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The metabolic costs of 'bent-hip, bent-knee' walking in humans

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Abstract

The costs of different modes of bipedalism are a key issue in reconstructing the likely gait of early human ancestors such as *Australopithecus afarensis*. Some workers, on the basis of morphological differences between the locomotor skeleton of *A. afarensis* and modern humans, have proposed that this hominid would have walked in a 'bent-hip, bent-knee' (BHBK) posture like that seen in the voluntary bipedalism of untrained chimpanzees. Computer modelling studies using inverse dynamics indicate that on the basis of segment proportions AL-288-1 should have been capable of mechanically effective upright walking, but in contrast predicted that BHBK walking would have been highly ineffective. The measure most pertinent to natural selection, however, is more likely to be the complete, physiological, or metabolic energy cost. We cannot measure this parameter in a fossil. This paper presents the most complete investigation yet of the metabolic and thermoregulatory costs of BHBK walking in humans. Data show that metabolic costs including the basal metabolic rate (BMR) increase by around 50% while the energy costs of locomotion and blood lactate production nearly double, heat load is increased, and core temperature does not return to normal within 20 minutes rest. Net effects imply that a resting period of 150% activity time would be necessary to prevent physiologically intolerable heat load. Preliminary data for children suggest that scaling effects would not significantly reduce relative costs for hominids of AL-288-1's size. Data from recent studies using forwards dynamic modelling confirm that similar total (including BMR) and locomotor metabolic costs would have applied to BHBK walking by AL-288-1. We explore some of the ecological consequences of our findings.

Keywords: *Australopithecus afarensis*; Biomechanics; Bipedalism; Computer modelling; Energy costs; Metabolic; Physiology

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Introduction

Stern and Susman (1983) have suggested that certain features in the postcranial skeleton of AL-288-1 *Australopithecus afarensis* should lead us to conclude that this early hominid was partially arboreal, and that as a consequence, when walking on the ground, bipedalism would have been 'compromised' and posture 'bent-hip, bent-knee'. Although costs of locomotion tend to account for only a small portion of total daily activity costs (Karasov, 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). It is thus of some importance to determine what the gait of this early hominid is likely to have been.

In an earlier paper (Crompton et al., 1998) we predicted the specific mechanical response of a segment inertial model of AL-288-1 to the joint motion typical of normal human bipedalism, voluntary bipedalism of untrained chimpanzees, and human 'bent-hip, bent-knee' bipedalism. We found that the skeletal proportions of AL-288-1 were incompatible with the first, but that kinematics of either normal erect walking or BHBK walking in the manner of humans could be sustained. However, the mechanical joint power requirements of the latter would have been much higher – approximately double – the costs of erect bipedalism. Further, our model predicted that positive work would be done primarily by the hip, and since the knee and hip muscles would be absorbing energy during much of the cycle, which could not be released as positive work. Unless energy exchange between segments occurred in such a way as to reduce inefficiency, core body temperature would rise considerably. Crompton et al. (1998) therefore suggested that all other things being equal, AL-288-1 would have been unlikely to adopt such an inefficient gait. Kramer and Eck (2000), also on the basis of inverse-dynamics modelling, then proposed — not only that this hominid could have been a mechanically effective upright biped – but that the (mechanical) energy cost of transport could have been about a third less than that of a modern woman walking at equivalent speeds. We have recently shown (Wang et al., 2003) that BHBK gait results in great reduction in the possibility of energy conservation by exchange of potential and kinetic energies, the mechanism which is known to be the basis of the efficiency of human bipedal walking.

We cannot of course measure metabolic costs directly in fossil species, but since the external forces engendered by AL-288-1's bipedalism almost certainly fell within the range of those which humans may, in certain circumstances, create (see eg. Li et al., 1996), it is reasonable to use experimental human gaits as a physiological model.

Very few studies have been designed to measure the effect of flexed hip and knee postures during during locomotion. However, a number of experimental studies exist on the effects of flexed lower limb joint posture on some of the primary physiological parameters, such as oxygen consumption and heart rate. Sato and Tanaka (1973) reported the effect of three different 'crouched' postures on both oxygen consumption and heart rate. They found 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; Table 1). Abitbol (1995) however, reported the effect of a '*bent-head, bent-knee posture*' (BHdBK) on oxygen consumption and blood flow in humans during locomotion. The posture was selected to mimic hypothesized posture of early hominids: the head and chest were leant forward, and hips and knees slightly flexed: at about 15°. The subject was allowed to shift the body weight from side to side

Table 1
The effect of posture on oxygen consumption and heart rate, from **1**: Abitbol, (1995) and **2**: Sato and Tanaka, (1973)

Posture and action	Oxygen consumption ($\mathrm{ml\,kg^{-1}\,min^{-1}}$)	Heart Rate ($\mathrm{beats\,min^{-1}}$)	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