	Fast
TA	32	49	58	53	57	59
GA	28	29	30	14	30	38
RF	-	15	18	47	46	49
BF	11	16	23	14	20	25
TOTAL	71	109	129	128	153	171

Table 5.2 The percentage of gait cycle for which each muscle is active, at each speed. Percent of gait cycle each muscle is active is then summed to produce total number of gait cycle units for which force is produced during each speed and posture.

In summary the total force difference between during normal and BHBK walking is shown in Table 5.2. During slow walking a BHBK posture leads to an increase from 71 to 128 units (80% increase), during medium walking BHBK produces an increase from 109 to 153 units (40% increase) and during fast walking BHBK produces an increase from 129 to 171 units (33% increase). Therefore the largest difference between normal and BHBK walking in the estimated time during which the muscles are producing force occurs at the slowest speed.

5.5 Discussion and Conclusions

Despite many years of research, the function of muscles during human locomotion is still not fully understood. Muscles reported to function during a particular stage of the gait cycle may not necessarily always be recruited during that phase. Patterns of muscle activity may also vary enormously between individuals.

This study endeavoured to record the activity of major superficial muscles of the lower limb during both normal and BHBK walking in humans. As protocol, electrode placement and normalisation methodology differs from study to study, it is difficult to compare data between studies. However, EMG data collected during this study for normal walking are fairly consistent with previously reported human EMG during walking. Data was given, for the rectus femoris muscle specifically, by Carlsoo and Fohlin (1969). They reported only minimal activity in rectus femoris in the final part of the swing and the first part of support, and suggested it may be entirely passive during gait. In the present study, during slow walking, rectus femoris was indeed found to display a peak of only 15% of MVC, corresponding to minimal activity. Greenlaw (1973) reports biphasic activity in rectus femoris, with a burst after heel strike and another during second double support, just before toe off. This, again, is consistent with rectus femoris activity recorded during fast walking in the current study. Carlsoo (1972), Greenlaw (1973) and Herman et al. (1973) report activity of the long head of the biceps femoris at the end of the swing phase and into early support, around heel strike: indeed, again, the long head of biceps femoris shows highest activity during the swing phase in the current study. However, Ishida et al. (1985) report high activity at heel strike, and slight activity is reported to continue throughout the stance phase. There was also an inconsistent burst reported by some authors (Carlsoo, 1972; Greenlaw, 1973 and Ishida et al., 1974), recorded at the end of stance, just before double support. This is consistent with the present study, and levels of activity did not increase above 10% MVC during this burst.

Ishida et al. (1985) only report low activity at heel strike for tibialis anterior. In the current study, normal walking produced moderate to high activity during heel strike, but activity is also noted during the swing phase (see section 5.4.2).

The same report reports activity in gastrocnemius lateralis during the latter half of stance phase. This agrees with data recorded in the current study. Data for GA (calculated as %MVC) was consistently higher in the current study than reported in the literature. The development of an MVC in GA was more difficult for subjects than in other muscles, although the resistance given was as large as possible, in the form of human weight. This phenomenon has also been recorded in previous research (Okada, 1972), who speculates that this phenomenon could be due to the specificity of the mechanical situation (when recording the MVC), as well as to the superior strength of this muscle.

Results from the current study indicate that as speed increases, peak muscle activity increases, but general activity patterns remain similar. The increase in activity with speed was noticeable for both gaits, but in both cases differences were more pronounced between the medium and fast gaits. An increase in muscle activity with speed is expected, due to conclusions made in previous studies that peak force in limb extensors increases with speed (Taylor, 1985). When muscle forces approach peak force during one gait, it is necessary to redistribute this force over time, usually resulting in a change to another gait (i.e. walking to running). The large increase in muscle activity in this study from medium to fast walking speeds, especially in the

BHBK gait, indicates that the subject may be more 'efficient' running at that speed ($2.0\ m{\cdot}s^{-1}$ in the current study).

The major differences seen in muscular activity between normal and BHBK walking of those muscles tested were detected in the rectus femoris and gastrocnemius muscles: activity increases in RF during BHBK walking, but decreases in GA.

Results of this preliminary EMG data show that the BHBK gait produces an increase in activity of tibialis anterior throughout swing, but especially at terminal swing, a point when it is inactive during normal walking. This is likely to be due to increased dorsiflexion during the BHBK gait, so that tibialis anterior has to be active for longer to lift the foot clear of the ground, while the ankle is still substantially dorsiflexed.

A decrease in gastrocnemius activity is noticeable during BHBK walking, probably again due to the increased dorsiflexion. Gastrocnemius may therefore cease to act as a plantarflexor of the ankle during BHBK gait. The gastrocnemius normally creates propulsive force during the end of stance. The lack of activity in gastrocnemius, which occurs during BHBK walking, implies that the propulsive forces in BHBK gait come from other muscles.

BHBK walking causes high levels of activity in the rectus femoris, which are almost continuous throughout stance phase. As both the hips and knees are flexed during the BHBK gait, RF seems to be acting isometrically to maintain this posture. However, the high and sustained activity in RF could be also due to RF replacing the function of GA in producing propulsive forces during stance. This agrees with data collected by Sutherland and colleagues (1988), which showed that a loss of activity in ankle plantarflexors (such as gastrocnemius) causes prolonged activity in RF. On the other hand, straight knees during stance allows for only a very small amount of activity in the knee extensors (Alexander, 1991). However, flexed knee gait increases activity in knee extensors, which presumably play an important role in regulating the knee flexion characterising BHBK gait, and work to counteract gravity in eccentric contraction. The increased length of activity in RF toward the end of stance may point towards RF acting to straighten the knee and thereby beginning to lift the heel passively at terminal stance (around 40% gait cycle, see Figure 5.10) prior to the start of swing. Rectus femoris also shows increased activity during hip flexion. This is likely to be due to the leg being lifted while still underneath the body. The pendulum action ceases to function in BHBK gait, and therefore the hip muscles and possibly RF would have to work actively to bring the leg forwards during swing.

In addition to a normal peak of activity in biceps femoris prior to heel strike to aid in decelerating the leg ready for heel contact, BF shows an increase in activity in mid to late stance during BHBK gait. This peak of activity is sometimes apparent during normal walking (Basmajian and De Luca, 1985), but is consistently present during BHBK walking. The BF may be acting in a BHBK gait to support the inclined upper body and also aid in propelling the body by knee flexion (Yamazaki et al., 1979). The long head of the biceps femoris works to stabilise the hip joint during a flexed joint gait, since a two joint muscle is more effective as a stabiliser of the joint than a one joint muscle (Ishida, 1991). It is likely that biceps femoris is also acting to counteract the increasing activity in rectus femoris during BHBK gait (ref??) as well as helping to stabilise the knee and hip joints.

Within this study, the muscle activity patterns during human BHBK walking seem quite similar to those reported in chimpanzee bipedal walking, by Ishida et al. (1974). In both, there is simultaneous contraction of the hip and thigh muscles, with delayed activity in the gastrocnemius. However, the human EMG still displays biphasic and triphasic patterns of activity of muscles during BHBK bipedal walking (as occurs during normal upright walking), whereas non human subjects (such as the common chimpanzee and the gorilla) display uniphasic patterns of activity (Tuttle et al., 1979a). Data also show similarities with human walking on an upward slope with an increase in quadriceps femoris and biceps femoris activity during stance. The knee flexion characteristic of BHBK gait may to some extent mimic the increased knee flexion and dorsiflexion with increasing grade (Lange et al. 1996).

In normal dynamic movement, very little work is done by the muscles against gravity. The momentum of the body and the pendular motion of the limbs (see section 1.5), allow for a smooth exchange of energy. In the BHBK gait the combination of a crouched posture with flexed knees requires that the quadriceps does extra work against gravity. This is similar to the case in some children with cerebral palsy (Winter, 1990). The best way to quantify this deficit would be using EMG, however at present it is impossible to accurately gauge the actual mechanical work done by the muscles from EMG data. The energy cost of muscle contraction for individual muscles would need to be quantified and calibrated against EMG data (Winter, 1990). At present no method has been developed to calculate metabolic costs in single muscles. However, Hogan et al. (1998) recently proposed that the duration of muscular contraction can significantly affect both the aerobic and anaerobic metabolic energy cost and fatigue of contracting muscle.

Inefficiency of increased muscle activity during gait

Antagonistic muscles contracting at the same time cause inefficiency. This is sometimes referred to as co-contraction (Winter, 1990). This occurs to a limited extent during 'normal' gait, for example at the ankle joint during walking. It is evident from preliminary data collected in the current study that increased co-contraction does occur during BHBK walking.

The least known cause of inefficiency at the muscular level is the transfer of energy between segments/muscles. This can occur when positive work is being done by one muscle group, while another muscle group does negative work (Winter, 1990). This is similar to co-contraction. During normal walking, it occurs during double-support, when one leg is generating energy for the push-off, while the other leg absorbs energy during weight acceptance after heel strike. The only way to quantify such inefficiency, is to calculate the muscle power at each joint, and calculate the proportion of phases when positive and negative work is being done simultaneously. This type of analysis is currently being done by other members in our research group (Wang, submitted paper).

It is possible that during BHBK walking, some muscles (such as RF) became over stretched beyond the elastic range of the cross-bridges, resulting in energy absorption rather than the elastic recoil more normally expected in the muscle-tendon complex (Baudinette, 1991; Rack and Westbury, 1974).

The EMG data collected during this study was undertaken in order to examine the proposed 'bent-hip, bent-knee' (BHBK) gait in 'Lucy'. This gait was proposed from analysis of anatomical evidence, but also because our closest relatives, the chimpanzees display this characteristic posture during their occasional bipedalism.

No studies, to my knowledge, have previously approached this problem by actually testing the muscular response to this gait in humans. Results of my experiments reveal a substantial increase in overall muscular activity and slight modifications in muscular activity patterns during BHBK walking. The increased flexion during BHBK walking increases foot contact time (the absolute amount of time the foot is in contact with the ground; see section 3.7), and therefore increases the duty factor (the percentage of each stride that the foot is in contact with the ground). High duty factors increase metabolic rate, as a reduction in time in which the leg is swung forward to the next step increases the force and work requirements during the swing phase (Alexander and Minetti, 1997). The probable eccentric contractions occurring in RF functioning to counteract gravity during BHBK gait would cause energy absorption within the muscles surrounding the knee joint. Energy absorbed in muscles that is not used to do work is likely to be stored as heat. Therefore, increased and prolonged eccentric contractions in RF could be linked to the increase in oxygen consumption and increased heat production measured during a BHBK gait (see Chapter 4).

However, the current study was neither comprehensive in the locomotory muscles studied, nor did it include enough subjects for reliability and statistical significance, hence more data should be collected.

In summary, it is apparent from this preliminary EMG data that the BHBK gait would probably have been fatiguing and therefore inefficient for early hominids. Therefore the BHBK posture is unlikely to have been practised during habitual gait.

CHAPTER SIX

GENERAL DISCUSSION AND CONCLUSIONS

"It seems unlikely that A.afarensis' morphology would have been preserved in the fossil record if it had not been adequately adapted to the more expensive activities which its niche required"

Crompton and Li (1995)

6.1 General Discussion

The objectives of this study were to assess the energetic cost of a BHBK gait to humans, as the basis of a model to predict the cost of a BHBK gait to early hominids. The energetic and thermal costs to a human walking both normally and with a BHBK posture have been determined in this study, and related to patterns of force production by muscles.

Initially, the energy expenditure in early hominids was estimated using previous estimates of body weight found in the literature. Total daily energy expenditure was estimated from body weight at 11209 $kJ \cdot day^{-1}$, of which between 8.8 and 17.5% is due to the cost of locomotion. It is likely that resting metabolic rates are underestimated when using the methods set out in Chapter 3, originally proposed by Karasov (1992). Katzmarzyk, 1996 stated that a substantial increase in energy expenditure (34%) can be assumed if animals live in an environment with a temperature greater than 25 °C (section 1.7). It is likely, therefore, that estimates calculated for total energy expenditure for *A. afarensis* in Chapter 3 are underestimated. As it is not possible to gauge the level of necessary correction to the total energy expenditure, the current estimate for total energy expenditure in *A. afarensis* given in this study should be considered as minimum daily energy expenditure.

Results from measurements of oxygen consumption in the current study during normal walking estimate a minimum cost of locomotion which agrees with values predicted for a mammal the size of man (Taylor et al., 1970). This contradicts work by Carrier (1984) who stated that the measured values for the energetic cost of locomotion are twice that of predicted values. He quoted a value of 0.212 $ml \cdot kg^{-1} \cdot km^{-1}$, which is not consistent with data collected in this study. Even at the highest speed of walking (2 $m \cdot s^{-1}$), cost of locomotion only approached 0.15 $ml \cdot kg^{-1} \cdot km^{-1}$ (see section 4.5.2).

This study shows that a BHBK posture during walking causes a significant increase in energy cost to humans in the BHBK gait. Oxygen consumption shows a significant increase of approximately 50% during BHBK walking when compared to normal walking. Heart rate shows an average 30% increase during BHBK walking. The physiological cost index of walking doubles during the BHBK gait when compared to normal upright walking. Rate of perceived exertion increases by two units for the same speed during a BHBK gait.

The thermal cost of a BHBK gait is significantly increased from that measured during exercise in an upright posture. The total increase in temperature during an exercise routine totalling half an hour is more than twice that of normal walking during the BHBK gait. In modern humans temperature regulation is effective between ambient temperatures of 10 and 30°C, where an increase in metabolism and ambient temperature is usually counteracted by evaporative sweat losses (Gisolfi and Wenger, 1984). As discussed in Chapter 4 (section 4.6.2), the higher the ambient temperature, the lower the activity must be in order to maintain a thermal balance and hence not expose our body to heat stress. The converse in also true, i.e. the lower the ambient temperature, the higher the activity level must be in order to retain a thermal balance (Fanger, 1970). Therefore when studying an environment with high ambient temperatures (e.g. >30°C), it is expected that its' inhabitants will display fairly low activity levels in order to limit thermal stress.

During physical exercise in which most of the major locomotory muscles are being employed maximally, the metabolic heat production can increase by a factor of 10 or more (equal to a work load of 500 W/m^2 {430 kcal/m^2}; Werner, 1993). Metabolic heat production during BHBK walking was estimated by measuring core temperature increase during exercise. During half an hour of sub-maximal exercise in a BHBK posture, the increase in core temperature was double that during exercise in an upright posture. A total increase of 0.7°C in core temperature resulted. If core temperature increases by 3.0°C or more, the central nervous system begins to fail, accompanied by circulatory failure, leading to irreversible tissue damage and death (Nadel, 1977). Nielsen et al. (1990) reported that it is indeed the rise in core temperature (rather than blood flow or substrate availability) during exercise in a heat-stressed environment (40°C) which forces an individual to discontinue exercise. The total time for recovery from exercise in the BHBK gait was estimated at 47 minutes for half an hour of exercise. Therefore a recovery period totalling approximately 150% of the time spent active should be assumed for individuals using the BHBK gait.

Taylor and Rowntree (1973b) estimated that sprinting cheetahs would refuse to run once their body temperature reached a critical level (40.5 °C). This would enable the cheetah to run for 1 km, which approximates the actual distance they pursue their prey in the wild. It seems in this case that fatigue is not as important as body temperature in determining how long the cheetah will run. It is possible that this may have also been true for early hominids, which would indicate that the significant rise in core temperature during BHBK may limit the amount of activity feasible during one day.

This study shows comparative results to estimates of energy expenditure and thermal stresses for BHBK walking to estimates produced by a computer model of 'Lucy'(see section 2.1). These results also agree with estimates calculated from predicted muscle power output in a study by Ishida (1991). Energy expenditure estimates from muscle power for joint-flexed walking were 216 percent higher than for normal walking (Ishida, 1991). EMG data for BHBK walking also correspond favourably with synthesised muscular force production of ape-type of walking in man by Yamazaki et al. (1979), where high muscular forces were predicted for ape-type walking in man for biceps femoris and the quadriceps femoris during stance. The increased cost of a flexed gait in the present study also agrees with the increased mechanical work cost of increased knee flexion during walking measured by Winter (1983). Winter predicted that the increase in work cost was due to the increase in bone-on-bone forces as knee flexion increases.

Results of the present study also agree with studies concerning increased compliance (i.e. increased knee flexion) in running gaits (McMahon, 1985; McMahon et al., 1986), where compliance increases oxygen consumption, and hence metabolic power, by approximately 50% due to increased anti-gravitational forces within the leg muscles.

After assessing early hominid morphology (see section 1.3.6) it does not appear that it would have been very difficult for early hominids to adjust their walking posture to upright bipedalism (Ishida, 1991). A postural adjustment such as this may have been effective in prolonging the foraging periods of early hominids. Since bipedalism may have also had some additional survival value (see section 1.2.), it seems that the Hominidae would have been more likely to have been fully upright behavioural bipeds (Ishida, 1991).

As determined in Chapter 5, the BHBK posture requires a substantial muscular stress in order to maintain equilibrium. During sprinting, muscles involved in locomotion are required to produce high speed and therefore a high power output. However, during sustained locomotion, muscles are required to be efficient and fatigue resistant (Alexander and Goldspink, 1977). During normal upright walking, 48-70% of the total energy used in locomotion comes from the transfer between kinetic and potential energy (Cavagna et al., 1976; Taylor, 1980). This leaves only 30-52% of energy to be supplied by the muscles. During BHBK walking, it is likely that less than half of the energy recovery from the pendulum motion of bipedal walking occurs (Wang et al., submitted paper), hence forcing the leg muscles to do proportionally more work (a substantial amount of which may not be positive mechanical work, see section 2.1) totalling 65-75% of the total energy input. It is therefore likely that the uneconomical BHBK bipedal posture could be not maintained for a long time in the early hominids. This type of locomotion, therefore, cannot represent sustained (habitual) bipedalism. For this reason, it seems very unlikely that this BHBK posture would have been a precursor of the erect posture seen in modern man (Kummer, 1991). The estimate for standing in BHBK posture is considerably larger than standing in a normal, upright posture. This suggests BHBK standing could prove substantially more problematic than BHBK walking for early hominids.

According to an in-depth biomechanical analysis of the australopithecine body shape by Preuschoft and Witte (1991), bipedal walking australopithecines were probably slow over long distances. Preuschoft and Witte deduced from australopithecine body shape that australopithecine characteristics are ideal for short rapid dashes over a few metres in length, with quick changes in direction.

Jungers calculated a humero-femoral index of 85 for *A. afarensis* (Jungers, 1982), which he indicates is evidence that hominids such as this has a lower stride length, and lower peak velocities, which infers substantial differences in the kinematics from the characteristic bipedal gait of humans. Wolpoff (1983), however argued that Lucy has a relative femoral length within the range of modern humans (see section 3.2). Therefore he concludes that Lucy's limb proportions cannot be used as evidence against a fully striding bipedal gait.

Charteris et al. (1982) reconstructed the gait of *A. afarensis* from the Laetoli footprints. He used the modern human relationship seen between step length, cadence and speed to conclude that these hominids were "strolling", and displayed a short stride length compared to their height. Alexander (1984) calculated walking speeds of hominids from the Laetoli footprints at between 0.53 and 0.75 $m \cdot s^{-1}$, which is consistent with slower walking speeds of modern humans. Tuttle (1987, in Boaz, 1988) confirmed this estimate by calculating walking speeds for hominids also in the slow range of walking speeds seen in modern humans. He estimated a stature of 1.2 m (see section 3.2), and walking speeds of between 0.48 and 0.56 $m \cdot s^{-1}$. Boaz (1988) addressed these slow walking speeds, and concluded that the relatively short lower limbs of *A. afarensis* should be a factor in assessing the relative walking speed of these hominids. By taking into account their short lower limbs, he concludes that if their range of possible walking speeds are taken into account, these speeds may not be particularly slow. Therefore it does not seem that australopithecines were making short rapid dashes at Laetoli (from the footprint evidence), but more likely that this bipedal locomotion was characterised by a sustained fully striding bipedalism of slow to medium walking speed.

It seems from the results of this study as well as evidence from previous studies in our laboratory (see chapter 2) that unless there was some over-riding advantage which offset the problems which accrue during BHBK walking, it seems that early hominids walked with an erect posture with straight knees and hips as soon as they became habitually bipedal. The major features of a bipedal gait would already have been present in an increasingly terrestrial proto-hominid arboreal ancestor (see section 1.3.5), and therefore a transition from arborealism to bipedalism from could have occurred quickly without a transitional phase (as argued by Rodman and McHenry, 1980).

Another possibility is that early hominids did not walk at all, so much as run. In running, the biomechanics are very different. During human running moderate knee flexion is normal, and a large amount of energy can be saved and returned by the elastic recoil of elastic tissues (such as the Achilles tendon, Alexander and Goldspink, 1977). Schmid (1991), however, feels that bipedal running in early hominids would have been unlikely due to the absence of the deltoid complex of the hip. In addition, the Laetoli footprints do not suggest running, since they are characterised by a walking step frequency (see section 1.3). Nevertheless. Carrier (1984) hypothesised that hominids might have been pre-adapted to endurance running for a variety of reasons (i.e. exceptional stamina of modern humans, presence of cholinergic sweat glands, reduced cost of transport, possible respiratory coupling). However, these characteristics are derived entirely from modern humans. More research is needed to determine the mechanics and energetics of hominids running before we can conclude that early hominids ran before they could walk.

It is not necessary in the theme of this thesis to postulate reasons (such as carrying, energetics, foraging possibilities) for the emergence of hominid bipedalism, although ultimately the freeing of the forelimbs from locomotion would have initiated the subsequent evolution of toolmaking and encephalisation in all later hominids. There is a possibility that hominids were scavenging if they did indeed walk upright as suggested by this study, as scavenging favours particular adaptations, one of which is the ability to travel long distances with a low expenditure of energy (Bertram, 1979). Since the rate of food consumption must be at least equal to energy expended during resting metabolism and activity, an estimate for average food consumption an animal must achieve in a day can be derived from total daily activity budgets, assuming oxidative metabolism (Nagy, 1987). Total daily energy expenditure estimated from body weight in Chapter 3 is 11209 kJ·day^{-1}. It can be assumed that this is an approximation to the average daily consumption of food necessary in early hominids. Scavenging meat from carcasses would improve the calorific return for the same amount of foraging effort (Potts, 1984; Bunn et al., 1988; Blumenschine et al., 1994), therefore providing a more effective way of fulfilling metabolic requirements. It is not essential within the confines of this study to be precise about the probable diet of early hominids, except to assert that their diets were likely to be somewhat eclectic, including a wide range of feeding items (Kurland and Beckerman, 1985).

Pennycuick hypothesised that early hominids were animals that attempted to improve the predictability of their food supply by maximising their foraging area. A large foraging radius has consequent selection pressure for a large body size, and locomotor adaptations that allow economical locomotion (Pennycuick, 1979). From ecological evidence (see section 3.4) it is possible that at the time of Lucy and other early hominids, the woodland environment was slowly being encroached by grassland. If this was the case, although savannah environments did not predominate, early hominids would find themselves having to cover long distances on the ground with very little cover when moving between fragmentary areas within the forest. An upright bipedal posture would facilitate economical locomotion between food patches, with the added benefit of having the upper limbs free for carrying, and increased visual distance for predator avoidance. Equally, a flexed hip, flexed knee posture would have limited australopithecines to short periods of activity. Further, the low efficiency of BHBK posture would select in favour of a small, rather than large, foraging radius, and therefore reduces the likelyhood of successful scavenging.

6.2 Conclusions

In attempting to understand the evolution of hominid bipedalism, it is important to study the behavioural and environmental contexts in which habitual terrestrialism first evolved. The research, therefore, must include an examination of these variables within both living humans and our closest living relatives, the great apes (Jablonski and Chaplin, 1994).

An understanding of how modern human bipeds walk is critical in examining the probable sequence in which the first bipedal hominid morphology was constructed (Jablonski and Chaplin, 1994).

The flexed-hip, flexed-knee posture first proposed for early hominids by Napier (1967) and again by Stern and Susman (1983) incurs a high energy cost to modern humans. A doubling in metabolic cost during exercise is apparent during the flexed joint posture. Thermal stresses are also doubled compared to the equivalent amount of exercise in a normal upright posture. Short bursts of locomotion in a BHBK gait may be possible, but due to the high thermal and muscular loads this would induce, a long period of recovery (150% of activity time) would be needed post-exercise. Early hominids adopting such a gait would be limited to small foraging radius and brief periods of activity, both of which make scavenging or hunting unlikely.

It is possible that early hominids could utilise a posture similar to the bipedal postures observed in other, non-human, primates. The bipedal posture seen in common chimpanzees, however, has been discounted for practise in the early hominid, 'Lucy', from data produced by a computer simulation of 'Lucy' walking with common chimpanzee kinematics (see Crompton et al., 1998). Bonobo and lowland gorilla type gaits results in stable walking, however the mechanical power output from these non-human primates is far in excess, even of that during human flexed joint walking (Aerts et al., personal communication). In addition, as no other primate, with the exception of modern humans, employs a fully upright bipedal posture habitually, it is unlikely that a posture showing similarities to non-human primate bipedalism could be employed by hominids on a routine basis. Running in a BHBK bipedal gait is possible, but this has not been researched fully enough (in the mechanical or physiological sense) to make any further decisions concerning running in early hominids.

6.3 Future Work

There are many possible improvements to this study, and a variety of future studies which could help to validate the conclusions set out in this thesis.

Many studies have assessed the locomotor morphology of 'Lucy', but most have concentrated on studying the lower limbs. Wolpoff (1983) investigated the lower limb proportions in Lucy, and concluded that her pelvic and hindlimb adaptations closely resembled those of modern humans, so that she was capable of locomotion in a fully striding bipedal gait. Wolpoff (1983) therefore suggested that the primary differences between Lucy and modern humans may be more apparent in the australopithecine forelimb. It is possible therefore that extending the type of assessment carried out by MacLatchy (1996) on the australopithecine hip, but moving the focus to the upper limbs of australopithecines may help to resolve the current arguments concerning Lucy's morphological adaptation one way or another.

Further direct comparison of bipedal walking in great apes and humans is important. Data should include normal walking with extended joints by humans compared to that of chimpanzees trained in upright walking; but also flexed joint walking, compared to the same in chimpanzees. To my knowledge, such studies have not been carried out previous to the present investigation. Repeating these experiments with weights being dragged (to add a horizontal force), or on a treadmill with a gradual increase in grade would allow the calculation of efficiency of the BHBK gait compared to the normal gait. Simultaneous video recordings (normal and high speed video) were made of each subject during measurement of the physiological variables discussed in Chapter 4, to permit analysis of the kinematics of the BHBK gait and allow kinematics to be correlated with physiological parameters. There was insufficient time, however, to analyse these data. The biomechanics of BHBK walking as a whole could be then be quantified and contrasted to the changes in oxygen consumption data, core temperature and muscle activity. When more data are available regarding the cost to humans of a BHBK gait in both walking and running, more secure inferences could then be made as to the likely postures and gaits of early hominids.

Similar physiological testing of humans trained in a BHBK posture would be invaluable. A single subject (such as presented in this study) does not provide enough data for any solid conclusions about the effect of training upon BHBK locomotion. Humans actually trained in BHBK walking on a treadmill would provide the best solution to this problem. However, the use of skiers (as in this study), fencers, table tennis players or others who regularly use a BHBK posture (children with cerebral palsy) would be also beneficial.

More information on muscle activity of humans walking in a BHBK posture would also be useful. This should include muscle activity data for iliopsoas, the major hip flexor in humans, and all heads of the quadriceps femoris, which extends the knee. Many more subjects would be needed for both human and primate EMG for solid inferences to be made concerning muscle activity changes during a BHBK posture in humans, and for comparison with non-human primate bipedalism. Comparison of muscle activity patterns before and after training would also be desirable, to assess the possibility of an increase in cross-sectional area after training in a BHBK posture.

Finally quantification of muscle efficiency could help to support other physiological data. However, the only way to quantify muscle efficiency is by calculating the muscle power at each joint, and calculate the proportion of phases when positive and negative work is being done simultaneously. This type of analysis is currently being done by other members in our research group (Wang et al., submitted paper). Comparison of this sort of data with measured EMG would be necessary before the full effect of BHBK gait on human locomotor mechanics can be quantified.

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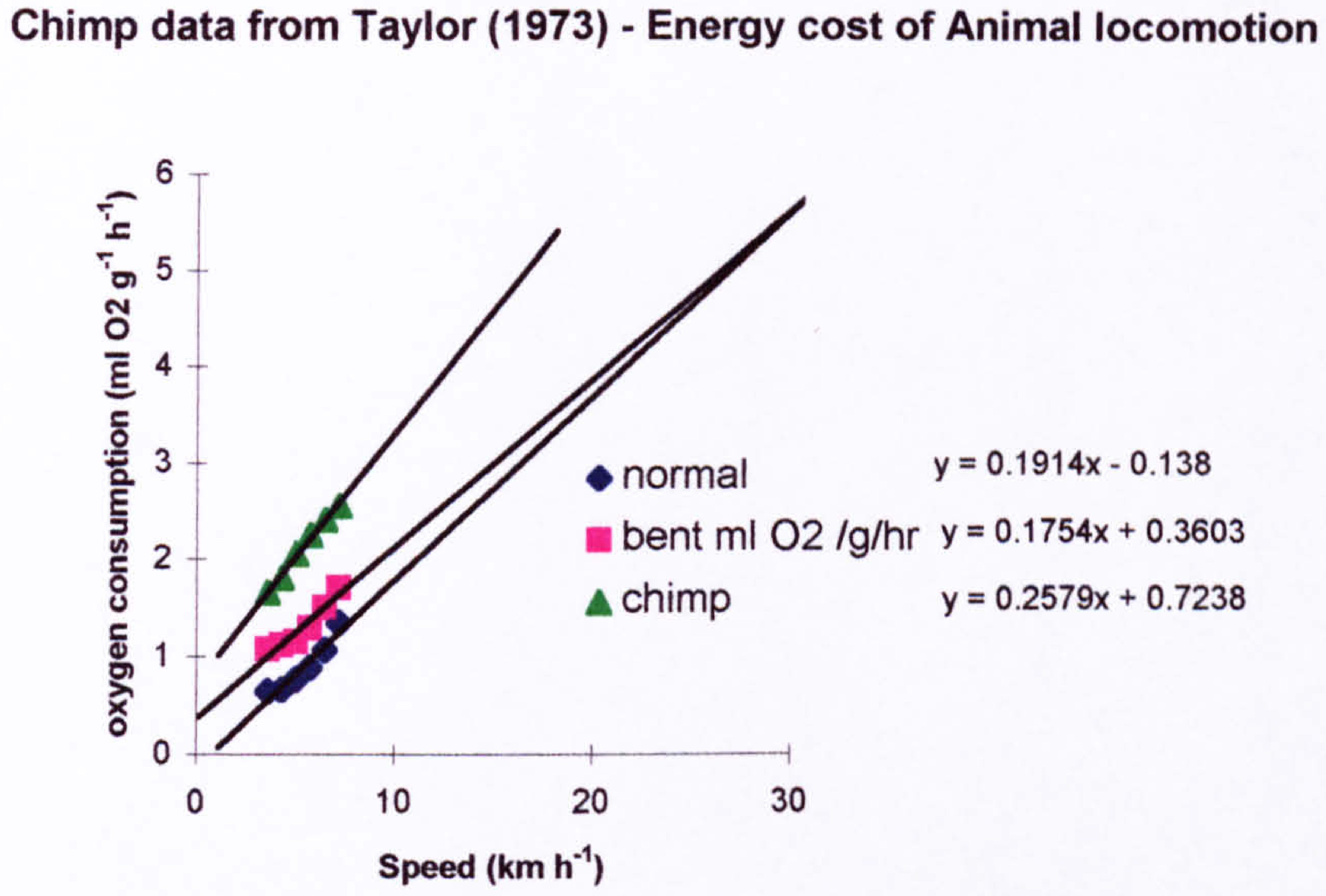
Appendix I

METs	Activity category	Specific category
5.0	Fishing and hunting	Fishing, general
4.0		Digging worms with shovel
2.5		Hunting, bow and arrow
6.0		Hunting, large game
5.0		Hunting, small game
5.0		Hunting, general
2.5	Home activities	Cooking, food-preparation
3.0		Child care, grooming, feeding etc
0.9	Inactivity, quiet	Lying quietly, reclining/Sleeping
1.0		Sitting quietly
1.5	Meetings, talking	Sitting
2.0	Walking	Walking, <2 mph, very slow, not carrying
3.0		Walking, 2.5 mph, carrying <24 lbs
3.5		Walking, 3.0 mph, moderate speed, not carrying
4.0		Walking, 3.0 mph, carrying <25 lbs
4.0		Walking, 3.5 mph, briskly, not carrying
4.5		Walking, 3.5 mph, carrying <25 lbs
5.0		Walking/downstairs/standing, carrying 25-49 lbs
6.5		Walking/downstairs/standing, carrying 50-74 lbs
7.5		Walking/downstairs/standing, carrying 75-99 lbs
8.5		Walking/downstairs/standing, carrying >100 lbs
6.0		Hiking, cross-country
6.0	Running	Jog/walk combination (jogging <10 mins)
7.0		Jogging, general
8.0		Running, 5 mph (12 min · mile^{-1})
9.0		Running, 5.2 mph (11.5 min · mile^{-1})
10.0		Running, 6 mph (10 min · mile^{-1})
11.0		Running, 6.7 mph (9 min · mile^{-1})
11.5		Running, 7 mph (9.5 min · mile^{-1})
12.5		Running, 7.5 mph (8 min · mile^{-1})
13.5		Running, 8 mph (7.5 min · mile^{-1})
14.0		Running, 8.6 mph (7 min · mile^{-1})
15.0		Running, 9 mph (6.5 min · mile^{-1})
16.0		Running, 10 mph (6 min · mile^{-1})
18.0		Running, 10.9 mph (5.5 min · mile^{-1})
9.0		Running, cross-country

Table AI.1 The energy cost of various human activities shown as multiples of 1 MET or RMR. (From Montoye et al., 1996)

MET = ratio of exercise metabolic rate to resting metabolic rate:
1 MET = RMR
5 METs = 5 x RMR

Appendix II



Chimp data from Taylor (1973) - Energy cost of Animal locomotion

Figure AII.1 Oxygen consumption against speed including normal, BHBK walking and also chimp bipedal walking. It should be noted that chimpanzee bipedal walking is higher than both normal human walking and BHBK human walking.

Appendix III

Scaling Ecological parameters to body weight

Ecological parameter	Units	Animal	Source
$DEE = 800\ M^{0.71}$	(kJ/day)	Mammals	(Garland, 1983)
$DEE = 753\ M^{0.67}$		rodents	(King, 1955)
$DEE = 802\ M^{0.66}$		howler monkeys	(Nagy and Milton, 1979)
$ICL = 10{,}678\ M^{0.70}$	(J/km)	Mammals from 0.01 to 260 kg	(Garland, 1983)
$BMR = 293\ M^{0.75}$	(kJ/day)	Mammals	(Garland, 1983)
$DMD = 1.038\ M^{0.25}$	(km/day)	All mammals	(Garland, 1983)
$DMD = 3.877\ M^{0.22}$		Carnivores	
$DMD = 0.875\ M^{0.22}$		Other mammals	
$Hrange = 14.9\ M^{1.083}$	(ha)	Mammals	(Garland, 1983)
$FBD = 436\ M^{0.541}$	(m)	Mammals	(Garland, 1983)
$DFD = 152\ M^{0.28}$	(km/day)	Mammals	(Garland, 1983)
$DFC = 152\ M^{0.738}$	(g/day)	Mammals	(Garland, 1983)
$FG/FB = 0.05\ M^{1.00}$	(g)	Mammals	(Garland, 1983)
FF = DFC / (FG/FB)	(bouts/day)	Mammals	(Garland, 1983)
ECT = 100 * (DMD x ICL)/DEE	in % DEE		(Garland, 1983)
substituting for values from Garland:			
$FF = 3.03\ M^{-0.262}$		Mammals	(Garland, 1983)
$ECT = 1.39\ M^{0.24}$		All mammals	(Garland, 1983)
$ECT = 5.17\ M^{0.21}$		carnivores	(Garland, 1983)
$ECT = 1.17\ M^{0.21}$		Other mammals	(Garland, 1983)

Table AIII.1 Scaling some ecological parameters to body weight in order to estimate total daily energy expenditure. Adapted from Garland (1983), King (1955) and Nagy and Milton (1979)

M = Body mass (kg)
DEE = Daily energy expenditure (kJ/day)
ICL = Incremental cost of locomotion (J/km)
BMR - Resting metabolism (kJ/day)
DMD = Daily movement distance (km/day)
Hrange = Home range area (ha)
FBD = Foraging bout distance (m)
DFD = Daily foraging distance (km/day)
DFC = Daily food consumption (g/day)
FG/FB = Food gained per foraging bout (g)
FF = Foraging frequency (bouts/day)
ECT = Ecological cost of transport (% DEE)

Calculation of ECT as a percentage of TDEE

From above (Table AIII.1), ECT = 100* (DMD x ICL)/DEE

Using data collected in Chapter 3:

Variable	*Homo* model	*Pan* model
ICL ($kJ \cdot km^{-1}$)	215	233
DEE ($kJ \cdot day^{-1}$)	12259	10335
DMD ($km \cdot day^{-1}$)	10	3.9
ECT as %	17.5	8.8

Table AIII.2 Using ecological data estimated for *A. afarensis* to find the ecological cost of transport (i.e. the percentage of energy cost that locomotion uses per day) (see Garland, 1983).

Appendix IV

Calculating total daily energy expenditure (TDEE) using Method A (see section 3.7, page 124) , i.e.:

$$\text{Total Daily energy expenditure } (\text{kJ}\cdot\text{day}^{-1}) = \Sigma\ (\text{activity cost} \times \text{time in activity})$$

where activity cost is a multiple of RMR, (e.g. for resting the activity cost is equal to 1.5 time RMR, totalling 274.5 kJ·hr^{-1}); and the time of activity is the time spent in each activity in hours.

Human model (data derived from !Kung activities, Lee, 1979):

Activity	**Time spent in activity (hrs)**	**Activity cost of activity (kJ·hr^{-1})**	**Total cost of activity (kJ·day^{-1})**
Sleep (RMR)	10	183	1830
Rest	4.5	274.5	1235.25
Gathering/Digging	3.0	732	2196
Tool making/fixing	0.9	457.5	411.75
Subsistence activities	2.4	457.5	1098
Housework (inc. cooking)	2.7	457.5	1235.25
Hunting	0.3	1098	329.4
Visiting	0.2	640.5	1281
Total (kJ·day^{-1})			**9616.65**

Table AIV.1 Activity budgets for human hunter-gatherers as a model for *A. afarensis*

Primate model (data derived from Chimpanzees, Clutton-Brock and Harvey, 1977a):

Activity	**Time spent in activity (hrs)**	**Activity cost of activity (kJ·hr^{-1})**	**Total cost of activity (kJ·day^{-1})**
Sleep	12	183	2196
Rest	3.96	274.5	1087.02
Feed	6.36	457.5	2909.7
Move	1.68	640.5	1076.04
Total (kJ·day^{-1})			**7268.76**

Table AIV.2 Activity budgets for chimpanzees as a model for *A. afarensis*

Appendix V

Conversion of speeds from metres per second to kilometres per hour, for comparison of speeds between Chapters 4 and 5.

m/s	to	km/h	km/h	to	m/s
1		3.6	4		1.11
1.2		4.32	4.5		1.25
1.4		5.04	5		1.39
1.6		5.76	5.5		1.53
1.8		6.48	6		1.67
2		7.2	6.5		1.81
2.2		7.92	7		1.94
2.4		8.64	7.5		2.08
2.6		9.36	8		2.22
2.8		10.08	8.5		2.36
3		10.8	9		2.50

Table AV.1 Conversion of speeds between units of $m \cdot s^{-1}$ and $km \cdot h^{-1}$

APPENDIX VI

Measuring energy cost in locomotion. Extra graphs for comparison between normal and BHBK walking.

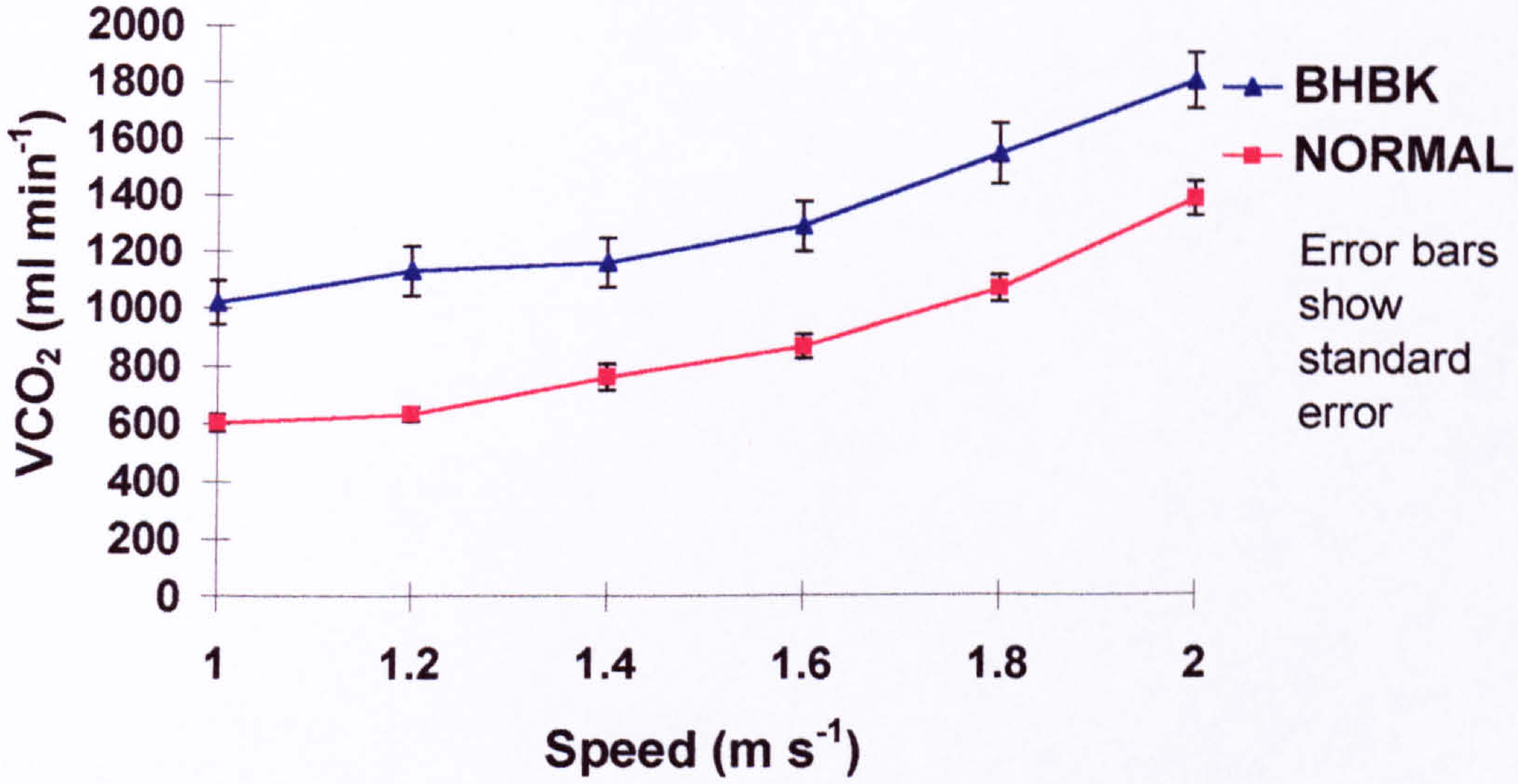


Figure AVI.1 VCO_2 (ml·min^{-1}) against speed (m·s^{-1})

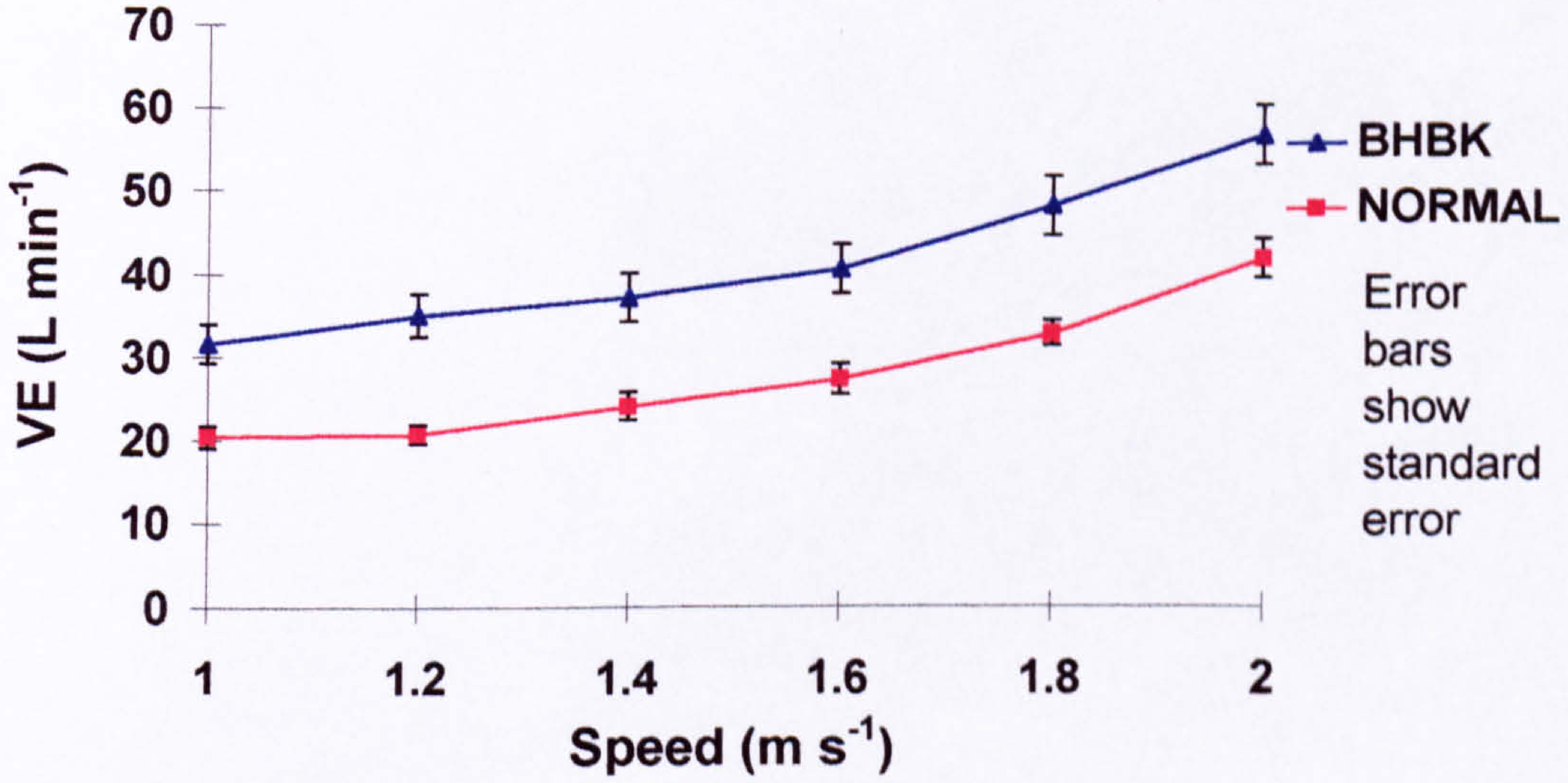


Figure AVI.2 VE (L·min^{-1}) against speed (m·s^{-1})

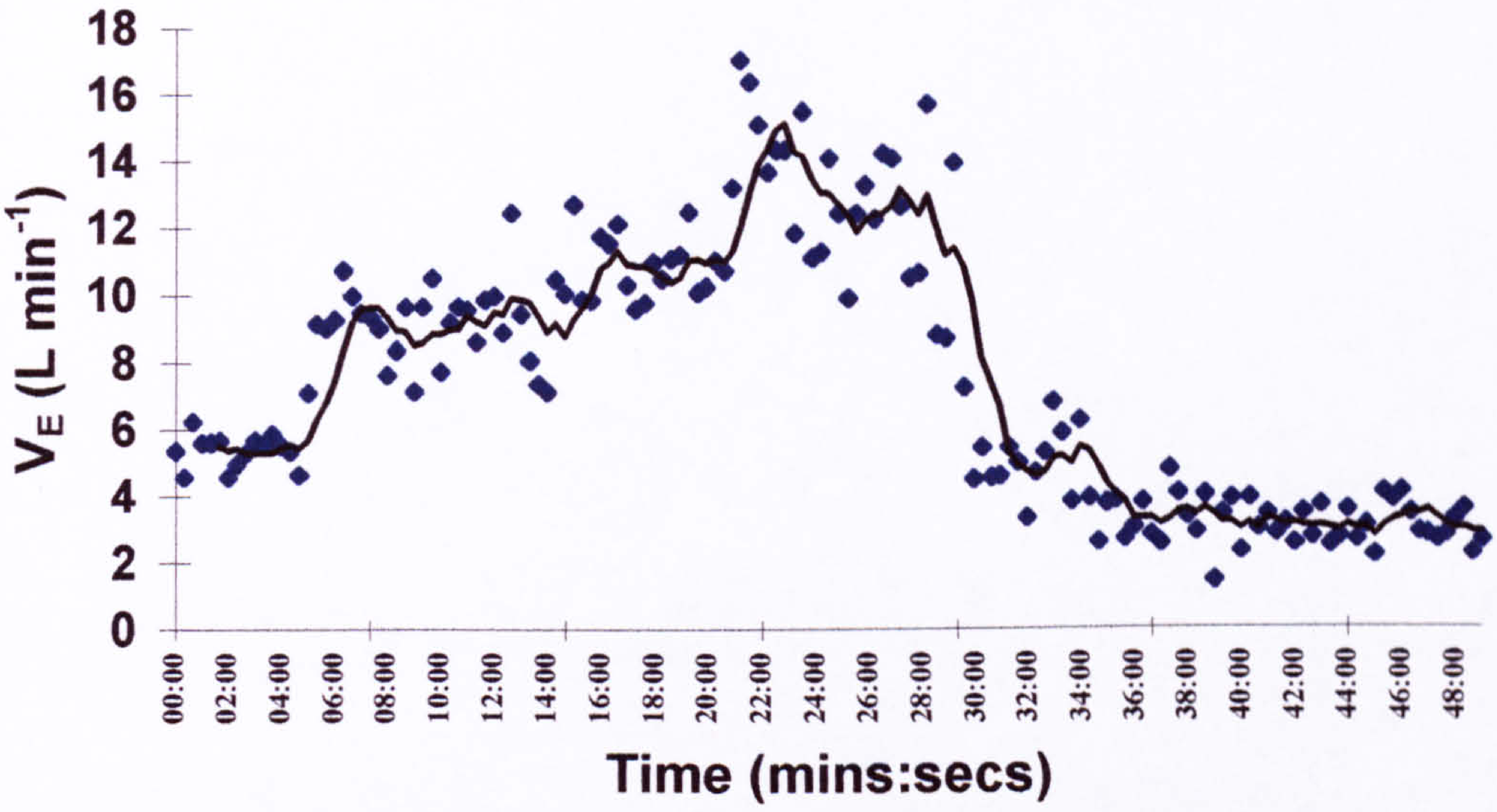


Figure AVI.3 VE against time for **normal walking**. Showing the relationship of VE with time, to predict the ventilatory threshold. A linear relationship can be noted until 21:00, then a non-linear relationship develops. This is estimated as the ventilatory threshold, and appears at speed 1.8 m·s^{-1}.

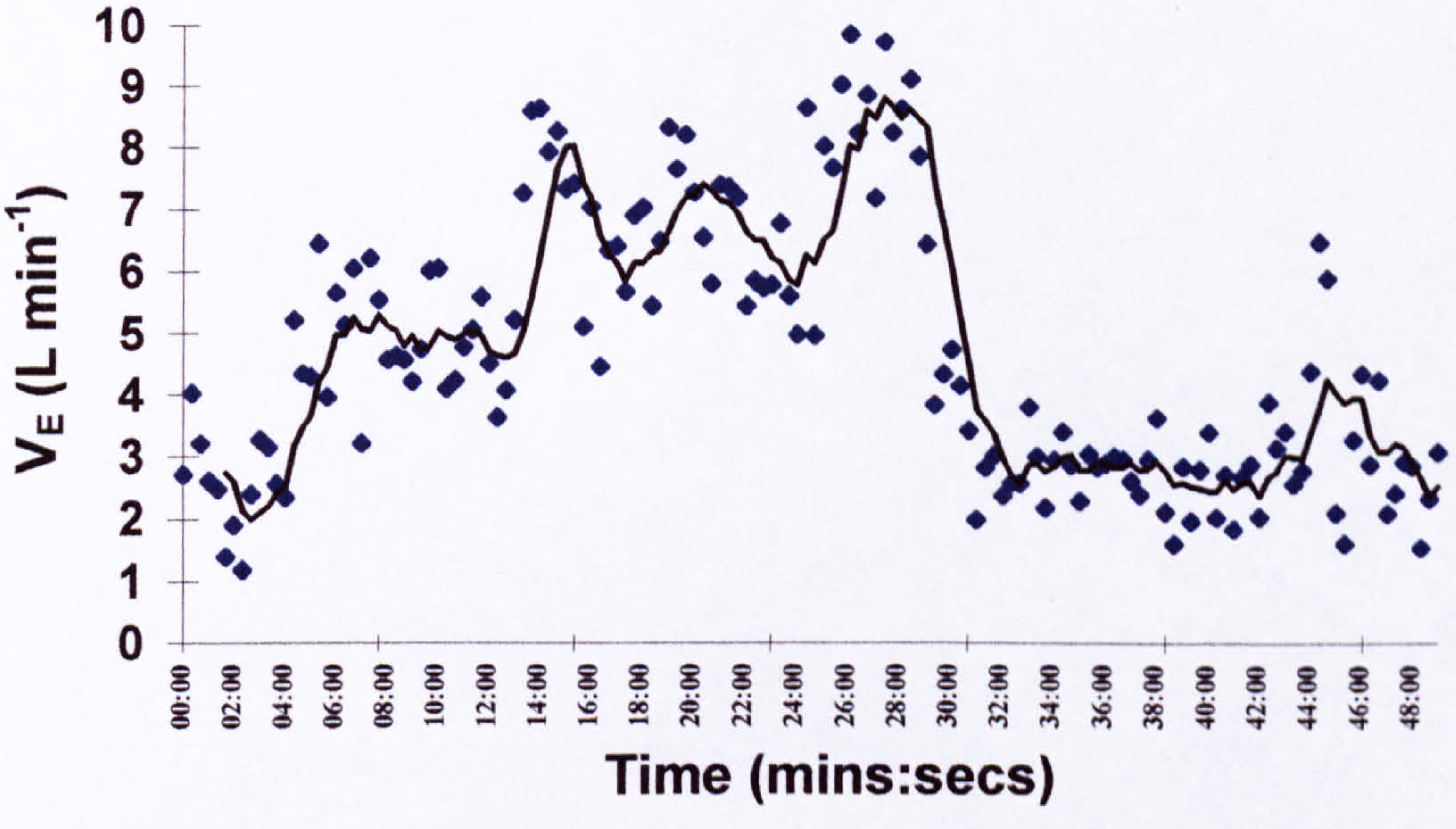


Figure AVI.4 VE against time for **BHBK walking**. Showing the relationship of VE with time, to predict the ventilatory threshold. A linear relationship can be noted until 13:00, then a non-linear relationship develops. This is estimated as the ventilatory threshold, and appears at speed 1.4 m·s^{-1}.

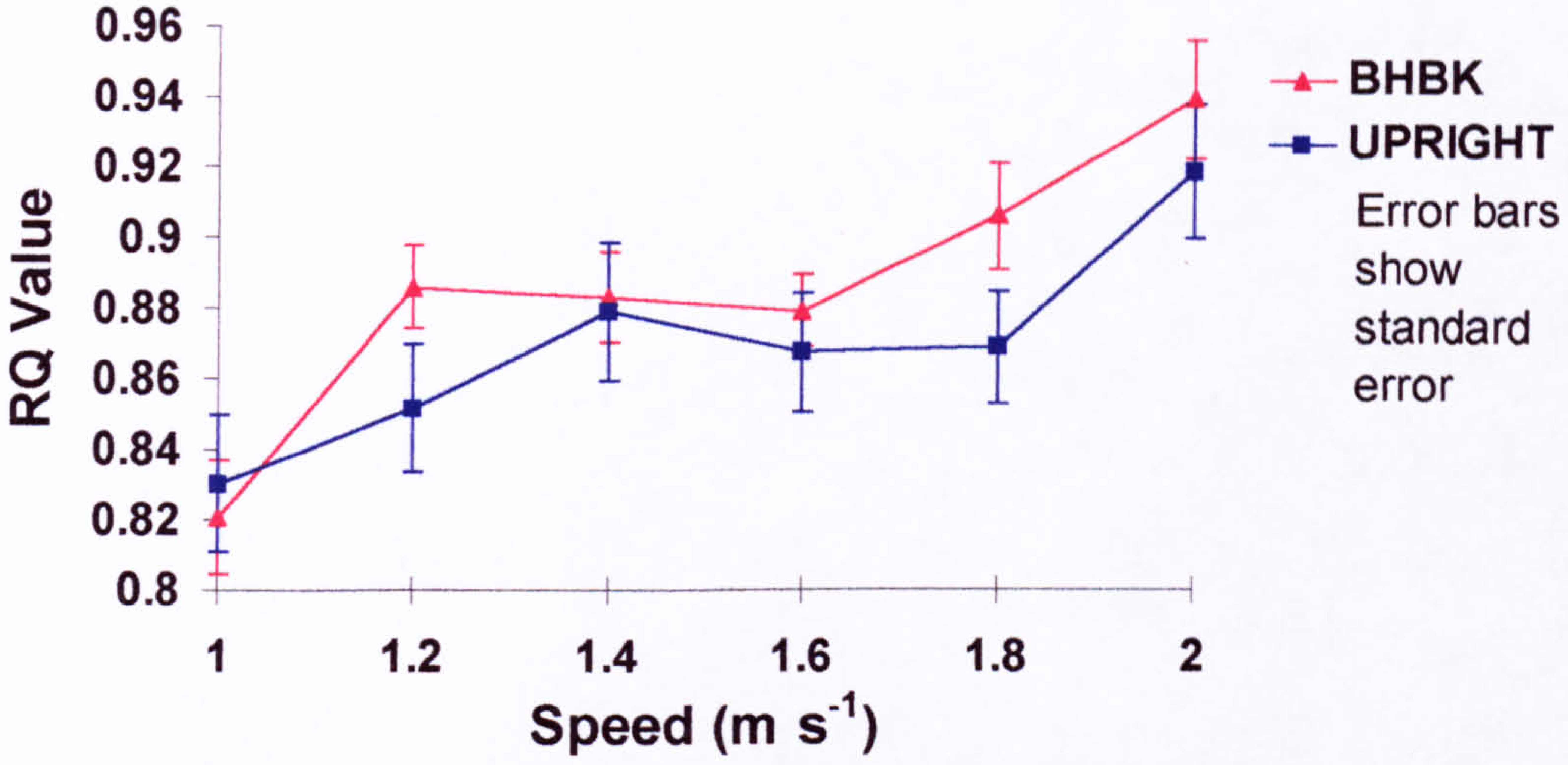


Figure AVI.5 RQ value against speed ($m{\cdot}s^{-1}$) for BHBK and normal walking.

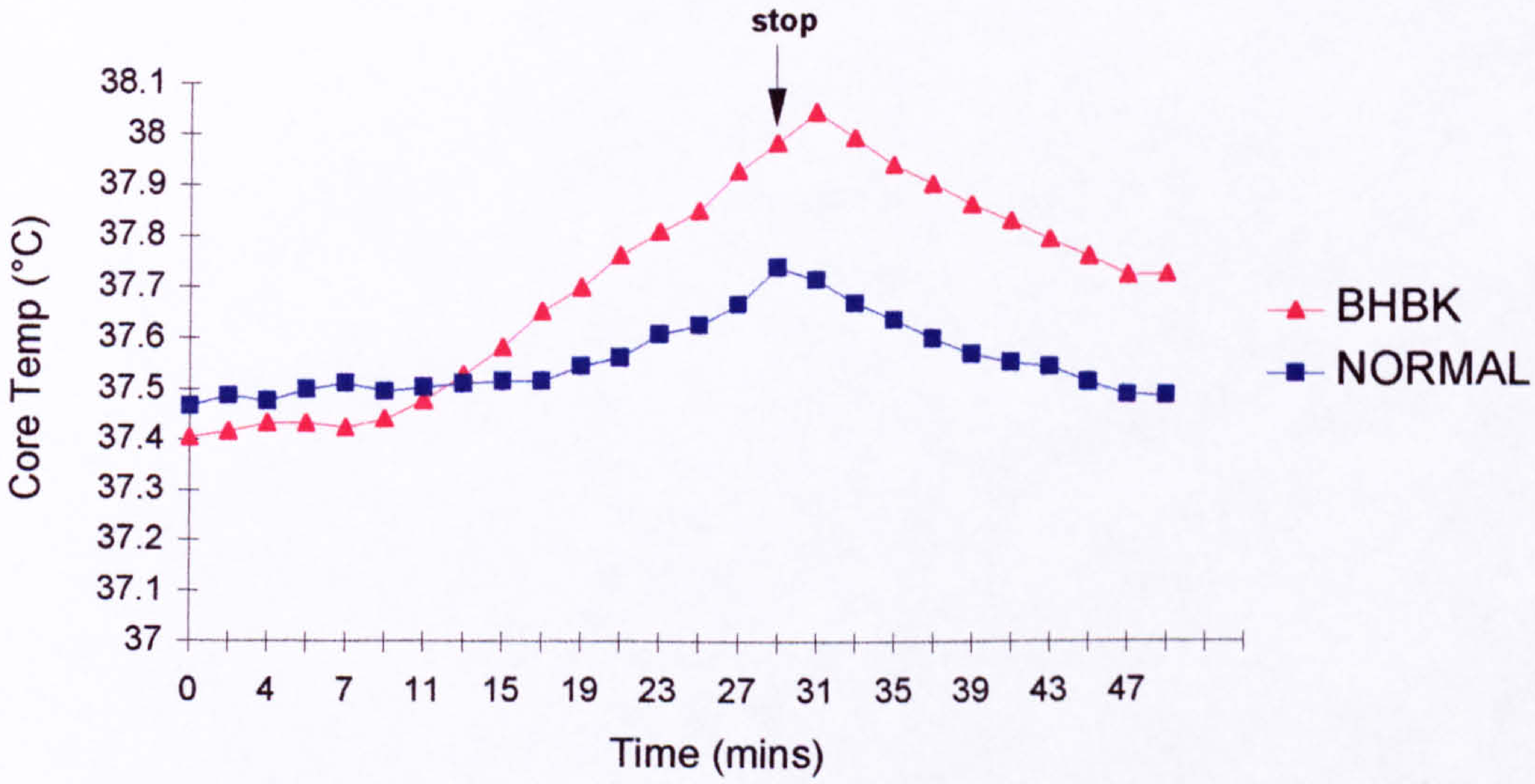


Figure AVI.6 Core temperature against time during normal and BHBK walking. Stop indicates the cessation of exercise (note how the core temperature continues to rise after exercise has stopped during BHBK walking).

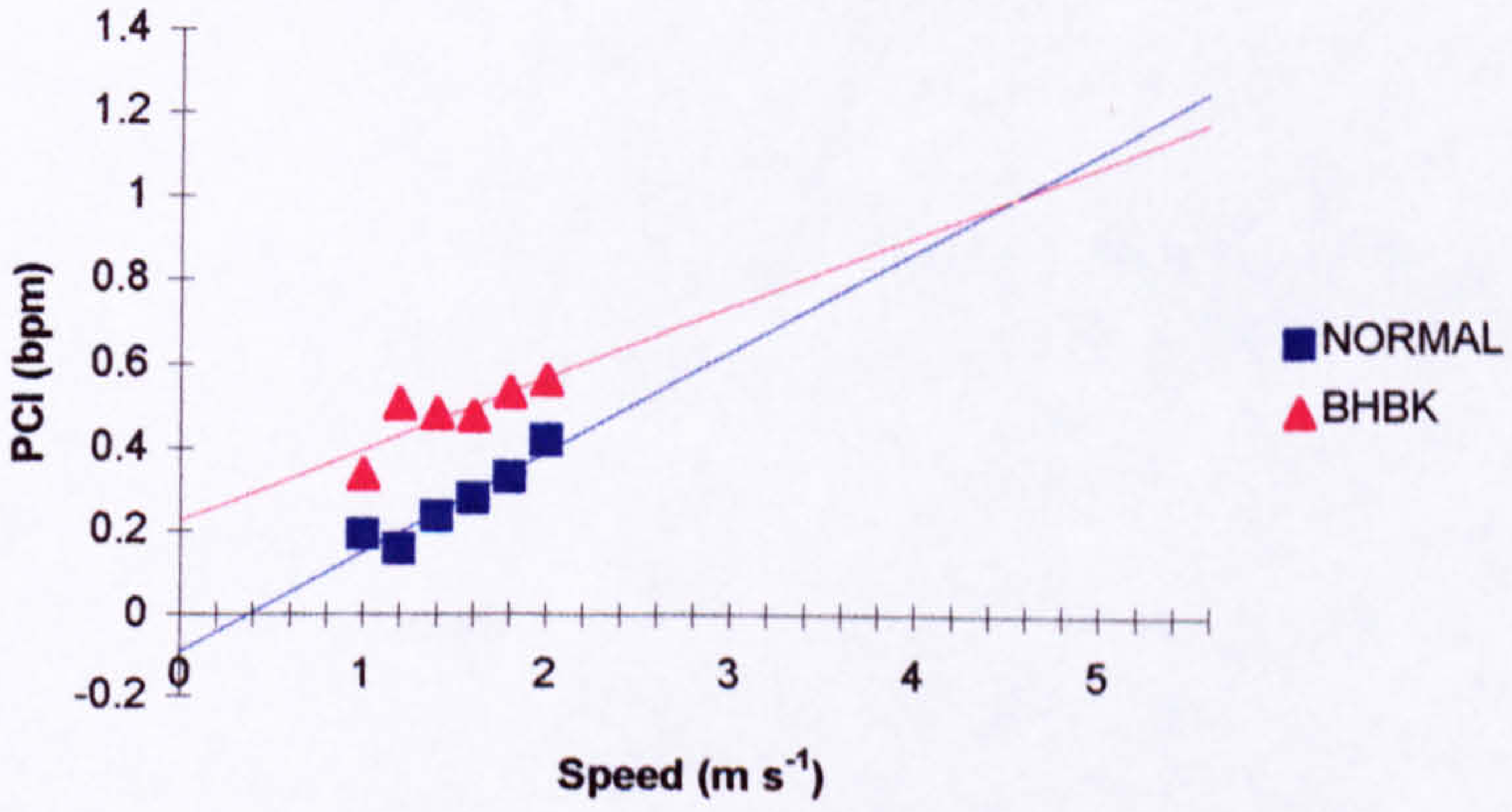


Figure AVI.7 Physiological cost index against speed for normal and BHBK walking Values cross at about 4.5 $m{\cdot}s^{-1}$.

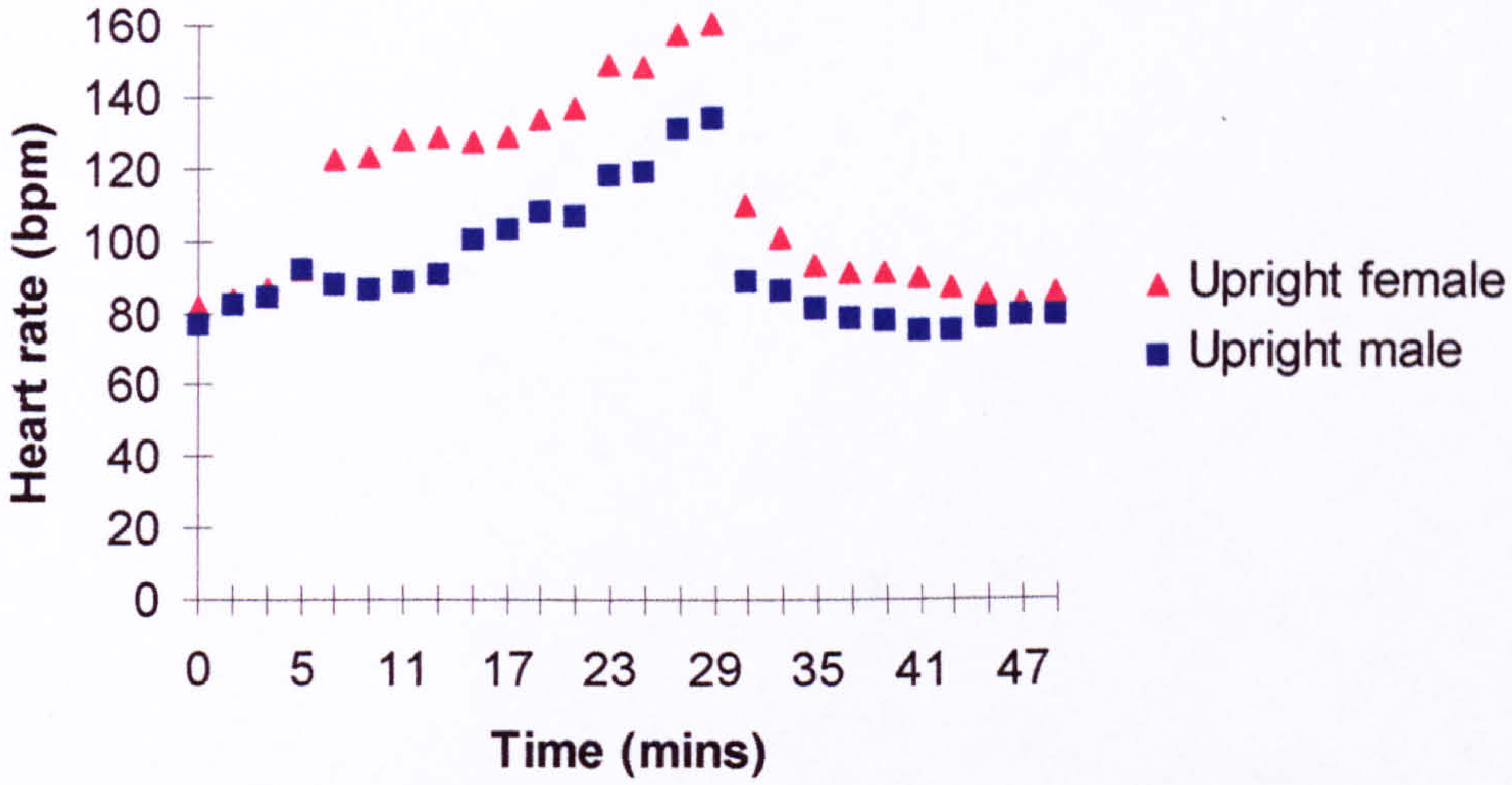


Figure AVI.8 Heart rate against time for normal walking in males and females

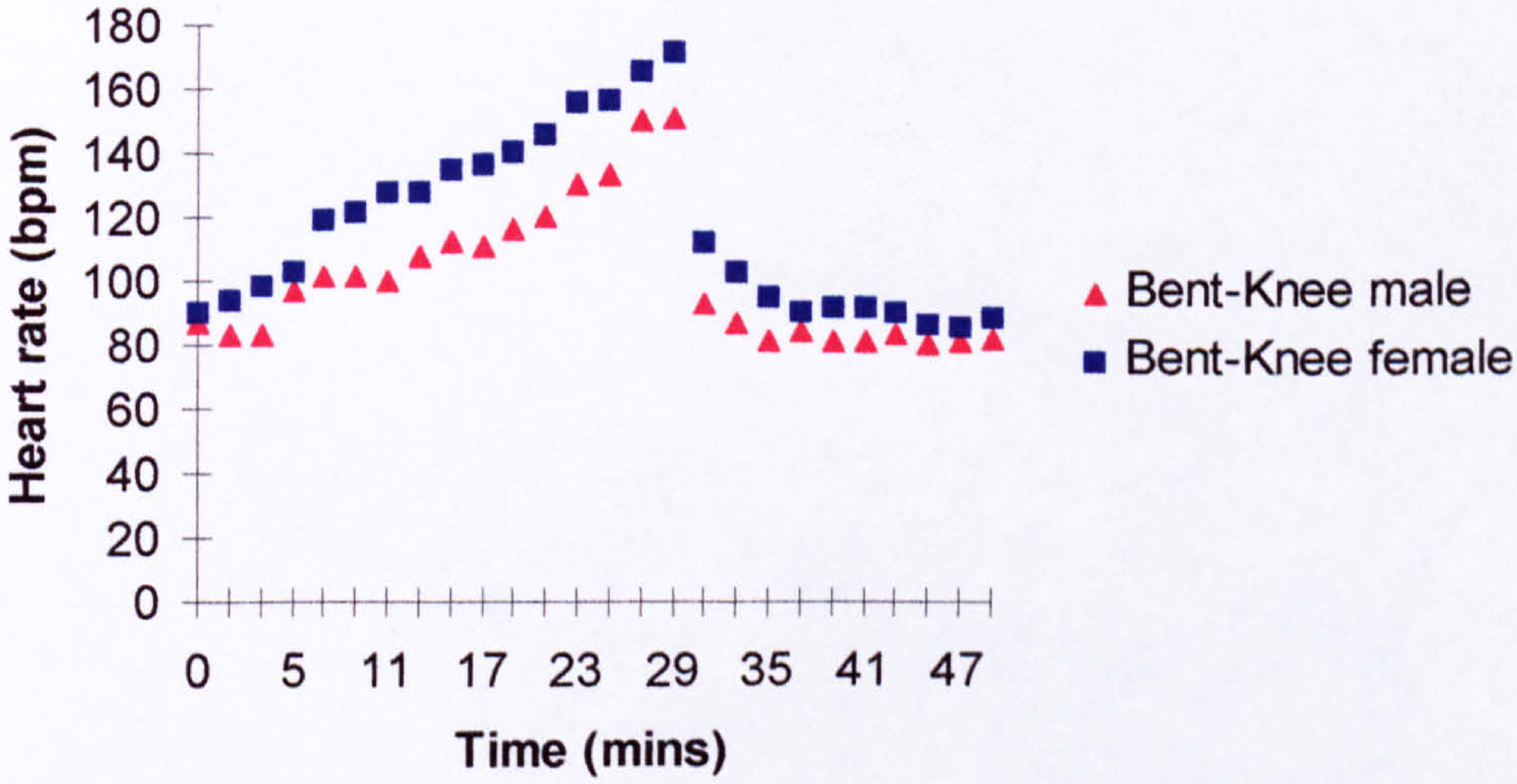


Figure AVI.9 Heart rate against speed for BHBK walking in males and females

Appendix VII

Example graphs of joint angle data in BHBK and normal walking:

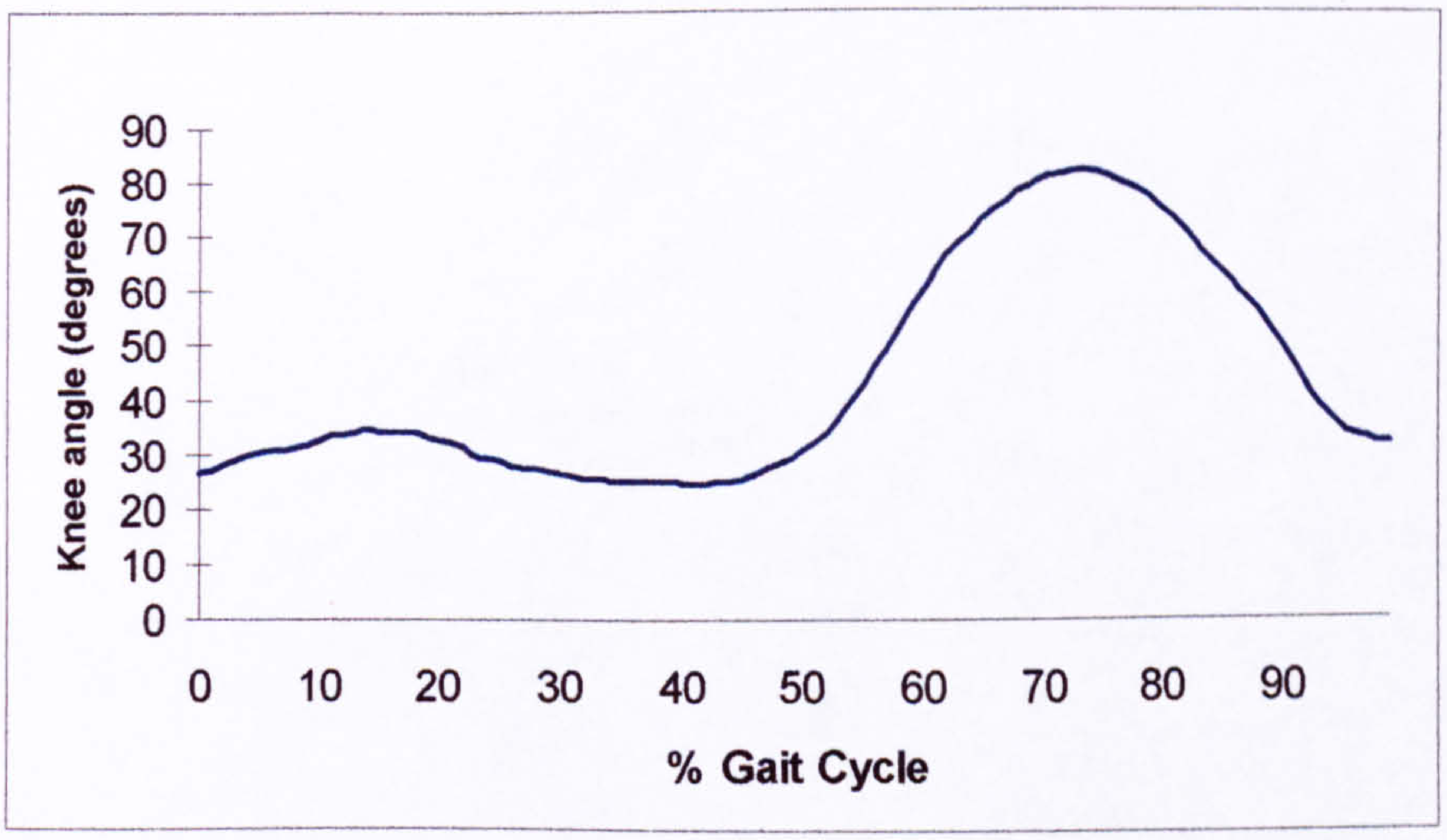


Figure AVII.1 Goniometer data for medium speed normal walking. Data shows knee angle (°) against % gait cycle from heel strike to heel strike. Note the brief flexion curve during early stance, followed by the maximal flexion curve during swing.

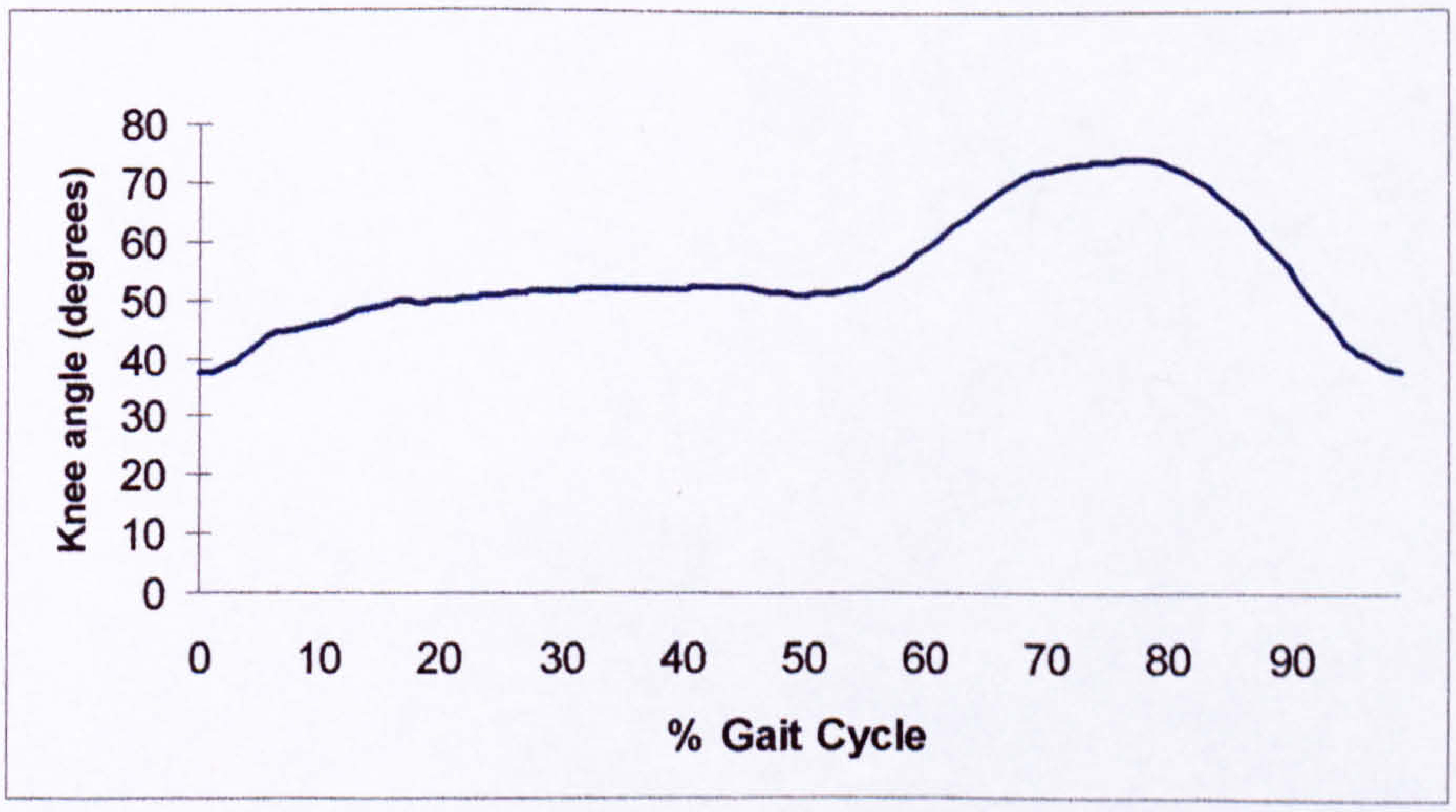


Figure AVII.2 Goniometer data for medium speed BHBK walking. Data shows knee angle (°) against % gait cycle from heel strike to heel strike. Note absence of the flexion curve during early stance. Maximal flexion is still seen during swing, but there is increased flexion throughout the gait cycle when compared to normal walking,

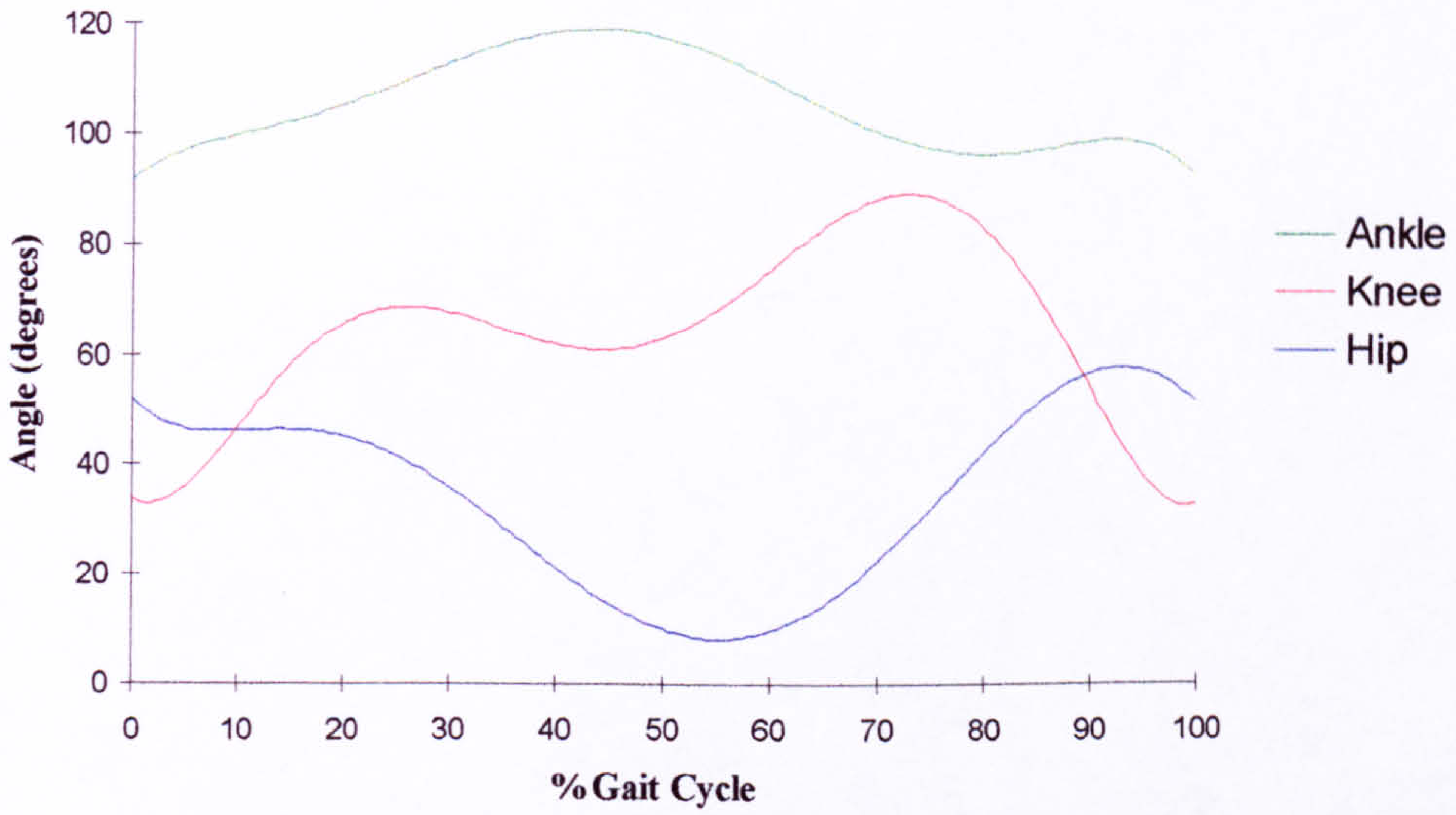


Figure AVII.3 Hip, knee and ankle angles during BHBK walking. Hip angle is measured as angle of flexion, knee angle is measured as angle of flexion, and ankle is measured as the angle between the foot and the calf (i.e. 90 degrees for no plantarflexion or dorsiflexion). Data kindly donated by Li,Y (pers. comm.). For normal flexion angle see section 1.5.

Appendix VIII

Heat balance during exercise in normal and BHBK postures during exercise for half an hour

(including evaporation, heat storage, metabolism, convection, conduction and radiation and total partitional heat exchange)

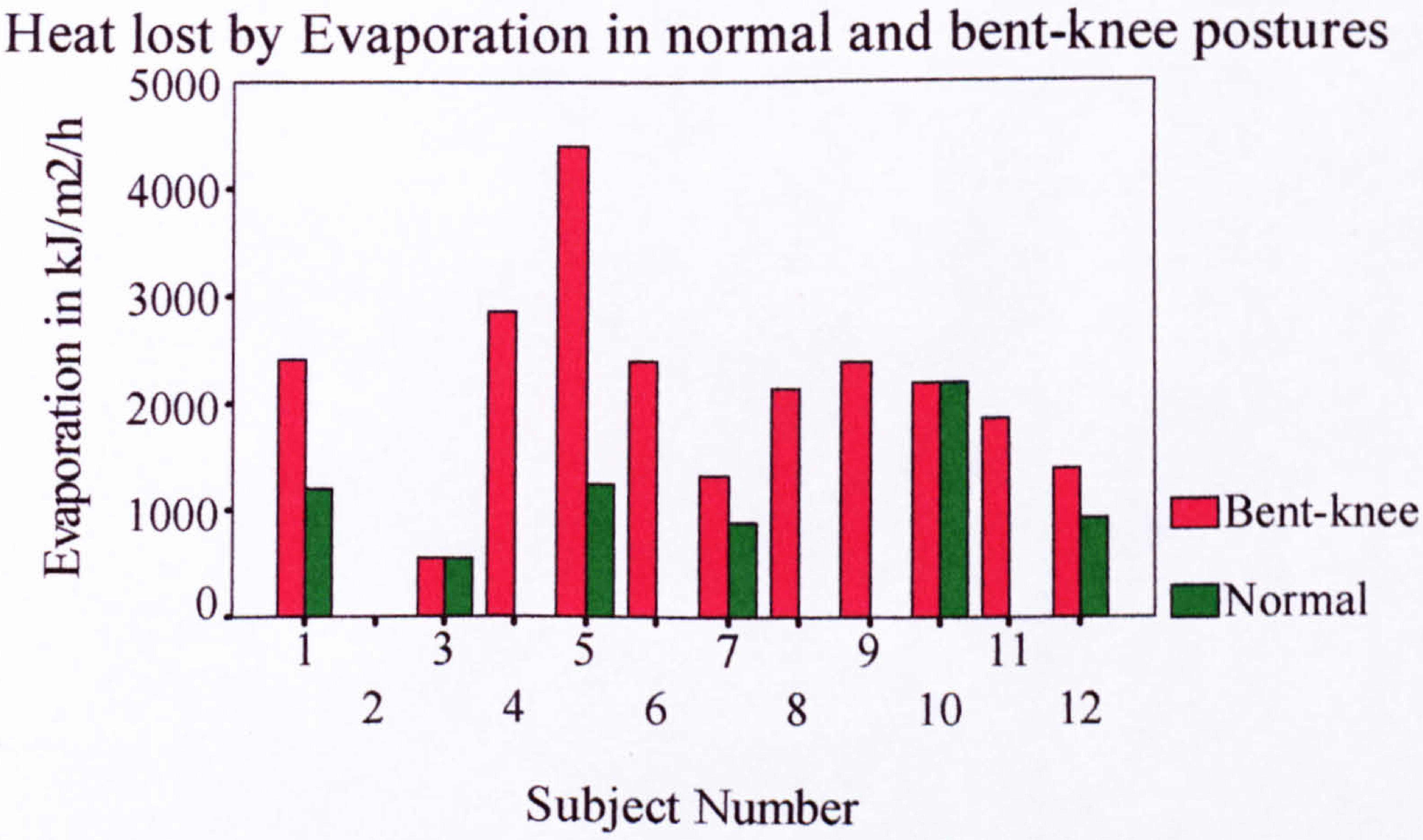


Figure VIII.1 Heat lost by evaporation (kJ·m^2·hr^{-1}) in normal and BHBK walking for all 12 subjects

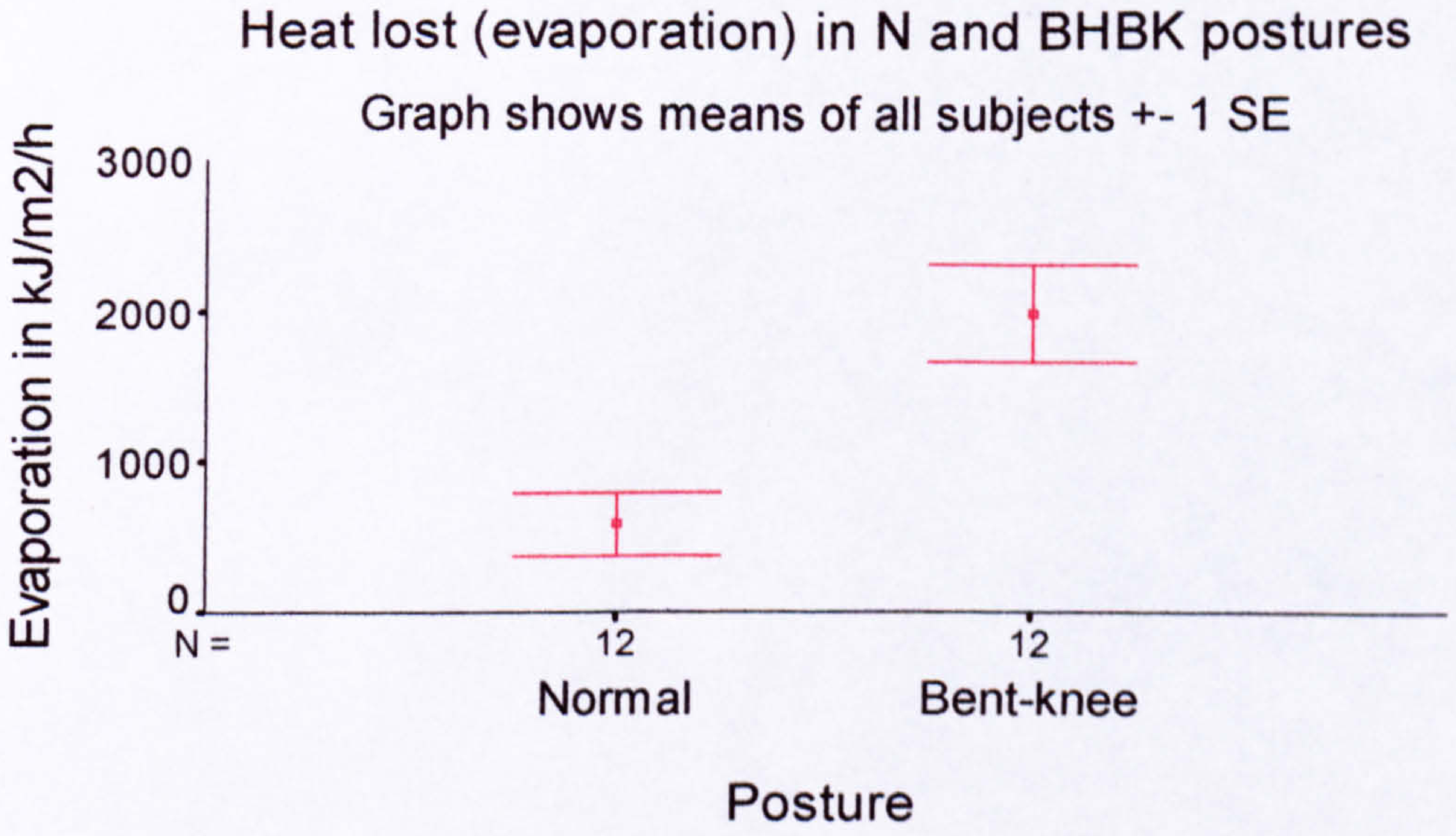


Figure VIII.2 Heat lost by evaporation (kJ·m^2·hr^{-1}) in normal and BHBK walking, showing mean ± standard error

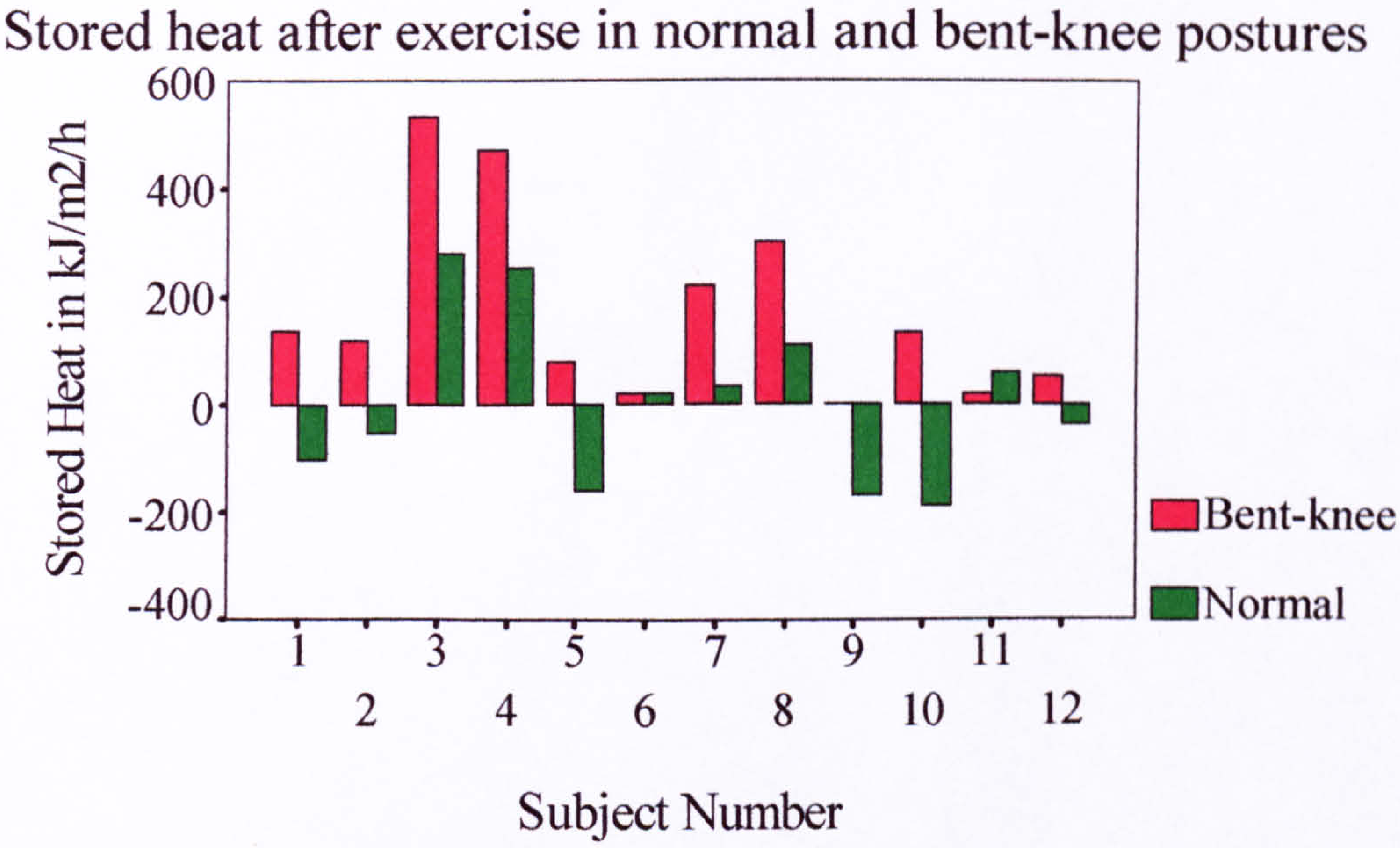


Figure VIII.3 Stored heat (kJ·m^2·hr^{-1}) in normal and BHBK walking, for all 12 subjects

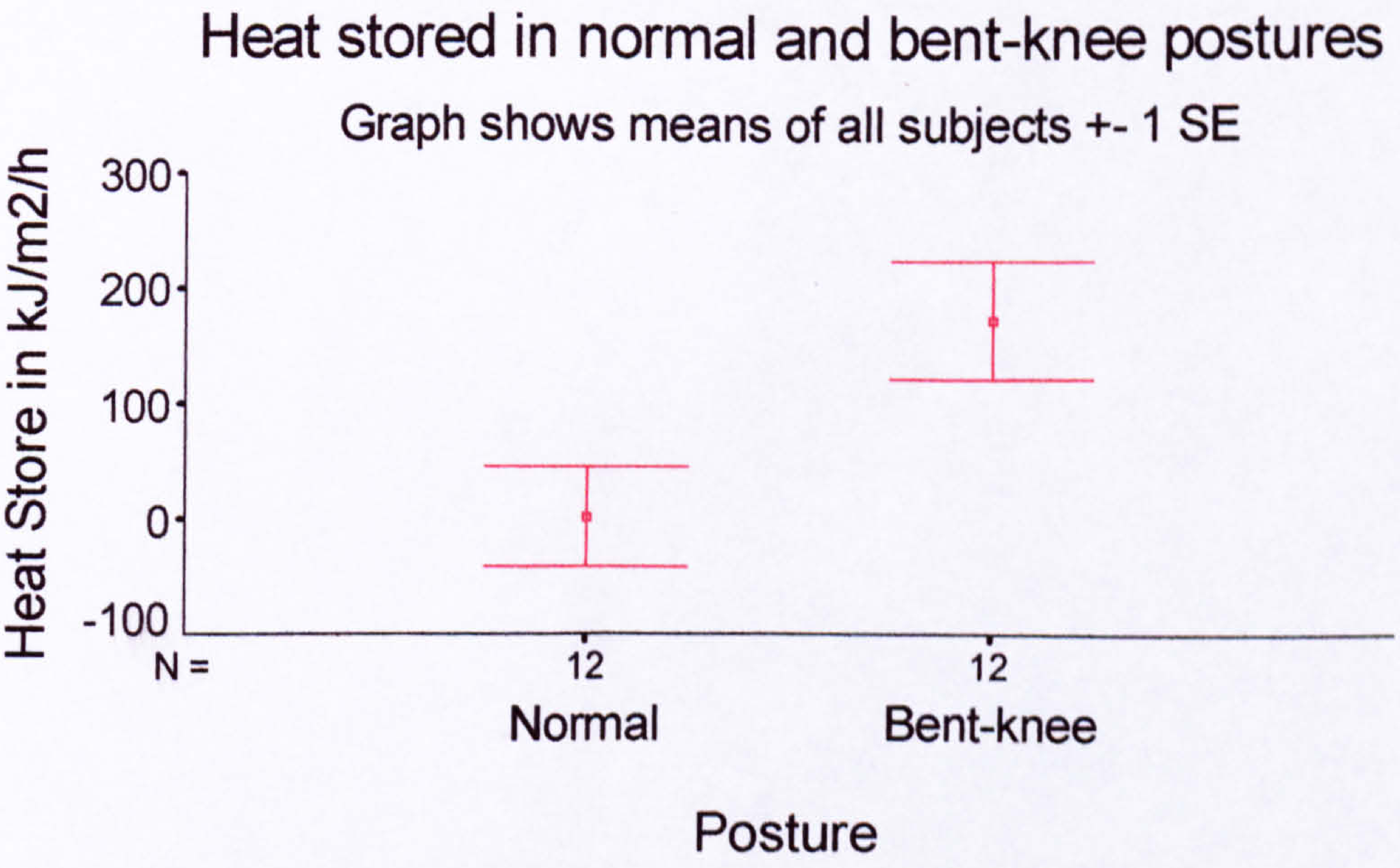


Figure VIII.4 Stored heat (kJ·m^2·hr^{-1}) in normal and BHBK walking, showing mean ± standard error

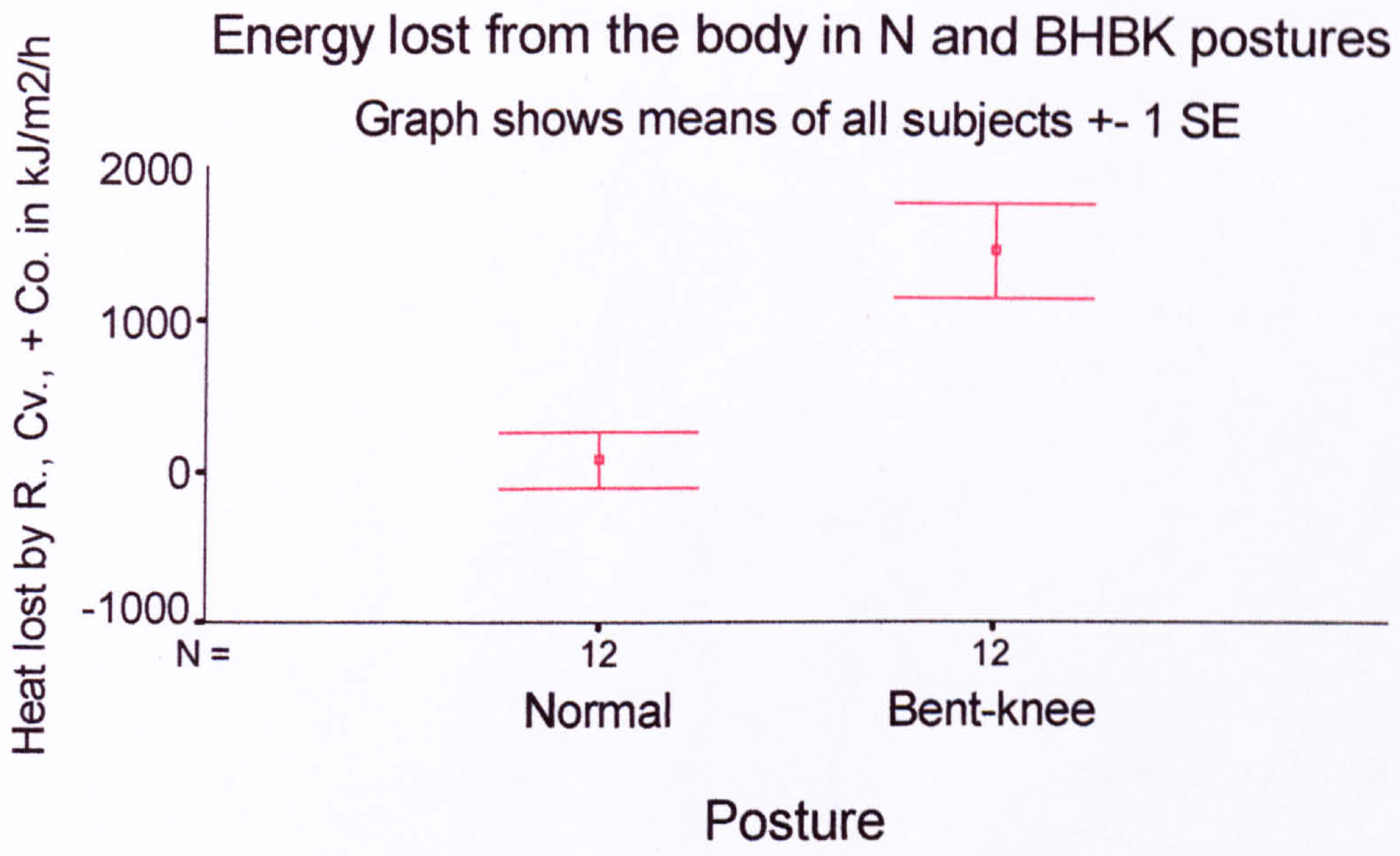
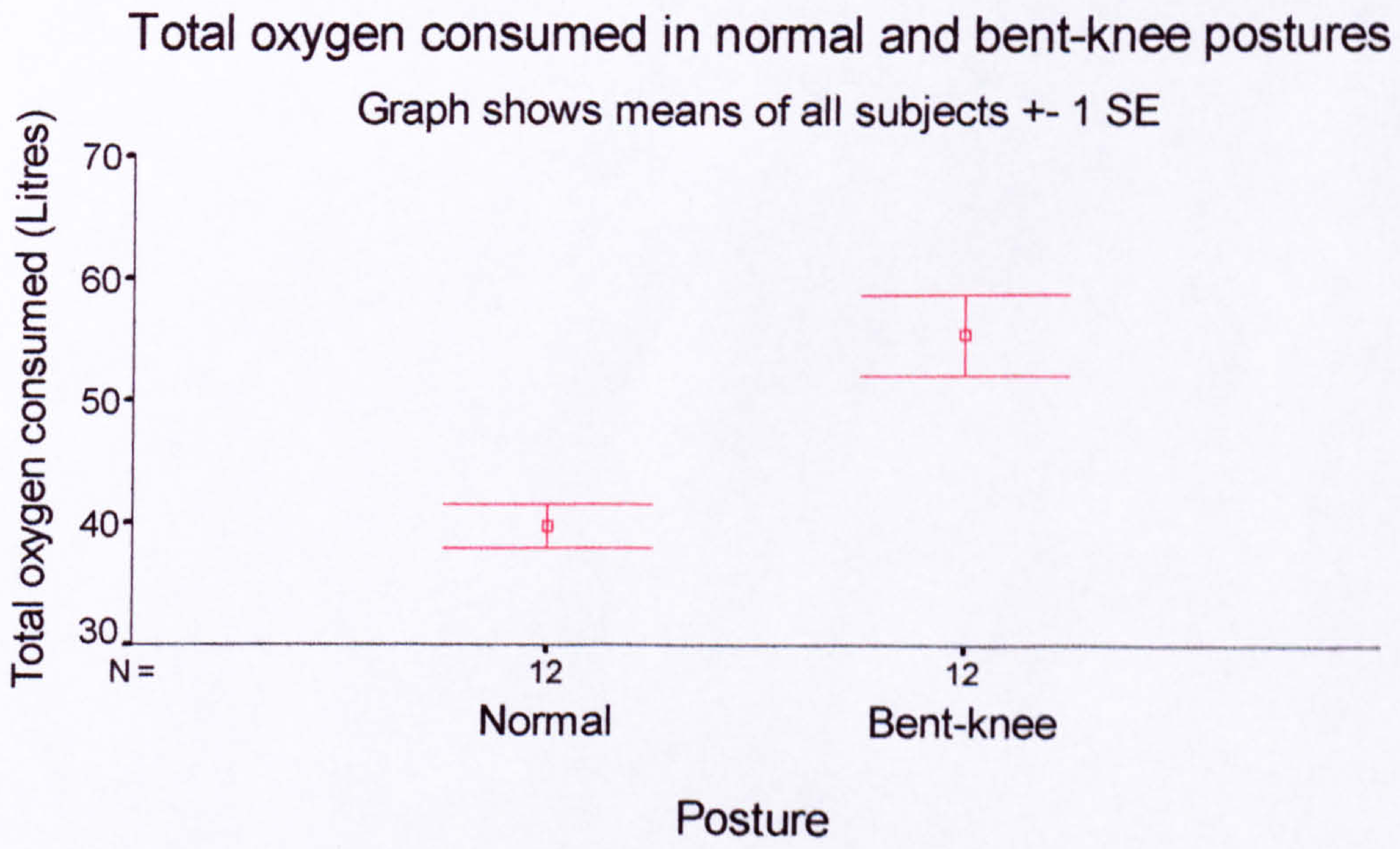


Figure VIII.5 Heat lost by radiation, convection and conduction (kJ·m^2·hr^{-1}) in normal and BHBK walking, showing mean ± standard error



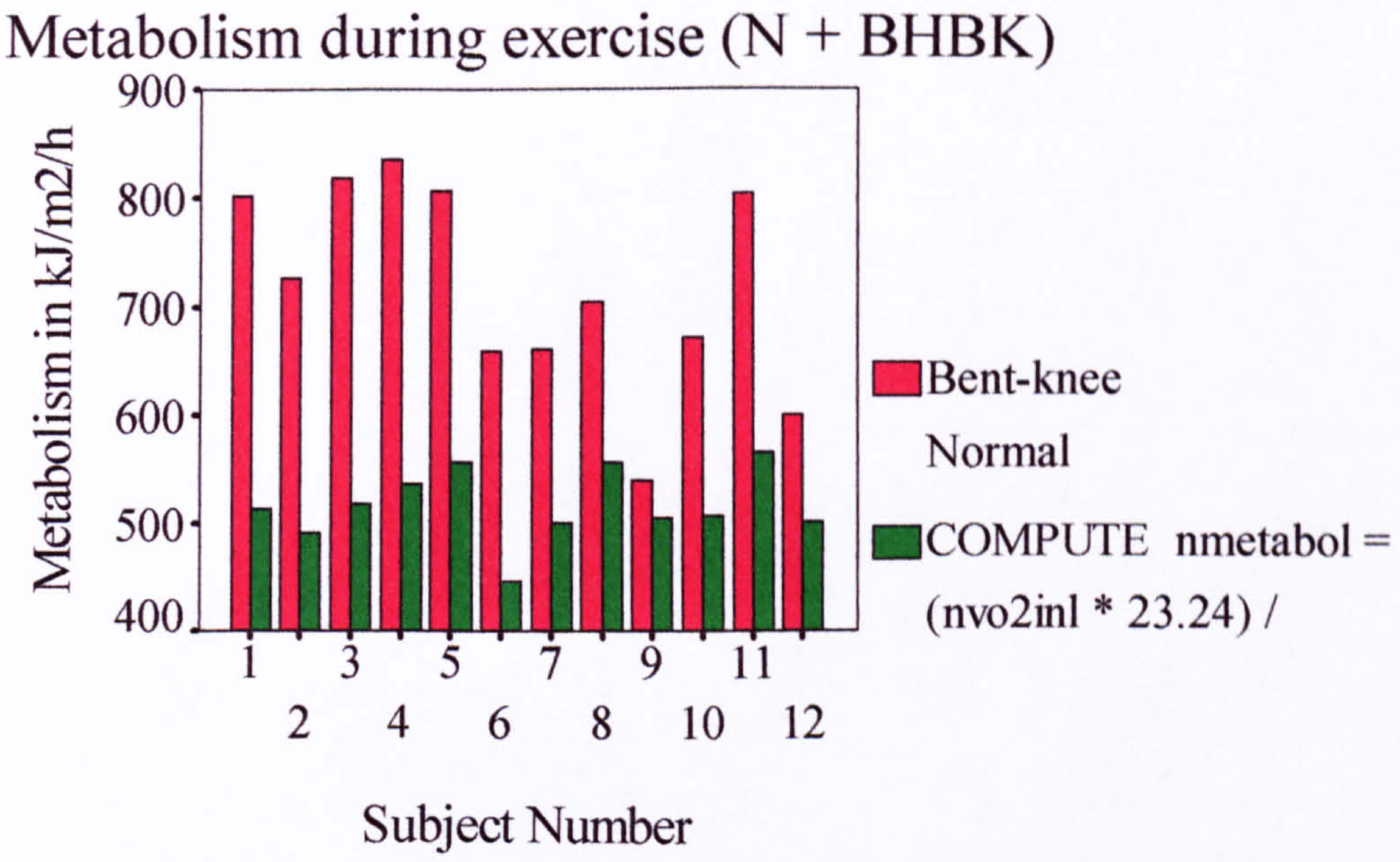


Figure VIII.6 Metabolic heat production (kJ·m^2·hr^{-1}) in normal and BHBK walking, for all 12 subjects

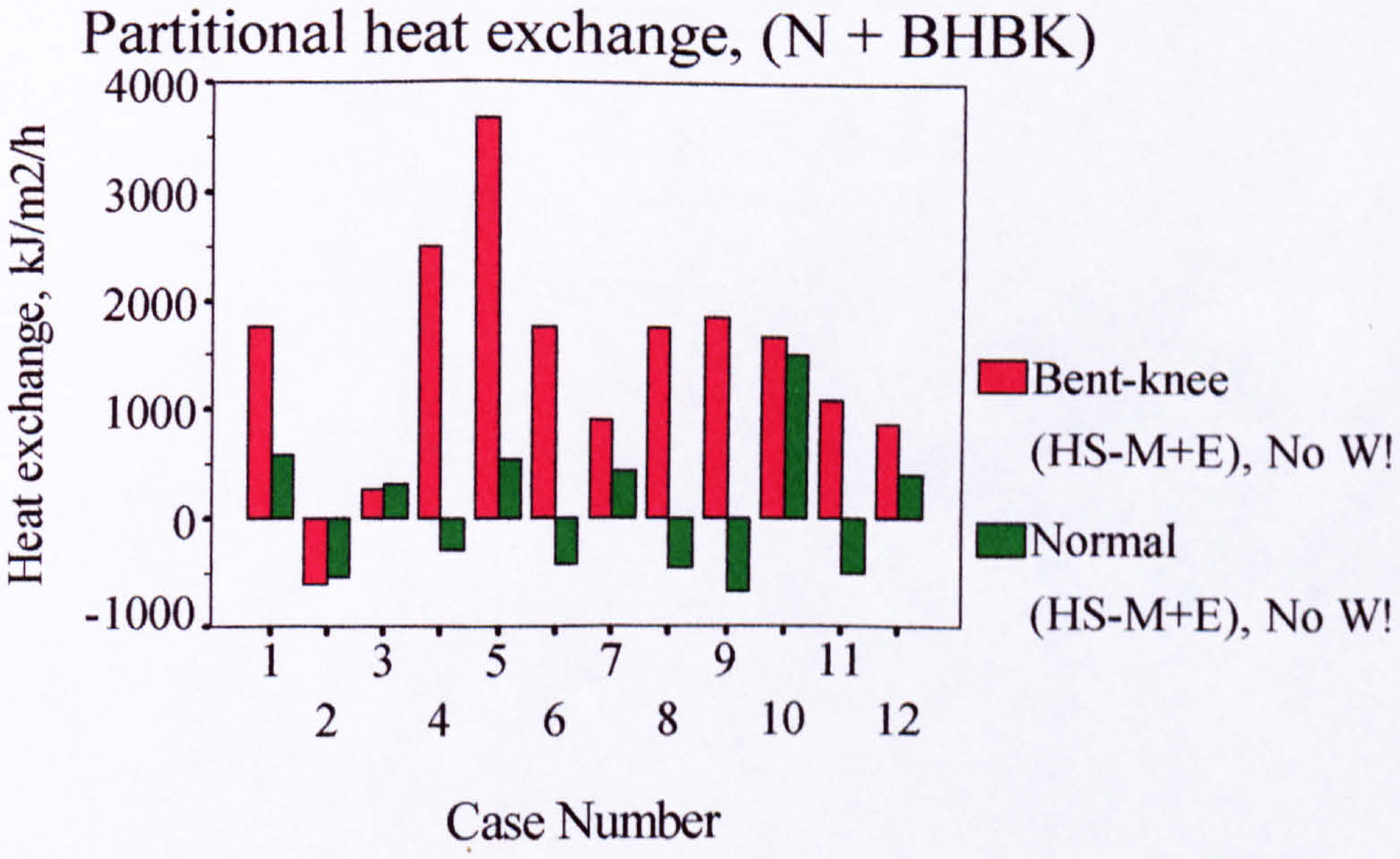


Figure VIII.7 Partitional heat exchange (kJ·m^2·hr^{-1}) in normal and BHBK walking, for all 12 subjects (not including Work in the equation)

Table VIII.1 OVERLEAF! Heat balance equations values for each subject including sex, age, height, weight, body surface area (BSA), resting metabolic rate (RMR), basal metabolic rate (BMR), pre and post exercise mass, pre and post exercise core temperature

Duration of exercise : (mins/60) hrs = 0.48 hrs.

BSA $= M^{0.425} \times H^{0.725} \times 71.84 \times 10^{-4}$

female RMR $= -161+10(M)+6.25(H)-5(age)$

male RMR $= 5+10(M)+6.25(H)-5(age)$

(equations by **Mifflin et al. 1990**)

Subject	1	2	3	4	5	6	7	8	9	10	11	12
	Jon	Ruth	Mark	Wang	Iain	Tracie	Shirley	Patrick	Penny	Alan	Olga	Tanya
Male/Female	M	F	M	M	M	F	F	M	F	M	F	F
height, cm	186	160	174	175	183	157	155	169	184	179	155	166
weight, kg	79	53	71	77	89	61	53	71	78	68	59	53
age	25	27	26	38	26	24	35	28	25	28	25	23
BSA (m^2)	2.033549	1.538759	1.851609	1.924542	2.114142	1.611234	1.503744	1.81288	2.006779	1.855671	1.57387	1.580381
RMR (kcal day^{-1})	1832.5	1234	1672.5	1678.75	1908.75	1310.25	1162.75	1631.25	1644	1663.75	1272.75	1291.5
BMR (kcal m^{-2} h^{-1})	37.54724	33.41438	37.63618	36.34522	37.61869	33.88318	32.21818	37.49215	34.13431	37.35732	33.69481	34.05032
Normal:core temp, pre	37.6	37.7	37.4	36.6	37.45	37.6	37.7	37.15	37.45	37.3	37.55	37.9
Normal:core temp, post	37.45	37.55	37.9	37	37.27	37.65	37.8	37.35	37.2	36.95	37.7	37.8
BHBK: core temp, pre	37.7	37.65	37	36.8	37.4	37.5	37.5	36.75	37.9	37.2	37.7	37.6
BHBK: core temp, post	37.9	38	37.95	37.55	37.5	37.55	38.15	37.3	37.9	37.45	37.75	37.75
Normal:mass, pre	79	52	71	78.1	89	60.7	53.4	71.6	78	68.3	59	52.9
Normal:mass, post	78.8	52	70.9	78.1	88.8	60.7	53.2	71.6	78	67.9	59	52.7
BHBK:Mass, pre	79	53.5	71.2	78.1	89.3	62.9	53.6	71.6	79.5	68.4	58.9	52.9
BHBK:Mass, post	78.6	53.5	71.1	77.6	88.6	62.4	53.3	71.2	79.1	68	58.5	52.6

Table AVIII.1 Data used in calculation of heat balance, for equations see legend (on previous page)

Appendix IX

Effect of skiing training on the energetic cost of a BHBK gait

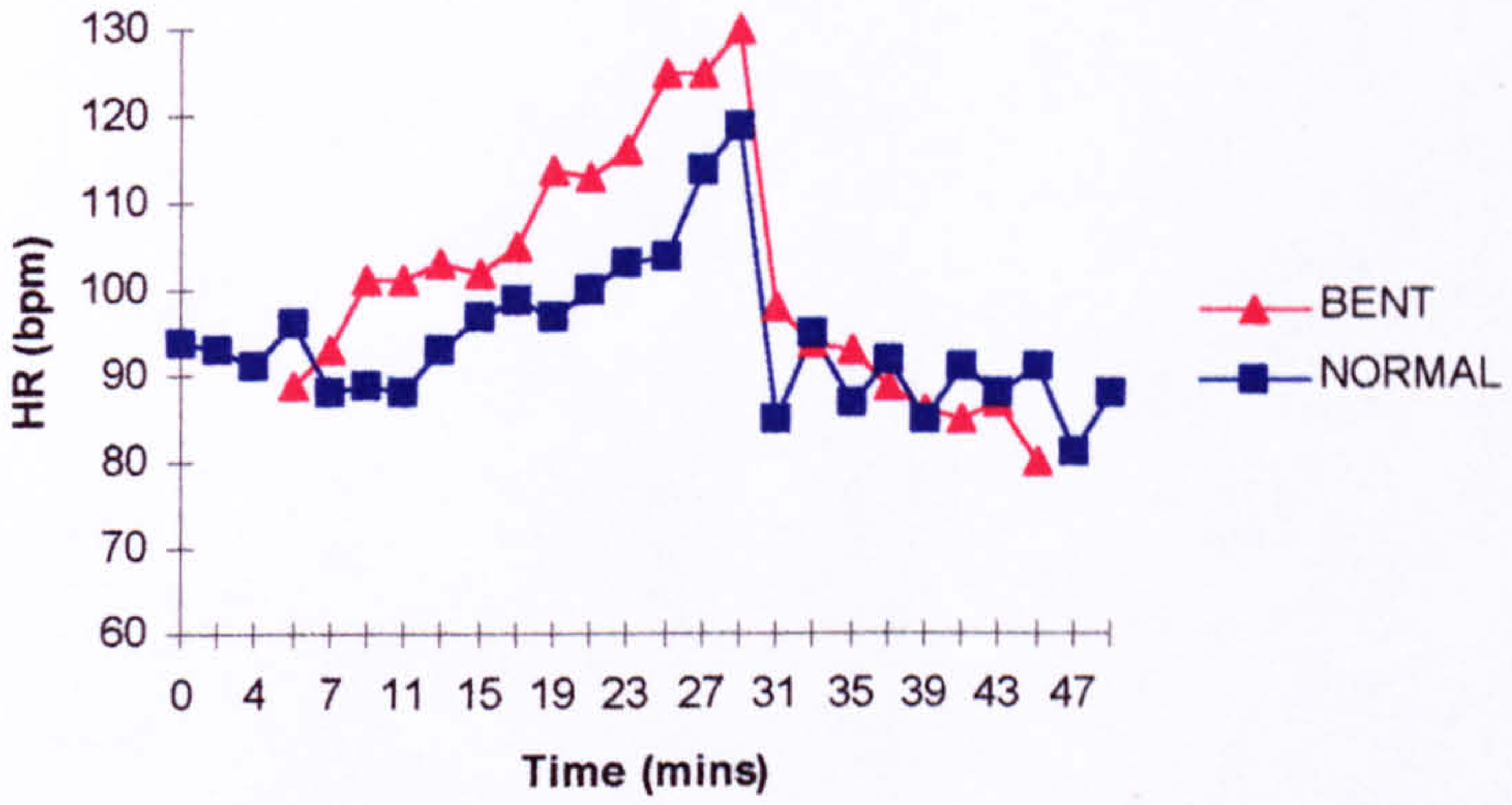


Figure AIX.1 Trained subject, change in HR during BHBK walking compared to normal walking.

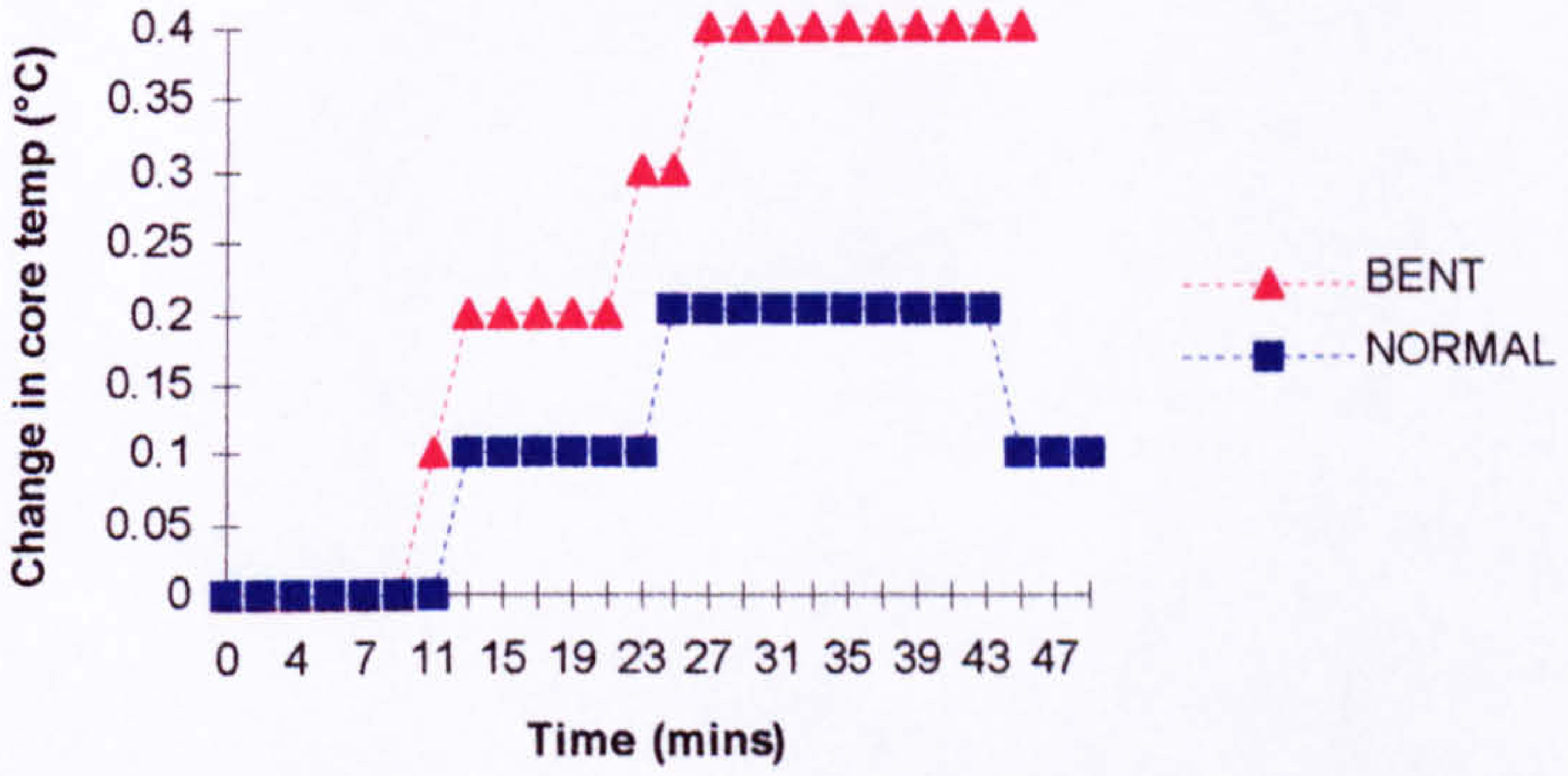


Figure AIX.2 Trained subject, change in core temperature during BHBK walking compared to normal walking.

Appendix X

Using data estimated for total energy expenditure to answer the question: "how far could a 37 kg hominid walk in one day??"

Using estimated from Low and Reed (1996), walking at the most efficient speed ($1.4\ m{\cdot}s^{-1}$ from their data) uses $167.842\ J{\cdot}m^{-1}$ for a 50 kg female.

Converting this to $J{\cdot}m^{-1}{\cdot}kg^{-1}$: $167.842 / 50 = 3.36$

Therefore for a 37 kg female the equivalent expenditure is :

$$3.36 * 37 = 124.21\ J{\cdot}m^{-1}, \text{ or } kJ{\cdot}km^{-1}$$

To find out maximum distance travelled, divide total expenditure (from estimations in chapter 3, after subtracting resting metabolic rate) by expenditure per kilometre:

$$(11209 - 4396) / 124.21$$

$$= 54.85 \text{ km per day}$$

To calculate distance walked during active day (assuming a 12 hour day)

$$54.85 / 2$$

$$=27.43 \text{ km per 12 hours}$$

APPENDIX XI

Time scale of primate evolution

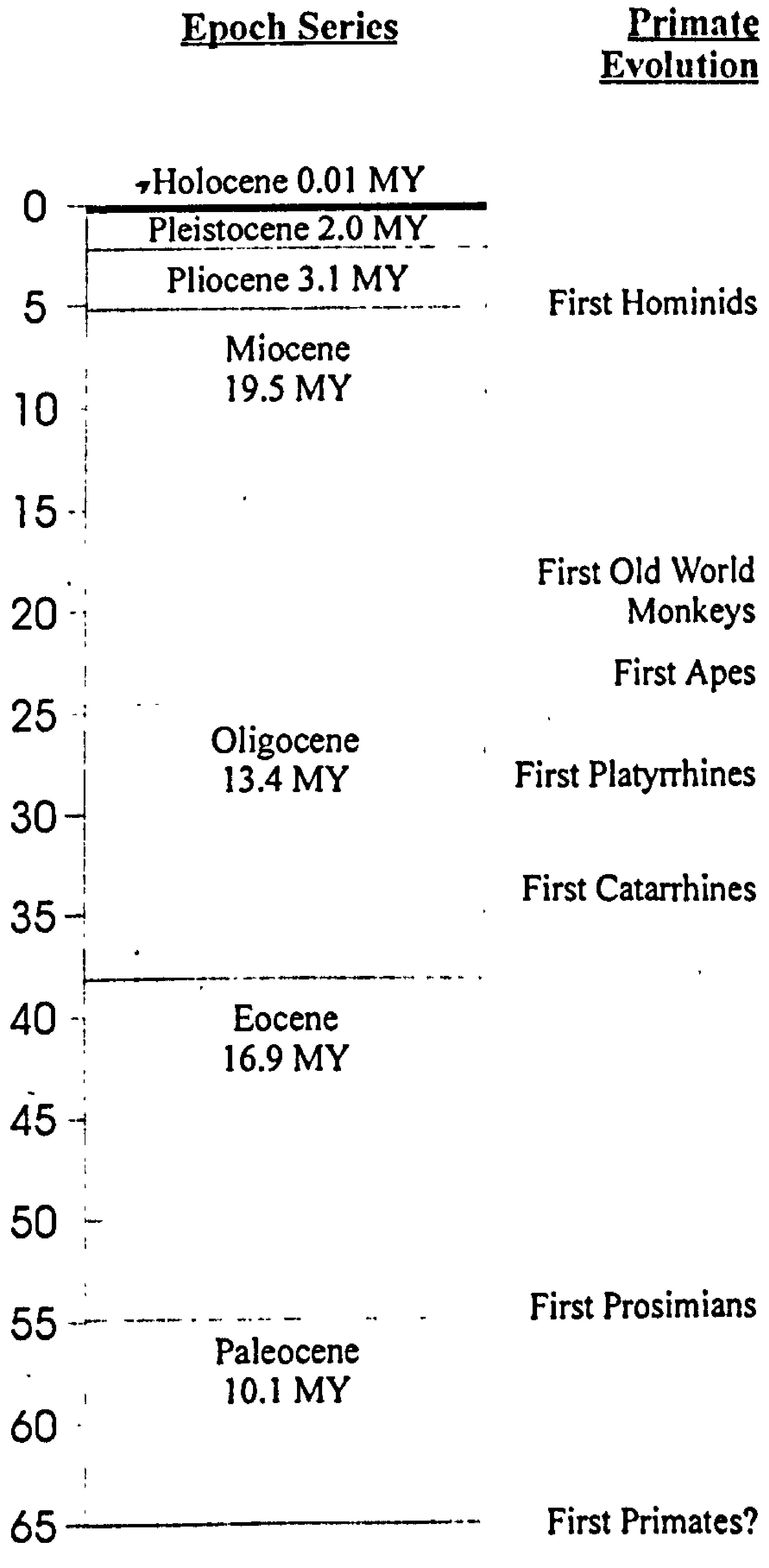


Figure AXI.1 Geological time scale of primate evolution showing the series of epochs from 65 MYA to the present day. The length of each epoch is displayed in millions of years (MY). The timeline on the left of the diagram represent millions of years ago from the present day (MYA). The major events in primate evolution are also shown for reference. 'Lucy' was dated to about 3.2 MY. Adapted from Fleagle (1988).

APPENDIX XII

Some general anatomical features of an upright biped, a generalised arboreal and terrestrial quadruped

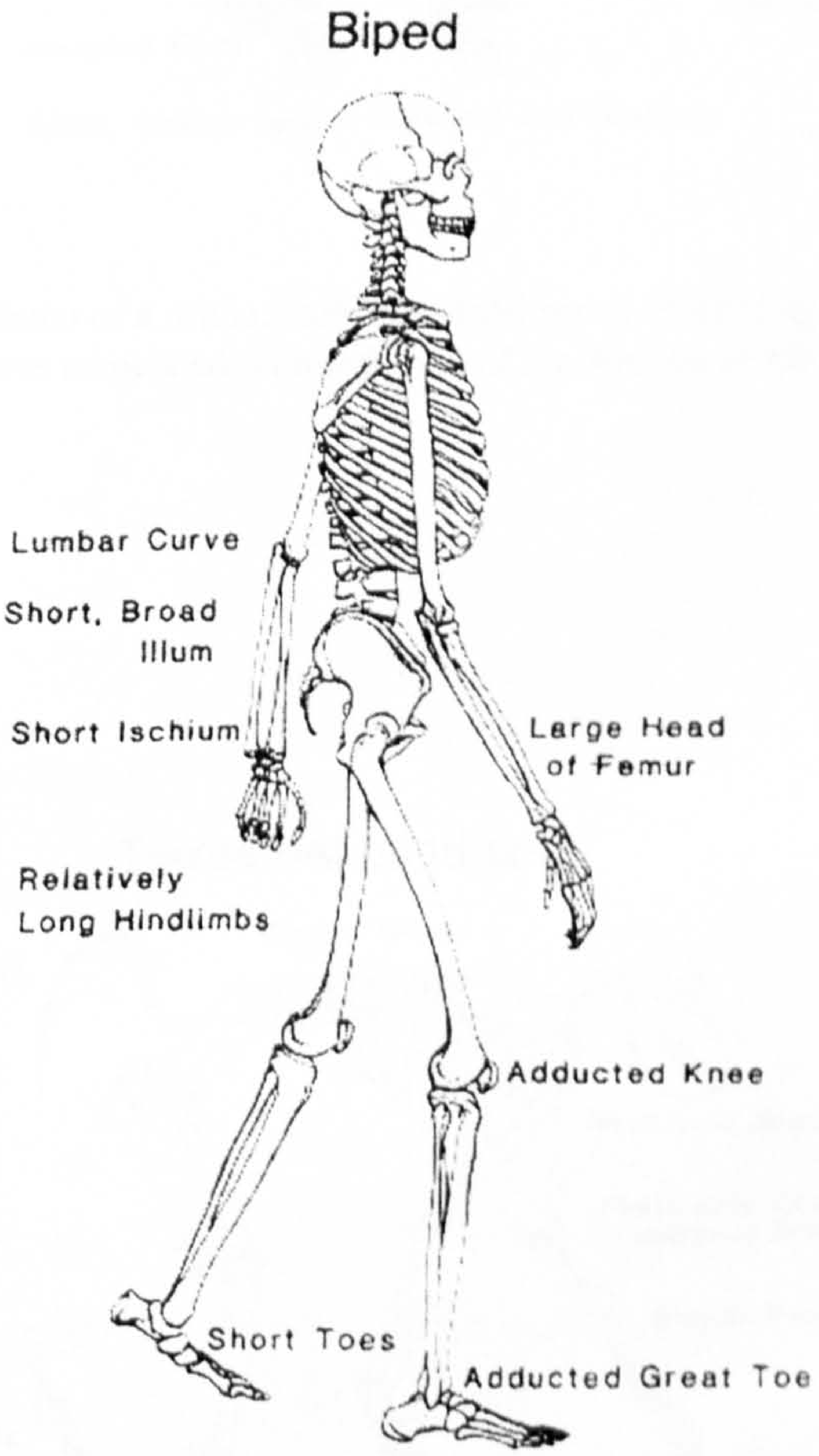


Figure AXII.1 The skeleton of a bipedal primate illustrating some of the distinctive anatomical features associated with that type of locomotion (From Fleagle, 1988)

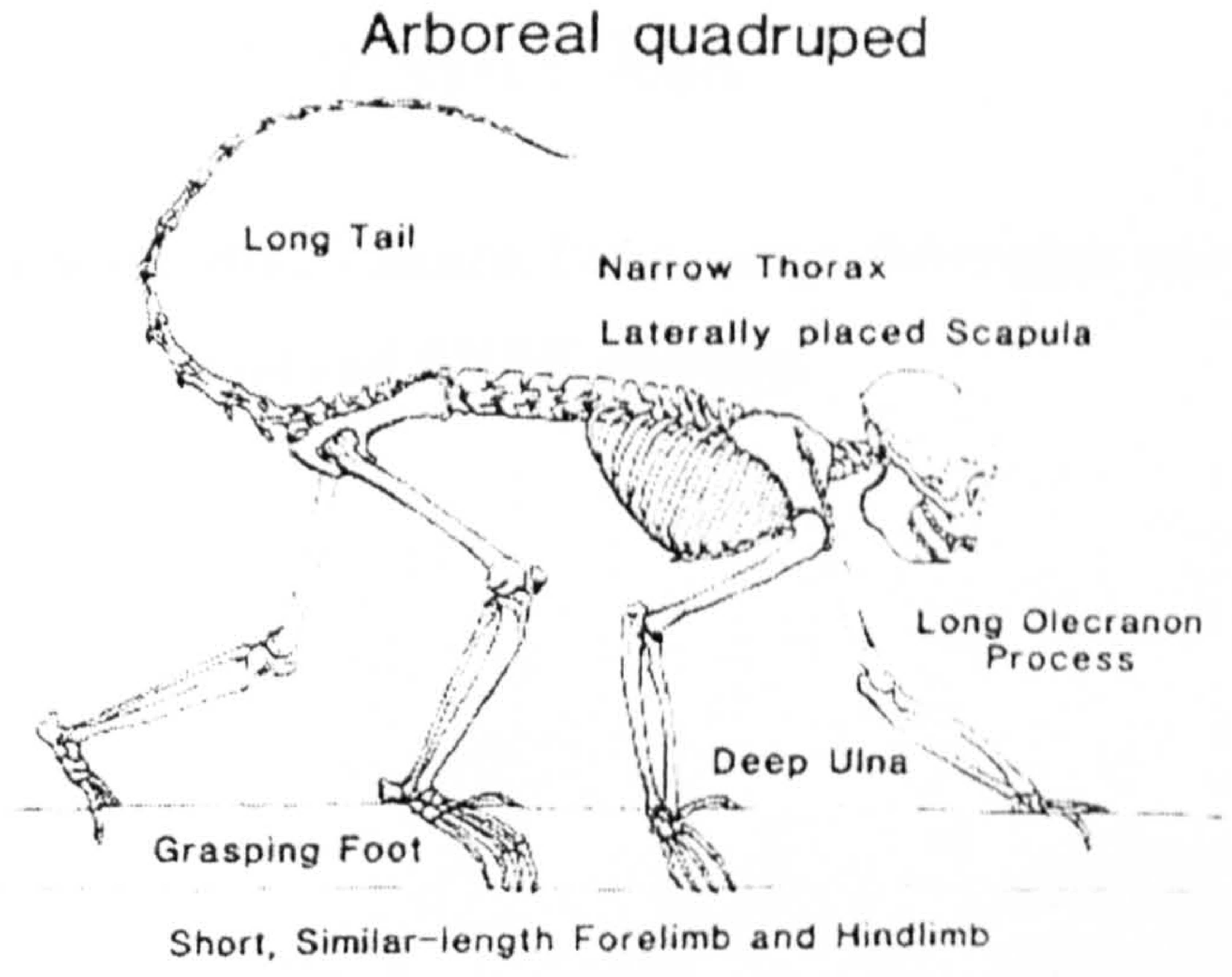


Figure AXII.2 The skeleton of a primate arboreal quadruped, illustrating some of the distinctive anatomical features associated with that type of locomotion (From Fleagle, 1988)

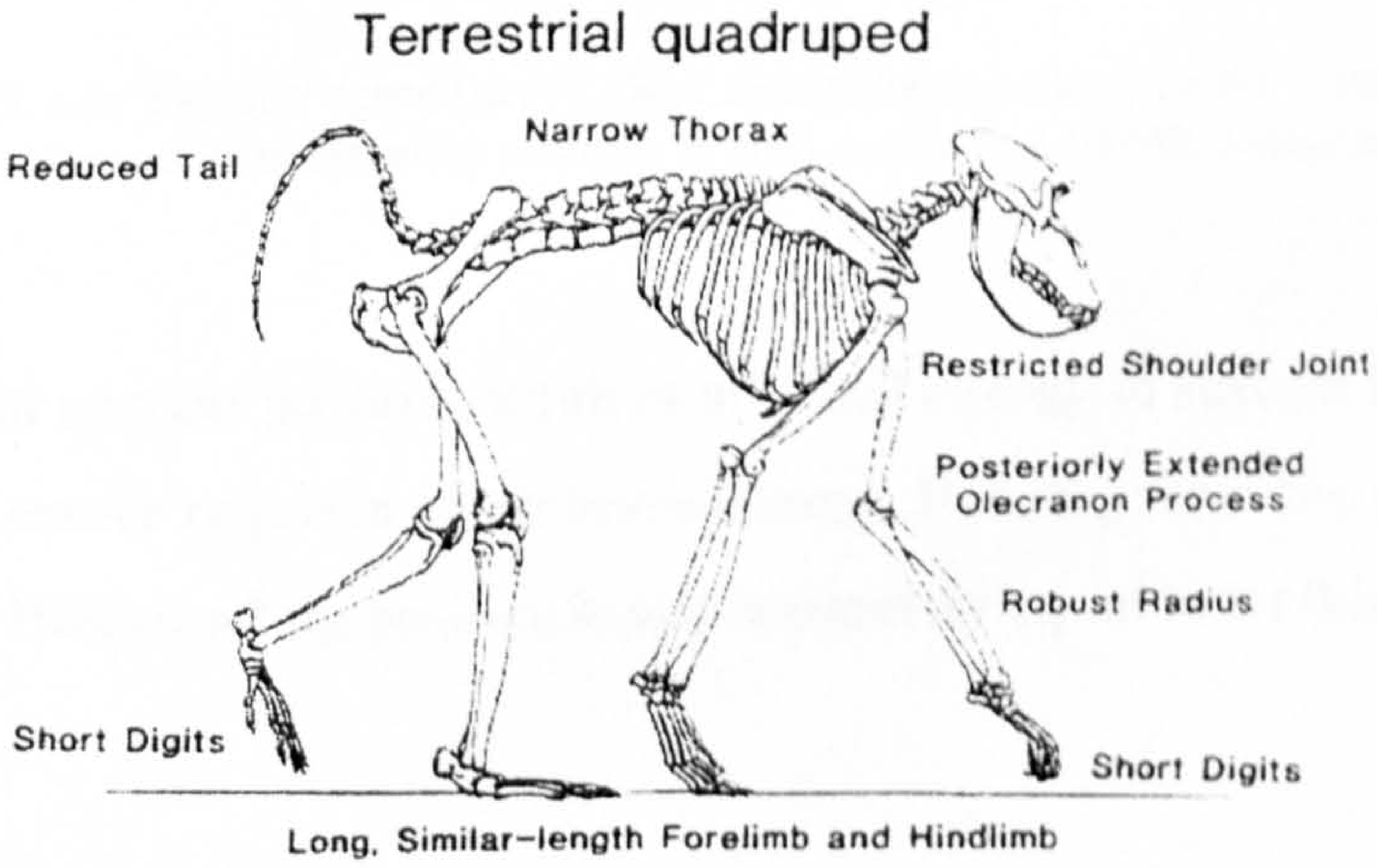


Figure AXII.3 The skeleton of a primate terrestrial quadruped illustrating some of the distinctive anatomical features associated with that type of locomotion (From Fleagle, 1988)

APPENDIX XIII

Measuring energy cost of standing posture. Extra graph for comparison between normal and BHBK walking.

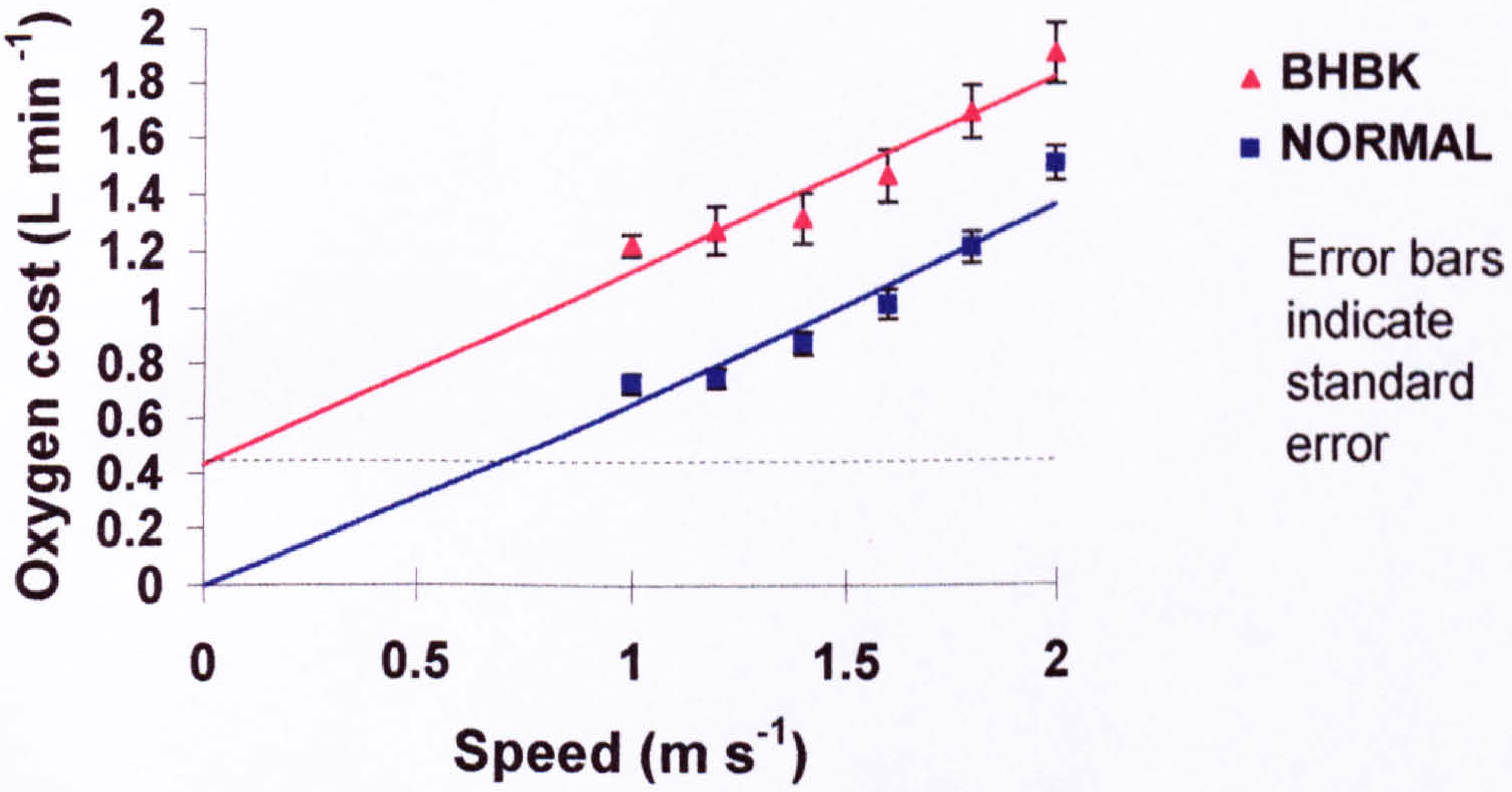


Figure AXIII.1 VO_2 (L·min^{-1}) against speed (m·s^{-1}). Back extrapolation to zero on the x-axis provides an estimate for the cost of maintaining postures in both normal and BHBK postures.

As expected, normal upright posture requires minimal energy to sustain it. However, BHBK posture requires much more energy. Reading from the graph, it is apparent that BHBK standing posture is approximately equal to walking at around 0.7 m·s^{-1}.

Appendix XIV

Publications

Carey, T. S. and Crompton, R. H. (1997). The energetics and bipedal locomotion of early hominids. 20th Annual Meeting of the American Society of Primatologists. June 27 - July 1, 1997. San Diego, USA **(Poster)**

Carey, T. S. and Crompton, R. H. (1997). The bipedal locomotion of early hominids. 5th International Conference of Vertebrate Morphology. July 12-17, 1997. Bristol, UK. Published in Journal of Vertebrate Morphology 232: 217-378 **(Oral presentation)**