

**Respiratory, postural and spatio-kinetic motor stabilization,
internal models, top-down timed motor coordination
and expanded cerebello-cerebral circuitry: a review**

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MOTOR STABILIZATION

ABSTRACT

Human dexterity, bipedality, and song/speech vocalization in *Homo* are reviewed within a motor evolution perspective in regard to

- (i) brain expansion in cerebello-cerebral circuitry,
- (ii) enhanced predictive internal modeling of body kinematics, body kinetics and action organization,
- (iii) motor mastery due to prolonged practice,
- (iv) task-determined top-down, and accurately timed feedforward motor adjustment of multiple-body/artifact elements, and
- (v) reduction in automatic preflex/spinal reflex mechanisms that would otherwise restrict such top-down processes.

Dual-task interference and developmental neuroimaging research argues that such internal modeling based motor capabilities are concomitant with the evolution of

- (vi) enhanced attentional, executive function and other high-level cognitive processes, and that
- (vii) these provide dexterity, bipedality and vocalization with effector nonspecific neural resources.

The possibility is also raised that such neural resources could

- (viii) underlie human internal model based nonmotor cognitions.

KEY WORDS motor stabilization; anticipatory postural adjustment; feedforward; internal models; preflexes; cerebello-cerebral circuits; bipedality; knapping; speech/song vocalization

1. INTRODUCTION

1.1. Motor stabilization and the evolution of novel motor capabilities

Motor stabilization—the capacity to adjust a movement to counteract a perturbation, or modify it to fit a particular circumstance—is central to the proficient execution of any action, whether done by an insect or by a human. The problem of movement instability is an ancient one faced by nearly every land invertebrate and vertebrate, and so, is neither recent nor unique to humans.

However, motor stabilization involves not only very ancient low-level processes such as muscle visco-elastic “preflexes” (Brown and Loeb, 2000; Nishikawa et al., 2007; van Soest and Bobbert, 1993), and stereotypical spinal adjustment reflexes (Heng and de Leon, 2007), but also more recently evolved high-level cerebello-cerebral cortex circuits that create top-down feedforward motor adjustments. The former are embedded directly in the musculoskeletal system, while the latter are based upon temporally accurate predictive internal models that simulate the complex dynamic interactions that happen in the musculoskeletal system (including attached artifacts and the environment) (Desmurget and Grafton, 2000; Doya, 1999; Ito, 2006; Ito, 2008; Kawato and Gomi, 1992; Wolpert and Kawato, 1998). Theoretically, these three biological processes of stabilization are very different due to the latter’s ability to support highly learnt task-determined and circumstance modifiable actions. Notably, the two low-level musculoskeletal system processes are restricted in that they can only enable the execution of a stereotypical and limited but highly reliable repertoire of pre-evolved movements. In contrast, stability based upon the predictive internal modeling—especially after many years of prolonged motor skill maturation as happens with humans—allows for top-down fractional-second multi-body part movement coordination—and so the execution and stabilization of a diverse range of nonevolved and cognitively enhanced motor skills. This article reviews evidence that in *Homo*, a shift occurred to the latter kind of mastery-based motor stabilization across the domains of hand control, anatomically aligned bipedality, and vocalization, and this produced the biologically unique motor faculties found in humans. Moreover, that this shift arose in *Homo* due to brain expansion.

1.2. Topics reviewed

This article in this context reviews the following interrelated issues.

Human motor abilities are biological novel. Each of the three major motor faculties that characterize humans (dexterity, bipedality and vocalization) on close examination show radical differences in their functional and neurological motor biology to their nonhuman motor equivalents (sections 2, 5, and 6).

This uniqueness has a similar nature in all three cases and links to enhanced feedforward stabilization. Human dexterity, bipedality and vocalization all in their proficiency show a common shift to a motor control ability based upon anticipatorily/feedforward control used to execute and stabilize highly practiced top-down timed coordinated movements across multiple motor elements (see section 4.3). Such accurate and precise timing of leant action adjustments can be seen in the task dependent timing of different muscles, for example, during the anticipatory stabilization of human specific motor expertise capacities involved in stone-tool knapping (section 2.1).

Stabilization by top-down adjustment derived from internal models across independent body/artifact movement units. The human ability to do top-down timed adjustment derives from the use of highly developed time-based predictive internal modeling of the body's kinematics, kinetics and action interactions (section 4). Many actions—such as knapping, anticipatory postural adjustment while standing, and vocal tract synchronization during human song and speech vocalization—can as a result be executed and stabilized by the use of several different and separated bodily movements that are actively orchestrated together in a centrally determined and precisely timed manner. This allows that correction movements can occur in the most effective ways at the millisecond exact times needed to counteract any disruptive perturbations or unwanted movement side-effects (section 3).

Top-down adjustment derived from internal models requires a protracted period to acquire expert mastery. Human motor function to acquire fully competent modeling requires extensive daily practice over many years. Humans, indeed, have a highly prolonged period of immaturity before adolescence and adulthood in which motor skills such as speech and walking are skillful without having full adult motor expertise, a motor mastery most notably shown in the extreme robustness of adults compared to children against unexpected disruption. This lack of full adult proficiency exists in spite of the fact that by adolescence such skills would normally have been in continual daily use for over ten years, and so in many respects already highly proficient. Likewise, the full mastery rather than mere skillfulness of the expertise needed for many specialized adult motor skills is only achieved in many cases, for example, in sport and musical instrument playing, after at least ten years of daily deliberate practice (see sections 2.7., 3.4., 4.2.1. and 8.2.).

Top-down adjustment derived from internal models interacts with higher-cognition. Internal models also enhance the higher level executive/ organizational control that provide actions with cognitive flexibility by enabling them to be (i) temporally planned and subtask set shifted in terms of hierarchized and sequentialized goal priorities, and (ii) monitored and modified during performance in regard to errors and error correction (sections 2.2. and 4.2.2.). Indeed, a key part of motor skill mastery lies in integrating motor faculties with cognitive ones that arise from such expanded higher internal model based abilities.

Nonhuman motor function is stabilized by evolved musculoskeletal system local preflexes and reflexes. In contrast, to humans, nonhuman motor control only enables a limited repertoire of highly evolved stereotypical movements. These are largely stabilized (though see comments in section, 4.5 upon nonhuman primates) within the musculoskeletal system through preflexes (section 3.2) and spinal adjustment reflexes (section 3.3). They lack as a result human levels of cognitive-motor complexity and task adaptability.

Human motor action involves multiple independent motor elements. Human task-determined actions usually consist of multiple motor elements (section 4.4.) that arise either

- (i) from the incorporation of artifacts (tools, projectiles, musical instruments, vehicles) into motor control, or
- (ii) from treating existing parts of the musculoskeletal system as independent control units that are otherwise in nonhumans animals “locked” together as nonindependent elements by the low-level stabilizing effects of musculoskeletal preflexes and reflexes.

Human enhanced motor stabilization arises from the expansion of cerebello-cerebral circuits. The internal model enhancement of human motor control arises directly from *Homo* brain expansion and its enlargement of cerebello-cerebral cortex circuitry (particularly involving the posterior parietal, ventral premotor and prefrontal areas). This expansion massively increased the capacity of *Homo* relative to non*Homo* brains to create musculoskeletal internal models with (i) fine-level temporal resolution, and (ii) the action-organization levels needed to provide enhanced higher cognitive control over them (sections 7 and 8.3.).

Human motor faculties share neural resources. In the case of each of the three major unique human motor faculties (dexterity, bipedality and vocalization), this internal model enhancement arises, at least in part, from internal model related attentional, executive and other capacities that are drawn upon as common, shared, and, to some degree, effector nonspecific neural resources (section 7.1.). This is evidenced, for example, in dual-task interference during which different areas of motor control (and even nonmotor faculties) are compromised in their performance when they attempt to concurrently employ such resources (section 7.1.2.), and the developmental neuroimaging correlates that exist between them, particularly in the cerebellum (section 7.2.4).

Motor innovations closely link to human evolution. Since the motor control of bipedality, dexterity and vocalization need not happen as concurrent activities during hunter-gathering (nothing required early *Homo* to walk and knap, at the same time, for instance), this raises the possibility that their enhancement evolved as a nonspecific cross-faculty pleiotropic adaptation.

- (i) brain expansion would have largely increased cerebello-cortical circuitry nonspecifically, and so
- (ii) the nonspecific availability of internal modeling that enhances motor skills. Further,
- (iii) the enhancement in each of the three motor faculties in the form of long-distance travel, high-energy food extraction tools, and more effective communication would have worked together in a highly synergetic manner.

The combined effect of them could have been responsible for the evolutionarily critical shift by early *Homo* to high-energy food—the hunter-gathering specialization of *Homo* until the recent advent of agriculture. This is because the enhancement and synergies involved would have created novel kinds of feedbacks leading to further motor function selection (section 7.2 and figs. 3 and 4). Notably, high-energy foods would support larger brains and the prolonged nonadult maturation period required for refining the internal models needed for acquiring highly developed motor skill mastery (section 8).

1.3. Evolutionary vs. Bernsteinian approaches to motor function

Motor control in this review is treated from an evolutionary perspective rather than a Bernsteinian one. Nikolai Bernstein (1896-1966) proposed that the scientific study of motor function was the study of motor coordination which he defined (inspired by engineering analogies) as the “overcoming excessive degrees of freedom of our movement organs, that is, turning the movement organs into controllable systems” (1996, p.41.), and “the process of mastering redundant degrees of freedom of the moving organ, in other words its conversion to a controllable system” (Bernstein, 1967, p. 127). This nonevolutionary problem defines the main research paradigm presently shaping contemporary studies upon motor function. This review takes this engineering inspired problem to be a noncentral issue that is readily managed by the brain (see section 4.3), and focuses instead upon motor function in terms of its performance as it has been (in all its neurological and functional complexity) actually evolved.

In particular, the evolutionary motor science perspective in which this review is carried out requires that the investigation of motor function satisfies three conditions:

- (i) ecological-survival validity,
- (ii) neurological-involvement validity, and
- (iii) developmental-mastery validity.

These methodological requirements need to be noted as much contemporary experimental research and theory upon motor function fails to fulfill them, and so lacks theoretical and empirical relevance to the issues raised and addressed in this review that are used to understand human motor evolution.

Ecological-survival validity

This concerns accounting for actually observed motor competences as expressed in maximally demanding circumstances, since this relates to motor functions as they have actually been selected. In the case of humans, this relates to the capacity of humans to engage in biological unique activities that are central to human biological fitness such as expert knapping, challenging bipedal balance (stable carrying; accurate throwing; in contemporary people, tennis volleys, soccer tackling) (for the novel nature of human bipedality see section 5), and human speech/song vocalization.

Neurological- involvement validity

This concerns accounting for the involvement of the parts of the brain as they are actually employed when motor functions are maximally challenged, and so the brain capacities that have actually been evolved to enable evolutionarily critical motor capacities. In the case of humans, these centre upon cerebello-cerebral cortex circuits including those that involve the prefrontal cortex (Slobounov et al., 2006; Suzuki et al., 2004).

Developmental-mastery validity

This concerns accounting for the fact that humans uniquely possess a prolonged maturation period, that includes the biologically novel stage of adolescence in which motor skills are mastered to a high degree of expertise (Bogin, 1999). This is reflected in the continued motor control refinement in bipedality, dexterity and vocalization (Assaiante and Amblard, 1995; Choudhury et al., 2007; Hirschfeld and Forssberg, 1992; Smith and Zelaznik, 2004) that occurs into late adolescence, and the fact that the acquisition of specialized hand skills (tool making, tool using and accurate throwing) can require at least ten years of daily practice if they are to be mastered at an expert level of motor competence (Ericsson and Lehmann, 1996). This need for a prolonged duration of human motor function is also known to be closely linked to the brain's neurological development and so the evolution of the human brain protracted maturation (Skoyles, 2008). Individuals that acquire specialized motor skills that require many years of practice, such as piano and violin playing, for example, show detectable physical changes in their brains (Amunts et al., 1997; Elbert et al., 1995; Hutchinson et al., 2003; Schlaug et al., 1995). This suggests that human motor skills have evolved such that they require extensive neural maturation before they can provide their full survival contribution to human evolutionary fitness. Any account of human motor control must account for why such prolonged maturation is central to the nature of human but not nonhuman motor skills.

Methodology and experimental research

Much general motor control theory implies that human motor coordination uses low-level processes, or that it can be studied effectively at this level. Such theory typically is based upon data gained from simplified or nondemanding tasks, for example, simple standing, repetitive actions like hand reaching to spatial targets, or even research extrapolated from nonhuman animals. The use of such experimental tasks, however, by their nature do not fully investigate the actual performance capabilities of humans. This is potentially problematic, particularly, if the above requirements are not respected, as it can led to theory fitting against potentially misleading data sets. For example, no one would expect that research done upon Formula One racing cars driven slowly around in circles in small car parks, however precisely measured and well researched, would led to accurate theories about the nature of their rather specialized and elaborate engineering. But this is essentially how many investigators at present methodologically research human motor abilities.

The issue is important. High-level models of motor function are argued here to be central to understanding human evolution. But, their existence has been rejected on the grounds that low-level models upon motor control can equally well account for available experimental data (for an example of this, Latash and Feldman, 2004). However, while such low level simplification can be important in understanding complex systems both in theory and experiment, it must be carried out with appropriate caution as to its limits of applicability, something that is not always the case in human motor control theory.

1.4. Overall plan of review

The review is organized into the following sections. In section 2, the *Homo* innovation in motor adaptation is exemplified with dexterity as shown in Pleistocene knapping. This is then followed by a discussion in section 3 of the processes involved in motor stabilization, and then in section 4, with a discussion of internal models and anticipatory motor adjustment. The uniqueness and motor stabilization of human bipedality is discussed in section 5, and that of human vocalization in section 6. In section 7, the possibility that human motor faculties share neural resources is reviewed in the evolutionary context that their employment need not be concurrent. Section 8, discusses specific opportunities with which to experimentally explore the neurobiological origins of human specific motor faculties. Section 9, provides a brief conclusion.

2. KNAPPING

To illustrate how the examination of motor stabilization might provide insights into human neurobiology, and the evolutionary specific nature of human motor control, consider knapping stone tools. Paleoanthropologically this dates back to 2.5 mya (Semaw et al., 1997), though the example examined below that allows the reconstruction of the manufacture of such stone

tools is young at ca. 2.34 mya (Delagnes and Roche, 2005). In knapping, an individual holds a core stone in the nondominant hand that they strike with a hammerstone held in their dominant one to produce flakes and a modified core (fig. 1.). Reconstruction of surviving flakes and cores shows (Delagnes and Roche, 2005) that this was done in terms of an overall knapping action plan (see fig. 2.). There has also been recent studies upon contemporary people as to the motor and the neurological processes involved (Marzke, 2006; Marzke et al., 1998; Roux and David, 2006; Stout et al., 2008; Stout et al., 2000).

Knapping is illustrated using the reconstructed knapping stones found at Lokalalei 2C (Kenya) (dated, 2.34 Myr) (Delagnes and Roche, 2005). The refitting group core stone 2 (Delagnes and Roche, 2005, p. 443) (9.4 cm long) together with the hammerstone 2 (9 cm) found at the same site are shown.

2.1. Need for impact stabilization

The success of knapping, first, has been found to depend crucially upon the hammerstone hitting an appropriately stabilized core. Electromyography research shows that there needs to be a millisecond timed scheduled stiffness adjustment to stabilize the hand holding the core that prepares the hand for the otherwise perturbing force of the hammerstone's impact (Marzke et al., 1998) (Fig 2 A and B). At the moment of impact, a coordinated loosening of hand grasp is also needed to protect the hand that "is brief enough that it does not allow displacement of the tool [hammerstone]" (Marzke, 2006: p. 248). If this timed anticipatory stiffness is prepared/relaxed incorrectly, not only could the hand be injured but also the core will not be stabilized when hit, and as a result—a defective flake or none—will be produced.

2.2. Need for overall manufacture plan

Second, knapping critically depends upon the executive formulation of an overall manufacture plan (Roux and David, 2006) and so abstract projectuality (Amati and Shallice, 2007) (see fig. 2). That is (i) having before commencement, a notion of the final product, (ii) an ability to treat each knap as intermediate stage to such a product, and (iii) capacity to modify the force, position and manner of each knap in terms of the changing debitage of the core to achieve the intended product (the knaps in fig. 2 A and C). Since cores can need secondary modification to enable knapping, and knaps can fracture the core in nonintended ways, it also requires, (iv) skill to identify errors and adjust new knaps to correct for them within the overall product making plan (as in fig. 2 B). Thus, the motor faculty of knapping requires cognitive specializations such as sustained attention, error detection, short- and long-term memory, action set shifting, and the hierarchization of ultimate and substage motor goals. For instance, the sequence illustrated in fig. 2 upon the refitted group core stone 2 found at Lokalalei 2C (Delagnes and Roche, 2005) could not have been done—as they were—2.34 myr by a brain that lacked the ability to organize its motor actions by such executive-type functions.

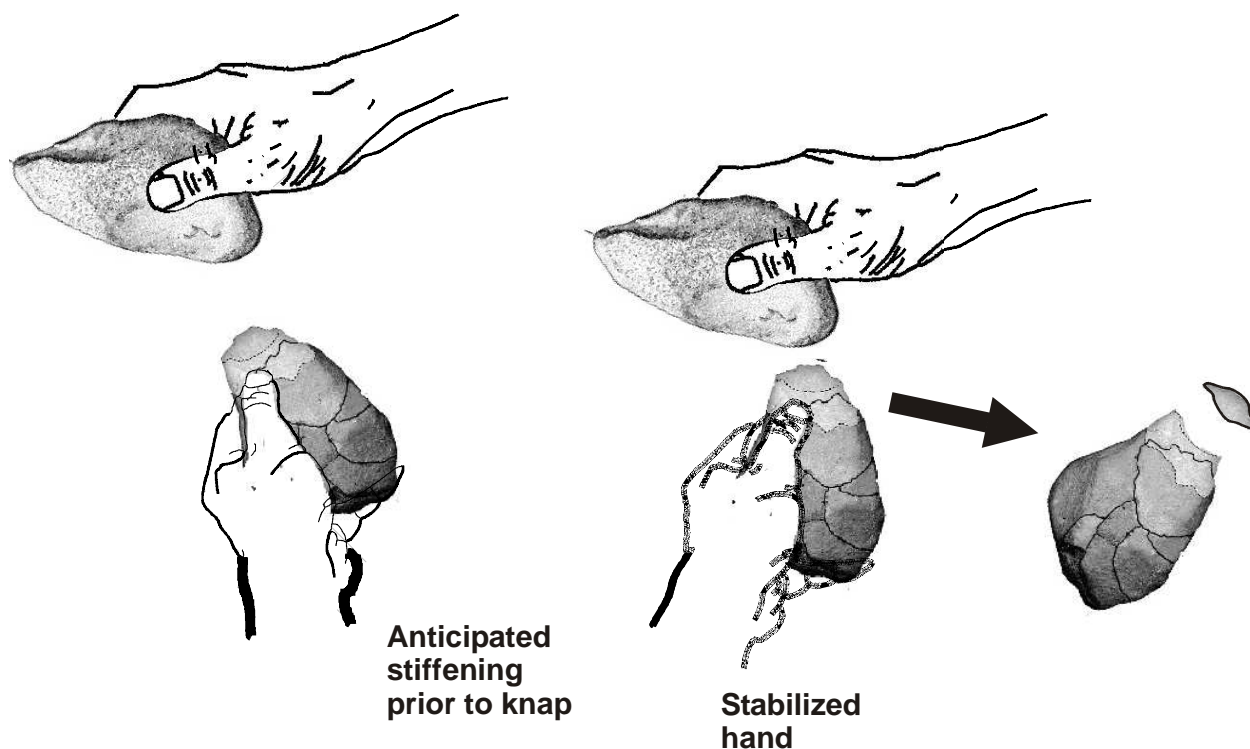


Fig 1. Knapping is illustrated using the reconstructed knapping stones found at Lokalelei 2C (Kenya) (dated, 2.34 Myr). The refitting group core stone 2 (9.4 cm long) together with hammerstone 2 (9 cm) found at the same site are shown.

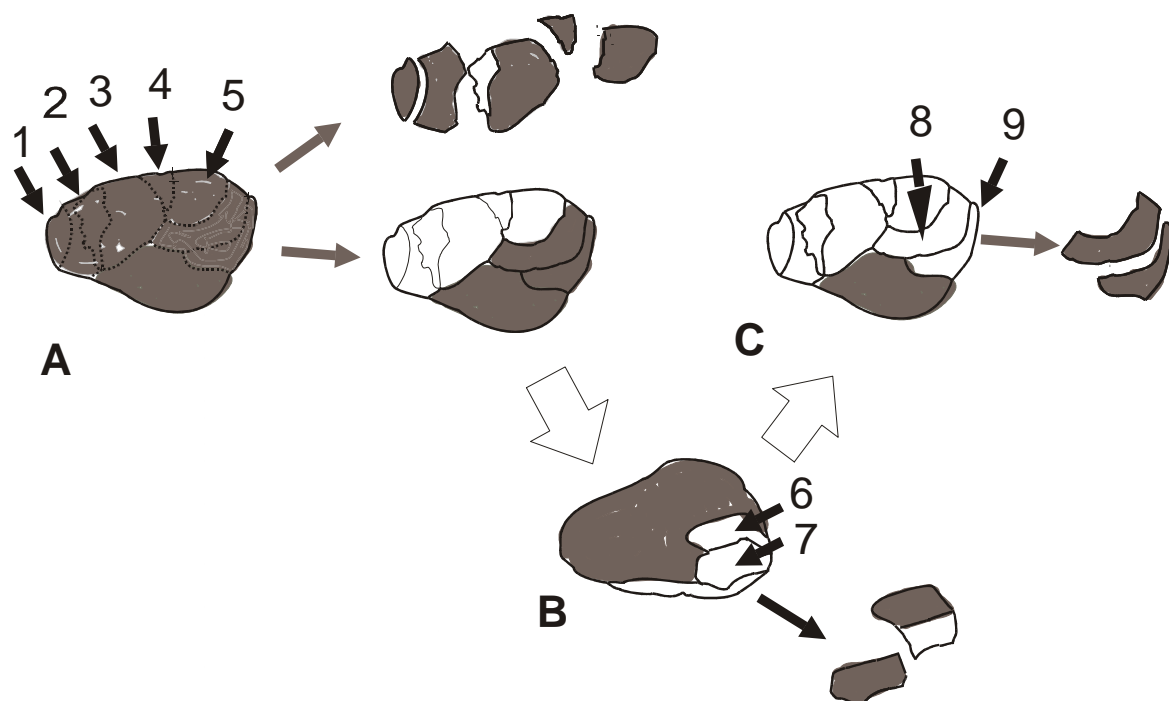


Fig 2. The refitting group core stone 2 was knapped into nine flakes. This happened in three stages. (A) five flakes, 1, 2, 3, 4 and 5 were knapped. (B) The knapper reshaped the core by removing a protrusion on the other side of the stone, (6 and 7 flakes) so creating an edge that was used (C) to make two more knaps, 8 and 9 (Delagnesa and Roche, 2005).

2.3. Human uniqueness

2.3.1. Stone tool making in nonhuman primates

No animal apart from *Homo* can anticipatorily adapt in a time accurate manner the stiffness in the core holding hand in regard to the hammerstone's impact force, nor engage in the executive function-like modification of motor control guided by the use of an action plan. Attempts to tutor the bonobos, to knap, for example, have been without success (Schick et al., 1999). This is not because they cannot use motor control to modify stones, nor because they lack the idea to make tools. Bonobos, such as Kanzi and Panbanisha are able to grasp the idea of stone modification—but they are only able to engage in this (even when shown how to properly knap) through (i) an initial uncontrolled “thrust percussive” method of throwing and braking stones on the ground, and (ii) later with more experience by a stabilization using the ground (Davidson and McGrew, 2005, see fig. 3 on page 800 in which Panbanisha holds a stone against the ground with her left hand). The former method of stone modification is also found in wild chimpanzees (Boesch and Boesch, 1990; Mercader et al., 2007). Both types of “thrust percussive” tool making is characterized by not needing the anticipatory coordination of the two hands, nor highly complex action planning.

Byrne (2005, p. 166) has noted “it may be very well that no living great ape is capable of learning the motor skill involved in aiming a powerful and accurate blow at an object held in the other hand: it is the combination that may be beyond them, because there is no doubt that living apes have both great limb power and delicate precision, in separate contexts”. Here this inability is identified as the lack of a capacity to coordinate energetic force in one hand, while the other engages in accurately timed adjusted stabilization against its quick forceful impact.

2.3.2. Reasons for human uniqueness

What has limited nonhuman primates from possessing the above noted motor dexterity needed to knap? One explanation might be human specific hand anatomy: (i) human fingers have optimal length to work with the human thumb (Napier, 1960), (ii) a stable and extended pulp region exists on the human thumb for aiding firm precision pinches and object holding (Susman, 1994), and (iii) human wrist bones allow for a power grip (Marzke et al., 1992). These musculoskeletal adaptations while optimizing the human hand for knapping, however, are not responsible for creating the motor capacity to anticipatorily stiffen effectively the core holding hand. In addition, human hand anatomy contrary to “long standing” assumptions is not completely unique to the human species as: “each of the features forming the human morphological pattern appears variably in at least one or more nonhuman primate species” (Shrewsbury et al., 2003: p. 41). Nor is refined finger control peculiar to humans: young chimpanzees, for example, appear to have more individual control over their fingers than humans (Landsmeer, 1993: p. 330).

2.3.3. Novelty of human motor control and knapping

The human specific motor control that underlies knapping is critically dependent upon its capacity to be organized within accurate time-based internal models (see section 4).

- First, these internal models allow the refined time prediction of the kinematics and kinetics of the musculoskeletal system of the upper body so that motor control can in a non-stereotypical timed manner stabilize “stiffness” in one motor element (the core holding arm) in regard to another independent motor element (the striking hammerstone) (Marzke et al., 1998).
- Second, such internal models allow the predictions needed to modify each temporally successive knap/stabilization in terms of the requirements of a complex action plan.
- Third, a factor not discussed in depth due to lack of space is aiding the generation of the intersegmental dynamic coordination of forces in the dominant hammerstone holding arm (Sainburg, 2002; Sainburg and Kalakanis, 2000; Wang and Sainburg, 2007) that is needed to accurately target the hammerstone and its strike impact on the core stone. Though the emphasize in this paper is upon stabilization, internal models also play a significant role in enhancing the voluntary capacities of musculoskeletal action (see section 4.3.2.).

In regard to motor ability, hand anatomy is secondary to the primacy of such human specific motor competence.

2.4. Nonhuman specific motor stabilization and its limits

Innovations to provide this motor control are needed if humans are to knap since from a biological perspective, the submovement stabilization of the core holding hand cannot be timed in a task-determined manner by the already existing stabling processes found in nonhuman vertebrates such as reflexes and spinal adjustment reflexes (see section 3.2 and 3.3 respectively).

Preflexes and spinal adjustment reflexes embedded locally in the body’s musculature underlie the motor stabilization of movements in nonhuman animals. They are unlike the anticipatory motor adjustment of proficiency since these can only be acquired through prolonged practice when mastering motor expertise in a particular task. Instead, reflexes and spinal adjustment reflexes are evolutionarily precustomized to provide specific stabilizations for (i) frequently encountered, or (ii) survival critical perturbations, that are faced during the execution of (iii) an evolutionarily limited repertoire of highly adapted stereotypical motor movements. This makes such musculoskeletal embedded stabilization mechanisms functional only for a few

highly evolved motor employments of the musculoskeletal system, not task-determined motor skills that require prolonged mastery.

Such lower-level musculoskeletal stabilization mechanisms are not able to offer the constantly modified time-based feedforward motor stabilization needed for knapping (and more generally, other practice-dependent forms of expert dexterity). First, when the two stones strike, it requires a task specific (not stereotypic) timed anticipatory coordination between the two hands that takes many years of practice and learning to master. Second, this anticipatory and timed adjustment must be situationally highly tailored as it is successively modified for each knap in terms of action goals (given the core's changing shape and intended core debitage). Third, knapping illustrates only one of the many different kinds of hand stabilizations that humans acquired through prolonged practice as they make and use diverse artifacts. Other kinds of motor stabilization with different task-determined time accurate coordination, for example, were needed by early *Homo* for the expert usage and making of tools that due to perishable materials—wood, bone, skin—are not preserved.

2.5. *Knapping and internal models*

The anticipatory stabilization needed for knapping reflects the existence in humans of the evolution of an expanded neurobiological capacity for (1) making time-organized internal predictive models of the kinetics, kinematics and action organization, and (2) the integration of them needed to engage in complex and practiced tasks (section 4). The increased ability in *Homo* to practice and refine such models allows *Homo* to engage in motor control that can for each occasion be exact and proficient in its anticipatory adjustments. As a result, motor control can stabilize effectively its actions to produce constant motor effects in spite of changing circumstances such as when a hammerstone hits a core stone of changing weight and shape. This top-down motor timed adaptation based upon internal models that characterizes proficient human motor control underlies not only for the expert and dexterous use of the hands (as in knapping) but (as will be argued below) also human bipedality (section 5) and human song/speech vocalization (section 6).

Although not discussed in a paleoanthropological context, internal model processes are well researched, especially in regard to their implementation in the circuits between the cerebellum and the cerebral cortex (parietal, motor, premotor and prefrontal areas) (Doya, 1999; Ito, 2006; Ito, 2008; Kawato and Gomi, 1992; Wolpert et al., 2003; Wolpert and Kawato, 1998). Such top-down internal model based motor adaptation is paleoanthropologically important because these circuits in humans are uniquely expanded compared to those in nonhuman primates (MacLeod et al., 2003), particularly in regard to the prefrontal cortex (Ramnani, 2006; Ramnani et al., 2006), and in preliminary evidence that *H. sapiens sapiens* underwent specific cerebellum enlargement at the cost of overall cerebral hemisphere size (Weaver, 2005). They are, moreover, known from studies upon cerebellar agenesis to be involved in

dexterity (Nowak et al., 2007), and from neuroimaging to be activated during knapping (Stout et al., 2008; Stout et al., 2000).

Further, humans have a prolonged nonadult stage in development, “adolescence” in which the relationship between gray matter and its connective white matter in the brain changes (Lenroot and Giedd, 2006). These changes can be specified linked to hand motor skill mastery. Learning to play the violin to an expert level thickens the connections between the two cerebral hemispheres (Schlaug et al., 1995), and acts to increase nearly threefold the area devoted to the left hand (Elbert et al., 1995). In keyboard players, there is an enlargement of the motor cortex that is proportional to the number of years that they have been practicing their instrument (Amunts et al., 1997). Musicians also have slightly expanded cerebellums—a difference that increases with the number of years that they have been practicing (Hutchinson et al., 2003). Consistent with these motor skill mastery changes in the brain linking to enhanced internal models, there is increased accuracy during adolescent in the internal models of hand movements, as well as improved fine-motor skills (Choudhury et al., 2007).

2.6. *Knapping, human uniqueness, and motor control summary*

Knapping illustrates four things.

- First, that humans can proficiently make actions that other animals cannot.
- Second, that though anatomy helps (the human hand is optimized for a power grip), this is not the explanation: what is critical is the timed adjustment and coordination of different movement elements made possible by time-exact internal models, a form of motor stabilization that cannot be done by the locally embedded reflexes and spinal adjustment reflexes that underlie the motor control of nonhuman animals. These models, moreover, provide the basis for the temporal and sequential goal hierarchization that allows for different body movements to be organized as part of a task action plan.
- Third, that the opportunity to base motor control upon such internal models depends upon something unique to *Homo*—expanded cerebello-cerebral cortex circuits including those with prefrontal areas, and also the existence of a prolonged nonadult maturation stage needed to refine and integrate them together as expert motor skills (Skoyles, 2008).
- Fourth, knapping, it can be added, is of great adaptive advantage (it provides sharp cutting implements essential for the extraction of high-energy foods such as bone marrow) (Dominguez-Rodrigo et al., 2005). This makes the origin of the internal model based motor stabilization central to any understanding of human origins. This is particularly so—if, as proposed below—that such internal models also underlie the biological distinctive character and utility of human bipedality and human vocalization

Knapping, thus, shows that there is an evolutionary link between changes in motor stabilization mechanisms (the shift from reflexes and spinal adjustment reflexes to accurately task timed anticipatory adjustments), and the evolution of what is peculiar to humans. Further, that this shift, identifies processes that are scientifically already well experimentally investigated.

3. MOTOR STABILIZATION

Motor execution consists of two complementary aspects: motor planning and motor stabilization. In motor planning, the brain selects commands to spinal and bulbar (brainstem) motoneurons that articulate musculoskeletal movement by determining various control parameters (suggestions have included λ settings, equilibrium points and joint torques) (Feldman and Levin, 1993; Kelso, 1992; Turvey, 1990). Such motor movements, however, need to be stabilized with submovements that counteract the disruption caused by the external environment, and the musculoskeletal system itself. For example, a foot might land in a hole, a hand while reaching for an object might shift the body, and with that, the hand itself (by shifting forward the standing body's centre of mass), or hitting one stone with another might make an unstable impact (as discussed above in knapping). These are not minor problems, and as illustrated with knapping, forestalling them in motor control is critical to the existence of human specific motor proficiency.

Motor planning also involves the contextual selection of movements for achieving particular ends. This is dependent predominantly upon the circuitry between the basal ganglia and the cerebral cortex (Grillner et al., 2005). This selection of movement commands is not discussed further here since this is widely discussed in the motor control literature. This evolutionarily orientated review, instead, focuses upon the second and generally ignored aspect of motor execution: the need to achieve such selected actions in a smooth and proficient manner. This, rather than the selected commands (as will be shown) is particularly central to understanding the unique dextral, bipedal and vocalization capabilities of humans.

3.1.1. Bernstein and motor stabilization

Bernstein recognized (though this is often ignored by neoBernsteinians) that accompanying submovements (which he called “background corrections”) were needed for planned movements to aid their stabilization (Bernstein, 1996, pp 111-112, 186-189). However, he assumed that such submovements after being acquired during the mastering of a motor skill quickly became automatisms that were carried out at a much lower level than the “superordinate controller” that organized motor execution (Bernstein, 1996, pp 188-189). As will be reviewed below, low-level automatic stabilization processes do exist in the form of reflexes and spinal adjustment reflexes, but it is critical—if the kinds of motor action mastered by humans are to be carried out—that their motor stabilizations is determined at a

high-level. This is because most forms of human motor execution depend upon task-determined adjustments that can only be timed and created in the context of the particular needs of a task as they are represented in its practice acquired internal models. Consistent with this, there is evidence that such submovement are initiated in the motor cortex alongside the primary movements they stabilize (Palmer et al., 1994; Palmer et al., 1996). Moreover, normal human motor stabilization is highly sensitive to the presence of current cognitive tasks—which would not be expected, if stabilization only occurred by low-level automatisms (de Hoon et al., 2003; Ebersbach et al., 1995; Hauer et al., 2003; Lundin-Olsson et al., 1997; VanderVelde et al., 2005; Woollacott and Shumway-Cook, 2002; Yardley et al., 2000). Indeed, where postural erectness is challenged and needs extensive stabilization, as for example on a tread mill or in an unusual virtual reality situation, the prefrontal cortex is activated (Slobounov et al., 2006; Suzuki et al., 2004).

3.1.2. Evolution and motor stabilization

From an evolutionary perspective, robust stabilization against perturbation is especially significant for the motor control of terrestrial biped animals.

Moreover, it is of particular importance for humans, as human are not only biped but also vertically upright in a manner that can quickly become unsteady, and so, unless effectively stabilized by correction movements, can result in falls and serious injury. Further, not only do humans require and acquire a particular robust means of stabilizing themselves (i) vertically, but as illustrated in knapping, also (ii) master hand skills that depend upon exquisite forms of stabilization if they are to control artifacts and manufacture them, and humans also engage in (iii) speech, that as shown below, only exists due to motor stabilization of pulmonary pressure created by respiration used in sound production by vocal articulators.

3.1.3. Open loop correction

The use of open loops that adjust motor execution directly with sensory feedback is one possibility for stabilization correction. However, the time delays involved in using direct sensory input can make movements ineffective or jerky (Desmurget and Grafton, 2000). Evolution has therefore created three other kinds of stabilization mechanism: (i) reflexes (Brown and Loeb, 2000; Daley and Biewener, 2006; Nishikawa et al., 2007; van Soest and Bobbert, 1993), (ii) spinal adjustment reflexes (Heng and de Leon, 2007), and (iii) feedforward time-scheduled motor adjustments. The first two are both processes that are local to the musculoskeletal system, while the third is top-down from the supraspinal brain based upon the “virtual” internal simulation of the musculoskeletal system, and so not directly part of it (Desmurget and Grafton, 2000; Doya, 1999; Ito, 2006; Ito, 2008; Kawato and Gomi, 1992; Kawato et al., 2003; Wolpert et al., 1998; Wolpert and Kawato, 1998).

3.2. *Prelexes*

Prelexes are an instantaneous and nonneurological means built physiologically into the musculoskeletal system to protect it from perturbation. They arise out of the nonlinear visco-elastic properties of muscles (Brown and Loeb, 2000; Nishikawa et al., 2007; van Soest and Bobbert, 1993) within the evolved skeletal and tendon configuration in which they work (Blickhan et al., 2007; Valero-Cuevas et al., 2007). As a result of nonlinear visco-elastic properties, perturbations cause a muscle to automatically act to make length and velocity adjustments that have been evolutionarily selected specifically to counteract common or survival critical movement disruptions. The effectiveness of their response arises from the fact that perturbations give muscles in their skeletal and tendon contexts, a different length, or make them change in length at a different velocity, from that originally commanded. The evolved nonlinear visco-elastic properties of muscles interact with these perturbation induced velocity and length differences such that the nonlinear properties of muscles counteract directly as they happen their disruptive effects.

For example, a quail's leg stepping into a hole (a common disruption against which evolution has tuned the nonlinear visco-elastic properties of its muscles) will cause a momentarily uncommanded velocity and length change in the muscles that span its various leg joints. This length/velocity discrepancy interacts with the nonlinear length- and velocity-force relationships that have evolved in response to such a disruption with the result that the leg extends further into the hole, and thus keeps the quail's body stable and upright (Daley and Biewener, 2006). It is the intrinsic musculoskeletal properties of a frog's leg, not neurally mediated spinal reflexes, that stabilize its wiping movements at irritants when the leg movement is perpetuated (Richardson et al., 2005). A human example of a prelex stabilization is when a person explosively jumps up from a squat position, and their leg muscles provide a zero time delay against perturbation from the vertical (van Soest and Bobbert, 1993).

Muscles provide the opportunity for prelex stabilization as they are not uniform simple structures (as suggested in most textbooks) but possess a highly composite and so evolvable internal visco-elastic structure. The deltoid "muscle", for example, comprises of at least seven segments with different bone attachments and neural control (Brown et al., 2007). Within each such segment, moreover, exists a more complex internal structure that goes down to one in which each muscle unit consists of a tendon, aponeurosis, and a fascicle of active contractile and passive elements (Brown and Loeb, 2000). Another composite factor is the variation in the internal architecture of the fiber orientation relative to a muscle's line of action, for example, as found in pennate muscles (Azizi et al., 2008). The potential heterogeneity of the different visco-elastic length- and velocity-force relationships of these subparts provides the opportunity for structurally complex muscle biocomposites with highly task-tuned nonlinear visco-elastic length- velocity- force relationships. Such composite structures within the musculoskeletal system can thus provide a direct physiological means by

which evolution can sculpt the visco-elastic reactions of the musculoskeletal system to perturbations so that it automatically acts to stabilize a movement without higher levels of control.

3.3. *Spinal adjustment reflexes*

The spinal cord (and the brainstem in its cranial nuclei) contains many stabilization reflexes that are stereotypical but also situational adjustable. For example, spinal adjustment reflexes enable that rubbing the ear of a standing dog will produce not only repetitive scratching movements of the same side rear leg, and also the motor adjustments in the other three legs needed to maintain stable standing. The sensory triggers of such adjustment reflexes are local to the body involving its surface, or are in the musculoskeletal system itself (such as spindle receptors in muscles and Golgi tendon organs). Such reflexes are created when such sensory input transmits to sensory neurons in the dorsal roots of the spinal cord and then to spinal motoneurons in the ventral roots that output to muscles. This makes it a process that is local to the musculoskeletal system. (A similar arrangement exists with cranial nuclei in the brainstem for bulbar reflexes involving reflex movements of the head, face, and eyes.)

Spinal adjustment processes have recently been found to carry out learned correction responses to perturbations even in the absence of supraspinal descending input (Heng and de Leon, 2007). “These findings indicate that, in addition to generating fast corrective response, the lumbar spinal cord generated some adjustments in hindlimb stepping patterns through experience” (Heng and de Leon, 2007, p. 8561). Such processes are also under descending cerebellar (van der Linden et al., 2007) and cerebral cortical (Kimura et al., 2006) control, and can even be modified voluntarily in humans after biofeedback training (Ludvig et al., 2007).

3.4. *Top-down feedforward motor adjustments*

A third means of stabilization against perturbation can be generated in a feedforward manner from supraspinal predictive internal models that simulate the musculoskeletal system virtually in neural circuitry (Desmurget and Grafton, 2000; Doya, 1999; Ito, 2006; Ito, 2008; Kawato and Gomi, 1992; Kawato et al., 2003; Wolpert et al., 1998; Wolpert and Kawato, 1998). These simulations allow the identification of counteracting submovements with appropriate timings that can be created to stop the occurrence of a perturbation, or otherwise stabilize an action. Importantly, since they are independent of the actual body, they can be developed for movements for which the body has not been specifically evolved, and in regard to qualities that are not immediate to a movement, such as its modification to fit an action plan. These correction movements can be executed prior to planned primary movements, or through constant sensory and motor input updating of internal models that change a movement as it happens (Desmurget and Grafton, 2000). Such feedforward motor adjustments are commanded from the motor cortex (Palmer et al., 1994; Palmer et al., 1996). The internal models themselves are generated in cerebello-cerebral cortex circuits (Doya, 1999; Ito, 2006;

Ito, 2008; Kawato and Gomi, 1992; Wolpert and Kawato, 1998). Controversy exists as to whether the models so acquired are stored in the cerebellum (Kawato et al., 2003), or cerebral cortex areas such as the parietal area (Wolpert et al., 1998). The actual submovements so scheduled for task mastered motor skills might be directly controlled from the cerebral cortex (Heffner and Masterton, 1983; Kuyper, 1958; Liscic et al., 1998; Ludlow, 2005; Maertens de Noordhout et al., 1999; Teitti et al., 2008), or involve in a hierarchical manner of delegation, lower areas in the supraspinal nervous system, such as the cerebellum and other subcortical areas (van der Linden et al., 2007), and/or, processes lower down in the spinal cord (Kimura et al., 2006; van der Linden et al., 2007). Related this top-down control, the supraspinal adjustment of long-latency (45-100 ms) reflexes can also draw upon the cerebello-cerebral internal models of limb dynamics (Kurtzer et al., 2008).

Due to their cortical nature and the prolonged maturation of cerebello-cerebral circuits, learning such feedforward capacities takes many years to acquire to its fullest adult competence. This happens not only to the mastery of “skilled” skills such as knapping but also apparently “unskilled” ones such as walking in regard to postural challenges caused by sudden pushes and shoves. Even at 14 years of age (Hirschfeld and Forssberg, 1992), humans, for example, are still improving their abilities compared to 10 year olds (who have by then already had nearly 9 years of bipedal experience) in maintaining balance while walking in response to unexpected forces (see also, Assaiante and Amblard, 1995). Reflecting this prolonged cortical mastery, there exists continued refinement of internal models during adolescence (Choudhury et al., 2007).

4. INTERNAL MODELS

Internal models enhance stabilization and motor execution in a task flexible way by offering musculoskeletal prediction of two kinds: forward and inverse (Desmurget and Grafton, 2000; Doya, 1999; Ito, 2006; Ito, 2008; Kawato and Gomi, 1992; Wolpert and Kawato, 1998). In forward prediction, an internal model mimics the input output relations that happen in a system. Thus, for motor control, a forward internal model provides a simulation of the outcome that would follow a particular change to the body. In inverse prediction, an internal model mimics a system in terms of identifying the inputs needed to produce a specific output. For motor control, an inverse internal model therefore gives a “retrospective” simulation of the movements that need to be done in a given musculoskeletal/ environment situation if the body is to achieve a particular motor result. Forward and inverse models can be useful not only for prediction but also for enabling control when sensory information is incomplete, noisy, or subject to delays (Desmurget and Grafton, 2000). Internal models in the brain have diverse and still largely unexplored functions beyond the musculoskeletal system such as the motor control of artifacts and tools (Imamizu et al., 2000), motor and environmental perception (Grush, 2004), motor and visual imagery (Grush, 2004), and even the interpersonal communication and coordination that happens in social interaction (Wolpert et al., 2003).

4.1. *Internal models and stabilization*

One motor use of the predictive capacities of internal models is the preparation of top-down timed movements that counteract perturbations. Forward prediction in this situation (i) enables the identification of the time sequence of disturbances that will accompany a movement, while (ii) inverse prediction allows the identification, given this predicted disturbance, of the motor adjustments and the timings of their execution elsewhere in the body needed to neutralize it, and so preserve motor stability.

An advantage of internal models for creating stabilization in this way is that they can use diverse sensory inputs and past experience to aid the prediction of likely instabilities, and identify corrective changes to prevent them that are unrestricted in regard to which particular parts of the body that they might employ. Further, they can create such stabilization with accurate timing that is constantly adjusted to the peculiarities of each particular instability situation. This is in marked contrast to spinal adjustment where not only are inputs limited but so are the body parts and timings that might be recruited to correct for instability. Further, the timings and body parts used in such low-level corrections cannot be flexibly altered given the task peculiarities of the primary movement they steady. Thus, the use of internal models radically changes the opportunity by which motor actions can be stabilized, and thereby the possibility of making them in a proficient task-determined manner.

4.2. *Cerebello-cerebral circuitry and internal models*

Cerebellar circuits are involved both in creating internal models (Doya, 1999; Imamizu et al., 2000), and in timing (Bares et al., 2007; Salman, 2002). Such circuits are cytoarchitecturally uniform irrespective of the information provided by the different areas with which they form input/output information processing loops (Bloedel, 1992). As a result, such cerebellar circuits can contribute the same kinds of computation to the timing and modeling needs of very different inputs and outputs, including those of task-determined motor control. The circuits in the cerebellum work both with cerebral cortex areas and subcortical ones (not discussed here due to lack of space). For the body, these cerebello-cerebral circuitry loops are made with the motor and posterior parietal cortices and concern musculoskeletal kinetics (the force and energy effects of movements and posture), and kinematics (their musculoskeletal configurational characteristics). But the cerebello-cerebral contribution to internal modeling is also open to the higher-order processes in the premotor and prefrontal cortices concerned with planning and monitoring events that are useful for enhancing the organization of motor actions (Ramnani, 2006). Thus, the cerebello-cerebral generation of internal models can involve such higher control factors as the anticipatory hierarchization of actions done in the ventral premotor area (Fiebach and Schubotz, 2006), and action hierarchization/sequencing carried out in the dorsal lateral prefrontal ones (Ramnani et al., 2006). Such high-level cerebello-cerebral input/output connections provide internal models with the complex planning and performance prediction abilities needed to

organize multi-stage actions (such as required for knapping). Though these levels of internal models are different with separate types of development, a key aspect of motor expertise also lies in the efficacious integration between them (see section 4.3.2.).

4.3. Feedforward adjustments

4.3.1. Motor component common to unique humans faculties

Feedforward related timed adjustment enabled by internal models underlies each of the three human motor faculties in their species specific uniqueness.

Dexterity, as shown above with knapping, needs accurately timed anticipatory adjustments in the nondominant holding hand to ensure the core is held steady—a passive type of stabilization. Such adjustments have also been found to be needed in the dominant upper limb and body (shoulder, upper arm, lower arm, wrist and fingers) for the stabilization of active movements, which in the case of knapping would involve the accurate aiming of an appropriately forceful blow with the hammerstone. (For evidence that these different stabilizations link to the nondominant and dominant hands, see (Sainburg, 2002; Sainburg and Kalakanis, 2000; Wang and Sainburg, 2007)). For an earlier identification of the link of the nondominant and dominant hands to these two forms of stabilization, see (Guiard, 1987).

The human form of bipedality (anatomical vertical alignment bipedality) depends upon the erect vertical body constantly making locomotive and upper body task-determined time-accurate anticipatory postural adjustments to maintain its centre of mass over a narrow foot base (Belen'kii et al., 1967; Bouisset and Zattara, 1987; Cordo and Nashner, 1982; Gelfand et al., 1971; Massion, 1992). It is interesting to note that the foot initiation of energetic human bipedal locomotion (when sprinting off from starting blocks) shows a similar nondominant side specialization for spatial body stabilization (Eikenberry et al., 2008).

Vocalization in both song and speech (section 6) requires (to give only one example of vocal stabilization) that the muscles controlling pulmonary pressure constantly adjust in a timed manner for upcoming phone and song note sequences of vocalizations (Ghazanfar and Rendall, 2008; Hixon, 1973; Ladefoged, 1960; MacLarnon and Hewitt, 1999; Proctor, 1986; Provine, 1996). Critically, these motor adjustments are also ones that cannot be done (or are interfered with) by reflexes and reflexes, suggesting that human evolution changed motor control both by expanding the role of timing in correction submovements (enabled by increased internal modeling), and also in parallel to this, by limiting the potentially disruptive involvement of reflexes and reflexes.

4.3.2. *Internal models, expertise and prolonged practice*

One issue in the evolutionary understanding of human motor control is that it can require extensive practice after apparently proficient skills are initially acquired. Notably, even seemingly simple and universal skills such as walking, talking and fine-finger dexterity continue to mature during adolescence (Assaiante and Amblard, 1995; Choudhury et al., 2007; Hirschfeld and Forssberg, 1992; Smith and Zelaznik, 2004). Moreover, highly specialized and culturally dependent motor skills such as those in music playing also require continuous daily attentive practice for at least ten years (Ericsson and Lehmann, 1996), and this produces MRI detectable changes in the brain (Amunts et al., 1997; Elbert et al., 1995; Hutchinson et al., 2003; Schlaug et al., 1995). It would seem that humans as a result have a unique capacity to gain a motor mastery in which skills are exquisitely refined in their performance over many years of daily practice.

In a skill such as knapping, this enhanced proficiency links to the ability to stabilize the core holding hand against the hammerstone strike, since, if this is done slightly incorrectly, the knap will either injure the hand, result in a useless flake, or stop the core being useable for further knapping. In locomotion, skill is needed to stabilize the body against unexpected perturbations that would otherwise cause a fall and possible injury. Stabilization is also critical if the upper body is to engage in complex upper body actions such as throwing. Musicians need to learn how to adjust their fingering in regard to different note combinations, the composer's playing instructions, and their personal phrasing and aesthetic interpretation. An important recent finding is that the accuracy of internal models continues to increase during adolescence (Choudhury et al., 2007). This suggests that the development required to stabilize the demanding specialized motor skills needed for adult life only exist due to the acquisition by the brain of complex predicative modeling, and that these processes are so extensive that they cause in it physical changes.

Consistent with this continual refinement is that active tuition is species specific to humans (for a review, see Csibra, 2007). Young humans, as a result, have the opportunity to sharpen up their internal model using the refinements acquired by others who have already mastered the skills they are acquiring. This could considerably broaden the types of culturally acquired motor skill mastered by humans, while also at the same time increasing the need for an expanded capacity for being able to engage sophisticated internal modeling to take advantage of such tuition.

4.3.2. *Interface between musculoskeletal stabilization and action planning*

It is the nature of task-determined actions that they are specific to the particular circumstances in which they take place, and this can alter each particular motor action. As a result of this dependence upon circumstances, the timing of anticipatory adjustments needs to be recalculated for each movement. In knapping, for example, with each strike, how the core

stone is held and positioned is different, while the knap itself needs to be modified in regard to the kinematics and kinetics of its individual force, angle and location upon the core (Roux and David, 2006). A knap done at the end will differ from that at the start since it will happen, for example, upon a smaller and differently shaped core. This makes such adjustment an ongoing activity that needs to be constantly modified as determined by higher-level action plans. Internal models, in consequence, for much of the motor control done by humans (such as knapping), must not only work out timed anticipatory adjustments in the musculoskeletal system, but also do so in constant interaction with movement changes determined by higher level action plans. Indeed, much of the skill of motor mastery could concern the ability to develop internal models both at a low and higher level so that they can adeptly interact together in this manner.

The opportunity exists for such communication between the various levels of internal models involved in motor control since their cortical areas are adjacent in the frontal lobe (with higher levels being anterior (prefrontal cortex) to lower ones (premotor and motor cortices). Further, in human evolution, the cerebello-cerebral cortex circuitry greatly expanded with the prefrontal cortex (Ramnani, 2006; Ramnani et al., 2006), and which enlarged the capacity for the modeling of the non-routine multi-level operations needed to organize motor action in the motor cortex with higher-level executive functions (Amati and Shallice, 2007). Consistent with this evolutionary change, white matter connections in the cerebral cortex, including the prefrontal cortex and corticospinal pathways continue to undergo refinement changes into adolescence and afterwards (Ashtari et al., 2007; Paus et al., 1999). Where the specific acquisition of highly practiced motor skills occurs, moreover, the cerebellum (Hutchinson et al., 2003), the cerebral cortical somatosensory motor areas (Amunts et al., 1997; Elbert et al., 1995), and the connections between them (Schlaug et al., 1995) can also undergo motor skill mastery related change.

One consequence of developing interactions between lower and higher levels of internal models is the ability to use higher level ones to monitor motor performance in other individuals. This is a crucial for the capacity to tutor, a phenomena, (which appears to be unique to the humans (Csibra, 2007)), that is based upon the identification of motor mistakes in another individual. It is also central to imitation where complex actions are copied in terms of the higher-level action organization observed in another's performance rather than the low-level particular kinematics of its particular movements (Whiten et al., 2006). Such imitation appears to be unique to humans (Whiten et al., 2004). Further, it has been recently found that low-level kinematics of actions—such as reaching and placing one of two wood blocks in the centre of a work surface with another individual (placing the other one) can vary in regard to whether they are done in cooperative, competitive or neutral context in spite of them involving the same movement (Georgiou et al., 2007). This effect requires that such movement kinematics are determined at a high-level where they can be shaped by issues of interpersonal interaction dynamics (see also Wolpert et al., 2003). This level of motor

cooperation could include the use of mirror neurons to anticipate in a complimentary interdependent manner the movements of others (Newman-Norlund et al., 2008).

4.4. Control over multiple elements

4.4.1. Degrees of freedom and musculoskeletal locking

Bernstein (1967; 1996) suggested that the articulated musculoskeletal system created a control problem for motor actions since any planned movement can be done in a great number of ways due to the articulated human body having an excessively large number of degrees of freedom. Bernstein's solution, and that of researchers following him (Feldman and Levin, 1993; Kelso, 1992; Turvey, 1990), is a superordinate controller that issues commands to subordinate mechanisms that organize movements in terms of functional "synergies". This approach to motor control, however, fails to take into account of the importance, particularly in nonhuman animals, of the capacity of recently discovered reflexes (Brown and Loeb, 2000; van Soest and Bobbert, 1993) and spinal adjustment reflexes (Heng and de Leon, 2007) to tackle the degrees of freedom problem of the body directly at a low-level.

A more basic problem with degrees of freedom as a "problem", however, is that neural networks can identify such degrees of freedom through carrying out, in effect, independent component analysis (Karhunen et al., 1997). This provides a means by which the brain can discover control strategies that for isolating motor-related vectors relevant to achieving a task from those that are irrelevant (Todorov, 2004). To take an example of such independent component analysis in a nonmotor faculty, consider the simulation of word meaning and its acquisition and use by Latent Semantic Analysis (LSA). LSA is a successful method of constructing semantic vectors based upon the extraction from textual input data of what are, in effect, hundreds of hidden degrees of freedom in which words and their meanings are located relative each other in a vast multi-dimensional semantic space (Landauer and Dumais, 1997; Landauer et al., 2007). This extraction of textual information in terms of hundreds of vectors provides an effective means of simulating actual performance data upon how people learn and use meaning, particularly in regard to their semantic context. Notably, it can explain experimental phenomena that has been previously intractable to computer modeling (Landauer and Dumais, 1997; Landauer et al., 2007). This suggests that at some broad level the multi-dimensional analysis it performs is also done in the brain as part of its learning and use of words and their meaning. The existence of this biocomputational capacity is important since Bernstein's problem is only a problem if human brains find it difficult to convert musculoskeletal information similarly into high-dimensional vector spaces that describe its various "latent" degrees of freedom. Since, LSA shows that such biocomputations can be readily carried out by the brain's neural networks, this argues that the degree of freedom problem identified by Bernstein (who died before the start of research into neural networks) is unlikely to be neurobiologically a major constraint upon the brain's capacity to control its body.

4.4.2. Preflexes and reflexes and degrees of available freedom

One degree of freedom problem, however, does potentially exist in the human body—that concerned with the lack of them. In the nonhuman body preflexes and reflexes act to restrict movement as part of the process by which evolution has selected a small set of survival critical actions so that they are done in a perturbation resistant manner (reducing perturbation involves putting limits upon the kinematic “envelop” in which movements happen). But, in humans such perturbation resistance (if not reduced) would place restrictions upon potential movements, and so could act to hinder higher motor cortex top-down control of the body. Thus, instead of too many degrees of freedom being a problem for motor control, it could be that due to preflexes and reflexes, that the evolution of human motor coordination faced the problem that its degrees of freedom were *insufficient*.

Bernstein, indeed, recognized the importance of the availability for motor control of having extra degrees of freedom: “enormously excessive degrees of freedom, apparently give us considerable advantages” (Bernstein, 1996, p. 37). And “An experienced master will always prefer an instrument with more degrees of freedom, that is, with fewer rails and props, than an instrument that might be easier to use but that also constrains the worker” (Bernstein, 1996, p. 37).

4.4.3. Overriding of preflex and reflex synergies

There is direct evidence, that increased involvement of the cerebral cortex in motor function in humans has led to the human neuromusculoskeletal system being “unlocked” in regard to some of the lower level perturbation resistance found in nonhuman animals to provide more degrees of freedom for top-down control.

First, reflexes in humans have been lost or come under greater inhibitory control. Humans initially show many “primitive” reflexes that are inhibited with increasing cortical maturation early in infancy (Schott and Rossor, 2002), but can emerge following cortical injury, or age-related frontal impairment (Schott and Rossor, 2002). Further, musculoskeletally more specific ones such as the reflexes that occur in other primates across the elbow are not found in humans (Illert and Kummel, 1999). Moreover, where reflexes occur, the human cerebral cortex can directly control their properties (Kimura et al., 2006). Indeed, humans can voluntarily learn to control them when trained with biofeedback (Ludvig et al., 2007), suggesting that humans have the capacity, if need be, to selectively limit their inappropriate involvement in movements.

Second, the human motor cortex has gained direct control of the musculoskeletal system that allows it to bypass spinal reflex processes. For example, the human cerebral cortex has considerably enhanced access to spinal motoneurons (Lemon, 2008) and so gained direct

control over finger and hand muscles (Heffner and Masterton, 1983; Teitti et al., 2008), and lower limb ones (Maertens de Noordhout et al., 1999). Similarly humans show direct control over the larynx and face (Ghazanfar and Rendall, 2008; Kuyper, 1958; Liscic et al., 1998; Ludlow, 2005).

Third, reflecting this increased freedom of control from reflexes, humans can do actions that nonhuman primates cannot perform such as control their breathing, and voluntarily suppress and activate (in the absence of sensory triggers) coughing and sniffing (see section 6.2.). Further, the human musculoskeletal system has evolved enhanced musculoskeletal flexibility, for example, humans are the only mammals that can anatomically make gymnastic backbends (Ward and Latimer, 2005).

4.5. *Precursors to human internal modeling*

Internal models are not specific to human motor control: what is unique instead is the substantial increase in their predictive abilities, the temporal accuracy and complexity of what they model, and the sophistication of the interactions that happen between the musculoskeletal and action planning and other cognitively related levels. In nonhuman animals, particularly apes and monkeys, internal models exist at a simpler and less developed level, and these can be an important component of their motor control (they have moderately developed cerebello-cerebral cortex circuitry). Indeed, research upon internal models has involved Japanese monkeys (*Macaca fuscata*) (Obayashi et al., 2001). However, such internal models are used only for single, not multiple element movement control.

For example, a chimpanzee hitting a nut placed upon a stone "anvil" with a hammerstone (Boesch and Boesch, 1990) would do this in regard to internal models and cortically mediated visual monitoring. Nut cracking, however, requires that that cortical motor control manipulates only one musculoskeletal element—the hand holding the hammerstone, and this does not involve synchronized time-scheduling between different body parts. The nut and anvil are passive to this action (though cortical processes are needed for their visual/tackle positioning relative to the percussive hand held stone). Nor does this task place strong demands upon interbody part stabilization. The human innovation (due to brain expansion and very prolonged skill and internal model maturation up to and after adolescence) is having highly accurate and refined internal models so that motor control can time the interactions of several motor elements (body parts and artifacts), and, moreover, do so in highly precise, complex, perturbation resilient, and hierarchically and cognitively organized ways.

It should be acknowledged, however, that the phylogeny of the internal model capacity is still poorly understood. It is known that the relative size of the cerebellum and the cerebral cortex has increased in the evolution from monkeys to apes (Rilling and Insel, 1998). While there is no specific research to show that apes have a better or different capacity to generate internal models than monkeys, this is likely in view of their enhanced motor abilities. Evolutionarily

apes engage a much more complex form of arboreal locomotion to monkeys that involves orthograde (vertical) scrambling or brachial swinging, rather than compliant pronograde (horizontal) quadrupedality (Povinelli and Cant, 1995). Anatomically, this is reflected in apes having a stiff spinal column (needed for upright locomotion) (Ward, 1993) with an absence of a tail (that functions in pronograde quadrupedality as an “inertia paddle”). Scrambling and brachial swinging require an exacting ability to anticipate and interaction with the surrounding “graspable” arboreal holds and support that would reasonably be inferred to depend upon the capacity to generate complex internal models “schemata” of the kinetics and kinematics of the interaction of the body and the immediate environment (Povinelli and Cant, 1995).

4.6. *Internal models and cognition.*

Though, it goes outside the core concerns of this review, it should be acknowledged that models since Kenneth J. W. Craik (1943, pp. 50-61) have been central to understanding human cognition. This raises the question whether their wider use derives from motor control related processes. In this context, one can observe that.

- Internal models provide a rich variety of frameworks to organize and consolidate motor related memories both short- and long-term (Shadmehr and Brashers-Krug, 1997). Such a role (together with sequential timing) could underlie the involvement of cerebello-cerebral cortical circuits in working and verbal memory (Fliessbach et al., 2007; Hayter et al., 2007).
- Motor control based around internal models allows for structural musculoskeletal matching between the brain’s own musculoskeletal system and that perceived in others (and so the possibility of exploiting “mirror neurons” for enabling complex imitation) (Mail, 2003; Oztop et al., 2006). Indeed, the enhancement of internal models in humans could be why mirror neurons exist in nonhuman primates without them producing the high-level imitative abilities found in humans (Whiten et al., 2004).
- Internal models in the motor system can be used to aid comprehension by enabling the prediction of the actions of other people (Grush, 2004; Wilson and Knoblich, 2005), and by simulating events described in language that emulate internally the properties of their various entities and their interactions (Pickering and Garrod, 2007).
- Once an action can be analyzed in terms of other states, it then becomes possible to map that action as an entity within another higher level model. Indeed, this is essential if stabilization is to be adjusted to each particular situation as determined by an action plan. In this way, not only can models be made of movements, but such models can become parts of abstract action schemata that are not themselves directly physical. The movements, for example, of tennis are organized not only to enable the volleying back

of tennis balls but also so that this is done within the constraints of arbitrary tennis rules. Thus, once the musculoskeletal system becomes organized in terms of models, then these models are potentially open to further modeling in terms of constructing other informational (including symbolic) structures.

5. BIPEDALITY

While the term “dexterity” is exclusively used of humans, the term “bipedality” is not. The simple act of positioning the body on two legs is widespread amongst terrestrial vertebrates (Alexander, 2004). Humans are, however, unique amongst extant animals in three respects. Humans use

(i) a biped bauplan (literally “building plan”) based upon anatomical vertical alignment (Borelli, 1989/1680, proposition CXXXV),

(ii) this fully extended upright posture is strongly robust against vigorous or disruptive perturbation, including those that occur when such bipedality is combined with expert upper body actions (such as accurate throwing, carrying saucers of easily spilt fluids), or when footing is temporarily or potentially lost (during trips and fights), and

(iii) this upright arrangement is constantly accompanied by an unconscious musculoskeletal “dance” of anticipatory and feedforward postural adjustments (Belen'kii et al., 1967; Bouisset and Zattara, 1987; Cordo and Nashner, 1982; Gelfand et al., 1971; Gurfinkel et al., 1971; Hodges et al., 2002; Massion, 1992).

This section argues that it is the uniquely enhanced capacity of humans for predictive internal models that by enabling continuous timed stabilizing adjustments, that allows humans, and only humans, to uniquely stand and move their body carriage in fully extended vertical alignment. Further, and again uniquely, that this allows humans to have the capacity to engage with robust stability in secondary (and quick center of mass shifting) upper and lower body part expert actions. Whether, and far, these traits characterized Australopiths is also discussed.

5.1. *Anatomical vertical alignment bauplan*

The human body is structured nearly entirely upon the compressive anatomical arrangement of bones, ligaments, joints and cartilage support “pads” (menisci). As a result, the human body lacks flexion between each of the body carriage segments—head, thorax, thigh, shank—as they are stacked in vertical alignment above each other. The ankle and metatarsophalangeal articulation in the feet are the only joints that humans properly flex normally in standing stance, and in the ground contact stages of walking. In running, the knee also is flexed but this links to the separate factor in which the running leg functions as a shock absorber when it hits the ground (Nigg et al., 1987). Remarkably, this anatomical vertical compressive alignment

bauplan is not employed, even occasionally, by any other extant terrestrial biped. Penguins and meerkats (temporarily) may appear to be spinally erect but they balance with a tripod use of their tails, and their bodies and legs are, on close examination, in fact flexed. Changes to foot anatomy (which reduced its flexion and enhanced its compressive stability) suggest the full development of such alignment dates at least to 2.2-2.36 myr and early *Homo* (Gebo and Schwartz, 2006b).

In contrast to humans, all nonhuman bipeds (birds, extinct dinosaurs and primates) use a variety of flexion biped bauplan in which the body carriage segments are angled relative to each other. In the case of nonhuman primates when they occasionally stand or walk bipedally, their limbs are flexed and their thorax is bent forward (Alexander, 2004; Okada, 1985; Schmitt, 2003). As a result, when upright they flex their legs and thorax in a "bent-knee, bent hip" or compliant manner (Alexander, 2004; Okada, 1985; Schmitt, 2003). Even anatomically aligned ratites such as ostriches limit such alignment to only one of their four leg joints (their extended "knee"—actually the joint between their tibia and tarso-metatarsus), and this in spite of appearances is slightly flexed with its body weight being only partial transmitted compressively directly down the joint (personal communication, Jonas Rubenson). Large ≥ 900 kg "graviportal" quadruped animals (Gregory, 1912) use alignment and compression but again this is confined to the legs, and they, of course, have the benefit of the stability that comes from a four cornered quadruped "support".

5.2. *Instability and bipedal risk of falls*

Borelli (1989/1680) was the first to note that the anatomical vertical alignment bauplan is intrinsically unstable and so needs constant musculoskeletal adjustment if fall and injury are not to occur: "the erect position is unstable as a result of the slipperiness of the joints.... They [humans] need their muscles to correct displacements and prevent falling" Borelli (1989/1680: p. 130) (see also Skoyles submitted).

Human anatomically aligned verticality is a particularly precipitous and unstable posture due to several factors.

- The erect standing body oscillates over a narrow support base at between 0.12. and 0.39 Hz (Thomas and Whitney, 1959).
- When humans walk, uprightness becomes unstable since the body spends 80-90% of the time supported only upon one leg.
- Running is even more unstable since at no time is the body supported except by one leg, and the body is engaged in leaps such that it might be in contact with the ground for only 27% of the time (Alexander, 1992).

- In fast walking the body axis is destabilized by a forward lean (Thorstensson et al., 1984; Weber and Weber, 1992/1825, Tables. VII and VIII).
- In upright standing, 2/3 of body mass of the erect human body (head, arms, thorax—HAT) is positioned 2/3 up a vertical pillar of unfixed body segments above a narrow foot support (each leg contains 0.161% of the total body mass (Winter, 1991, Table 3.1)).
- Humans, constantly engage in diverse upper body voluntary movements, such as lifting objects with hands that, because they are high above the foot support base, can quickly move the body's centre of mass off-balance (Cordo and Nashner, 1982).
- In running, the body leaps and carries considerable forward moment and requires an elaborate counter-torquing by the upper body to counteract the lateral torque produced with each step (Witte et al., 1991).
- When running, the body faces the problem of its feet tripping and stumbling on uneven, rough and slippery ground (Hsiao and Robinovitch, 1998).
- Unlike chimpanzees and gorillas that have slightly longer arms than legs (the ratios respectively are 1.017 and 1.164) (Reno et al., 2005), humans have shorter arms than their legs (ratio 0.712). Thus, if humans lose upright balance, they cannot safely fall upon their hands (unlike other apes) (see Skoyles, submitted).

This lack of stability and the need for constant postural adjustment particularly in fast walking and running puts the body at risk of postural and locomotive interruption due to falls, and more importantly, creates the risk of severe leg injury, and as a result, temporary or even permanent immobilization. This is because the kinetic energy held in the upright adult human body compared to that needed to break a femur bone is “an order of magnitude greater than the maximum value of the work to fracture and nearly twenty times the average work to fracture (Lotz and Hayes, 1990: p. 698). In addition to this, as humans get taller in stature, the strength of their long support bones fails to keep up in their osteological strength with the forces that impact upon them from standing height falls. A child can fall, for example, with only a bruise but an adult can suffer a substantial injury. (The effect is marked and nonlinear: osteological strength decreases at the square root relative to increased height; for a review of the riskiness of bipedally see Skoyles submitted).

5.3 Stability and engineering

The flexion biped bauplan, in contrast to anatomically aligned bipedality, provides opportunities for low-level self-stabilizing. When upright, putting support limbs or the body at an angle allows that shifts of the body's center of mass over its support base can be corrected

by changing slightly that angle. Even simple spring arrangements such as found in articulated (anglepoise) lamps can be arranged to do this automatically (French and Widden, 2000). Not only does flexion allow this greater opportunity for quick equilibrium management, but flexed limbs and thorax, can be further initially angled such that preflexes and spinal adjustment reflexes are to optimal for aiding this automatic adjustment. This option to stabilize the upright body, however, does not exist if limbs and the thorax are not angled. Instead, the extended erect body to maintain its centre of mass over its feet must actively and constantly shift masses distant to the legs including changing the posture of the spine and thorax (Hodges et al., 2002). The need for such changes due to the precariousness of human unflexed uprightness is illustrated by the fact that they are even made to correct the shifts in the centre of mass projection created by respiration (Gurfinkel et al., 1971; Hodges et al., 2002).

5.4. *Utility of the human bauplan*

The anatomical vertical alignment bauplan of humans would not have arisen without advantages that compensate for its intrinsic instability and unsafeness. These are significant. Notably, humans can economically stand erect for long periods since they use only 7% more energy standing than when laying down; in contrast a 10 kg dog when quadrupedally standing uses 70% more than when supine (Abitbol, 1988). This is because anatomical alignment does not require energy expenditure to maintain muscles in a state of flexion. A further utility of the anatomically aligned bauplan is that when walking, the stiff compressive axis through the upright body allows it to temporarily store potential energy (in the form of a raised center of mass at midstance) from forward kinetic energy (such locomotion is also known as strident or inverted pendulum walking) (Cavagna et al., 1976). In such strident walking, the stiff leg temporarily vaults up the mass of the body and so stores potential energy that can be reused to swing forth the leg to make the next step. In contrast, bent knee, bent hip walking used by other primates in their occasional bipedalism requires about four times the energy due to the need in addition to moving the body forward of maintaining flexed muscles in a constant state of tension (Sockol et al., 2007). There are also likely to be other advantages linked to enhanced maneuverability of the upper body (Skoyles, in preparation).

The existence of these advantages raises the problem of why evolution has only exploited them in one extant primate. Given the instability of bipedal anatomical alignment, this suggests that evolution has only found in the particular case of *Homo*, an effective means to balance constantly such an intrinsically unsteady and difficult to stabilize anatomical aligned posture, particularly when engaging in complex forms of bipedality such as rough ground running and doing upper body actions (such as carrying and throwing). It is suggested here that this was linked to brain expansion, and the consequently increased ability to constantly engage in top-down anticipatory postural adjustments.

5.5. *Australopithecine bipedality*

Considerable controversy exists over the nature of Australopithecine terrestrial bipedality as to whether it was stiff gait (and so anatomically aligned) (Latimer, 1991; Lovejoy, 2006; Ohman et al., 1997), or compliant (Stern, 2000; Susman et al., 1984). Evidence arguing for anatomical alignment and stiff gait are musculoskeletal features such as femoral bicondylar angle, and the increase in total cancellous bone in primary joints of lower limbs (Latimer, 2005). Another factor is the biomechanical modeling of the efficiency of hominin walking (Crompton et al., 1998). A further factor is that macaques after initial training in bipedal erect standing can be trained successfully in semi-anatomical aligned strident walking (Hirasakia et al., 2004). This argues that the primate engagement in stiff gait walking is only to a limited extent related to lack of anatomical adaptation, otherwise it could not be acquired by behavioral modification as in macaques. This suggests other nonanatomical factors (such as ecological utility) are responsible for its hominin adoption, with anatomical changes being secondary to these behavioral ones.

The above listed instability factors are greatest for fast walking and running, that are specific to *Homo*. Foot anatomy of pre*Homo* (unlike *Homo*) suggests that their feet (Berillon, 2004; Gebo and Schwartz, 2006a) were not optimal for running, as was the lack of the lateral stabilization provided by a *Homo*-like gluteus maximus, (Lieberman et al., 2006). Bramble and Lieberman (2004) have identified diverse musculoskeletal adaptations needed for endurance running in *Homo* that are absent in pre*Homo* hominins. Thus, the stabilization problem faced by *Homo* is much more severe than that faced by Australopiths. Since the balancing for slow walking can be acquired by modern trained bipedal macaques (Hirasakia et al., 2004)), this level of postural stabilization is likely to be within the already existing postural capacities of pre*Homo* brains.

Further, Australopiths were less at risk from falls than *Homo*.

- They had shorter stature than *Homo* so the impact forces that result from falls would be smaller as the relative bone strength to resist them increases in a positive nonlinear manner (by the square) with height.
- The Australopith habitus in contrast with that of *Homo* was more padded and covered with fur which would have better absorb impact forces.
- As their arms were longer than their legs, they could fall upon their hands from a lower body height, and if they injured a leg, they more easily adopt a quadruped gait and so avoid lower limb injury and immobilization.

These habitus factors (that Australopiths share with other apes) have been argued elsewhere (submitted) relate to the need to minimize the injury risk of arboreal falls. However, they would have also as a side consequence allowed Australopiths to be bipedal without also needing an highly developed capacity to stabilize the upright body. In contrast, *Homo*

individuals when running without the protective habitus of earlier hominins and arboreal apes would place themselves at constant risk, given the body's momentum, of immobilization if they slipped or tripped injuring a lower limb. Preventing this requires considerable motor skill not only in controlling body falls in such circumstances, but also the ability to integrate into locomotion visual and other information about the rough ground ahead to constantly make safe footings.

How might we understand Australopith bipedality? An important factor here is that human bipedality even in simple walking and standing radically changes after childhood as internal model competence expands, in terms of motor qualities such as greater postural robustness (Hirschfeld and Forssberg, 1992), and stabilization of the head and vision (Assaiante and Amblard, 1995). This changes involves a reorganization in how the erect body is controlled (Assaiante and Amblard, 1995). An adult flexibly adapts their balance mobility across their head, upper arms, lower arms, hands, thorax and any held objects. However, they are "locked together" in children as they lack the sophisticated adult ability needed to stabilize and control all their separate degrees of freedom as a single kinematic mobility (Assaiante and Amblard, 1995). Early *Homo* show minor anatomical changes such as to the distal femur at adolescence (Tardieu, 1998) that suggest this change to a more sophisticated stabilization of balance only occurred in *Homo* evolution. The more simple "locked together" anatomical alignment found in modern children not present before *Homo* adolescence would have been adequate for the more limited locomotion needs of Australopiths. Thus, while anatomical aligned bipedality may be unique to hominins, the combination of this with highly developed internal model based postural adjustment might be a developmental limited to adult and adolescent *Homo*.

5.6. Vertical alignment bauplan, internal models and cerebello-cerebral circuits

Research since the 1960s shows that humans (as Borelli suggested three centuries earlier) stabilize their upright bodies by continuous musculoskeletal adjustment (Belen'kii et al., 1967; Bouisset and Zattara, 1987; Cordo and Nashner, 1982; Gelfand et al., 1971; Gurfinkel et al., 1971; Hodges et al., 2002; Massion, 1992). In this, motor commands that will cause a forward displacement of body mass such as moving an arm forward to reach an object, are accompanied by top-down timed anticipatory postural adjustments that ensure that it is accompanied by an equal and opposite counter-positioning of body mass (Cordo and Nashner, 1982). Not only do such adjustments stabilize the body but such timed postural submovements accompanying walking steps help to propel them and make locomotion more steady and efficient (MacKinnon et al., 2007). Feedforward processes incorporating sensory inputs into internal models (Desmurget and Grafton, 2000) are also likely to be particularly important, where anticipation is limited such when making stepping reactions if erectness is threatened (Hughey and Fung, 2005; Marigold et al., 2003; Pai et al., 2006; Zettel et al., 2002); and the organized control of body collapse so it falls in a manner that minimises injury (Hsiao and Robinovitch, 1998).

Consistent with this dependence of human bipedality upon continuous timed postural adjustment, there is considerable evidence that normal human bipedality is supraspinal and involves the cerebellum working with the cerebral cortex. Dual-tasks, for example, show that postural adjustment requires cognitive resources used by other motor faculties such as vocal articulators (repeating syllables, talking) (de Hoon et al., 2003; Lundin-Olsson et al., 1997; VanderVelde et al., 2005; Yardley et al., 2000), dexterity (Ebersbach et al., 1995), and even higher cognitions such as spatial tasks, mathematics and Stroop (Hauer et al., 2003; Maki and McIlroy, 2007; VanderVelde et al., 2005; Woollacott and Shumway-Cook, 2002). The close study of maintaining stance and walking shows that it is stabilized by central control (Morasso and Schieppati, 1999), and involves cerebello-cerebral cortex circuits (Jacobs and Horak, 2007; Maki and McIlroy, 2007). It can include—if balance is particularly challenging—also the involvement of the prefrontal cortex, for example, when people walk on treadmills (Suzuki et al., 2004), or if a person stands in a virtual reality that lacks visual clues as to the floor and the ceiling (Slobounov et al., 2006). People can motor empathize with the postural upright stability in other individuals (Cheng et al., 2005; Slobounov et al., 2000), and this occurs through cortical mirror neurons (Cheng et al., 2005). This is all suggestive or consistent with a dependence upon postural adjustment based upon cerebello-cerebral cortex predictive internal models.

5.7. Noninternal model bipedal alternatives

Anticipatory postural adjustments and such internal model based top-down stabilization, it needs to be noted, is not required, however, for all forms of bipedal stiff standing and walking. Mechanical toys and robots can be designed such that their passive mechanical properties can cause them to walk in a human-like stiff manner on flat surfaces (Collins et al., 2005; Fallis, 1888). Empirical research suggests that stable upright posture can be achieved with only an open loop ankle stiffness control (Winter et al., 1998), or a closed loop involving muscle spindle and monosynaptic spinal feedback mechanisms (He et al., 1991). Robots have even been designed that can recover from perturbations during walking with only open loop methods of stabilization (Mombaur et al., 2005). Consistent with this, people with cerebellar agenesis or cerebellar dysfunction (developmental, lesion, or alcohol intoxication) can stand and walk with compromised supraspinal processes (Titomanlio et al., 2005, see particularly the associated video to this case report), as can those with spinal cord injuries when given partial hoist support following intensive multi-year physiotherapy (van Hedel et al., 2005).

However, from an evolutionary perspective, the existence of such non-top-down supraspinal internal model based bipedal stabilization mechanisms is less relevant than it might appear. This is because such mechanisms are too limited in their perturbation resistance to enhance an individual's survival fitness, as would have happened when the evolution of human motor abilities occurred during the Pleistocene. People who are “drunk”, for example, maybe able to stand and walk but such inebriated individuals lack exact temporal organization in their movements, and as a result, they are, in many respects disabled, as they easily fall, or are

limited in what they can do in a stable manner. Modern human locomotion, moreover, is much easier in terms of maintaining upright balance than it was in Pleistocene times: the modern walking environment is mostly paved, flat, often carpeted, and kept clear of footing hazards by health and safety legal requirements to minimize accidents. In contrast, the Pleistocene environment was rough and full of unexpected footing hazards that could potentially trip or slip up walkers and runners. The concern in this review is exclusively with the processes that enable the exquisite and highly robust balance shown by human adults when engaged in evolutionarily exacting upper body biped skills (such as accurate throwing), or challenging circumstances (avoiding trips and slips where there are footing hazards as when rough ground running), as only these are relevant to the past selection of human specific bipedal motor functions.

5.8. Summary of human bipedality and internal models

This brief discussion of human bipedality provides preliminary evidence to suggest that like dexterity, its uniqueness derives from anticipatory timed motor stabilization based upon internal models. Another source of evidence is that neuroanatomically, like dexterity, lesion and neuroimaging shows that it depends upon the cerebello-cerebral cortex circuits (Ioffe et al., 2007; Jacobs and Horak, 2007; Maki and McIlroy, 2007; Morton and Bastian, 2004) including prefrontal ones (Slobounov et al., 2006; Suzuki et al., 2004) that underlie such internal models.

6. HOMO VOCALIZATION

6.1. Humans are unique vocalizers

The art of vocalization is widespread amongst animals. Birds are, in particular considered, to be exquisite songsters. While speech, is appreciated to be biologically unique to humans, human song, in an albeit hidden way, is also biologically unique. Bird song, unlike humans song, is done with minibreaths between each syllable (with the exception of high frequency "trills" at $ca. 30s^{-1}$ in canaries, and $16s^{-1}$ in cardinals (Suthers et al., 1999)). Birds can do this because they use a different respiratory apparatus to mammals. This employs anterior and posterior air sacs to create a unidirectional airflow through their lungs, and this allows for the insertion of such minibreaths in between their song notes (Suthers et al., 1999).

Such minibreaths suggest bird vocalization is built upon low-level reflexive processes that ensure adequate concurrent respiration. Humans, whether in speech or song, in contrast, produce multiple vocalization upon prolonged single out-breaths, a phenomena called "thoracic breathing", that in terms of normal respiration is distinct from the everyday nonvocal and reflex controlled form of "quiet" respiratory breathing (Ghazanfar and Rendall,

2008; Hixon, 1973; Ladefoged, 1960; MacLarnon and Hewitt, 1999; Proctor, 1986; Provine, 1996). As with the human uniqueness in bipedality and dexterity, this respiratory phenomena is argued here to link to an unique competence in accurately timed motor stabilization (in this case the stabilization of subglottal pulmonary pressure) that results from expanded cerebello-cerebral circuits and internal modeling that overrides a lower level of reflex and motor control. Further, this capacity for such timed control in vocalization, even more than for dexterity and bipedality, allows for the construction of the novel kinds of complex motor executions; in this case, the interarticulator actions in the vocal tract that create the phonetic features that provide different phones with their distinct phonetic identities (Lofqvist and Gracco, 1999).

There exist several unique related traits in human vocalization.

6.1.1. Hierarchically stringing of units

Humans generate vocalizations strung together at several levels of hierarchical organization. Such vocalization can be made up of speech phones (syllables, words, clauses, sentences), or song notes (beats, meter, phrases, melodies).

6.1.2. Diverse recombinable units

Human vocalization is done in regard to a large set of recombinable phone/note units (most languages contain 20 to 45 vowel, consonant, and diphthong phones; there are 12 semitones in an octave and most singers can range across several). The International Phonetic Alphabet (International Phonetic Association, 1999) lists for consonants 12 places and nine types of articulation that can be either voiced or unvoiced (plus five types of anterior release clicks); for vowels it lists five positions and seven manners (plus being rounded or not). In addition, it notes the existence of three kinds of suprasegmentals stress (seven types), tone (15 types), and intonation (four types). Such features create a large pool of potential phones: for example, in one sample of 317 human languages, there were 757 different kinds of phones (Maddieson, 1981).

6.1.3. Diverse uses and modes of production

Humans modify and use their vocalizations in diverse mastered ways as distinct as falsetto, esophageal speech (after laryngectomies), yodeling, whistle speech, throat singing, and entertainment ventriloquism. Further, some human hunters learn to imitate the vocalizations of their prey to stalk them (Willerslev, 2004).

6.1.4. *Optional subcomponents*

The various components of human vocalization provided by the lung (pulmonary), glottis (vocal cords), larynx, and supralaryngeal vocal tract can be isolated, omitted, or used for other purposes. Humans can, for example, speak without glottal phonation, as in whistle speech, or without normal pulmonary pressure and phonation as in esophageal speech or buccal-source speech (also called ‘Donald Duck’ talk). (In this, the vocal tract is partially blocked by the back of the tongue, and teeth, cheeks, and oral pressure is created by the tongue that causes the arches in the back of the mouth to vibrate (Smith, 1994: p. 4221). Following spinal injuries, the pulmonary control of thoracic breathing can shift to being based upon the diaphragm without employing the normally used abdominal and intercostal muscles (Meyer, 2003). Respiration control is used for nonvocalization activities such as playing woodwind and brass instruments. In addition to such respiratory control, saxophonists and clarinetists can modify their instrument’s sound in the altissimo register by changing their vocal trait resonance (Chen et al., 2008; Fritz and Wolfe, 2005).

6.1.5. *Unique amongst primates*

Human vocal capacities are of particular biological interest because no nonhuman primate makes any comparable vocalizations. This is in spite of nonhuman primates already having many of the required competences: they can produce singularly some of the phonetic units of human speech (Richman, 1976), hear them (Steinschneider et al., 1982), and if trained, can comprehend the pronunciation of spoken words (Savage-Rumbaugh and Lewin, 1994), and intersperse vocalizations with human and other conspecific interactors in a conversational manner (Savage-Rumbaugh et al., 2004). However, even with these vocal-related advantages, while nonhuman primates can be tutored to communicate with gesture and sign-board based languages, they cannot be tutored to talk (Hayes, 1951). The language tutored, Kanzi, for example, is no more able in his vocal interactions than to contextually modulate the spectral and temporal features of his vocalizations—a notable contrast to his considerable abilities to communicate manually with a sign board (Taglialatela et al., 2003). This is odd since gesturing and sign board pointing would seem of comparable motor complexity to speech, and, nonhuman primates already use vocalization (unlike sign boards) to communicate. Indeed, evolution has enhanced nonhuman ape vocalization in a manner not found in humans in the form of vocal sacs (Ghazanfar and Rendall, 2008; Nishimura et al., 2007). The shape of the hyoid bone in a partial *Australopithecus afarensis* skeletal suggests interestingly that preHomo hominins also might have possessed such vocal sacs (Alemseged et al., 2006, p. 300). Such vocal sacs enable chimpanzees (and perhaps other apes) to produce very loud piercing calls that in the case of chimpanzees are made of two simultaneous tones that are three octaves distant from each other (Yerkes and Learned, 1925, pp. 61-62).

6.2. *Unlocked vocal chain*

Much less is understood about motor stabilization in human vocalization than for bipedality and dexterity, (it is known though that the vocal articulators adjust quickly after perturbation (Gracco and Löfqvist, 1994)). Research upon attempts to teach higher apes to make voluntarily vocalizations suggest a link to an unique human ability to control the respiratory/vocal tract musculoskeletal system. There are two such accounts (Furness, 1916; Hayes, 1951); both report difficulties in directly controlling the vocal apparatus. The account provided upon Viki is most detailed.

Viki could create some speech sounds but this depended upon her first being prompted with external help (Hayes, 1951). Keith (her human speech tutor) trained Viki by positioning his fingers in her mouth to open and shut them to form speech syllables. This was because Viki could make an “asking sound” but without such external help she could not modify it on her own into other sounds. As his wife Catherine Hayes noted in her book upon Viki (1951: p. 67.): “She soon got the idea and began to inhibit her asking sound until Keith’s fingers were on her lips. If he was too slow in getting ready, Viki often took his hand and put it in the helping positions”. Much earlier William Furness (1916) reported upon his attempts to teach an orangutan. In order to say “cup”, he used a spatula to push her tongue make to the /k/ phone: “after several lessons .. she would draw back her tongue to the position even before the spatula had touched it, but she would not say *ka* unless I place my finger over her nose. The next advance was that she herself would place my finger over her nose and then said it without any use of the spatula” (Furness, 1916, p.284).

To take the case of Viki, she could create the pulmonary pressure and phonation needed for a particular “asking” vocalization, and she could also manipulate her lips to create a different one (as evidenced when triggered to do so by Keith’s hand). What she could not do, or found very difficult, was combine them as independent motor elements so she could pronounce on her own a new type of nonevolved vocalization. The nearest she could do was use another part of her motor system (her hands) to get hold of Keith’s hand to reshape her mouth, and so use this indirect and external means to control her vocal articulation. A similar phenomena seems also to have characterized the attempts of Furness’ orangutan to vocalize. This suggests that nonhuman apes have problems unlocking the separate musculoskeletal elements that make up the vocalization chain to create the motor coordination that underlies the motor production of human speech. That the nonhuman vocal chain should be locked in this way makes evolutionary sense in the view of the critical importance of the links of respiration to cardiovascular and locomotion (Lee and Banzett, 1997), and that the larynx is involved not only in phonation but also in several survival critical reflexive actions such as swallowing, respiration and cough (Ludlow, 2005).

Reflecting this innate locking, while breathing is under voluntary control in humans (Loucks et al., 2007; Simonyan et al., 2007), it is difficult to train in nonhuman primates such as

chimpanzees (Hayes, 1951: p. 69). Humans also seem unique in related voluntary respiratory abilities such as suppressing and voluntarily activating (in the absence of sensory triggers) coughing and sniffing (Simonyan et al., 2007). Nonhuman vocalizations, when made, moreover, are nearly always done in emotional contexts and performed in a highly stereotypically and a genetically determined manner. This is evidenced in the strong correlations that exist between the vocalizations of chimpanzees and bonobos (in spite of them being two species), a correlation that does not exist, in contrast, for their manual gestures (Pollick and de Waal, 2007). The human brain control needed for voluntary respiratory such as that for exhalation and the production of sound syllables also seem to be closely related in that they involve similar cerebello-cerebral circuit activations (except for the auditory cortices) (Loucks et al., 2007).

6.3. Subglottal pressure stabilization

To control pulmonary pressure requires that thoracic muscles can stabilize lung exhalation as a separate motor control element in a time sensitive manner from the later ones in the vocal chain involved in phonation (voicing), vocal resonance change (vowels), and its gestural modification (consonants). There is here a direct parallel with anticipatory adjustment used in human bipedality and dexterity, but in regards to the stabilization of the motor parameter of pulmonary pressure below the glottis (vocal cords). This, for functional speech, needs to be maintained at a constant level (for a given degree of loudness) throughout successive strings of vocalizations in spite of this producing considerable decrease in lung volume (Hixon, 1973; Ladefoged, 1960; Proctor, 1986). For this pulmonary pressure stability to exist requires that the muscles controlling it are anticipatorily adjusted in regard to each upcoming vocalization and its particular subglottal pressure needs (which might vary, for example, in regard to its individual phones, vocalization loudness, and prosodic stress and emotional emphasis). There also needs to be in regard to forthcoming speech and song pauses action planning of thoracic muscles as to when to refill the lung (Whalen and Kinsella-Shaw, 1997).

6.4. Time-scheduling and phone articulation construction

Humans not only engage in thoracic breathing but also when articulating phones, engage in exquisite “dexterity” of the vocal tract. The reason for this, I suggest, is that in nonhuman animals, pulmonary pressure and the vocal tract are restricted by reflexes to articulating a limited set of evolved vocalizations. But because human vocal tract actions are “unlocked” from such reflexes in humans by direct cortical control (Ghazanfar and Rendall, 2008; Kuyper, 1958; Liscic et al., 1998; Ludlow, 2005; Teitti et al., 2008), it can be synchronized and motor coordinated in complex sequences of diverse and differently timed glottal, laryngeal and supralaryngeal movements. It is this ability to combine as independent motor elements glottal phonation, laryngeal/ supralaryngeal gesture and vocal tract modifications (Lofqvist and Gracco, 1999) with timed anticipatory motor adjustment that, could be

responsible for enabling the human motor system to create, and then string together, its rich diversity of speech phones into spoken words (as noted in section 6.1.2.).

If glottal phonation, for example, can be adjusted independently and anticipatorily to the rest of the vocal chain, it can be time-schedule synchronized to create speech sounds that differ in the timing between their glottal onset and their acoustic shaping by vocal tract gestures (voiced/ unvoiced contrast; glottal phones). Likewise, if the laryngeal shape is not reflexively locked to articulators higher up the vocal chain, then its resonance “vowel” quality can be changed independent of them so that vowel vocalizations can be conjoined in a time exact manner with a great variety of gestures in different vocal tract locations (bilabial, labio-dental, dental, alveolar, post-alveolar, retroflex, palatal, velar, uvular, pharyngeal, epiglottal, and glottal), and manners (nasal, plosive, fricative, approximant, trill, tap/flap, and their lateral variants). As a result, vowels can be provided with diverse kinds of associated consonantal sounds. For example, using data from the International Phonetic Alphabet (International Phonetic Association, 1999), the movement of the lips (bilabiality) can create six consonants depending upon their timing with the on-start of phonation in the glottis (voiced vs. unvoiced), the presence or not of nasality (/m/) (created by soft palette opening), and how that lip movement is carried out (plosive, /p/, /b/; fricative, /ɸ/, /β/; or trill, /ʙ/). The lips with such top-down control can create further pronunciations such as anterior release “click” consonants that do not even use pulmonary air pressure. This motor ability to independently stabilize different vocal components explains the diversity, that was noted in sections, 6.1.2. and 6.1.3 with which the human vocal apparatus can be used.

In this context, it is interesting to note that internal models in the cerebellum upon the auditory signal of phone production have been suggested to underlie phone perception (Callan et al., 2006), vocal tract articulation (right side) (Callan et al., 2007) and speech prosody (left side) (Callan et al., 2007). There is evidence that phone perception involves processes used in its production (Liberman et al., 1967; Pulvermuller et al., 2006). This research suggests that there may be a considerable opportunity to explain phenomena already identified in phonetic and speech sciences with the internal model processes that became more complex when the human brain expanded.

6.5. Possible link to syntax

As with knapping, the nature of internal models allows that such musculoskeletal level predictive internal models can engage in complex hierarchical interaction with higher internal model ones. As noted in section 6.1.1., it is a peculiarity of human vocalization that it is made in the context of several layers of hierarchical organization that concern not only productive ones (such as in speech syllable, word, phrase, and sentence) but also those involved in communication such as semantics, syntax, pragmatics and emotions. There is even evidence that the speech production system does not only aid the perception of speech (Liberman et al.,

1967; Pulvermuller et al., 2006) but provides prediction and imitation abilities that also aids higher level language comprehension (Pickering and Garrod, 2007).

Of particular importance in this context is that strings of phones are made into units that are organized and arranged in planned syntactic ways. This syntax level directly interacts down upon the lower musculoskeletal ones—a phenomena that can be seen in the way that syntactic tense can modify vowel vocalization such as in "swim", "swum", "swam". This suggests that the syntax and musculoskeletal levels are in some way closely interlinked. While any ideas in this area are necessarily preliminary, this raises the possibility that the internal models needed for low-level musculoskeletal control of the vocal tract could have created the opportunity by which higher-level models are constructed in motor control upon them so that the speech units that they create can be structured to support communication and semantics. It is interesting to note that the Broca's area, a brain region in the premotor cortex traditionally associated with syntax, and more recently, syntactic working memory (Fiebach et al., 2005), has also been recently identified as underlying the anticipatory hierarchization of actions (Fiebach and Schubotz, 2006). This is consistent with lower motor level models in vocalization providing the basis for the development of higher-level ones that have come in their organization of lower ones to possess what are analyzed as syntactic functions.

6.6. Summary of vocalization and internal models

These brief observations show that human vocalization and voluntary respiration control could gain their evolutionary novelty like human dexterity and bipedality from top-down internal model timed motor stabilization. Like them, this is consistent with them being linked to the cerebello-cerebral cortex circuits (Callan et al., 2007; Callan et al., 2006; Dresel et al., 2005; Loucks et al., 2007; Murphy et al., 1997; Schulz et al., 2005; Spencer and Slocumb, 2007). Further, like dexterity and bipedality, the kinematics of speech production continues to be refined into adolescence and after (Smith and Zelaznik, 2004).

7. HUMAN BRAIN EVOLUTION

There are two possibilities by which top-down time accurate motor feedforward adjustment might have evolved to underlie the human uniqueness argued above to exist in dexterity, bipedality and speech/song vocalization.

- (1) That it was independently selected in each case, or
- (2) that (as will be argued below) it was a result of a common pleiotropic selection (namely, for increased cerebello-cerebral cortex circuitry linked to brain expansion).

The reason for proposing the latter is that empirical research (section 7.1) suggests, at least provisionally, that the above three domains of motor enhancement use partially overlapping and shared neural resources. Given that the actions of bipedal locomotion, dexterity and

vocalization need not, and in fact rarely, occur together, enhancement by sharing common neurological components would be optimal. This is because it would provide three talents for the adaptive cost of one—a phenomena that economists call “economies of scope”. Thus, the human evolution of the above faculties could have been part of one common brain expansion linked general motor control enhancement pleiotropic adaptation.

Note, a qualification needs to be made in regard to speech. In both dexterity and bipedality, it has been argued above, that it was stabilization enhancement rather than motor primary execution that was improved by an increased ability to time motor movements (though this is not to deny that their execution would not have been enhanced also to some degree). However, in speech, accurate interarticulator time-scheduling is critical to the generation of the particular identities of phones (Lofqvist and Gracco, 1999), suggesting that this might have required a further additional enhancement of internal modeling beyond that needed to enable human dexterity and bipedality. This prerequisite is unique to speech language since gesture-speech does not require such tight time control of its articulators which instead depend upon the accuracy of their visuospatial processing (Campbell and Woll, 2003). Thus, the enhancements needed for full speech may (unlike bipedality and dexterity, for which there is paleoanthropological evidence for an early origin in *Homo*) might have only existed since the rise of the present human species, with earlier *Homo* only having “protospeech” vocal capacities. This would be consistent with it depending upon cerebellum expansion and related brain changes that seems to have occurred specifically to *H. sapiens sapiens* (Weaver, 2005).

There are two steps of argument here. (i) How good is the evidence for such neural sharing? And (ii) would such pleiotropic evolution make any sense for understanding the specific changes that happened to *Homo* from an evolutionary perspective? There also a third issue (discussed in section 8): how far can this issue be researched to provided new data into the role of internal models and timed enhancement of motor control that arose in human evolution?

7.1. Shared neural resources

7.1.1. Cerebellum and cerebral cortex nonspecificness

Cerebellar circuits are cytoarchitectonically uniform with differences in their processing arising from their inputs and outputs (Bloedel, 1992; Ito, 2006). Prefrontal cortex areas—one of the cortical regions to which the cerebellum connects and forms circuits—lack specific domains and instead apply their functions adaptively where they are relevant to motor and nonmotor tasks (Duncan, 2001). Parts of the cortical motor system such as the posterior parietal cortex also show evidence of not being effector specific as, for example, they control both eye saccades and hand reaches (Levy et al., 2007). Cerebral cortex areas are more generally open to represent different parts of the body as shown after hand amputations when sensorimotor networks shift from representing the hand to the face (Elbert et al., 1994), a

situation (including also the feet) that arises naturally in those born without arms and hands (Kamping et al., 2004). The corticospinal tract also is not strongly tied to specific motor domains: surgical intervention after brachial plexus avulsion, for example, can reestablish arm and hand control by reinnervation to spinal motoneurons that previously controlled respiration (Carlstedt et al., 2004). More generally, research upon developmental neural plasticity (such as that upon those born blind), argues that considerable functional reassignment of function can occur during development upon the brain's neural networks (for a review of the importance of such noninnateness of neural circuit function to human evolution see (Skoyles and Sagan, 2002)).

7.1.2. Dual-task evidence of neural sharing

Interference occurs between tasks when done at the same time such as between bipedal balance and dexterity, for example, when walking while opening and closing a coat button (Ebersbach et al., 1995); and with vocal articulation as when standing and repeating syllables (Yardley et al., 2000). In the elderly such conflicts become more evident (probably due to impairments that curtail the effective functional "size" of their brains), and extend to balance and language to the degree that some individuals cannot both walk and talk (de Hoon et al., 2003; Lundin-Olsson et al., 1997). Dual-task interference can derive from several factors including bottlenecks in drawing upon limited general attentional resources, but the effects are specific here as balance (Hauer et al., 2003; VanderVelde et al., 2005; Woollacott and Shumway-Cook, 2002), for example, is more effected by spatial higher cognition tasks than nonspatial ones (Vander Velde and Woollacott, 2008; VanderVelde et al., 2005). This suggests that they share processes in common.

7.1.2. Cross motor entrainment and priming

Entrainment occurs across different motor faculties. While this for anatomical and physiological reasons might be expected between walking and breathing, it also occurs where there are no functional couplings such as between eye movements and finger movements, and finger movements upon breathing patterns (Raßler et al., 1996). Further, certain pairs of tasks are impossible to time independently of each other such as reciting nursery rhymes with proper intonation while tapping a 1-3-123 rhythm (Peters, 1977) see also (Ramachandran, 2006). Priming effects also occur across vocal, manual and ocular motor effectors (Eimer and Schlaghecken, 2001). These effects are consistent with motor faculties using shared processes in common.

7.1.4. Developmental correlation and neural overlap

Consistent with the existence of neural sharing is that the early infant acquisition of bipedality correlates with enhanced executive skills at the age of 33-35; moreover, half the activated voxels in the cerebellum linked to such adult executive skills also link to those that

retrospectively associated with early bipedality (Ridler et al., 2006) (see also further comment in section 7.3). In this context, it should be noted that frontal activations in infants as young as 6 months accompany the maturation of motor skills such as eye saccades depend upon internal models, and, then only later in adults, shift to posterior areas when they become highly automated (Csibra et al., 2001). It would thus seem that motor skills such as bipedality and eye saccade control depend critically upon prefrontal neural resources, even though this ceases, in most normal circumstances—at least when unchallenging—once they are fully mastered.

7.1.5. *Subprocesses in common*

Functional imaging shows that motor skills (and indeed nonmotor ones) share subcomponent processes in the brain. For example, the concentration needed to mentally count targets of a particular color and shape activates an "attention hotspot" in the lateral cerebellum that is identical to one briefly activated at the onset of the motor act of responding to every member of a series of targets (irrespective of color or shape) (Allen et al., 1997) (see also more comment below). Another study has found the existence of a general and widespread sharing of cortical areas in the human brain by different cognitive tasks, with an average sharing of 5.97 (range 1-38) tasks per cortical area (Anderson, 2007).

This diverse variety of evidences suggests or supports the idea that some of the neural circuits employed by the three major human motor faculties are not necessarily tied to specific musculoskeletal effectors. At least some aspects of the enhancement of their motor control as a result could therefore derive from the cross-sharing of neural resources.

7.2. *Synergetic enhancement in high-energy food hunter-gathering.*

Pleiotropic selection of such shared neural resources would make particular sense if economies of scope applied to enhancing skills that also worked synergistically together (but never concurrently) in strengthening the evolutionary fitness of *Homo*. This appears to be the case with the three human unique motor faculties, and the human unique subsistence niche: high-energy food hunter-gathering.

Paleoanthropological isotopic evidence suggests that Australopiths eat a predominately vegetarian diet (Spoonheimer et al., 2006; Teaford and Ungar, 2000), and that this changed with *Homo* to one dominated by high-energy foods acquired by wide territory based hunter-gathering (Foley, 2002). The actual nature of the high-energy foods acquired by hunting and gathering is controversial with early *Homo* having been variously suggested to having engaged in purposeful small game hunting, the extraction and cooking of tubers (O'Connell et al., 1999), passive scavenging (Shipman, 1986), power scavenging (chasing off predators from their kills) (Bunn, 2002), big game (Dominguez-Rodrigo, 2002) and persistent "running down" hunting (Liebenberg, 2006). The existence of a shift to high-energy foods, however, is

not in question since the concomitant brain expansion and the prolongation of immaturity in *Homo* could have only occurred in the context of the increased ability to acquire calories (Foley, 2002). In particular, human children have double the resting metabolism of adults in their cerebral cortex between 4-10 years of age related to the needs of brain development (Chugani, 1998; Skoyles, 2008, for a review). This increase causes the brain to consume 60% of their total body resting metabolism since it combines a doubling of metabolism with a total resting body metabolism in children that is around half that of adults (Skoyles, 2008). This would have made humans, as a biological species, particularly vulnerable to disruptions in the availability of high-energy foods so requiring that they had also evolved the skills that could always ensure with good reliability that they were obtainable.

No other primate engages in a comparable form of life-style. Three factors, notably make it a difficult option: high-energy foods (of whatever nature, tubers, game or carcasses) tend to be widely dispersed (big game animals alive or dead are sporadic, tubers occur only in scattered locations), hard to access (deep in the ground, marrow locked in bones), and require for their maximum exploitation information sharing (tubers occur in patches, large animal carcasses and game occur rarely), information storage (seasonal movements of animals, degree of harvesting of tuber areas) and social collaboration (sharing of information, the care of infants while hunter-gathering) (Aiello, 1996). Thus, hunter-gathering has a highly synergetic need for diverse motor competences to come together: those that enable (i) travel over wide areas, (ii) extracting hard to access foods, and (iii) effective information transfer between individuals.

In consequence, an evolutionary self-sustaining feedback process would occur if an adaptation arose that enhanced the multiple motor skills that worked synergistically together in hunter-gathering, and that they were not concurrently employed. Moreover, such feedback could self-maintain itself producing yet further opportunities for evolutionary change. This would suggest that the pleiotropic enhancement of motor faculties through expanded cerebello-cerebral cortex circuitry and top-down stabilization might have been an important mechanism (and one that is researchable, see below in section 8) in giving rise to, and then acting to shape, human evolution (see fig 3).

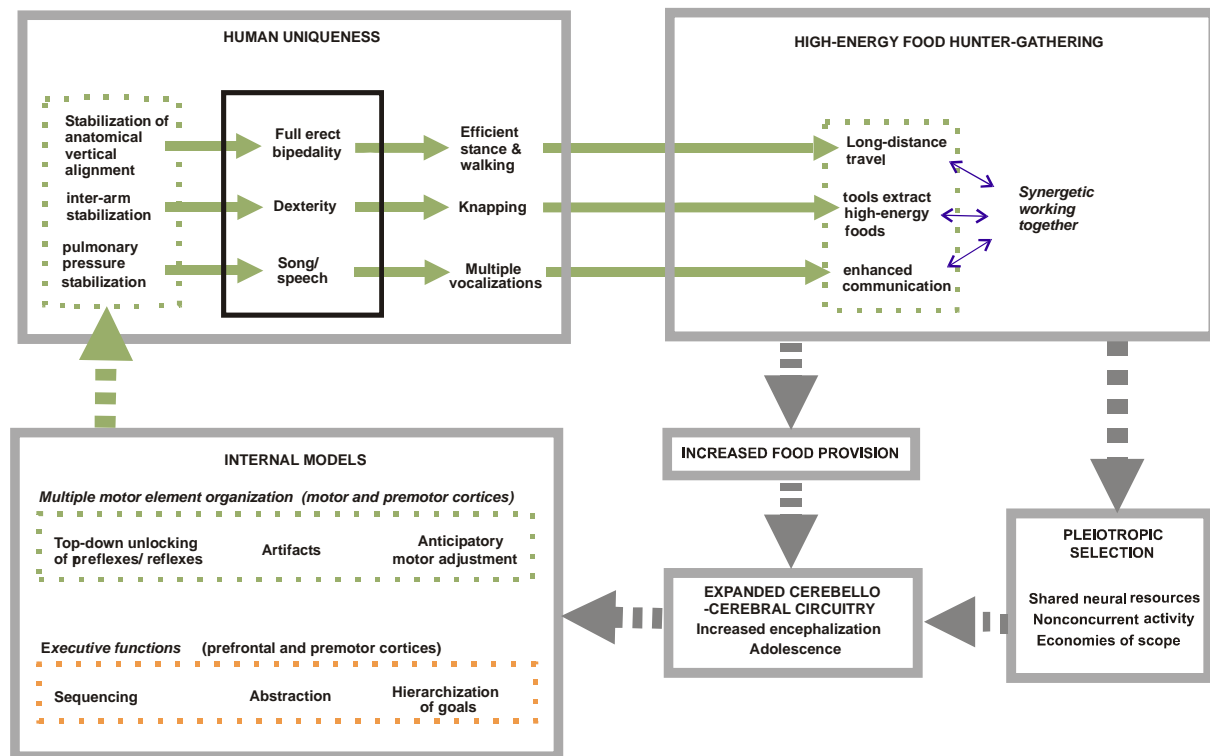


Fig. 3.

Outline of the main components of the proposed motor theory in the context of *Homo* origins. In the center of HUMAN UNIQUENESS is listed each of the major motor faculties: bipedality, dexterity and vocalization. To the left of them are the motor stabilizations that underlie their uniqueness, and to the right, the unique behavioral competence that they enable. To the right of HUMAN UNIQUENESS, lines connect behavioral competences to *Homo* ecological behavior in HIGH-ENERGY FOOD HUNTER-GATHERING. For example, the stabilization of anatomical vertical alignment bipedality allows efficient stance and walking, and so enables *Homo* to engage in long-distance travel. The three ecological behaviors are shown to act synergistically together with each other and also the social competences that derive from executive functions that also derive from INTERNAL MODELS (shown by a link running at the bottom). HIGH-ENERGY FOOD HUNTER-GATHERING is shown to link to PLEIOTROPIC SELECTION. The motor faculties are not concurrently done, and so permit the possibility of them relying upon shared neural resources (economies of scope). HIGH-ENERGY FOOD HUNTER-GATHERING also results in INCREASED FOOD PROVISION. This supports the prolonged nonadult stage of adolescence and increased encephalization and so EXPANDED CEREBELLO-CEREBRAL CIRCUITRY. This produces an increased capacity for INTERNAL MODELS and so the HUMAN UNIQUENESS.

7.3. Neural resource sharing and nonmotor faculties

This theory of shared neural resources faces the "problem" that some of the empirical support that motor skills share neural resources comes from evidence that such sharing occurs between motor and nonmotor skills. If a motor task shares an attentional subprocess with an higher cognitive one (Allen et al., 1997), then it is reasonable to assume that other motor faculties will also share that attentional subprocess. Likewise, if developmentally a motor ability such as bipedality correlates not only in terms of a later competence for executive function but also in 48% of its voxels in the cerebellum (Ridler et al., 2006), it is reasonable to assume that the subprocesses responsible for this is also shared to a similar or greater extent with other motor faculties.

No particular division exists in the prefrontal cortex between motor areas and nonmotor areas as it is activated as much by motor tasks as nonmotor ones (Duncan, 2001). The prefrontal cortex, indeed seems to act both as a higher area for planning, sequencing, monitoring and selecting appropriate motor actions, and as an area for doing these computational operations for cognitive processes (Abe et al., 2007; Mushiake et al., 2006; Slachevsky et al., 2003). As noted above, internal models can underlie a diverse range of nonmotor-type cognitions. This argues the enhancement found in the three major human motor faculties could have endowed the *Homo* brain with abilities that would have changed cognition more generally than just by enhancing motor functions.

This is consistent with the existence of close links that have already been suggested or found to exist between the motor system and general cognition. The founder of child development science, Piaget, argued that the initial stage of cognitive development upon which the intellect was built was a sensorimotor period (Piaget, 1928). The work mentioned earlier that links early bipedality and executive skills (Ridler et al., 2006) is inspired by the theory of cognitive dysmetria by which the cerebellum coordination of movement is conjectured to underlie a coordination also of thought (and impaired in its coordination in schizophrenia) (Andreasen et al., 1998). The nature of concepts has been suggested to be grounded upon the sensory-motor system (Gallese and Lakoff, 2005). Anticipation of events in the external world has been proposed to use the motor system (Schubotz, 2007). Action words associate with the motor parts of the brain that control their actions (Pulvermüller et al., 2000). Mentally, counting or putting any elements into an order series activates hand motor circuits (Andres et al., 2007). Phenomena such as the short-term phonological buffer represent nonmotor ideas in terms of their phonological articulations (Baddeley et al., 1984), and in ASL speakers, manual gestures (Wilson and Emmorey, 1997). Silent reading and "inner voice" associate with electromyographic activity in the vocal tract (Sokolov, 1972). Moreover, purely mental activities recruit respiratory and cardiovascular stress responses (Brod et al., 1959). This recruitment suggests that they use processes that had originally a motor function, and that when they are activated, that this in a vestigial manner still prepares the body for a physical

response. Thus, diverse phenomena are consistent with motor control enhancement found in humans having effects beyond those directly enhancing motor functions.

The idea that motor processes used in motor control might also underlie nonmotor cognitions is not novel. The greater complexity of motor control needed for arboreal clambering of apes has been suggested to underlie their greater self-awareness cognitive abilities (Povinelli and Cant, 1995). Most of those researching motor internal models assume that they also underlie cognitive ones (Imamizu et al., 2000; Ito, 2006; Ito, 2008; Wolpert et al., 2003). For example, “We further speculate that the cerebellum assists information processing in cerebral areas by providing general internal models of extended controlled objects in the external world such as concepts, symbols and languages (Imamizu et al., 2000, p. 195).

This raises a question for the nature of human evolution. If human evolution pleiotropically enhanced motor faculties, might it not also have pleiotropically enhanced *both* motor and nonmotor ones? High-energy food hunter-gathering in modern humans is highly dependent not only upon motor skills but also cognitive planning, communication and social cooperation. This suggests a second loop might need to be added to that suggested for motor enhanced long-distance travel, tool making and use, and vocal communication linked to cognition (see fig. 4).

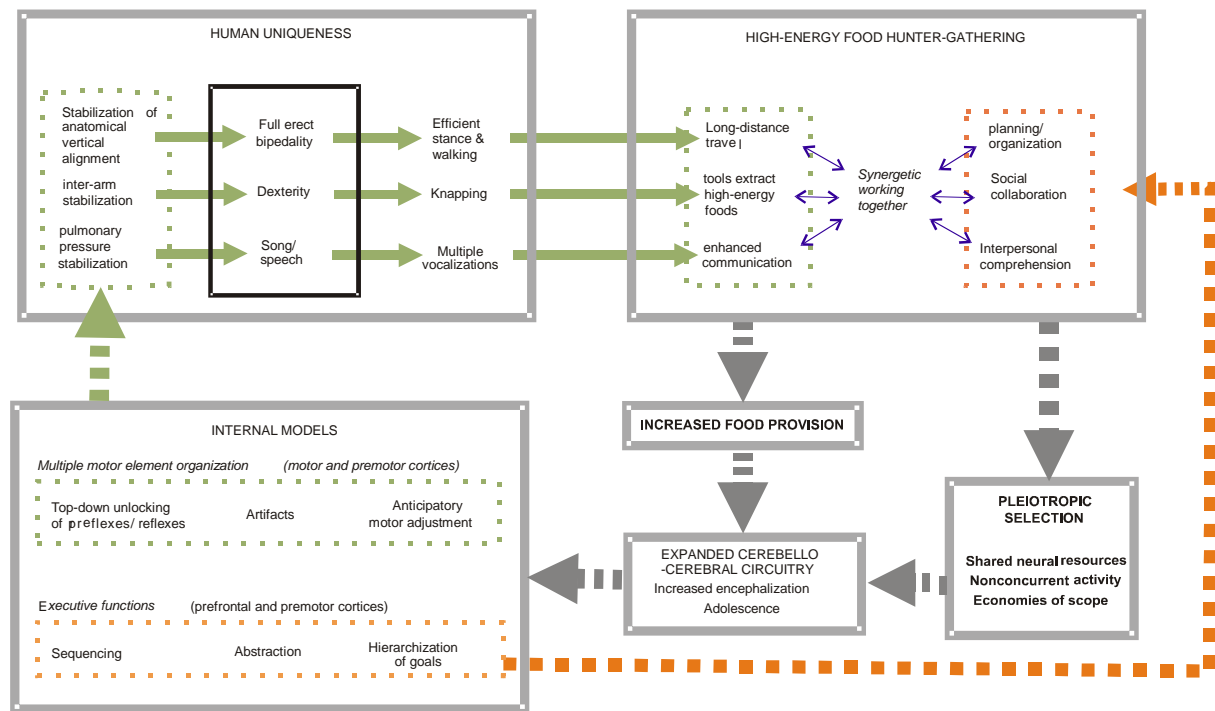


Fig 4.

Another loop is added to the boxes in fig 3 that starts from the bottom of INTERNAL MODELS in the “executive functions” box. This enables nonmotor functions that enhance HIGH-ENERGY FOOD HUNTER-GATHERING, and so INCREASED FOOD PROVISION for EXPANDED CEREBELLO-CEREBRAL CIRCUITRY and so better INTERNAL MODELS.

8. EXPERIMENTAL IMPLICATIONS

This review presents two levels of observation. First, it identifies a previously unappreciated neurobiological commonality between human dexterity, human bipedality and human vocalization that is also a characteristic that separates them from superficially similar activities done by closely related nonhuman primates. Second, it identifies how human evolution might have selected cross-motor faculty enhancement by exploiting economies of scope by the use of shared neural resources. Both observations are interesting in that they identify novel opportunities for research into motor processes and human origins. These possibilities will be briefly reviewed.

8.1. Neurodevelopment correlations

The opportunity to empirically explore neural resource sharing is raised particularly by Ridler et al (2006) and their finding that the age of acquiring bipedality links with later executive skills,

for example, that they share 48% of their cerebellar voxels in common. Three notable things exist about this research. First, prior cognitive theory does not predict this strong link between bipedality and executive functions. Second, this research at present is unique in its exploration upon such developmental correlations. Third, it investigated only two of a large number of possible evolutionary relevant motor and nonmotor cognitions. In the context of this review article, this type of research can be predicted to potentially identify many other motor-motor and motor-nonmotor correlations. More importantly, such research could identify the differing contribution and role of neural resources sharing between motor and nonmotor faculties in terms of their degrees or not of overlap, and so provide information about how past selection might have acted through them to shape the human brain.

8.2. *Adolescence*

Another research issue is the evolution of adolescence. This is unique in occurring only in humans but there is much uncertainty as to its developmental role (Bogin, 1999). Research suggests it is a period of refinement of internal models (Choudhury et al., 2007), and also of motor skills (Assaiante and Amblard, 1995; Choudhury et al., 2007; Hirschfeld and Forssberg, 1992; Smith and Zelaznik, 2004). But human children would seem superficially to have mastered motor skills to an apparently adequate level of proficiency already before adolescence. One factor is that the adolescent body undergoes various changes such as lengthening of its trunk and legs, and, after this, an increase in muscular strength (Bogin, 1999). However, such body changes will require only the minor modification of previously acquired motor skills. Another possibility is that skills mature during adolescence in a less obvious manner such as in regards to their robustness against unexpected and complex perturbations. Such stability would have been particularly important to Pleistocene high-energy hunter-gathering adults. Contemporary humans live in a carpeted and artificially flat world, in contrast, premodern people walked and ran bare-footed on an environment littered with footing hazards that could trip them. Moreover, they faced the possibility of unexpected predators and so a need for locomotive proficiency such that they did not stumble when they ran to escape. Superiorly enhanced skills acquired during adolescence therefore might have once had a much greater importance to survival than in contemporary people. Indeed, it is possible that the physical changes that happen in adolescence have, in part, been delayed until the brain can safely embody a taller, stronger and so more difficult to stabilize body before it starts to do more demanding adult activities. A capacity for motor enhancement could therefore be expected that might seem redundant in contemporary humans (except in activities that uses it for recreation such as music, dance and sport). Nonetheless during adolescence such capacities would still continue to be acquired, and be closely linked with adolescence neurological changes such as the development of greater accuracy in internal models.

8.3. Encephalization links to internal model dependent motor and cognitive capacities

An additional research related issue is the evolution of the increased human encephalization index. Brain size both absolute and relative to body size has increased from Australopiths up to *H. sapiens sapiens* (Rightmire, 2004). Further, intriguingly, a shift of brain volume between the cerebral hemispheres to the cerebellum has been argued to have occurred between early Neanderthal and Cro-Magnon *H. sapiens* and extant humans (Weaver, 2005). In the context of this review article, one would expect brain size differences to closely link to the human capacity to engage in motor stabilization, the shared use by different motor faculties and nonmotor ones of neural resources.

The opportunity to explore them exists: occasionally research and clinical case papers report the existence of individuals with small brain size yet apparently normal cognition (for a literature review of such individuals in the context of the IQ debate, (see Skoyles, 1999). Indeed, modern humans with normal range IQ exist with brains as low as 750 cc, and so in the low range for *H. erectus* (Skoyles, 1999). For example, children that have hemispherectomy (removal or functional disconnection of one of the two cerebral hemispheres) have (assuming a normal initial sized brain) 548 cc of cortical tissue removed leaving them with a brain of around 823 cc (750 cc if female) (Skoyles, 1999). Clinical accounts of such individuals report that they can have normal or higher than normal IQ, for example, P.G., had a Wechsler verbal test IQ of 118, and a performance one of 94; 15 years later, the Wechslers remained relatively unchanged at 121 (verbal) and 91 (performance) (Griffith and Davidson, 1966). Individuals with hydrocephalus can have a markedly reduced cerebral hemispheres and yet can be cognitively normal: for example, the case of the white collar worker recently described with accompanying MRI scan in the *Lancet* (Feuillet et al., 2007). Other cases are described in Skoyles (1999). There is, however, as yet little attempt to study such individuals to investigate the link between brain size, human cognition, and its evolution. Even the more limited variation found in normal brain imaging recruitment is rarely studied except in the context of IQ. For example, one study (Giedd et al., 1996) recruited 624 4-18 year-olds, of which after carefully screening with psychometric tests, and a psychiatric interview, only 112 meet their stringent criteria for 'normality'. Within this group striking variance was found in cerebral hemisphere volume ranging from 735 cc (a 10 year-old male) to 1470 cc (a 14 year-old male) (Giedd et al., 1996, Fig. 4). A 10 year-old male old has a brain at least 95% the size of an adult, and given normal proportions this individual's total brain size would be 850.7 cc, and 888 cc as an adult, calculations in (Skoyles, 1999). Thus, even in carefully selected MRI scanning studies, normal individuals exist with low brain volumes.

Research upon such individuals could provide a new source of data upon the factors that shaped past human selection, particularly if combined with measures of different motor/nonmotor faculty proficiency, timing of motor stabilization and coordination, and neural resource probes involving dual-tasks, entrainment and cross-faculty priming. For example, does the capacity for motor stabilization and timing accuracy in internal models link to the

size and so availability of cerebello-cerebral circuits? Is there such a link with cerebello-prefrontal ones? What is the relationship between brain size and shared neural resources (for example, in the context of the development correlations found in (Ridler et al., 2006))? Do individuals with smaller brains compensate by increased cross-faculty neural sharing, or do they experience timing related proficiency ceilings upon their motor skills? If modern humans traded-off cerebral hemisphere volume for enlarged cerebellums, is there population variation in the relative size of these two parts of the brain, and if so, how does it correlates with motor execution—particularly in speech—and nonmotor skills, and their cognitive development? The phenomena identified in this review are therefore within the domain of present research, and provide the opportunity for more detailed investigation.

9. CONCLUSION

This article has reviewed the stabilization accomplishments in the three major motor faculties (dexterity, bipedality, and vocalization) that distinguish humans from nonhuman animals, and has identified a trait that closely links with the cognitive capacities that associate with increased encephalization. This trait is the much greater use of feedforward control in the accurate timing in motor control, particularly that required for the top-down stabilization against perturbation. Such feedforward control is known to link to cerebello-cerebral circuitry, and this circuitry has markedly expanded in *H. sapiens sapiens* compared to *H. sapiens* archaic (Weaver, 2005), and in humans generally compared to other nonhuman primates (MacLeod et al., 2003). This review has further identified that such a change would most parsimoniously occurred if the three major human motor faculties shared neural resources. There is preliminary evidence from dual-task research that this is indeed the case. These observations are interesting in that they identify novel opportunities for research into motor processes and human origins.

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