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The relative cost of bent-hip bent-knee walking is reduced in water

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Abstract

The debate about how early hominids walked may be characterised as two competing hypotheses: They moved with a fully upright (FU) gait, like modern humans, or with a bent-hip, bent-knee (BK) gait, like apes. Both have assumed that this bipedalism was almost exclusively on land, in trees or a combination of the two. Recent findings favoured the FU hypothesis by showing that the BK gait is 50–60% more energetically costly than a FU human gait on land. We confirm these findings but show that in water this cost differential is markedly reduced, especially in deeper water, at slower speeds and with greater knee flexion. These data suggest that the controversy about australopithecine locomotion may be eased if it is assumed that wading was a component of their locomotor repertoire and supports the idea that shallow water might have been an environment favourable to the evolution of early forms of "non-optimal" hominid bipedalism.
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1. Introduction

Even before, but especially after Johanson et al. made the discovery of the fossilised hominid known as 'Lucy' (AL 288-1) (Johanson and Edey, 1981), there has

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been debate about how putative ancestors labelled 'australopithecines' might have moved. Most (e.g. Lovejoy, 2005; Stern and Susman, 1983), but not all (e.g. Sarmiento, 1998), support the notion that generally they moved bipedally but there remains a clear disagreement as to which gait they were likely to have adopted (Ward, 2002; Stern, 2000). Some workers (e.g. Lovejoy et al., 1973; Jungers, 1982; Crompton et al., 1998) favour a fully upright (FU), very human-like gait, whilst others (e.g. Berge, 1994; Stern, 2000) propose a different, more ape-like, bent-hip, bent-knee (BK) gait. Recently, direct measurements of energy consumption on human subjects (Carey and Crompton, 2005) showed that the BK gait is 50%–60% more costly than FU in humans on land, depending on the speed, and that core body temperature rose by 0.3 °C in 30 min by adopting a BK gait, suggesting that it would have been maladaptive in hot, equatorial habitats. This raises the question of whether there are any environments where a BK gait might not have been as maladaptive from a cost of locomotion point of view.

Almost all the theorising by workers in the scientific literature about the possible modes of locomotion of australopithecines to date has been in the context of terrestrial, arboreal or a mixture of the two environs. Serious consideration about how they might have moved in water, or its possible impact on the origins of hominid bipedalism has been conspicuous largely by its absence, although there is a growing body of literature about hydrotherapy and its beneficial effects in exercise regimes for the elderly and post-operatively (see, for example Teramoto et al., 2000; Shono et al., 2001; Fujishima and Shimizu, 2003; Sundelin et al., 2004; Hotta et al., 2004; Barela et al., 2006).

The lack of scientific investigation into the wading hypothesis of bipedal origins is peculiar, considering that the palaeoecological contexts for many of the australopithecine finds have been distinctly "wet and wooded" (WoldeGabriel et al., 2001), climatically variable (Potts, 1998) and dominated by local wetlands (Johanson et al., 1982, p. 391), and that predominantly terrestrial quadrupedal great apes appear to predictably switch to bipedalism in shallow water (Kuliukas, 2002; see discussion this paper).

In response to the Carey and Crompton (2005) study which showed that a BK gait was 50–60% more costly than a FU gait on land, we decided to test the hypothesis that moving in water should reduce the effect of gait on the cost of locomotion and thus open up a new line of enquiry into the phenomenon of the evolution of hominid bipedalism.

2. Materials and methods

Thirty fit and healthy volunteers (14 males, 16 females, means and standard deviations, respectively, for age = 39.13 and 15.36 years, weight = 76.54 and 15.25 kg, height = 1.72 and 0.10 m, BMI = 29.51 and 3.70 kg/m^2) were involved in a series of wading experiments with approval granted by the University of Western Australia Ethics Committee.

The experiments were designed to calculate the energy consumption of various walking trials administered to each individual following a counterbalanced design. Each set of trials was performed on the same day and examined the effects of speed,

depth of water and degree of knee flexion on the cost of locomotion. Typically the volunteer either walked along one end of a pool or waded from side to side at a given depth, speed and knee flexion, for about three minutes in order for their oxygen consumption to reach a steady state. The speed was maintained by synchronising the volunteer's location against a series of markers along the pool. Knee flexion was measured as the angle the tibia makes *away from* the continuation line from the femur. The degree of knee flexion was maintained by suspending a cord across the pool at a height corresponding to the eye-level of the volunteer whilst standing with bent knees. Once steady state was reached, expiratory gases were collected via a Douglas bag for about 1 min and subsequently analysed to calculate the rate of O_2 consumption and CO_2 production. Heart rate was recorded before and after each trial and used to ensure the volunteer was rested before the next trial in the set.

Paired student's *t*-tests were used to compare the differences in oxygen consumption ($V \cdot O_2$) for BK and FU on land and in water, and two-way unbalanced ANOVA followed by Fisher LSD *a posteriori* tests, using Genstat for Windows software, were adopted where depth and knee flexion variables were compared. Statistical significance was accepted at the $p < 0.05$ level.

3. Results

In agreement with Carey and Crompton (2005), we found that the cost of a BK gait (Fig. 1a) with 50° knee flexion (BK50) at 0.3 m/s was approximately 57% higher (student's *t*-test, $p < 0.05$) than an FU gait on land. However, when similar experiments were conducted in chest-deep water, also at 0.3 m/s, there was no significant difference in the gross energetic cost of locomotion between FU and BK gaits, ($p = 0.631$, Fig. 1a).

In waist-deep (0.96 m) water and at higher speeds (0.5–0.6 m/s), the difference in energetic cost between the two gaits was approximately 18% ($p < 0.001$; Fig. 1b).

As knee flexion increased, there was a greater difference between the cost of FU and BK walking on land, but this effect was diminished in water (two-way, unbalanced ANOVA, substrate: $F = 33.40$, $p < 0.001$, flexion: $F = 14.27$, $p < 0.001$; Fig. 2).

We also found that it was about 73% more costly to move with an FU gait in water than on land, but that this ratio gradually diminished as knee flexion increased. Walking with a knee flexion of 60° or more was actually found to be just as costly (no significant difference) in water as on land. The effect of increased knee flexion on the cost of standing still was also found to be 50–70% more than a FU posture on land, with the cost falling away as water depth increased up to 1.4 m, where there was no significant difference between postures (two-way, unbalanced ANOVA, flexion: $F = 19.86$, $p < 0.001$, depth: $F = 6.20$, $p = 0.004$; Fig. 3).

Finally, as with walking on land, we found that the cost of locomotion per metre travelled was highest at very low speeds (< 0.2 m/s), reached lowest levels in the mid-range (between 0.3 and 0.7 m/s at this depth) and then rose again as maximal speeds were reached, with the FU gait being 20–25% less costly over the 0.3–0.7 m/s range (Fig. 4).
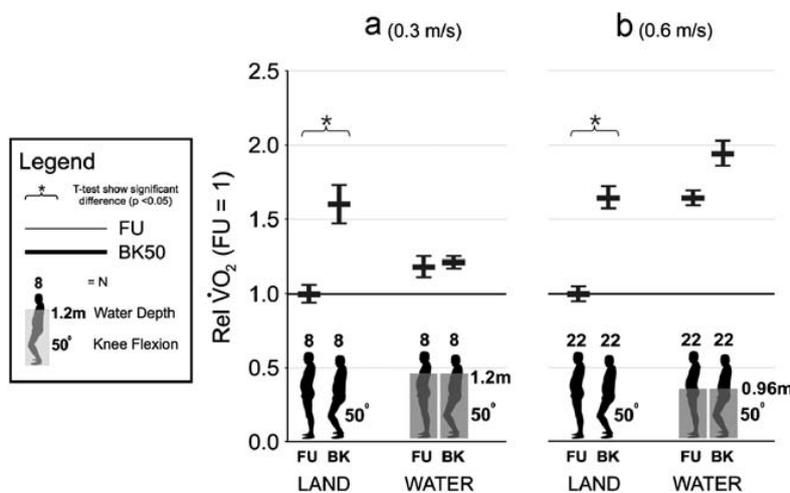
Fig. 1. Relative cost of walking with FU and BK gaits on land versus (a) chest-deep water at 0.3 m/s or (b) waist-deep water at 0.5–0.6 m/s. All results for each panel are expressed as means ± S.E.M. relative to the cost of the FU gait on land. ✳ indicates statistically significant difference at $p < 0.05$.
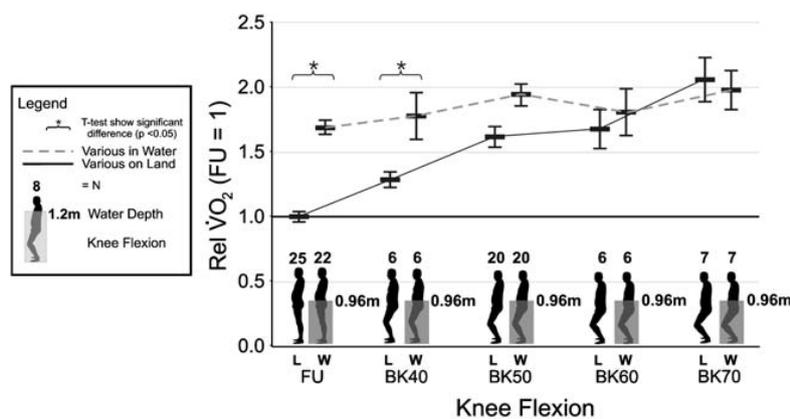

Fig. 2. Relative cost of walking with FU and BK gaits on land versus waist-deep water at 0.6 m/s with varying knee flexion. All results are expressed as means ± S.E.M. relative to the cost of the FU gait on land. ✳ indicates statistically significant difference at $p < 0.05$.

4. Discussion

The results of this study show that the cost differential of BK compared to FU gait is less in water than on land. This 'gait-cost equalising effect' varies with the angle of knee flexion, depth of water, body height and speed of movement. The greater the knee flexion, the deeper the water and the slower the speed, the less is the differential between the cost of movement of a BK gait compared to the cost of a FU gait. Under some conditions (e.g. knee flexion greater than 60° at speeds less than 0.3 m/s
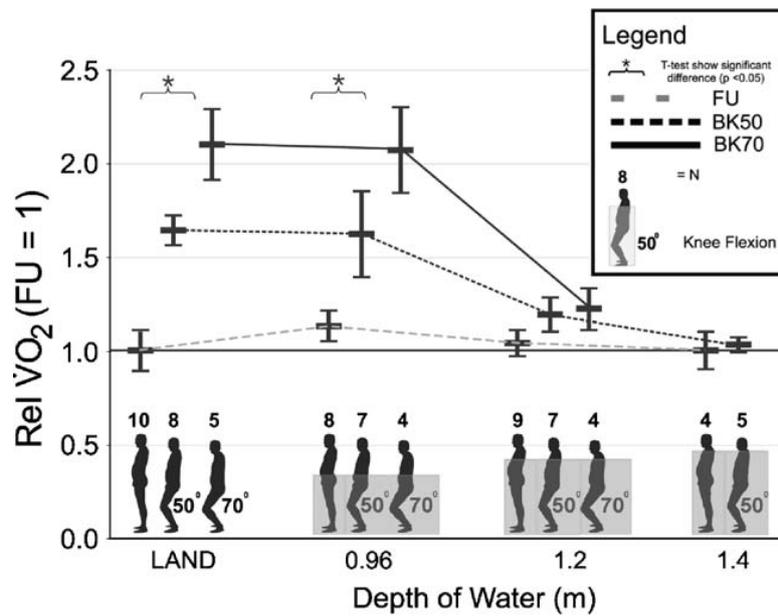
Fig. 3. Relative cost of standing still on land and in varying water depths and knee flexions. All results are expressed as means ± S.E.M. relative to the cost of standing still FU on land. ✳ indicates statistically significant difference at $p < 0.05$.
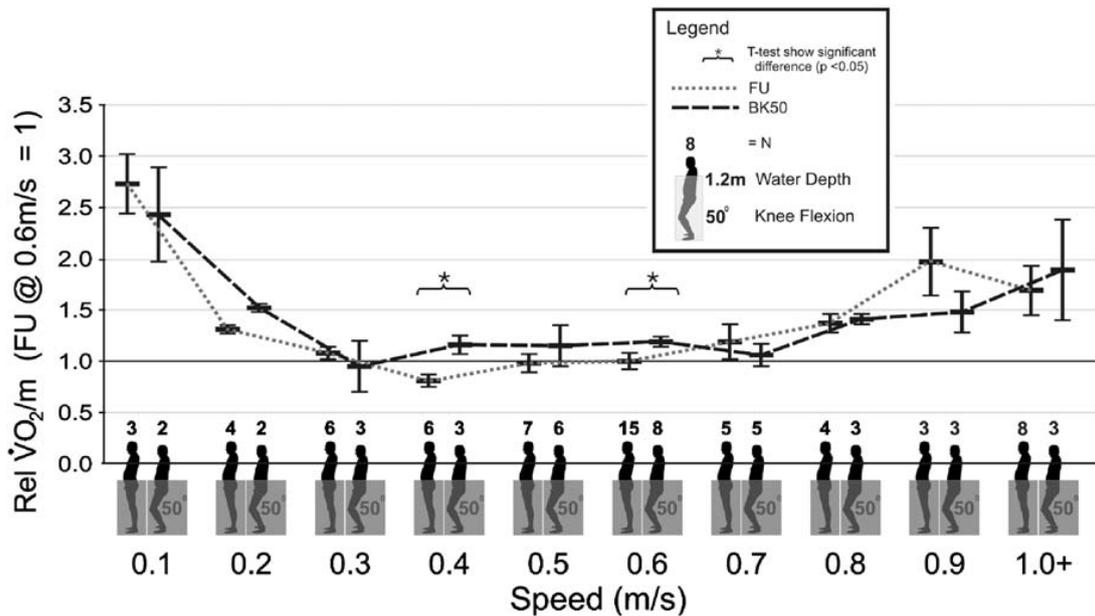
Fig. 4. Relative cost of wading with FU and BK (50°) at varying speeds in 0.96 m water. All results are expressed as means ± S.E.M. relative to the cost of wading with FU gait at 0.6 m/s. ✳ indicates statistically significant difference at $p < 0.05$.

in depths of water about the xiphisternum level) the cost of moving in water is not significantly different from that on land.

These findings may have a bearing on some important issues in the debate about the evolution of hominid bipedalism, generally, and about the possible mode of locomotion of early hominid bipeds such as *A. afarensis* in particular: Assuming that

the results of this study would be as valid in the typical muddy substrata found in flooded forest habitats as we found in our ideal swimming pool experiments, they suggest that for early hominids not yet anatomically specialised for human-like bipedalism the cost of moving through shallow water bipedally may have been less affected by gait in water than on land.

Although there is good evidence, for example from Laetoli, that australopithecines walked on land habitually (Leakey and Hay, 1979) and moving through water bodies would have entailed significant predation risks from crocodiles and territorially defensive hippopotami, there is good reason to suppose that early *Homo* always retained a significant ecological relationship with waterside habitats, along with their australopithecine-like forebears.

Firstly, it is likely that early *Homo* needed to maintain an adequate water budget for thermoregulation, in the context of mobility and stealth activity in semi arid tropical mosaics (Wheeler, 1991, 1992) and would therefore have been unlikely to have wandered too far from drinking water. Such locations, including gallery forests adjacent to rivers, swamps and lakes would also have attracted game ungulates for the similar reasons, and contained usable lithic materials with the potential for tool-making.

Secondly, as tropical rainforest made way for savannah in the Plio-Pleistocene, woodland would not have shrunk in a random manner but systematically, closer to permanent water courses in the form of gallery forests. Our early hominin ancestors, like most forest adapted species, are likely to have clung to these forest refugia (Hughes, 1988; Meave et al., 1991) placing them closer to water courses, paradoxically, the more arid the climate became. Riparian forests are prone to seasonal flooding, a phenomenon likely to have exposed these hominins (Reed, 1997, p. 309) to the need for occasional movement through water and it has been suggested that habitats such as the Okawango inland delta, may have acted as relatively food-rich refugia for taxa, including early hominids, adapted to forests (Wrangham, 2005).

Thirdly, some *A. afarensis* palaeohabitats indicate a close association with water including Taharin (KHN-TH 13510), whose faunal assemblage was described as "including lacustrine animals and those that would be found along a lake margin and in the catchment area" (Hill, 1985, p. 222), Hadar (AL 288-1) dominated by local wetlands (Johanson et al., 1982, p. 391), Denen Dora (AL-333) associated with distinct water channels, and the Dikika area (DIK-1) described as a "river-dominated delta system" (Wynn et al., 2006, p. 332). The association with waterside niches is even stronger in some earlier hominids (e.g. *Sahelanthropus tchadensis,* Vignaud et al., 2002) which, according to some recent studies, have "apparent adaptations for bipedality… close to or even antedating accepted dates for hominin/panin divergence" (Thorpe et al., 2007, p. 1330). The anticipated objection of taphonomic bias in this evidence can be countered, most importantly, by simply understanding that although death close to water courses does not have to indicate a more aquatic life style, it certainly does not provide evidence against it. The matter at hand is simply the question as to whether such habitats may have provided sufficient selection pressure to favour increased levels of bipedality. Indeed,

considering those current models of ape-human divergence that place the phenomenon in the context of wooded-savannah mosaics, it is difficult to see how such scenarios differ from the habitats of extant chimpanzees. If such a slight (or even non-existent) shift in habitat is perceived to have been sufficient to drive early hominin evolution it can only be suggested that waterside habitats could be more powerful in doing so.

It is worth considering which habitat settings might provide the most feasible setting for bipedal wading. Extant great apes have been observed moving quadrupedally in very shallow water. Fruth reported quadrupedal wading in bonobos in the context of foraging for invertebrates in shallow forest streams (interviewed in De Waal and Lanting, 1997, pp. 79–82.) Chimpanzees have been reported moving quadrupedally in shallow water too (Kortlandt, 1999, pp. 27–31) and gorillas have been observed moving quadrupedally in shallow swampy 'beis' in the Congo in the context of gathering roots and shoots of aquatic sedges (Parnell and Buchanan-Smith, 2001).

However, in deeper water there is good evidence, including photographic and film, that chimpanzees (Karlovski, 1996; Tutin et al., 2001; BBC/Discovery Channel, 2002), bonobos (Myers-Thompson, 2002, p. 24; Kuliukas, 2002), gorillas (Doran and McNeilage, 1998:124; Parnell and Buchanan-Smith, 2001; Breuer et al., 2006) and orang-utans (Ellis, 1991, p. 56; Sommer and Ammann, 1998; Galdikas, 1999, pp. 72–80) tend to switch to bipedal locomotion (Fig. 5), often in the context of foraging for food. As we can find no reports of other mammalian taxa that share this locomotor behaviour, other than brief instances of postural bipedalism seen in film footage of the grizzly bear (*Ursus arctos*), bipedal wading would seem to be an almost unique characteristic of *Hominoidea* amongst mammals.

One of the two species most closely related to humans, the bonobo (*Pan paniscus*), perhaps the extant species most closely associated with the general body shape of *A. afarensis* (Zihlman et al., 1978), has been shown to habitually move both bipedally and quadrupedally with a knee flexion typically much greater (40–130°) than that in humans (0–75°) (D'Aout et al., 2002). Such general body shapes, therefore, may be seen as ideal candidates to benefit from moving through water bipedally, as shown in this study.

We propose that the results of this study should be considered in the light of the fossil evidence, provided earlier, linking the palaeohabitats of early hominins to waterside habitats, and in the context of a climatically variable time period in human evolutionary history (Potts, 1998). It is suggested, in that context, that this study indicates that intermittent wading in seasonally flooded habitats, either for food or as a necessity to cross flooded open patches of woodland, could have been a significant factor in leading some apes on an evolutionary trajectory towards obligate bipedalism. Furthermore, our findings might help to satisfy the apparently contradictory concerns of palaeoanthropologists about the putative gait of the australopithecines. The suggested instability of the FU posture in australopithecines (Berge, 1994; Stern, 2000) would certainly not be as great, and concerns that a BK gait would have been too energetically costly and likely to have resulted in overheating (Crompton et al., 1998; Carey and Crompton, 2005) may be

Fig. 5. Chimpanzee (*Pan troglodytes*) female, with infant, wading bipedally in approximately 75 cm deep water at the Conkuati reserve, Congo. Photo: Philippe Vallas/HELP International.

eased, if it is assumed that at least some of their bipedal locomotion was performed in water.

We believe this study should stimulate further research in a number of areas. It would be useful to repeat this experimental protocol in various natural habitats to determine how the results might be affected by real world under-foot substrates. It should also be possible to conduct research into the shape of the australopithecine hip and, specifically, how this shape differs biomechanically from the human form. A 3D morphometric geometric study of the pelvis and femur should be able to yield enough data to determine the kinds of hip movements this hominid could perform with a biomechanical advantage better than the human form. Then, further similar studies to this one, varying gait by including components of lateral motion (e.g. twisting and sideways), could be done to test the hypothesis that the hip movements, found to be most effective in the australopithecine hip, might be explained as some adaptation to efficient wading.

Acknowledgements

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