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Human balance, the evolution of bipedalism and dysequilibrium syndrome

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Summary A new model of the uniqueness, nature and evolution of human bipedality is presented in the context of the etiology of the balance disorder of dysequilibrium syndrome. Human bipedality is biologically novel in several remarkable respects. Humans are (a) obligate, habitual and diverse in their bipedalism, (b) hold their body carriage spinally erect in a multisegmental ‘‘antigravity pole’’, (c) use their forelimbs exclusively for nonlocomotion, (d) support their body weight exclusively by vertical balance and normally never use prehensile holds. Further, human bipedalism is combined with (e) upper body actions that quickly shift the body’s center of mass (e. g. tennis serves, piggy-back carrying of children), (f) use transient unstable erect positions(dance, kicking and fighting), (g) body height that makes falls injurious, (h) stiff gait walking, and (i) endurance running. Underlying these novelties, I conjecture, is a species specific human vertical balance faculty. This faculty synchronizes any action with a skeletomuscular adjustment that corrects its potential destabilizing impact upon the projection of the body’s center of mass over its foot support. The balance faculty depends upon internal models of the erect vertical body’s geometrical relationship (and its deviations) to its support base. Due to the situation that humans are obligate erect terrestrial animals, two frameworks – the body-and gravity-defined frameworks – are in constant alignment in the vertical z-axis. This alignment allows human balance to adapt egocentric body cognitions to detect body deviations from the gravitational vertical. This link between human balance and the processing of geometrical orientation, I propose, accounts for the close link between balance and spatial cognition found in the cerebral cortex. I argue that cortical areas processing the spatial and other cognitions needed to enable vertical balance was an important reason for brain size expansion of *Homo erectus*. A novel source of evidence for this conjecture is the rare autosomal recessive condition of dysequilibrium syndrome. In dysequilibrium syndrome, individuals fail to learn to walk bipedally (with this not being due to sensory, vestibular nor motor coordination defects). Dysequilibrium syndrome is associated with severe spatial deficits that I conjecture underlie its balance dysfunction. The associated brain defects and gene mutations of dysequilibrium syndrome provide new opportunities to investigate (i) the neurological processes responsible for the human specific balance faculty, and (ii) through gene dating techniques, its evolution.

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Introduction

Humans are biologically novel in several respects including language, dexterity and complex culture. One trait which tends to get overlooked is bipedality. This is perhaps because two legged locomotion is biologically common. However, the manner in which humans stand, walk and run only occurs in our own species.

Briefly, the human body is arranged vertically such that the head, trunk, legs and feet and their links in the neck, spine, pelvis, knees, and ankles dynamically balance together to form an upright ‘‘antigravity pole’’. Since these segments and their points of articulation are not fixed, and the downward force of gravity never stops, the erect body exists always an inch or two away from falling. There is no locomotive use of holds, as with other primates. That the body is constantly upright is due to the unending skeletomuscular adjustment of posture (in the manner of a segway scooter or iBOT wheelchair). The habitual stance of no other animal has this total dependence upon the maintenance of vertical balance.

Here I propose a new theory about the nature and evolutionary uniqueness of the balance faculty responsible for human erectness, and the etiology of a rare autosomal recessive condition, dysequilibrium syndrome, in which this balance faculty is developmentally defective. The core of my theory concerns the evolution of a novel addition to the primate

balance processes that enables humans to engage in their proficient bipedality: the internal models of the nongravitational z-axis body image.

The separate processing of gravitational and nongravitational information by the human balance faculty has already been established by neurologists [1, 2], and by those studying the biomechanics of human balance [3]. Building upon this, I propose that:

(a) the z-axis body image arose from the unique geometrical situation of terrestrial bipeds. In such bipeds, the constant perpendicular uprightness of body axis to the ground support (egocentric geometry) is put in direct alignment with the gravitational vertical (allocentric geometry);
(b) that the advantages of this alignment only came to be fully exploited for balance when hominid brain size expanded with the evolution of *Homo erectus*;
(c) that it has a close integration with higher cognition. As a result, the bipedal balance faculty has the same species specific relationship to humans as other higher cognition dependent faculties such as language or dexterity;
(d) that it is a defect in this balance faculty that underlies the rare autosomal recessive balance disorder of dysequilibrium syndrome [4–6];
(e) and that the cognitive, neurological, and genetic impairments of dysequilibrium syndrome and other developmental balance disorders provides a window with which science can study the information processing, neurology and evolution of human bipedality.

Human bipedalism

Bipedalism, as a descriptive term for the use of two legs for standing and locomotion, can be applied to a variety of animals. These include, as an occasional method of locomotion, primates (such as macaques, chimpanzees, bonobos, gorillas), birds (in general, and as a specialization in flightless ones such as penguins, ostriches and emus), extinct reptiles (Tyrannosaurus rex), certain lizards and even cockroaches [7]. However, human bipedal posture and anatomy are unique in four fundamental ways.

(a) Humans are habitual and obligate bipeds that engage in a wide and diverse variety of erect locomotions (walking, running, skipping, jumping, dancing), and apart from a brief period in infancy, normally (unlike all other primates) do not engage in any form of quadrupedalism. Other obligate bipedal mammals such as kangaroos exist, but they hop rather than walk or run.
(b) Humans hold the carriage of their bodies upright in a spinally erect posture in which each body segment is balanced on top of each other. Anatomically this involves moving forward in the skull, the foramen magnum (the hole through which the spinal cord enters the head), [8]. Further, other anatomical changes exist that increased the range of movements which could be used to stabilize the body, such as an enhanced flexibility of the spine for lower back movements [9] (humans are the only mammals that can make gymnastic backbends [9]). The bodies of meerkats and penguins are also spinally erect but in contrast to humans they stabilize their uprightness tripod-like with stiff tails.
(c) Humans use their upper limbs exclusively for nonlocomotion such as manipulation, clubbing, carrying, throwing, and arm gestures. In contrast, the upper and lower limbs of nonhuman primates engage regularly both in locomotion and nonlocomotion, and as a result, neither of them are exclusively specialized. Human lower limbs, in contrast, are exclusively adapted for plantigrade walking (human toes are, for instance, the only primate ones which are not opposable), and the upper limbs likewise are specialized for power grips and finger thumb pinches [10].
(d) Humans lack prehensile tails and feet with which they can balance and support their body weight by holding and clutching surfaces. Instead, humans in their normal upright posture hold the weight of their bodies up entirely through constant and dynamic skeletomuscular adjustments so that its body mass rests vertically down through its arched feet on the ground. These anatomical and postural traits exist due to the human brains capacity to make appropriate stabilizing skeletomuscular balance adjustments. Further, the human brain can make these adjustments not only when humans stand, walk or run but also when humans superimpose upon these gaits other secondary movements. I review these secondary movements since they show that human evolution selected the human brain to have balance abilities that are considerably more skilled than those needed merely for simple bipedal erect standing or walking.

Movements while bipedally erect

Upper body activities

Due to human hands being free from locomotion, humans engage in a diverse variety of motor activities that quickly shift the center of mass of their upright bodies. Examples include throwing projectiles, clubbing, racket players returning volleys, parents piggy back carrying children, and two or more hunters carrying an animal carcass. Since these movements shift body mass considerably above the support area provided by the two legs, they are particularly likely to disrupt body balance. To prevent this happening, the body needs to make synchronized compensating postural adjustments. This is a constant though hidden process when erect: even an activity such as respiration that might be thought to only marginally shift the body's center of mass still requires regular postural changes [11].

Transient unstable positions

To be stable, static bipedal posture requires that the ground projection of the body's center of its mass is vertically above its base support. However movement introduces other factors. An important one concerns the velocity and direction of the center of mass relative to its base support [12]. For example, the vertical projection of the center of mass can be still be dynamically stable outside its support base provided it has an appropriate inward velocity [12]. This means that erect humans can engage movements that temporarily lack firm balance, for instance, during dancing, fighting and tackling and kicking footballs. Making such body actions out of transiently unstable postures, however, requires the existence in the brain of a balance faculty that can accurately determine and make the skeletomuscular adjustments needed to keep the erect body stable.

Height

When erect, humans stand taller than most other primates and do so upon a narrow foot ground contact area (compared to their height). As a result, humans stand on a particularly slender foot support. Further, the center of mass in the human body is usually high due to human legs taking up a large percentage of total height. Since the risks of falling over links to the height of the position of the center of mass above the ground, and the area of its support base, this greatly increases the demands made upon balance skills.

Tallness further increases the risk of bone and joint injury after a fall. This risk is strongly nonlinear with momentum on impact increasing with height to the power of 3. 5, and released kinetic energy, to the power of 4 [13]. The disadvantage of height is further increased in humans by short arms that are far off the ground (arms are roughly 70% leg length whereas chimps are 10% longer), and lack the robustness (which they otherwise would have if they were used in locomotion) to safely break falls.

Stiff gait

Bipedal walking can be done in two biomechanical ways: stiff gait (also known as inverted pendulum), or compliant gait (also known as bent-hips bent- knees) [14]. In stiff gait walking, the center of gravity moves up and down as an inverted pendulum. In this, the kinetic energy of the leg stance that moves the body forward is converted by raising the center of mass in the step phase into potential energy that can be reused in the next leg swing to create a new forward leg movement. In compliant walking, individuals lack this reuse of energy since the center of gravity of the body is kept fixed by hip and knee bending [14]. Compliant walking is how nonhuman primates walk bipedally, either as an occasional part of a primate's natural locomotive repertory (as with chimpanzees, gorillas and bonobos), or when they acquire bipedality permanently following injury or birth defects to their forelimbs [15].

Compliant walking maintains the body's center of mass in a constant position and so makes the body posturally stable. However, stiff gait by creating a postural instability with its constant raising then lowering of the body's center of mass turns walking into a ''series of falls' 'in which periods exist of potential body instability. As a result of this, stiff gait walkers unlike compliant ones face a constant risk of falling, for example, if they misstep or trip up.

Whether the stiff gait walking goes back to Australopithecine species is controversial. Arguments from anatomy question whether they were stiff walkers [16] but computer simulations in regard to gait efficiency suggest that they were [17]. Even assuming that they were stiff walkers, from a balance perspective they would have faced fewer problems than later humans due to the lower center of mass of their bodies caused by their smaller statue and shorter legs (as a proportion of total body height). The *Australopithecus afarensis* individual AL-288-1 (Lucy) was 1. 05 m tall, while the

H. erectus individual KNM-WT 15000 (Nariokotome Boy) would have been as an adult1. 85 m. Given the nonlinear increase of kinetic energy released upon falls with increasing body height [13], Nariokotome Boy would have fallen with the release of over nine fold more kinetic energy than Lucy. Thus, walking by H. erectus, and its descendent Homo species including modern humans, created a need for a capacity for reliable and robust balance that was not present, or at least not so important, for earlier australopithecine species.

Endurance running

The body when running is unlike that in walking in three respects: (1) it reuses forward kinetic energy through elastic absorption in tendons and ligaments. The pattern of absorbing and releasing energy stored in tendons biomechanically makes running a series of controlled leaps. As a result of this it (2) spends periods during which neither of its legs are on the ground, and (3) due to forward momentum, it possesses considerable potential energy. Running therefore puts the body at particular risk of tripping (the instability of the leaps lacking ground support), and when it does trip up, due to its large momentum, of severe injury. Long distance running is peculiar to humans. While nonhuman primates such as gorillas can run, they can only do so for short distances. Australopithecine species are also not thought to have been capable of sustained running [18]. In contrast, since H. erectus, humans have possessed specialized adaptations that allow them to engage in long-distance endurance running [19]. Given the risks, skilled balance is particularly needed if running is to be safe. An important factor is the ability for balance to incorporate information provided by higher cognition in regard to the unevenness of the ground ahead. In premodern periods, a runner needed to make footings that avoided vegetation, obstructions and holes that might trip them up.

The human biped need for balance abilities

The above noted secondary motor activities add greatly (often combined together at the same time) to the competence of the balance abilities required to keep the biped human body upright. An indication of the sophistication of these abilities is that children do not develop adult competence in even apparently simple bipedal activities as walking and running until the age of seven [20]. Indeed, the sophistication of the balance abilities that evolved suggest that we should revise our ideas about human bipedality. Instead of viewing it as another kind of bipedality, it should be seen as an entirely new form of locomotion – a kind of gymnastic ‘‘flying’’ on two legs (witness human sport and dance) – since no other biped engages in the above kinds of secondary movements.

The human balance faculty

Internal models

If the body’s center of mass goes outside its base of support, body instability starts within 100 ms [21]. Since it takes longer than 100 ms for the brain to detect an instability and then make compensating changes to posture, well-organized balance corrections must be initiated in advance. The nature of such forward feed corrections will invariably be complex. Consider an arm lifted from the side of the body to reach an object. This will need the skeletomuscular system to slightly shift back the legs to counterbalance the otherwise change forward in the location of the body’s mass. But the exact nature of this correction will depend not only upon that arm action but the pre-existing posture and tilt of the rest of the body. Humans have evolved a specialized ability to make the balance calculations required for such corrections, and spontaneously, without any awareness, carry them out. But how does this process work and how did it evolve? One way of approaching these questions is in terms of the internal models of the body image used by the brain to link posture, balance and verticality.

First, we briefly review motor control and the internal models it employs.

(1) Actions carried out by any body part are done within a neural model of its surrounding action space. These models will include the action space made by the effects of gravity upon the whole body. The brain models both physical space (in the parietal cortex), and closely related to this, the space defined by potential movements (in the motor cortex) [22] both of which involve the space in which balance occurs.

(2) The brain models its relationship to the environment in two kinds of framework. (i) The egocentric framework in which external entities are located in terms of the body itself as a referent. In this framework, objects and events are processed in terms of the body such as left, right, behind or in front, above or below. (ii) The allocentric framework in which external entities are located in terms independent of the body. In this framework, entities are defined with aspects of the environment such as compass pointings (such as north or south), and relative position to other nearby objects and events. An important allocentric referent in the external environment is the ‘‘earthcentric’’ up and down provided by gravity.

(3) Actions have many skeletomuscular consequences which with development become automatically modified so that an action is carried out smoothly. For example, muscles often exist in agonist and antagonist pairings (such biceps and triceps). The coactivation of activation and inhibition of agonist and antagonism muscles is dependent upon the context of the type of movement intended [23]. To do this, the brain must model how the skeletomuscular system interacts given different intended movements. Balance is special case of this in which the skeletomuscular system is modeled in regard to the effects of movements upon the body’s center of mass and postural stability.

(4) These models are constantly active and part of the body image. Those that contribute to balance control effect even simple erect standing. Though in theory, standing could be achieved using only peripheral servo-style intrafusal stretch reflexes, standing has been found to use centrally generated adjustments [24, 25].
Gravitational information and anticipation

These models need reliable information about the relationship of the body to the vertical, particularly small deviations in its slant. However, the direct sensing of gravity is not appropriate for this task. The information provided by gravisensors is limited to the particular body part in which they are located, while the vertical projection of the center of mass of the body concerns body as a whole. The gravisensors provide information, moreover, only after an instability has started, and then with a time lag.

Reflecting this, little evidence exists that vestibular input is used directly for the on-going maintenance of human body balance, though it is employed in stabilizing single body parts such as the head in the vestibulo-ocular reflex [26]. An important example of the nongravitational control of balance is shown in the ‘‘moving room illusion’’ [27]. In this, a standing individual sees what would normally be static ‘‘wall’’ surfaces move. Their brain attributes this visually seen motion in the outside world to their own upright body deviating from the stable upright [27]. As a result, the brain instructs the body to make movements to counteract this falsely detected body motion with the result that it sways backward and forward [27]. This happens in spite of the body’s gravisensors correctly detecting that the body is not deviating from vertical. Children in their earliest erect posture and first steps depend also upon nonvestibular inputs for the upright [3], and they are even more easily unbalanced than adults by a swaying visual environment [28]. Direct gravitational clues also fail to provide upright information when vision is blurred: a major problem in aviation before the existence of attitude indicators was that pilots lost their sense of vertical orientation when in clouds [29]. Individuals with bilateral labyrinthine dysfunction can still walk in spite of the loss of the use of their vestibular gravity sensing otoliths [30].

Geometry and vertical information

Information about body deviations from the vertical can be inferred from the body image’s geometrical relationship to the environment. This is because human obligate terrestrial bipedality combines having a continuous upright posture with this happening upon a flat and stable horizontal support base. Human bipedality, as a consequence, puts the vertical spinal axis of the body image in near constant alignment with gravity. This link between gravity and the vertical body is peculiar to humans since it exists only for obligate terrestrial bipeds. Notably, it does not exist, for great apes since they spend only a small part of their time bipedally, and much of that involves arboreal standing upon tree branches that are slanted, flexible and unsteady– a situation that prevents a constant link existing between an upright body and the direction of gravity. Thus, a consequence of humans being habitual and regular terrestrial bipeds is that one of the egocentric axes of the body image – the one that runs through our spines from our feet to our head – is put in a constant alignment with the gravitational vertical one of up and down. In geometry, the alignment shared between these two frameworks is in the third or vertical z-axis. Accordingly, in humans the geometry of internal models based around the body’s z-axis can be used to detect body deviations from the gravitational vertical. The information used to detect postural deviations can be derived from many sources including proprioceptive sensors in the ankles and other body parts, golgi organs in the tendons, plantar pressure sensors cutaneous receptors in the feet, reafferent motor copies about body movement, vestibular inputs, optic flow and the observed horizontal and perpendicular surfaces in the surrounding environment [3].

Due to the z-axis alignment, cognitive processes that evolved in the motor system to model egocentric frameworks can be redeployed to process geometrical posture deviations and so detect deviations of the body from the gravitational vertical. This can be used to create not only compensating body adjustments when movements happen but train the motor system to create them in advance.

A similar principle of creating balance from detecting geometric tilt deviations is used by segway scooters (US Patient 6, 779, 621). These maintain a stable platform for the human standing and holding its scooter stick by detecting angular (or tilt) deviations from an implied vertical and making appropriate adjustments to ensure that its projection of the center of gravity is over the scooter’s wheel support.

Spatial information processing and balance

The models underlying the z-axis body image exist due to the brain’s capacity to process spatial relationships. As might be predicted from this, research finds a close link between the processing of human balance and that of spatial information.

An individual's posture stability is impaired if they engage at the same time in spatial tasks (though not nonspatial ones). Vice versa, a person's ability to engage in spatial tasks is impaired by challenges to their postural stability [31, 32].

Human balance due to its high dependence upon internal models draws upon most parts of the cerebral cortex. For instance, since these anticipations link to planned motor behavior, the models used for balance draw upon the prefrontal cortex competences [33]. The visual system is able to detect stable from unstable erect postures in others [34]. Human balance therefore involves the whole brain and is not – as in many nonhuman quadrupeds – confined to the lower brain parts such as the cerebellum.

Dysequilibrium syndrome

Given the central role of the balance faculty in human biped standing and locomotion, it might be expected that it could be impaired during developmental. The impairment of this faculty would, however, not underlie all individuals with balance problems since balance can also be affected by dysfunction to sensory input or the motor coordination needed to make balance adjustments.

Only one developmental condition exists that can be directly attributed to the central impairment of the balance abilities needed for bipedalism: the very rare autosomal recessive balance disorder of dysequilibrium syndrome. The following account of this syndrome is based on the work of Bergt Hagberg and colleagues in Sweden [5], the more recent research upon the North American Hutterites cases [6], and its likely identification in large family in Turkey [35]. Individuals with dysequilibrium syndrome usually are mildly retarded and born with hypoplasia of the cerebellum (particularly the vermis) and variable hypoplasia of the cerebral cortex. However, though they have minor cerebellar signs, the cerebellar hypoplasia does not result in marked cerebellar ataxia as they can show agile motor control. For example, the dysequilibrium women in Turkey can do skilled crotchet work [35]. In spite of this spared motor development, they are crippled by an inability to stand erect and walk *bipedally*. As a result, the dysequilibrium individuals in Turkey use their spared motor abilities to walk and run on their legs and arms as proficient quadrupeds [35].

The bipedal impairment of individuals with dysequilibrium syndrome does not link to direct sensory or balance impairment. However, they suffer cognitive impairments, notably, spatially- related dysfunctions such as a poor sense of direction, length, area, weight and amount [5]. Linked to this is an impairment in the internal models that relate the posture of their bodies to the surrounding ground support. For example, lacking the ground orientation they provide, these individuals do not know how to fall without trauma – in the earlier Swedish sample, affected individuals were noted to drop back without a stepping reaction and so went down ''like a felled pine'' [5] (p. 43). As Bengt Hagberg [5] notes they ''lose the safety of the floor as a point of reference'' (p. 34).

Hagberg in the 1970's on the basis of his observations [5] identified their bipedal balance problems as arising from ''an inability—located at different levels in different cases—to integrate a normal proprioceptive inflow''. And that 'the body image functions on a subcortical level seems to be congenitally detective. Secondarily, this results in an impaired development of the body image and the spatial relationships on the cortical conscious level'' [5].

In the 30 years since Hagberg offered this analysis [5], it has been appreciated that erect balance requires internal models to process the body's z-axis. In this context, his description takes on a new significance since an overlap exists between the spatial characteristics of the z-axis body image and the spatial and body defects of dysequilibrium syndrome. This overlap suggests an explanation in which the balance defects of the dysequilibrium syndrome arise from a selective impairment to the brain's capacity to process the models that underlie the z-axis body image. As noted above, erect balance skills draw upon spatial ones. In dysequilibrium syndrome, failure in the development of spatial abilities, or their integration with motor coordination, would impair the brain's ability to model and make the anticipations needed to maintain a balanced erect body. Without the geometrical contribution to balance, there would still remain the direct gravitation sensation of the vertical – but this would be insufficient by itself to enable normal human biped locomotion. However, it might allow bipedal locomotion of a defective and restricted kind. Those with dysequilibrium syndrome after prolonged developmental delay, for instance, can often stand erect and aided by physiotherapy learn to walk, presumably with such processes, though in an abnormal ''tin solder'' or cerebellar (truncal) ataxic manner [35].

It is noteworthy that the individuals in Turkey with dysequilibrium syndrome, though they were capable after physiotherapy of such walking, originally mastered on their own a highly coordinated quadrupedal gait [35]. This can

be explained by the fact that quadrupedal walking and running locates the body's center of gravity in a near ground position compared to that in erect walking and running, and so considerably reduces the need for complex balance control. Further, if balance during quadrupedal locomotion is lost, the body does not fall very far so it does not suffer injury.

The evolution of human bipedality

Is bipedally primary an anatomical adaptation?

The anatomy of primates, particularly apes, can readily adapt to bipedal locomotion, in spite of its evolution for quadrupedalism. As noted above, great apes as part of their locomotive repertory occasionally walk bipedally, and can even do this permanently following forelimb injury or developmental defect. In the opposite direction, the recent Turkish cases of dysequilibrium syndrome demonstrate that the human skeletomuscular framework though evolved for bipedality retains the ability to acquire proficient quadrupedalism [35]. This situation exists because the skeletomuscular changes associated with bipedalism are either (1) nongenetic and induced by the activity of bipedal locomotion such as lordosis, femoral- neck-shaft angle, or that (2) they are innate but they only act to optimize bipedality. For example, the leg arm length ratio (also known as the inter- membranal ratio) in the above human quadrupeds though higher than normal (a roughly . 90 ratio instead of . 72) is still markedly less than chimpanzees and gorillas (respectively, 1. 07 and 1. 18). As a result, they have to hold their pelvises up in the air due their legs being much longer than their arms – which compromises their gait [35].

This argues that what distinguishes human bipedality from other forms of bipedalism is not primarily anatomy but balance skills. In support of this, while nonhuman primates spontaneously engage in the nonbalance demanding compliant walking, they can be taught to walk in the balance demanding stiff variety if they are first trained to stand erect, and only then encouraged to walk [15]. The lack of bipedality but with a preserved capacity for quadrupedality in individuals with dysequilibrium impairments also is consistent with the key role of balance [35].

H. erectus and erect balance

Several sources of information suggest that enhanced balance abilities arose with H. erectus.

- The vestibular canals take on the enlarged size of humans with *H. erectus* [36]. Since the vestibular organs play a key role in balance, this suggests that balance had an importance for *H. erectus* that it did not have for earlier Australopithecine species.
- There was an increase in height between Australopithecine species and *H. erectus*. As noted, the risk of injury from falls increases in a strongly nonlinear manner with height. Australopithecine species therefore retained a small statue for which bipedal falls would not result in serious harm, while *H. erectus* was able to grow to a height in which falls could produce serious bone injuries. This suggests that *H. erectus* had acquired sufficiently sophisticated balance control that such falls during normal life rarely happened.
- As noted above, there is a close link between cerebral cortical processing abilities including those in the frontal cortex and balance. Between australopithecine species and *H. erectus*, there was a marked increase in brain size particularly of the cerebral cortex. Such an increase would have provided increased numbers of cortical circuits with which to model the anticipation needed to control erect balance.
- Only with *H. erectus* did balance become sufficiently competent to allow for endurance running [18, 19].

Together this argues that a radical enhancement of erect balance competences occurred between the Australopithecine and Homo species. Two hypotheses can be proposed. First, that the z-axis processes discussed above arose first with the Homo species with the earlier bipedality of the Australopithecine species being dependent upon gravitational processes. Alternatively, the early Australopithecine species could have acquired the z-axis processes but these were underdeveloped. For example, that the integration of z-axis processes and gravitational ones could required extra neural circuits that only came available with the increased encephalization of *H. erectus*.

Predictions and implications

Neurology

At present, acquired brain lesions have allowed neurologists to locate the gravitational and non-gravitational components of human balance respectively to (i) the cerebellar-cerebral circuits centered upon the vestibular area in the

posterior insular cortex, and (ii) the ventral posterior and lateral posterior nuclei of the posterolateral thalamus and the associated cortical projections [2]). MRI scans of the brain abnormalities of those with dysequilibrium syndrome will be able to confirm this and extend these observations [4, 35].

Genes and dating the evolution of human bipedality

Researchers can infer the evolutionary history of genes from their inter-and intraspecies DNA coding differences. Genes critical for human uniqueness have been dated as to their evolutionary onset [37]. At present this research has been confined to genes concerned with brain size and language. Recently abnormalities, for example, in speech and articulation have been linked to FOXP2, agene that shows evidence of positive selection in humans compared to chimpanzees [38]. The two above suggested scenarios of the origin of human bipedally can therefore be distinguished if sufficient genes responsible for human balance can be identified.

Genes involved in the species specific balance abilities of humans, however, are still mostly unidentified as there is no recognized mutation that links to them. The conjecture made here is that the mutations that cause dysequilibrium syndrome involve such genes. Dysequilibrium syndrome is likely to be a multi-etiological condition (with subtly different phenotype impairments) caused by mutations in many different genes. Further, there exist other conditions that involve developmental balance impairments but which are insufficiently severe to cause the crippling impairments of disequilibrium syndrome, and these might potentially also have a genetic origin [39].

Already one gene has been located for the dysequilibrium syndrome found amongst the Hutterites [4, 40]. The genetic dysfunction of the Turkish individuals has been located on chromosome 17p, though the particular gene in this DNA patch has not been as yet identified [41]. It is likely that with advances in genetic analysis that many more DNA loci will be linked to developmental balance disorders making it possible to reconstruct in detail the evolutionary story of the human balance faculty.

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