Brain evolution in *Homo:* The "radiator" theory[1]

Dean Falk

Department of Anthropology, State University of New York at Albany,
Albany, NY 12222
Electronic mail: *df356@albny1vx.bitnet*

Abstract: The "radiator" theory of brain evolution is proposed to account for "mosaic evolution" whereby brain size began to increase rapidly in the genus *Homo* well over a million years *after* bipedalism had been selected for in early hominids. Because hydrostatic pressures differ across columns of fluid depending on orientation (posture), vascular systems of early bipeds became reoriented so that cranial blood flowed preferentially to the vertebral plexus instead of the internal jugular vein in response to gravity. The Hadar early hominids and robust australopithecines partly achieved this reorientation with a dramatically enlarged occipital/marginal sinus system. On the other hand, hominids in the gracile australopithecine through *Homo* lineage delivered blood to the vertebral plexus via a widespread network of veins that became more elaborate through time. Mastoid and parietal emissary veins are representatives of this network, and increases in their frequencies during hominid evolution are indicative of its development. Brain size increased with increased frequencies of mastoid and parietal emissary veins in the lineage leading to and including *Homo*, but remained conservative in the robust australopithecine lineage that lacked the network of veins. The brain is an extremely heat-sensitive organ and emissary veins in humans have been shown to cool the brain under conditions of hyperthermia. Thus, the network of veins in the lineage leading to *Homo* acted as a radiator that released a thermal constraint on brain size. The radiator theory is in keeping with the belief that basal gracile and basal robust australopithecines occupied distinct niches, with the former living in savanna mosaic habitats that were subject to hot temperatures and intense solar radiation during the day.

Keywords: australopithecine; bipedalism; brain evolution; brain size; comparative neuroanatomy; human evolution; paleontology; thermoregulation; vascular physiology

1. Introduction

The theory presented below resulted from two serendipitous and unrelated events. The first was a conversation that I had with my auto mechanic, Walter Anwander (a whiz), who completely rebuilt the engine of my 1970 car. One day, while enumerating the wonders beneath the hood, Walter pointed to the radiator and said, "The engine can only be as big as *that* can cool." I didn't think much about it at the time.

The second event was more to the point. In January of 1987, I received a letter from a French physiologist named Michel Cabanac whose team had determined that emissary veins contribute to the regulation of brain temperature. Commenting on the suggestion that vascular and venous sinus systems were modified in early hominids as a byproduct of bipedalism (Falk 1986a; Falk & Conroy 1983), Cabanac noted that during the course of hominid evolution, brain thermolytic needs would have increased with increasing brain size. He further suggested that I consider the evolution of emissary veins in *Homo* from this new perspective. Cabanac's suggestion is largely responsible for this paper.

2. Bipedalism, brain size, and neurological reorganization

Twenty years ago, the leading theory of hominid brain evolution was based on a cyclical model that postulated a

feedback between bipedalism, freed forelimbs, tool production, hunting, and brain enlargement (Washburn 1960). This theory has lost favor in the last decade however (Washburn 1982), largely because of the discovery in Laetoli, Tanzania of fossilized footprints that show early hominids were bipedal long before brain size began its dramatic increase, i.e. 3.5 million years ago (Leakey & Hay 1979). Cranial capacity is a close approximation for brain size (Hofman 1983) and is therefore used in its place in many evolutionary studies. The mean cranial capacity of the earliest known bipeds was not much larger than the average brain size of living chimpanzees, and its increase was gradual during the course of evolution in gracile and robust representatives of the genus *Australopithecus* (Falk 1987b). Thus, the proposed cyclical interaction between bipedalism and brain size was lacking in the earliest known hominids.

It was not until some two million years ago that brain size began increasing dramatically, and then it did so in another genus, *Homo* (Falk 1987b). But what meaning may we attach to increased brain size? Comparative studies of cranial capacity in various hominids are made confusing by the fact that body size also increased during the course of hominid evolution. (A full discussion of allometric considerations is beyond the scope of this paper. See Falk 1980a; Holloway & Post 1982; Jerison 1982 for reviews.) Although relative brain size (brain size to body size) may be more meaningful than absolute brain size in evolutionary studies, efforts to estimate its value are hampered by difficulties associated with identifying

the correct species for fossil long bones used to estimate body size. We may be able to estimate that such and such a fossil femur probably came from an individual that was approximately x feet tall and weighed approximately y pounds, but what good is this information if we cannot be sure of the species (and sometimes the genus) represented by the femur? Add to this the well known fact that there appears to be little correlation between brain size and intelligence in modern human populations (Tobias 1971), and it becomes clear that one must interpret brain size cautiously.

In addition to the increase in brain size that took place during hominid evolution, reorganization seems to have occurred in the spatial relationships and connectivity of the component parts of the brain (Holloway 1975; see also Galaburda & Pandya 1982). This concept of "neurological reorganization," developed most notably by Holloway (1975), is extremely important for thinking about hominid brain evolution. As Holloway puts it (1975, p. 34): "One cc of chimp or australopithecine cortex is not equivalent to one cc of modern human, Neanderthal or *Homo erectus* cortex."

Neurological reorganization occurs not only across species, but reorganization or "plasticity" can also occur within the brains of *individual adult* primates (Altman 1987; Fox 1984). For example, dynamic changes in response to surgery have recently been demonstrated for finger representations in the somatosensory cortex of adult owl monkeys (Clark et al. 1988). Similarly, electrical stimulation mapping of human patients has led Ojemann to conclude that (1983, p. 195): "The exact cortical sites related to a language process may not be stable over time even in adult life, expanding or shrinking in relation to facility with a particular function." These results are viewed by many as surprising because they contradict the long-held view that the cerebral cortex is basically hard-wired by the time adulthood is reached (see also Altman 1987; Kaas 1988).

This newly emerging dynamic view of the primate cerebral cortex provides a basis for understanding how new behaviors (e.g. bipedalism) can directly cause cortical reorganization. Richards (1986) has recently incorporated information about the plasticity of cortical maps into a discussion of the origins of bipedalism in hominids. In a welcome departure from the cliché of bipedalism "freeing the forelimbs," Richards suggests that enslavement of the foot rather than freeing of the hands caused neurological reorganization in the first bipeds. To wit: Once feet became weight-bearers (for walking) instead of graspers (a second pair of hands), areas of cortex previously used for foot control were reduced, thus freeing up cortex for other functions. This idea is consistent with cortical maps of human and nonhuman primates. Generally speaking, foot representations of humans (Penfield & Rasmussen 1950) are relatively small and buried medially within the brain; whereas those of rhesus monkeys (Woolsey 1958) and chimpanzees (Woolsey 1964) appear to be larger and extend onto the lateral surfaces of their brains. (Hand representations appear to be large in cortical maps for all three species.) Richards' hypothesis finds recent support from Rakic's (1988) discussion of the "radial unit hypothesis" that explains how a cortical area might shift its representation so that a "cytoarchitectonic area can be introduced during evolution."

But where does this leave us? We see that brain size increased dramatically during the known fossil record for *Homo* that began some two million years ago, but that it did not increase appreciably in the australopithecines (Figure 1). To be specific, in two million years, mean brain size doubled from roughly 700cm^3 to 1400cm^3 in *Homo* (Falk 1987a), and "the tempo of rising encephalization accelerated as cranial capacity itself increased" (Godfrey & Jacobs 1981), i.e. brain size increased "auto-catalytically" (ibid). Although it is well known that brain size is not highly correlated with intelligence in living people, it is also true that the known fossil record for *Homo* coincides with a cultural record that began with a few clunky stone tools (Foley 1987), led slowly to the gorgeous artistic endeavors of the Upper Paleolithic (Marshack 1985), arrived more quickly at the computer age, and has brought us rapidly to the beginnings of a revolution in biotechnology. Comparing ourselves to our closest nonhuman cousin, the chimpanzee (with whom we share a common ancestor that may have lived around five million years ago, Sarich 1971), we can safely surmise that somewhere along the line: (a) the capacity for language developed in hominids (Falk 1980b; 1983; Holloway 1983; Tobias 1981; 1987; Toth 1985) and (b) so did human-like intelligence. Thus, contrary to the situation *within* our species today, increasing brain size may indeed have been causally associated with increasing intelligence during the course of evolution in *Homo*.

One thing is for sure: Bipedalism has been thoroughly disengaged from its hypothetical interaction with brain enlargement. Or, put another way, the feet went first. What accounts for this breech birth of the genus *Homo*? Many workers have suggested that one behavior such as language (Darwin 1871; Olivier 1972), or hunting (Ardrey 1976; Hewes 1973; Krantz 1968), or throwing (Calvin 1982; 1983a; 1983b; 1986a; 1986b) was primarily responsible for human brain evolution. Although I believe that the search for such "prime movers" is highly speculative and that these theories do not lend themselves well to hypothesis testing (Falk 1980a), the seeds planted by Walter Anwander and Michel Cabanac have led me to a prime mover theory of hominid brain evolution that ties together the origin of bipedalism in early hominids with the enlargement of brain size much later in the genus *Homo*. And a mechanistic theory at that.

3. Cranial blood flow and posture in humans and other animals

A column of fluid whose orientation changes from horizontal to vertical is subject to increased gravitational (hydrostatic) pressure along a gradient that runs from top to bottom due to the weight of its contents (Schmidt-Nielsen 1979). In keeping with this, pressure gradients differ across the jugular vein depending on posture (Caro et al. 1978). Reclining humans drain blood from their heads mainly through their jugular systems, but upright individuals do not. Instead, humans in vertical positions drain cranial blood primarily to their vertebral plexus of veins (Batson 1944), especially during expiration and forced expiration (Eckenhoff 1970). The vertebral plexus is a large valveless vascular network that extends from the cranium to the coccyx. It is composed of the external
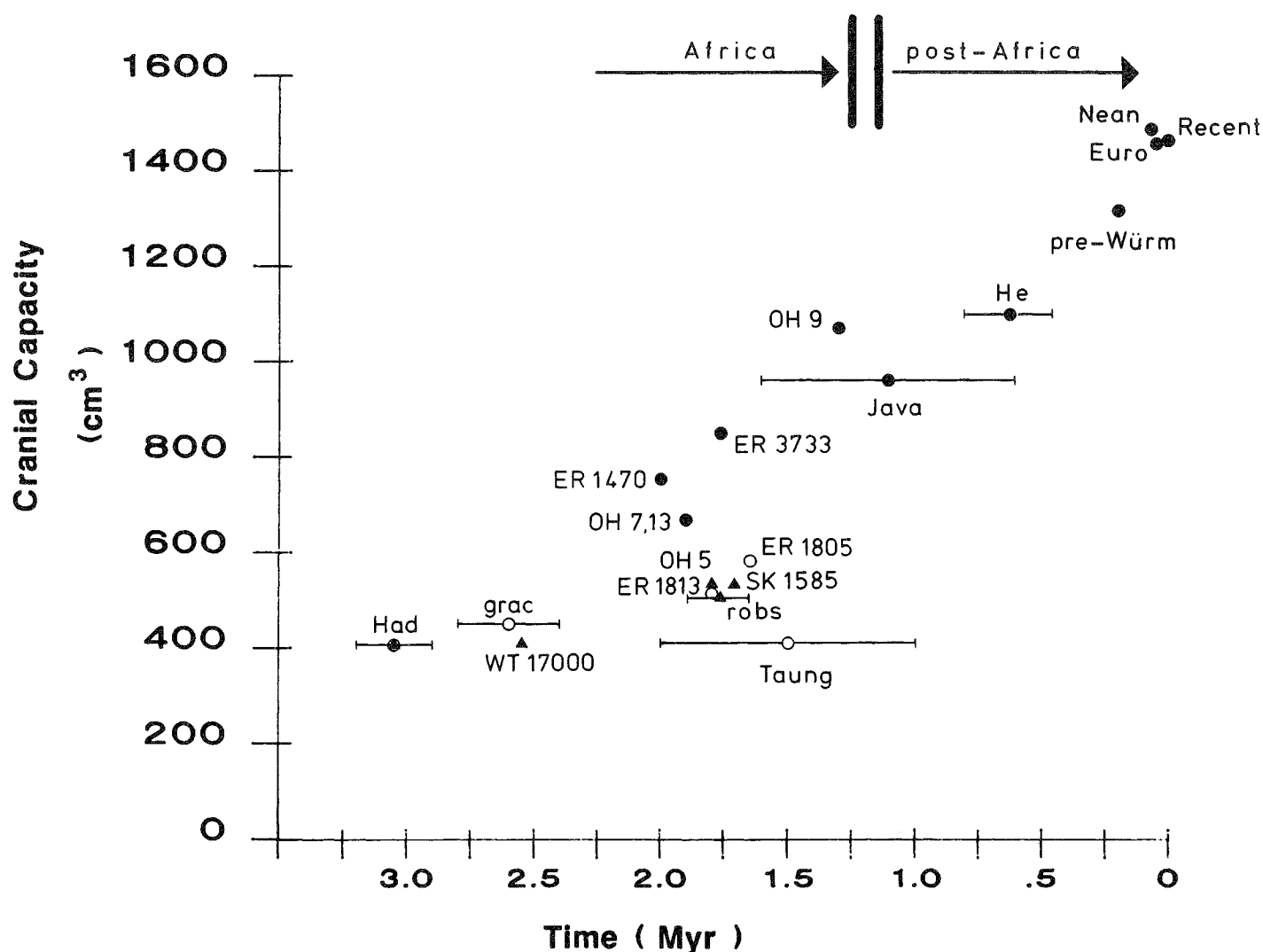
Figure 1. Mean cranial capacity plotted against time. Had, Hadar specimens; open circles & *grac*, gracile australopithecines; triangles & *robs*, robust australopithecines; filled circles, *Homo; Java*, Java *Homo erectus; He, Homo erectus; Nean*, Neanderthals. Horizontal bars indicate time ranges. Reproduced from Falk 1987b.

vertebral plexus, the internal venous plexus, and communicating veins, and it has connections with the dural sinuses and emissary veins. The finding that blood drains to the vertebral plexus in an upright posture is well documented and has important implications for patients undergoing surgery of the head and neck (Gius & Grier 1950). (For a more thorough review, see Falk & Conroy 1983.)

But what are the mechanisms that cause blood to drain to the vertebral plexus in upright humans? In order to approach this question, one must consider various factors (in addition to gravity) that contribute to the hemodynamics of different postures. For example, action of the heart produces viscous flow pressure to compensate for resistance to flow within the blood vessels themselves (Badeer 1985, Schmidt-Nielsen 1979). Viscous flow pressure drops from the aorta to the right atrium, and this fact is reflected in the relative thickness of the walls of arteries (thick) and veins (thin). In addition, since the veins have the lowest viscous flow pressure and are more compliant, gravitational pressure effects appear to be more pronounced in the venous than the arterial system (Badeer

1986, p. 210). Diversion of blood from the jugular vein to the vertebral plexus shifts the flow to a greater number of vessels that have smaller diameters. This acts to decrease the relative viscosity of blood (blood behaves as an anomalous fluid in this case, Schmidt-Nielsen 1979, p. 109) and facilitates its flow through capillaries.

Other factors contribute to the hemodynamics of upright posture. As noted above, blood flow fluctuates in jugular veins of upright humans in response to breathing (Eckenhoff 1970). Specifically, blood flows preferentially away from the jugular vein (and into the vertebral plexus) when intrathoracic pressure is elevated during expiration. On the other hand, during inspiration when intrathoracic pressure is low, blood flows through both jugular and vertebral systems. It should be noted, however, that there is much interest but little established information about the further effects of respiration on the venous system (Caro et al. 1978).

Other animals, such as arboreal snakes (Lillywhite 1987a; 1987b) and giraffes (Hargens et al. 1987; Pedley 1987), have a variety of adaptations that permit maintenance of blood circulation when their bodies are held

vertically. Arboreal snakes have hearts that occupy more anterior positions, special mechanisms for regulating arterial blood pressure, and specific movements that facilitate venous cardiac return and that prevent pooling of blood (Lillywhite 1987a; 1987b). Standing giraffes also have several features of the peripheral circulation that inhibit oedema. These include thick-walled arterioles, tight skin and fascia in the lower legs ("antigravity suits"), valves that prevent back-sloshing in long veins, and "muscle pumps" in the legs that squeeze blood up out of the lower veins (Hargens et al. 1987; Pedley 1987). The pressure gradient down the jugular vein of giraffes appears to be in the direction opposite to that expected for a standing column of blood. These "venous pressures are interesting and deserve further investigation" (Hargens et al. 1987, p. 60). Along these lines, it would be interesting to test the hypothesis that blood is shunted from the jugular system to a (more laterally dispersed) vertebral plexus of veins in upright giraffes.

Numerous factors must be taken into account in attempting to specify the mechanisms responsible for preferential flow of blood to the vertebral plexus in upright humans. The evidence regarding jugular vein pressures in giraffes offers insights that may be helpful for clarifying the situation in humans. A siphon model has been suggested to explain the circulation in the head and neck for both giraffes (Badeer 1986) and humans (Burton 1972; Eckenhoff 1970). This model depends partly on the premise that blood pressures in head vessels are theoretically subatmospheric. This would be the case if blood pressures were determined only by gravity, or if head veins were contained within rigid walls that could not collapse, as is the case for dural sinuses. However, as Pedley (1987) points out, the empirical evidence for giraffes (Hargens et al. 1987) shows that the 16 mm Hg blood pressure at the top of a giraffe's neck is far from the −100 mm Hg reading expected on the basis of gravity. Pedley therefore rejects the siphon model and suggests instead that the giraffe reading is due to viscous flow pressure in association with a collapsed jugular vein. In keeping with this, there has been at least one report (Goetz & Keen 1957) of a collapsed jugular vein in a standing giraffe.

What about the situation for upright humans? As is the case for giraffes, empirical evidence is hard to come by. One source (Ganong 1971) states that venous pressure in parts of the body above the heart is decreased by gravity, and that neck veins collapse above this point. However, the pressure along the collapsed segments is said to be zero instead of subatmospheric. Another widely cited text (Burton 1972) estimates venous pressure at the top of the head to be 39 mm Hg instead of the −44 mm Hg predicted by gravity alone. It is noteworthy that the latter example is similar to the case just discussed for the giraffe. Furthermore, as is the case for giraffes, the jugular vein of humans is often reported to be in a collapsed state (Pedley 1987). Alternate routes for cranial blood flow are provided by the vertebral plexus of veins in humans, but remain to be demonstrated in giraffes. In sum, it seems that viscous flow pressure *and* hydrostatic pressure (gravity) play important roles in the circulation of the head and neck of both giraffes and upright humans, and that other mechanisms such as "muscle pumps" and "antigravity suits" may come into play for humans as well as giraffes (Pedley 1987).

In monkeys that are lying down or in vertical positions with their heads held down, blood flows preferentially to their jugular systems; when they are standing with their heads held up, it flows to the vertebral plexus (Dilenge & Perey 1973; Epstein et al. 1970). Since the latter position is not the norm for monkeys, one must conclude that they rely a good deal more on their jugular systems in day-to-day activities than do humans. As put by Dilenge and Perey (1973, p. 336): "Indeed, since man is in the upright position most of the time, it is logical to think that it is the vertebral plexus rather than the internal jugular veins which is the major pathway of cerebral venous return in man."

In short, the hemodynamics associated with body posture in mammals are subject to various pressures, including gravity. Data for arboreal snakes and giraffes suggest that evolutionary changes in habitual posture are accompanied by adaptive changes in the circulatory system due to altered hydrostatic pressures. Humans are just as subject to gravity as other mammals, and the vertebral venous plexus is the major channel of cerebral venous drainage in upright (but not supine) humans. Since this is not the case for semiterrestrial nonhuman primates (including apes – see below), and since posture is of key importance for blood flow, it is reasonable to speculate that the shift in emphasis from the jugular vein to the vertebral plexus to drain blood from the cranium in upright humans originated with selection for bipedalism in early hominids (Falk 1988).

3.1. Venous sinuses and veins in the hominid fossil record

Fossilized cranial remains may be studied in an effort to determine the routes by which blood was channeled from the cranium to the vertebral plexus of veins (Falk & Conroy 1983). Such studies have revealed two different strategies for delivering cranial blood (Falk 1986a; Falk 1988), each of which characterized different groups of fossil hominids. On the one hand, an unusual enlarged occipital/marginal (O/M) sinus system was present in robust australopithecines (*Paranthropus* or *Australopithecus robustus*, *Australopithecus boisei*) and the early hominids from Hadar, Ethiopia (*Australopithecus afarensis*). On the other hand, representatives of a developing network of small veins can be traced forward from gracile australopithecines (*Australopithecus africanus*) to modern *Homo sapiens*.

3.1.1. Robust australopithecines and the Hadar early hominids. Tobias (1967; 1968) was the first to describe an interesting variation of the cranial venous sinus system that characterizes robust australopithecines, and Holloway (1981a) first noted that such a configuration is also present in the Hadar fossil material attributed to the earliest known hominids, *Australopithecus afarensis* ("Lucy"). Both groups of hominids possessed an enlarged occipital/marginal (O/M) sinus system that either supplemented or replaced the transverse sinuses that connect with the sigmoid sinuses in most hominids and pongids (Figure 2). Normally, living people have very small occipital/marginal sinuses that do not leave marks on the inside of the crania. For example, Tobias (1967) showed that only 6% of 211 modern people had enlarged O/M sinuses, while less than 2% had sinuses that were as

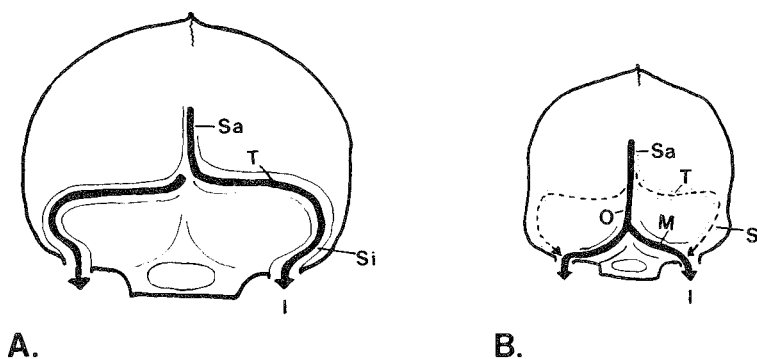**A.**   **B.**

Figure 2.   Occipital views of typical cranial venous sinus systems in modern humans (A) and fossil robust australopithecines and the Hadar early hominids (B). In A, blood flows from the superior sagittal sinus (and the straight sinus within) to the transverse-sigmoid sinuses and then exits the cranium via the internal jugular veins. The transverse-sigmoid system is reduced or missing in B, in which a large portion of blood is drained through the occipital/marginal sinus system to the vertebral plexus of veins that is near the foramen magnum. As illustrated, the O/M sinus can also deliver blood to the internal jugular vein depending on postural and respiratory constraints (see text). Abbreviations: I, internal jugular vein; M, marginal sinus; O, occipital sinus; Sa, superior sagittal sinus; Si, sigmoid sinus; T, transverse sinus. Reproduced from Falk & Conroy 1983.

dramatically enlarged as those of early hominids. Thus, more blood appears to have been channeled through the O/M sinus system in the Hadar hominids and robust australopithecines than is the case for extant humans.

Blood that exits the cranium through the O/M sinus system is distributed differently from that which takes the transverse/sigmoid route. In a dissection of 100 human cadavers, Browning (1953) found that nine had appreciable O/M sinus systems. The O/M sinus delivered blood exclusively to the jugular bulb in only two of the nine specimens; in three cadavers, the sinus delivered blood to the jugular bulb and to the vertebral plexus of veins that is associated with the spinal column. In the remaining four specimens, the O/M sinuses connected only with the vertebral plexus. Thus, in the majority of humans with enlarged O/M sinus systems, blood is drained to the vertebral plexus of veins instead of, or in addition to, being delivered to the internal jugular system. Therefore, in keeping with the literature (Batson, 1944; Das & Hasan 1970; Gray 1973; Padget 1957) and contrary to Kimbel (1984), one must reject the notion that the O/M and transverse/sigmoid sinus systems are functionally equivalent.

An enlarged O/M sinus system appears to be fixed in the australopithecine species under discussion, that is, it occurs in *all* scorable specimens (6/6 *A. afarensis* specimens from Hadar and 7/7 robust australopithecines; Falk & Conroy 1983; Falk 1986a; Tobias and Falk 1988). (For reasons detailed elsewhere [Tobias & Falk 1988], to demonstrate the lack of an enlarged O/M sinus in a fossil hominid one needs an occipital fragment that is in good (uneroded) condition and that includes the internal occipital protuberance, internal occipital crest, and both sides of the foramen magnum.) On the other hand, O/M sinuses occur in only 20% (1/5) of the scorable specimens representing another early contemporary species, the South African gracile australopithecines (Tobias & Falk 1988). (A sixth gracile australopithecine has recently been

scored as lacking an enlarged O/M sinus system [Conroy et al. 1990]. The frequency for O/M sinuses in South African gracile australopithecines is now ⅙ or 17%.) These are remarkable facts that led, in part, to the conclusion that: "*A. afarensis* was directly ancestral to, or shared a common ancestor with, robust australopithecines." (Falk & Conroy 1983, p. 779) It is noteworthy that Olson (1981) reached a similar conclusion for totally different reasons. Despite the controversial nature of hominid systematics (Clark 1988; Eckhardt 1986; Falk 1986b), it seems reasonable to speculate that selection for bipedalism in the common ancestor of the Hadar fossil hominids and robust australopithecines resulted in adaptations for delivering blood to the vertebral plexus of veins that included fixation of an enlarged O/M sinus system (Falk & Conroy 1983).

3.1.2. The gracile australopithecine through *Homo sapiens* lineage. Since *Homo sapiens* is bipedal and lacks fixation of an enlarged O/M sinus system, there must be another mechanism for delivering blood to the vertebral plexus of veins when humans are awake and upright. As it turns out, this function is accomplished in extant humans by a widespread network of small veins, including multiple connections with the small occipital/marginal sinus (Padget 1957), the basilar plexus of veins, the rete canalis hypoglossi, and the occipital vein (Gray 1973). The vertebral plexus of veins in humans also receives contributions from the posterior condyloid, mastoid, occipital, and parietal emissary veins (Gray 1973; see Figure 3). The contributions of these cranial emissary veins to the vertebral plexus are well known (Gius & Grier 1950; Eckenhoff 1970), and of extreme importance for the present study because emissary veins pass through foramina of the skull and their presence can therefore be investigated in the hominid fossil record.

An earlier *comparative* study by Boyd (1930) suggests that a network of emissary veins was selected for during
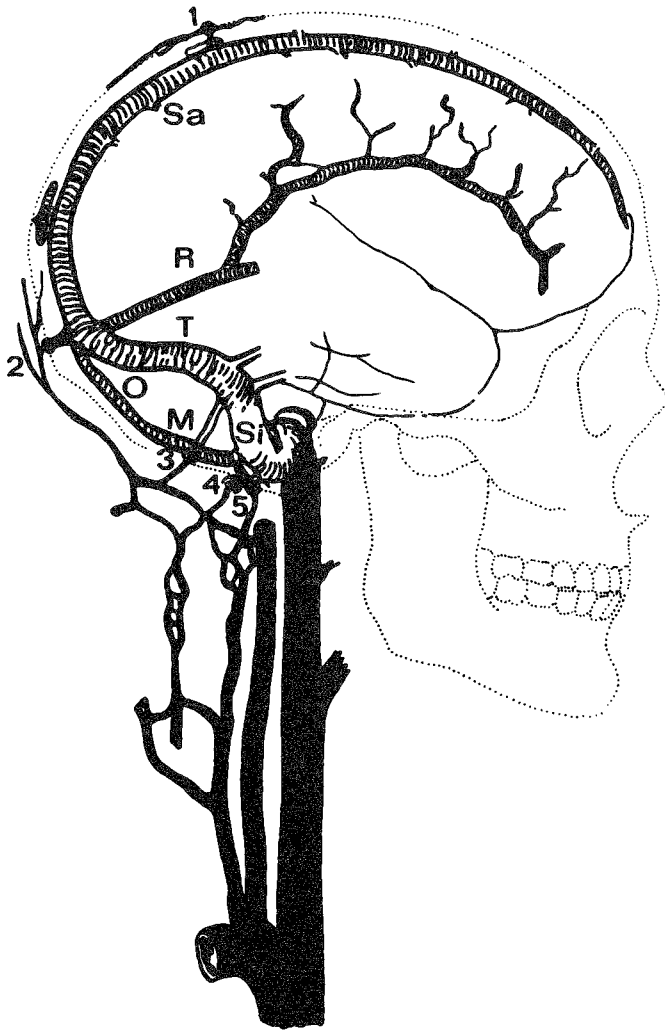
Figure 3. Venous sinuses and emissary foramina. Abbreviations for sinuses: R, rectus; others as in Figure 2. Emissary foramina: 1, parietal; 2, occipital; 3, mastoid; 4, posterior condyloid; 5, hypoglossal. Emissary veins transversing these foramina communicate with the vertebral plexus of veins. After Gray 1973.

hominid evolution. Specifically, Boyd found that the frequencies of parietal, mastoid, and condyloid foramina were much higher in humans than in gorillas or chimpanzees. Boyd's (1930) findings provide further incentive for applying the second method available to paleontologists, the direct method, to the question of the origin of emissary veins, i.e., examining frequencies of emissary foramina in the hominid fossil record itself.

In 1984 I was able to undertake such a study and to confirm Boyd's findings (Falk 1986a). Although sample sizes for various species of fossil hominids are small, as one moves forward in the hominid record the data show marked increases in the frequencies of both mastoid and (later) parietal foramina (Falk 1986a). Figure 4 summarizes these results and includes data for an enlarged O/M sinus. (See Falk 1986a and Tobias & Falk 1988 for a discussion of other foramina and a more thorough analysis).

It is important to emphasize that Figure 4 reveals information about only the *osteological* indications of cranial blood routes and not the routes themselves (which

have long since perished). Furthermore, information is provided for only two emissary foramina that represent a much wider system of emissary veins (Cabanac 1986). Thus, the trend for mastoid and parietal foramina and the trend for an enlarged O/M sinus system merely provide glimpses of the development of cranial venous circulation during hominid evolution. (This is discussed in more detail in section 4.1.2.) Although all hominids were bipedal, Figure 4 reveals that the circulatory systems of different groups became adapted to bipedalism in two distinct ways.

3.1.3. Two types of hominids/two ways to drain blood.
Because of the changed gravitational forces associated with the reoriented columns of fluid (blood) discussed above, selection for habitual bipedalism in hominids *had* to be accompanied by changes in their circulatory systems. As Figure 4 summarizes, different pathways for delivering blood to the vertebral plexus of veins were selected in different species of hominids. In keeping with the facts that African apes are not habitually bipedal and that they normally do not hold their heads and necks completely upright even when their bodies appear to be vertical (Goodall 1986; Dilenge & Perey 1973), the frequencies for an enlarged O/M sinus, as well as for parietal and mastoid foramina appear to be low, i.e., below 25%. This may be taken as the ancestral, or primitive, condition for hominoids.

Robust australopithecines and the Hadar early hominids, however, are characterized by fixation of an enlarged O/M sinus system. The frequencies of parietal and mastoid foramina are low for robust australopithecines, i.e. near those of apes. (The Hadar specimens have not been scored for emissary foramina; see Figure 4).

Still another condition characterizes the lineage leading from gracile australopithecines to extant *Homo sapiens*. The frequency of O/M fluctuates around that for apes and appears to decline through time (although it should be noted that Figure 4 smooths data that are presented in more detail in Falk 1986a). The reverse is true for the mastoid and parietal foramina, i.e., their frequencies increase through time, as expected from the comparative data from larger samples of *Homo sapiens* and African apes (Boyd 1930; Falk 1986a). It appears, then, that the circulatory systems of the Hadar-robust and gracile-*Homo* lineages were modified differently in conjunction with selection for and refinement of bipedalism. Elsewhere (see section 5, Falk 1988), I have discussed the systematic implications of these data. What is important for the present discussion is the conclusion that a network of emissary veins was selected for in conjunction with bipedalism *only* in the lineage leading to and including *Homo*. That is a key to brain evolution in our genus!

4. Evolution of the radiator

4.1. Human brains are heat sensitive
Brains are extremely active metabolically and produce excessive heat. They are also heat sensitive organs (Cabanac 1986). Nevertheless, when an animal exercises, the temperature within the cranium is kept cooler than that of the body (Baker 1979; Caputa 1981). Many animals (numerous carnivores and ungulates) are able to sustain
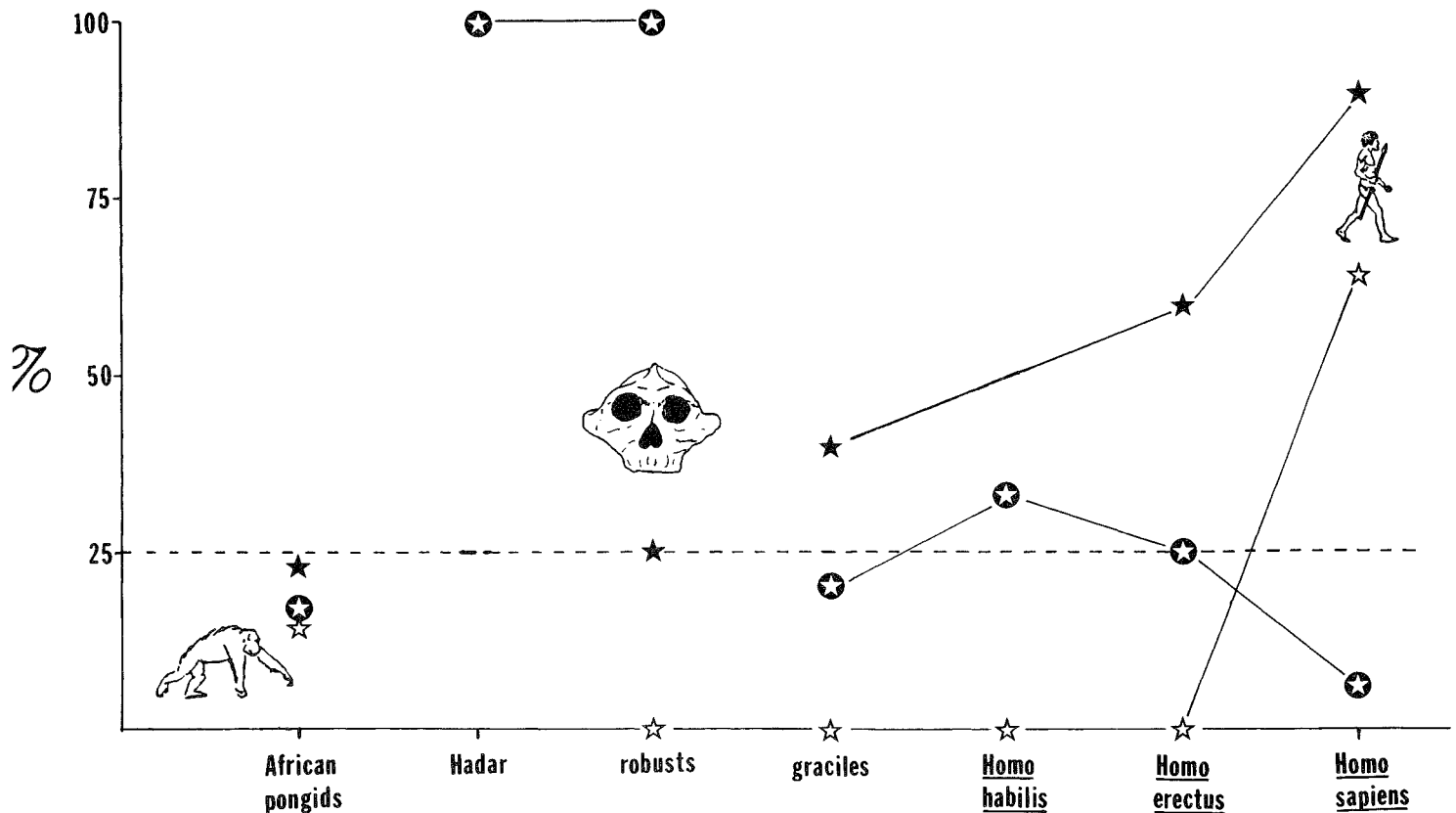
Figure 4. Frequencies of emissary veins versus enlarged O/M sinuses, data from Falk 1986a and Tobias & Falk 1988. Solid stars, mastoid foramina; open stars, parietal foramina; stars within circles, enlarged O/M sinuses. The Hadar and robust australopithecines and the gracile australopithecine through *Homo* lineage have different systems for draining blood from the cranium. In the former, an enlarged O/M sinus has been selected for and fixed whereas emissary foramina of robust australopithecines occur in frequencies approximating (or less than) those of apes. The reverse situation is approached for the latter lineage, i.e. frequencies for O/M fluctuate around those for apes, and high frequencies of emissary foramina are selected for over time. Mastoid and parietal emissary veins are representatives of a wider system of innumerable tiny emissary veins that join the subcutaneous veins outside the skull to the inside of the cranium (Cabanac 1987, and see text). Besides draining blood to the vertebral plexus, the latter arrangement has the added benefit of providing a means for cooling the brain under conditions of hyperthermia (see text). Modified after Falk 1988.

acceptably cool brain temperatures during exercise because they possess an arterial network known as *the rete mirabile*, or wonderful net. Arterial blood within this network is cooled as it flows to the brain because the rete loses heat to the relatively cooler venous blood that surrounds it in the cavernous sinus at the base of the brain. Thus, the rete acts as a "countercurrent heat-exchange network" in various mammals including dogs, sheep, cats, lambs, oxen, wolves, and hyenas (Baker 1979). On the other hand, numerous animals, including human and nonhuman primates, do not have retes, and it seems reasonable to assume that humans inherited their lack of a rete from their primate ancestors.

Human brains are particularly sensitive to abnormally high temperatures:

A rise of only four or five degrees C. above normal begins to disturb brain functions. For example, high fevers in children are sometimes accompanied by convulsions; these are manifestations of the abnormal functioning of the nerve cells of the overheated brain. Indeed, it may be that the temperature of the brain is the single most important factor limiting the survival of man and other animals in hot environments. (Baker 1979, p. 136)

Brain temperature in humans (Brinnel et al. 1987; Caputa 1981) and rhesus monkeys (Baker 1979; 1982; Hayward & Baker 1968) is determined by a number of factors, including the temperature of arterial blood supplying the brain, rate of blood flow, and rate of metabolic heat production by the brain. As discussed below (section 4.1.2), the temperature of the base and surface of the brain can also "be influenced by direct heat exchange through the scalp or through the base of the skull" (Baker 1982). In general, arterial blood is cooler than the brain it supplies. As arterial blood circulates, it removes heat from the brain. Thus, venous blood leaving the brain is warmer than the arterial blood supplying it.

The relatively great cooling needs of human brains have been attributed to at least two characteristics that developed during hominid evolution: First, brains of *bigger bodied* mammals such as humans are particularly susceptible to hyperthermia because the ratio of cerebral to resting metabolic unitary rates (per units of body mass) increases with body size (Caputa 1981). For example, the ratio is 2.6 for mice, 8.5 for dogs, and 21.4 for elephants (ibid.). Furthermore (continuing along allometric lines), human brains are relatively larger than those of other animals, including nonhuman primates, and this charac-

teristic is itself associated with greater cooling needs (Cabanac & Brinnel 1985).

Second, heavy exercise (Bortz 1985; Caputa 1981; Taylor 1974) as well as high environmental temperature (Wheeler 1984; 1985; 1988; Zihlman & Cohn 1986; 1988) present threats of overheating. Humans tolerate sustained exercise, such as running, as well as or better than other animals, including many predators (Bortz 1985). It is interesting that human tolerance for sustained running has been attributed to selection for persistence hunting in early hominids living in hot environments (Bortz 1985; Carrier 1984; Fialkowski 1986). Because humans have more stamina for exercise than many mammalian cursors, they must be able to dissipate metabolic heat for longer durations (Carrier 1984). (The role of environmental temperature and exercise is discussed further in section 5.1.)

4.1.1. The cerebral cortex may be at greater thermal risk than the brain's interior. A recent debate about selective brain cooling in exercising humans (see below) has focused on *deep* brain temperatures and the question of whether or not the tympanum is an accurate reflector of this temperature (Cabanac 1986; 1987; Nadel 1987; Shiraki et al. 1988). In both monkeys (Hayward & Baker 1968) and humans (Aschoff et al. 1971 cited in Brinnel et al. 1987), *deeper* regions of the brain measure approximately 0.5°C. higher than aortic arterial blood. In keeping with this, esophageal temperature (thought to be a good indicator of aortic blood temperature) was reported to be 0.5°C. below temperature in the lateral ventricle and 0.7°C. below the temperature in white matter directly above the ventricle in an unanesthetized human (Shiraki et al. 1988). On the other hand, *superficial* regions of the cerebral hemispheres of monkeys (Hayward & Baker 1968) measured only 0.1°C. warmer than the arterial blood, i.e., hemispheres of monkeys are coolest in their exteriors and warmer towards their centers. The subcutaneous scalp of monkeys is cooler still, measuring −0.45°C. cooler than arterial blood (ibid.) Consistent with this, temperature of the frontal dura mater in one human patient measured 1.0°C. below that of the esophagus (Brinnel et al. 1987).

These facts suggest that the human brain is likely to have a temperature gradient similar to that of the monkey's brain. Thus, it is reasonable to hypothesize that the human cerebral cortex is maintained at a slightly lower temperature than the hemisphere's interior. If so, the cerebral cortex, rather than the interior of the brain, should be more susceptible to damage from increased temperature of arterial blood caused by hyperthermia. Brinnel et al. (1987) show that temperature of the tympanum may be the best indicator to date of the responses of brain structures at greatest thermal risk, i.e., superficial structures such as the cerebral cortex or dura mater, to changes in environmental temperature.

4.1.2. Cabanac's physiological research: A cooler for the brain. Cabanac & Brinnel (1985) have independently described a cooling mechanism for human brains on the basis of physiological studies on the same two emissary veins (the parietal and mastoid) that were studied in the hominid fossil record and depicted in Figure 4. Specifically, the direction of blood flow in these valveless veins was recorded in human subjects during conditions of

hypothermia on the one hand, and exercise-induced hyperthermia, on the other. During hypothermia, the blood in these veins either did not flow or flowed slowly from the brain out to the surface of the skull. During hyperthermia however, the blood flowed rapidly from the skin of the head into the cranial cavity. Thus, under conditions of exercise-induced heat stress, the parietal and mastoid emissary veins serve to deliver blood that has been cooled by vasodilation in conjunction with evaporation of sweat from the scalp *into* the braincase. Along these lines, it is noteworthy that humans have the greatest sweating capacity for a given surface area of any known animal (Cabanac et al. 1984; Newman 1970) and that the density of sweat glands on the forehead is three times that of the rest of the body (Cabanac 1987). During hyperthermia, blood also flows inward in the ophthalmic vein that drains blood from the forehead (Cabanac 1986; Caputa et al. 1978) and these three emissary veins together provide a glimpse into a larger system that cools the human brain:

> . . . innumerable anastomoses join the rich subcutaneous venous plexus of the cephalic head to the intracranial sinuses. Most of these emissary veins are microscopic, but some are quite visible and constant. . . . Since, during hyperthermia, blood flows inward in three big emissary veins located at three widely separated loci of the head, it is likely that this process takes place in all the vasodilated skin of the head and that the innumerable emissary veins collect blood from the skin to send it inward through the calvaria. (Cabanac 1986, p. 42)

In short, Cabanac's team has described a radiator for cooling the human brain. As shown above, the parietal and mastoid emissary veins that "represent" this radiator increased in frequency during the course of evolution in the lineage leading from gracile australopithecines to *Homo sapiens*, but not in the robust australopithecines. Thus, the network of emissary veins had dual functions in the lineage in which it was developed: (1) to deliver blood to the vertebral plexus of veins as required by the constraints of gravity on a biped, and (2) to cool the brain under conditions of hyperthermia. Furthermore, brain size increased dramatically in the lineage that developed the radiator but remained conservative in those early hominids that did not (i.e., those with a fixed enlarged O/M sinus system). See Figure 1.

Cabanac's work provides insight into the perplexing question of why bipedalism preceded the dramatic increase in brain size in *Homo* by at least 1.5 million years (so-called mosaic evolution). Figure 5 plots the increase in brain size (as a percentage of the modern mean value of 1400 cm³) with the frequencies of emissary and parietal foramina provided in Figure 4. These data strongly suggest that elaboration of the radiator network of veins took place during the increase in brain size that occurred in our lineage.

If basal gracile australopithecines occupied a savanna niche with a good deal of heat stress as many have argued (Bortz 1985; Carrier 1984; Zihlman & Cohn 1986; and see section 5.1.), one can easily see the selective value of the dual function radiator. To wit, it delivers blood where it has to go in a biped (to the vertebral plexus) and also serves to cool the brain under conditions of hyperthermia. Figure 5 suggests that the radiator released a thermal constraint that limited brain size in other hominids. That is, as the
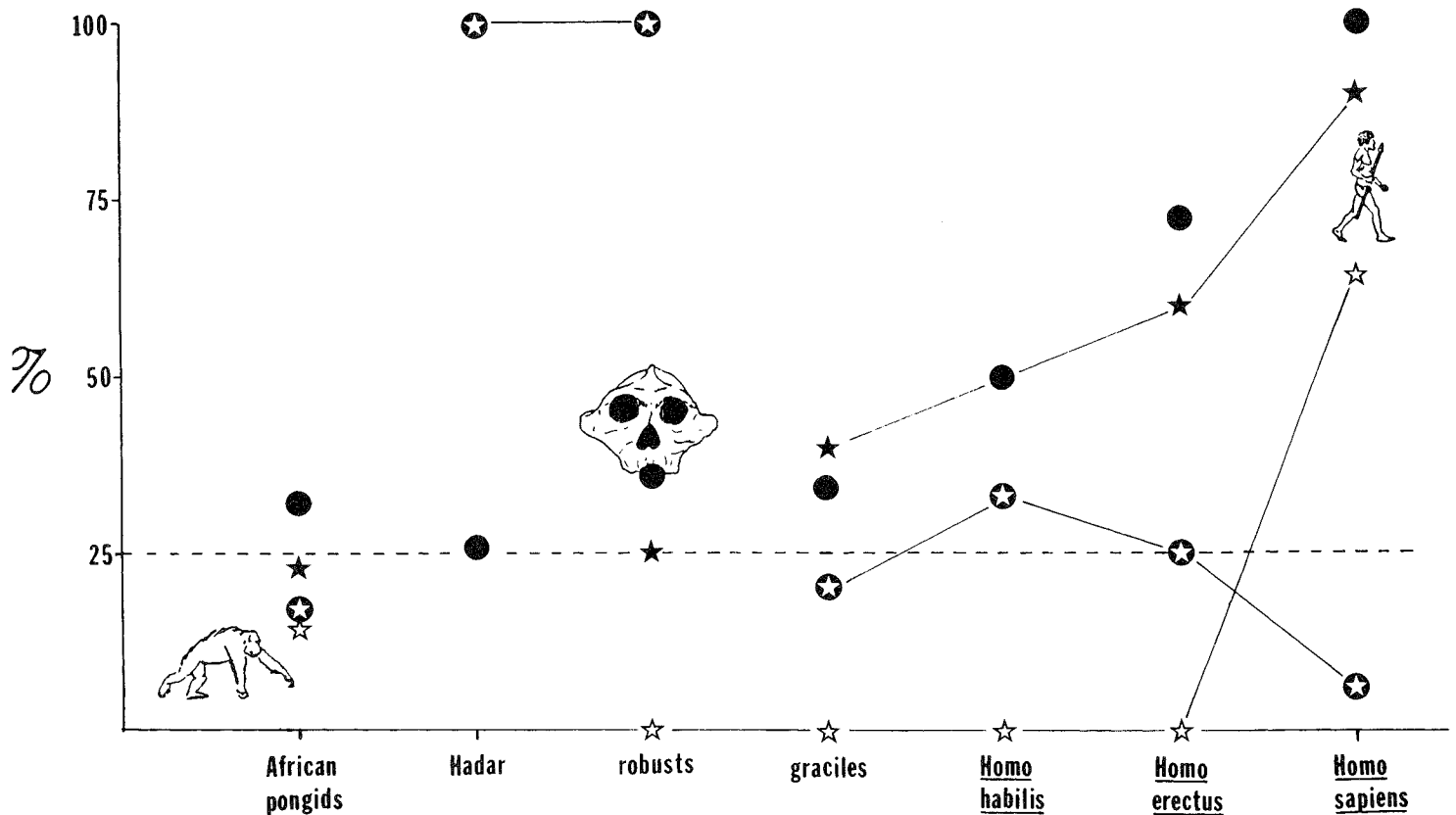
Figure 5. Mean cranial capacity (filled circles) as a percentage of the average capacity for extant *H. sapiens*, plotted against Fig. 4. Hominid cranial capacities from Falk (1987b); estimates for Hadar are based on AL 162-28 and AL 333-105. Pongid capacities are from Tobias (1971). Notice that both brain size and frequencies of emissary foramina increase from gracile australopithecines through *Homo*. Selection for the radiator of *all* emissary veins (not just their mastoid and parietal representatives) appears to have released a thermal constraint that limited brain size in other hominids and pongids. See text for discussion.

network of veins became more complex during hominid evolution, it became a better cooler and selection for brain size was thus facilitated. (To quote my mechanic, "the engine can only be as big as *that* can cool.")

4.1.3. Fialkowski's heat stress hypothesis. Drawing from the computer sciences, Fialkowski (1978; 1986) earlier suggested that increased brain size during hominid evolution provided structural redundancy that prevented cognitive impairment due to heat stress:

> My hypothesis . . . is that the increase in size and complexity of the hominid brain (at any rate, the early stage of the process) was largely a side effect of an evolutionary response to considerably increased heat stress under conditions of primitive hunting. This hypothesis is based on certain physiological data and on von Neumann's mathematical demonstration that the reliability of a complex system can be maintained in spite of a decrease of reliability of its elements provided that the number of elements and of their interconnections is increased. (Fialkowski 1986, p. 288)

The radiator theory presented here agrees with Fialkowski's basic premise that increased brain size was a byproduct of thermoregulatory factors. Although the two theories differ in the details of how heat stress interacted with the evolving brain, both views are mechanistic and should be viewed as complementary.

5. Systematic implications of the radiator theory

Figure 6 presents an evolutionary model (based on a cactus) that incorporates the evidence regarding cranial blood flow. It is much simpler than other models that are currently favored by paleontologists and, in fact, is compatible with the theory that John Robinson developed several decades ago (Robinson 1963). The major split at the base of the cactus is between basal robust australopithecines (on the right) and basal gracile australopithecines. As discussed above, *all* scorable specimens representing the righthand stem are characterized by enlarged occipital/marginal venous sinuses. Thus, at least those Hadar specimens that could be scored for this trait appear to be ancestral robust australopithecines. (It should be noted, however, that some workers have suggested on the basis of postcrania that the Hadar specimens may contain more than one species. See Falk [1988] and Tuttle [1988] for discussions.) The 1986 discovery of a robust australopithecine dated at 2.5 million years ago from Kenya (WT 17000: Walker et al. 1986) is compatible with this interpretation, since this fossil is viewed by many as a possible intermediary between the Hadar specimens and other more recent East African robust australopithecines, such as ER 406.

One scorable cranial fragment from Laetoli (a site in Tanzania that is represented by footprints in Figure 6)
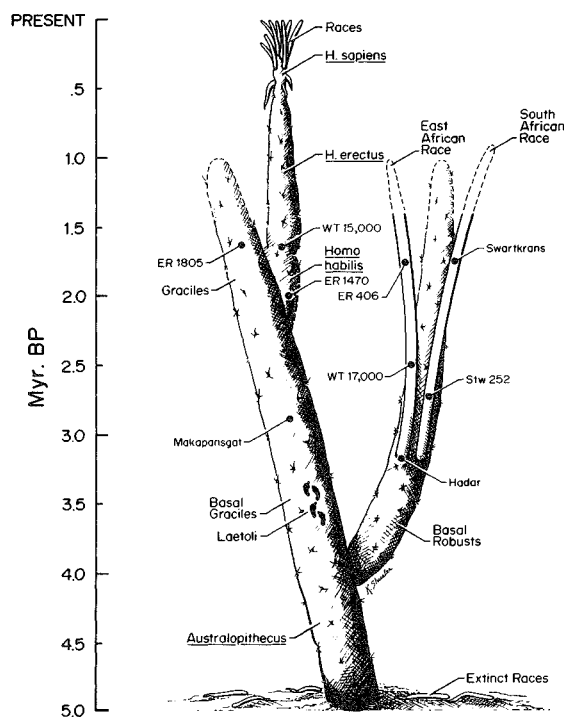
Figure 6. A phylogenetic cactus that summarizes the author's view of hominid evolution. Modeled after the "Old Man" cactus (*Opuntia vestita*). The left side of the cactus represents gracile australopithecines from Laetoli forward to ER 1805 (with Makapansgat representing *Australopithecus africanus*). The genus *Homo* branches from the gracile side of the cactus. ER 1470 is the oldest *Homo habilis* and WT 15000 is the oldest *Homo erectus* shown on this stem. The right side of the cactus contains only robust australopithecines (called *Paranthropus* by some paleontologists). It should be noted that the placement of Hadar on this cactus is controversial, as is the separation of Laetoli and Hadar populations. Some workers would place ER 1805 on the *Homo* branch (but see Falk 1983), and others might not agree that Stw 252 belongs on the robust branch (but see Clarke 1988). See text for discussion. (Reproduced from Falk 1988.)

lacks an enlarged O/M sinus (Kimbel 1984) and this is compatible with other evidence that separates the Laetoli from the Hadar specimens (Tuttle 1985; 1987; 1988 and see Falk 1988 for further discussion.) At the top left, the genus *Homo* can be seen peeking around the gracile stem from which it branches at some as yet unknown point prior to 2.0 million years. As noted earlier, both brain size and the network of radiator veins increased dramatically in this stem of the cactus.

Robinson was the first to realize that the numerous australopithecine fossils from South Africa that were believed to represent many species separated into just two groups, robust (*Paranthropus robustus*) and gracile australopithecines (*Australopithecus africanus*), and it was he who formulated the famous "dietary hypothesis." Specifically, robust australopithecines were characterized by enormous back teeth and huge, flat faces that provided anchorage for massive chewing muscles. Still other chewing muscles were anchored on a sagittal crest on top of the skull. Since markings on the skulls for neck muscles indicated erect posture, it appeared to Robinson that *P. robustus* was essentially a bipedal chewing ma-

chine – and one that used its enormous molars to crush and grind tough roots, bulbs, and other gritty vegetable matter. As strict vegetarians, these early hominids had lost the large front teeth for tearing meat or processing nonvegetable foods. Robinson believed that robust australopithecines had relatively smaller brains than gracile australopithecines (but this is now problematical, see Falk 1988), and that they were probably incapable of sophisticated tool use compared to the latter species.

According to Robinson, gracile australopithecines had larger anterior teeth and much smaller molars than robust australopithecines. The upper face and cheeks were also less massive in the region where chewing muscles that operate the back of the jaw attach, and this combination of features resulted in faces that were "dish-shaped" rather than flat. Gracile australopithecines lacked sagittal crests; their skulls appeared to have higher foreheads and to be more rounded than skulls of robust australopithecines. Robinson believed that gracile australopithecines were slighter in body build and this contributed to his thinking that they were bigger brained relative to body size than their robust contemporaries.

In short, Robinson placed gracile australopithecines in a completely different niche from robust australopithecines. They lived in more open regions that were drier and therefore less conducive to the growth of plant foods than were the moist forest regions that *Paranthropus* preferred. Gracile australopithecines retained the large anterior dentition of their ancestors that was useful for processing all kinds of food, including meat, and Robinson believed that tool-use in conjunction with obtaining meat was at a premium in this species. He also thought that intelligence was selected for in gracile australopithecines and that they alone eventually gave rise to *Homo*.

Australopithecines have now been found in East as well as South Africa, and many of Robinson's ideas are supported by recent evidence. Today's literature reaffirms the herbivore/omnivore dichotomy between robust and gracile australopithecines (Brain 1988; Grine & Kay 1988). New evidence supports Robinson's belief that robust australopithecines seem to have evolved in moist forest environments. For instance, Shipman and Harris (1988) have shown that the early robust australopithecines from East Africa were usually associated with closed/wetter habitats than contemporaneous nonrobust hominids. Lucy's curved finger and toe bones also suggest that the Hadar fossil hominids spent a good deal of time in forested habitats (Stern & Susman 1983). It should be further noted that although the evidence on relative brain size for the two groups of hominids is inconclusive because of lack of reliable information about body sizes (Falk 1988), brain size apparently remained conservative throughout evolution in both groups of australopithecines but eventually "took off" only in descendants of gracile australopithecines, i.e., in *Homo* (Figure 1). (This is true despite recent interesting speculation, based on finger bones from Swartkrans, about the possible tool-making abilities of robust australopithecines; Susman 1988.)

5.1. The radiator theory meets the savanna hypothesis

The idea that our earliest hominid ancestors abandoned forests and woodlands and refined bipedalism on the African savanna has had a long history. Several workers

have stressed the importance of persistence hunting (that is, running down animals during the heat of the day) and have suggested that it was a major advantage of bipedalism in savanna habitats as well as *the* prime mover of hominid evolution and/or brain evolution (Bortz 1985; Carrier 1984; Fialkowski 1978; 1986; Krantz 1968). Most of these authors state that persistence hunting in early hominids would have necessitated the development of thermoregulatory mechanisms for dissipating metabolic heat, usually citing sweating and hairlessness as examples. The problem with these, as with other prime mover theories (Falk 1980a), is that they implicitly put too much stress on one sex (males). As Zihlman puts it (personal communication):

> It is the activity level that is important and hunting isn't the only behavior to suggest high activity. In fact, hunting is mostly a male activity and reinforces the bias on passive women. What about their locomotion? They were out . . . gathering food, carrying, etc., any kind of vigorous work will cause individuals to overheat.

Although hunting may be overemphasized in the contemporary literature, the wider notion that important thermoregulatory adaptations occurred in early hominids that occupied savanna mosaic habitats appears sound. As discussed above, the radiator network of veins apparently began evolving in ancestral gracile australopithecines that were living under savanna mosaic habitats comprised of "patches" ranging from gallery forests to open grasslands. Presumably both sexes spent a good deal of time exploiting the scattered resources of open African grasslands that were subject to hot temperatures and intense radiation during the day (Zihlman & Cohn 1986). Sustained exercise under such conditions would have created thermal stress for early hominids; Wheeler (1984; 1985; 1988) and Zihlman and Cohn (1986) have argued convincingly that functioning eccrine sweat glands, reduced body hair, and dark skin evolved as a functional complex in response to living on the African savanna. What better addition to this complex than a radiator network of veins that both cools the most heat sensitive part of the body (the brain) and simultaneously provides new drainage routes required by the pressures of gravity on a reoriented (because of bipedalism) vascular system?

5.1.1. Wheeler's physiological hypothesis. Wheeler (1984; 1985; 1988) offers an important theory that accounts for the development of bipedalism in early hominids. Unlike many efforts to explain bipedalism, Wheeler focuses on physiological factors associated with thermoregulation in hot savanna habitats. His ideas provide relevant information about the early part of the hominid scenario and fit well with the later scenario described by the radiator theory.

According to Wheeler, protohominids that foraged for food during the heat of the day risked overheating because they lacked carotid retes. When it is hot, quadrupedal savanna mammals seek shade and thus reduce their heat loads. Early hominids that foraged in patchy habitats, however, were already semi-erect (i.e., preadapted for bipedalism, possibly because of a brachiating ancestry) and were therefore able to reduce heat loads by postural means – namely, bipedalism (Wheeler 1984 p. 94): ". . . when the sun is overhead, an upright hominid presents only about 40% of the area that it would if it was

in a quadrupedal position. A biped therefore experiences a much lower radiant heat load throughout the most stressing period of the equatorial day. . . ." Thus, postural changes allowed early hominids to open a noon-day scavenging niche (Blumenschine 1986; 1987) while other scavengers rested. Put another way, early hominids created their own shade (so to speak) and were able to eat too.

Most savanna mammals have pelages that protect the skin from direct solar radiation. However, body hair also restricts air flow over the skin and therefore inhibits cooling by evaporation. Wheeler suggests that once bipedalism was achieved, hair reduced on body surfaces that were no longer exposed to direct solar radiation from the sun at its zenith. Only the head and shoulders continued to be at risk, and these areas remained protected by hair. (According to Cabanac & Brinnel 1988, baldness in extant males appears to be a thermoregulatory adaptation.) A naked skin and associated cutaneous sweat glands (Wheeler 1985) allowed increased evaporation and therefore whole-body cooling. According to Wheeler, such whole-body cooling released a physiological constraint on brain size and thereby made the subsequent increase in brain size in *Homo* possible. Add to this the changes in the vascular system of the head and neck that were initiated by changed hydrostatic pressures associated with reorientation of posture, and you've got the radiator theory! In other words, it's not just lower-body sweating, cooling the arterial blood supplying the brain, that is responsible for "keeping a cool head" (Cabanac 1986). Heads sweat, too. Indeed, they sweat profusely, as anyone who participates in serious jogging or aerobics (or manufactures headbands) will attest. The brain has its own network of veins that reverses the direction of blood flow under conditions of hyperthermia and brings cooled blood into the cranium (ibid.). Just like my car, the brain has a radiator.

5.2. The radiator released constraints on brain size

The *combination* of thermal stress associated with a savanna mosaic environment (Wheeler 1984; 1985; 1988) and changed hydrostatic vascular pressures associated with bipedalism triggered multiple thermoregulatory adaptations in gracile australopithecines, including selection for the radiator network of veins. Furthermore, frequencies of parietal and mastoid emissary foramina (Figure 4) show that the elaboration of the radiator network of veins continued throughout most of the evolution of *Homo*, even after this genus radiated out of African savanna habitats to other environments. Indeed, Figure 5 suggests that brain size increased with continued elaboration of the radiator. It therefore seems plausible to speculate that during the early development of the network of radiator veins, thermal constraints that had previously kept brain size in check in hominids were released. Subsequently, the brain "took off" in *Homo,* so much so that today it is three times the size one would expect for a nonhuman primate of equivalent body size (Falk 1980a).

The only other group of mammals whose relative brain size approximates our own (after allometry has been accounted for) are the cetaceans, or sea mammals (Jerison 1973; 1978). During their evolution, ancestral cetaceans went through a major change of habitat that presumably

impinged on thermal and gravitational conditions, i.e., they shifted from terrestrial to aquatic environments. Although it is beyond the scope of the present paper, it would be of great interest to explore the thermoregulatory mechanisms for maintaining brain temperature in this order of mammals, as well as the relationship between such mechanisms and the evolution of the brain. [See also: Glezer et al. "Implications of the 'initial brain' concept for brain evolution in Cetacea" BBS 11(1) 1988.]

6. Beyond the radiator theory

The radiator theory is mechanistic. The dramatic increase in brain size in *Homo* is viewed as a side benefit of earlier vascular changes that occurred because of thermoregulation and the pressures of gravity associated with a new postural niche. So far, nothing has been said about the selective pressures that acted on the brain once it had acquired an adjustable radiator and *could* get bigger. I am going to indulge briefly in such speculation, but it should be realized that this final section is just that – speculation that is separate from the radiator theory.

As noted earlier, various workers have attributed hominid brain evolution to *one* prime mover such as warfare, language, tool production, throwing, or hunting (see Falk 1980a for a review). However, there seems to have been resistance to the possibility that hominid brain size increased as a result of selection for intelligence, at least in part because brain size does not correlate highly with intelligence in living people (e.g., Radinsky 1979). I find this resistance puzzling, for several reasons. First, relative brain size increased in parallel during the evolution of many groups of mammals (Jerison 1973; Radinsky 1978; 1979). (It should be noted, however, that thermoregulation may not have been a problem because these increases were modest in comparison to that which occurred in *Homo*.) Because Passingham (1975b) calculated significant rank correlations for (a) neocortex/medulla volume and response to novel objects and (b) neocortex/medulla volume and learning set performance for many species of primates, it appears that "intelligence" may have been related to the increase in brain size for various groups of mammals across the Cenozoic.

It also seems obvious that intelligence in its multi-faceted sense (which is the best way to go, since it is a notoriously difficult concept to define) would have been adaptive for early hominids. [See also Sternberg: "Sketch of a componential subtheory of human intelligence" BBS 3(4) 1980.] Simply put, hominids that (a) stayed alive and (b) successfully bred would have been selected for. Many aspects of "intelligence" would presumably have facilitated such selection. For example, Richards (1989) offers a "physiomorphic model" in which he details the evolution of an *open-ended behavioral repertoire* from environmentally induced enhancement of imitational skills. Others (Cheney et al. 1986; Byrne & Whiten 1988) have suggested that *social intelligence* was strongly selected for because socially skilled hominids would have had differential access to food and mates. Similarly, selection for left hemisphere *time sequencers* would have been of enormous importance for the development of *language*, as Calvin (1982; 1983a; 1983b; 1986a; 1986b) points out (although he suggests that the primary selection is related

to throwing); and such selection may even have facilitated the *perception of time* itself. With the latter would have come a concept of death (burial of the dead), the ability to worry about the future (e.g. to fantasize escape routes), and a proclivity for looking both ways when crossing the street (or ravine). Surely these behaviors were and are adaptive. Humans are speculative, language bearing, and fretful to a degree that exceeds nonhuman primates, including our closest "cousin," the chimpanzee. It is time to view these aspects of mind within an evolutionary framework. I suggest that intelligence *was* adaptive for hominids (see also Van Valen 1974) and that furthermore, when controlling for allometry and comparing species (not individuals), bigger brains were and are better brains.

NOTE
1. This paper is dedicated to the memory of Leonard Radinsky (1937–1985).

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The multiple obstacles to encephalization

M. Maurice Abitbol[1]
Department of Obstetrics and Gynecology, University Hospital, State University of New York at Stony Brook, Stony Brook, NY 11794.

Multiple problems had to be solved before encephalization could proceed.

1. The average body weight of a normal human adult is 85 kg and the average brain weight is 1700 grams or 2% of the total body weight. Cerebral blood flow (CBF) is 1000 ml/mn, approximately 12 to 15% of the total cardiac output (Scheinberg 1975). At rest the brain consumes $\frac{1}{4}$ to $\frac{1}{3}$ of the total oxygen intake and 70% of the total glucose consumption; glucose is the only substrate used by the brain. The brain is always working, even during sleep (Ingvar & Risberg 1967). Therefore, CBF had to be increased.

2. What makes the above figures even more dramatic is the fact that, unlike any other organ, the brain has no oxygen or glucose stores and is therefore entirely dependent on a constant and well regulated blood supply; short interruptions of blood flow to the brain (less than 8 minutes) can bring brain tissue death and permanent cerebral dysfunction (Zwiebel 1982).

3. The brain also is subject to and must adapt to severe hemodynamic changes during different postures (Abitbol 1989).

4. The brain needs a solid bony "box" (the skull) for protection.

5. In addition, this "burning furnace" (the brain) needs an efficient cooling system to prevent overheating.

6. The return of venous blood from the brain to the heart has to be safely secured without any obstruction.

7. Encephalization is already in progress while the fetus is in utero. How does the mother provide blood, oxygen, and glucose at a much greater level than in any other mammal? The histology of the human placenta is different. In the suidae, six cellular layers lay between the maternal and the fetal blood (epitheliochorial placenta); in felidae and canidae there are four cellular layers (endotheliochorial placenta); in primates, the placenta is hemochorial, that is, the maternal blood flows freely under high pressure around the fetal vessels of the placenta; in primates there are two cellular layers; in humans during the third trimester of pregnancy there is only one cellular layer between maternal and fetal blood and the exchange of oxygen and nutrient is very high. At term, the woman diverts up to 40% of her cardiac output to the pregnant uterus, as the maternal blood volume increases by 50% during pregnancy (Pritchard et al. 1985).

8. The encephalized fetal head at term has to be delivered through a maternal pelvis which has been completely remodeled by erect posture, and the fit can be very tight (Abitbol 1987).

The problems for a successful encephalization are therefore numerous and one can understand why it took about one million years before hominid encephalization began. As stated by Scharrer (1960): "Without proper development of the vascular system, the human brain could not have attained its present level of differentiation." And yet "knowledge of the ontogeny and phylogeny of the vessels within the brain is still somewhat meager" (Craigie 1938). This problem has been dormant for many years, since there was no way to study the arterial system in fossil hominids. The breakthrough occurred with Falk and her associates, who thoroughly investigated the cerebral venous system in primates (by definition the venous return is equal to the arterial output). They grouped together in a coordinated system all the anatomical observations on venous endocasts of extinct and extant hominids, added observations of their own, and formulated ingenious concepts concerning the phylogeny of the vascular system during the hominoid evolution: (a) They used the enlarged occipito/marginal sinus system of the robust and Hadar australopithecines to demonstrate the hemodynamic difficulties during the early attempts at erect posture; (b) the jugular vein versus the vertebral vein route also sheds light on the alternate routes used by the returning blood during different postures; (c) the increased frequency of the mastoid and parietal emissary venous system during the evolutionary process becomes logical; (d) the cooling of the brain (just as important as the arterial supply and the venous return) has been elegantly explained. Thanks to Falk, we now have as much information on CBF, if not more, as we would have gotten from well preserved arterial remains.

It is not important here to decide whether Falk's theories completely explain the evolution of cerebral blood flow in primates or if they will need further revision. What is important is that a new approach to anthropology has been described, namely, vascular anthropology, and it will play a role.

The last sentence of Falk's target article relates to a bigger brain: I could not decide whether she implies that the future of *Homo sapiens* is in an even bigger brain. I personally believe that there is room for such a speculation (Grusser & Weiss 1985).

NOTE
1. M. Maurice Abitbol, M.D. Department of Obstetrics and Gynecology, Jamaica Hospital, 89th Avenue & Van Wyck Expressway, Jamaica, NY 11418.

Brain evolution in *Homo:* the "hood" theory

Robert A. Barton*
Department of Psychology, University of Sheffield, Sheffield S10 2TN, England

One day, as my motor mechanic and I were peering into the bowels of my venerated automobile, he tapped the hood with his wrench and sagely observed: "The engine can only be as big as there's space for under that." I didn't think much about it at the time.

But later I was reflecting on what the mechanic had said, and it struck me that what was true of my car's engine was also true of my brain! My brain could only be as large as my cranium permitted, and, in evolution, the skull-size constraint would have had to be removed to enable hominids to become large-brained. The only link now required to elevate my idea to the status of a "theory" of brain evolution, was some explanation of how hominids in the lineage leading to ourselves were able to develop these large skulls. "Then, hey presto! You've got the hood theory!", I thought to myself excitedly. Unfortunately, at that point my brain overheated.

The pastiche is, perhaps, not altogether fair. Falk has provided a useful synthesis of comparative information about venous drainage from the cranium, and argues, plausibly to my mind, that the predominant system found in later hominids (including ourselves) is related to the adoption of an upright stance, and, in addition, performs a brain thermoregulatory function. What I take issue with is the idea that this, in any important sense, "explains" the evolution of large brain size. There are a number of constraints on brain size, of which thermal factors are only one variety. For example, the brain is a metabolically expensive organ to run, so the development of large brains must be supported either by higher metabolic rates overall, or by allocation of a greater proportion of the metabolic output (Martin 1981; Armstrong 1983). All such constraints (including skull size!) must be slackened during the evolutionary expansion of the brain. But the demonstration of such constraints, and the mechanisms by which they are released, has no necessary bearing on the *causes* of brain enlargement.

Falk emphasises the link between bipedalism and the way the system of venous drainage from the brain subsequently evolved; the reorganisation of cranial blood flow due to changes in gravitational forces paved the way for the radiator. The radiator was in turn a necessary adaptation for keeping the brain cool during mid-day scavenging in a hot, open environment. Thus, bipedalsm resulted in preadaptations which dictated the type of cooling system that then evolved. Robust australopithecines didn't need the same elaborations because they inhabited a cooler, more shady environment. Nothing wrong so far. It is when Falk leaps from these arguments to the conclusion that the "prime mover" of human brain evolution has been discovered that the issues become muddied. Was the radiator an adaptation for running about at midday on the savannah (only mad dogs, Englishmen, and gracile australopithecines . . .)? Or was it the mechanism by which larger brains came to be cooled as they evolved? Falk seems to want to have her cake and eat it. On the one hand, we have an argument for the selective value of the radiator in the context of hominid foraging ecology (which has no necessary corollary as far as brain size is concerned), on the other hand, a suggestion as to the mechanism by which thermoregulatory constraints were overcome during the evolution of large brains. In neither case do we have a "prime mover."

Falk is perhaps implying (although this is not clearly stated), first, that temperature regulation of the brain was the only critical constraint preventing it from getting bigger, and second, that the radiator was so *efficient* a cooling system that, once the basic mechanism was in place, it preadapted hominids for brain expansion beyond that possible in other phyla. No evidence is

presented for this, however, and it does not seem particularly plausible. Nevertheless, the idea could be tested by following Wheeler's (1988) approach in modelling the thermoregulatory properties of the different systems.

In the final section of the paper, Falk goes beyond the issue of constraints to discuss selection pressures. But, here we are on boggy ground indeed. Selection for "intelligence" is posited as an alternative to selection for abilities in warfare, tool-making, hunting, and so forth. This seems a spurious distinction to me. There may have been resistance to considering selection for general intelligence in human brain evolution, simply because it is too imprecise a concept (see Macphail 1982; Whiten & Byrne 1987). Thus, theories have tried to isolate specific aspects of intelligence, or specific sensory processing abilities, which might have been important (an enterprise of arguable worth, admittedly, when not supported by solid comparative evidence). Falk's assertion that "hominids that . . . stayed alive and . . . successfully bred would have been selected for" is an unfortunate tautology. As for looking both ways before crossing the street, I've known dogs that do that; you don't need a particularly big brain, just the right kind of training experience.

I like the cactus in Figure 6 (despite some rather uncladistic-looking multiple branching points), and look forward to Steven Jay Gould rewriting his famous essay (Gould 1977a) as "Bushes, ladders and cacti in human evolution." Gould, like Falk, is the progenitor of interesting ideas about mechanisms in human evolution; neoteny, for example, is seen as a mechanism facilitating a suite of changes, of which increased brain size is one (Gould 1977b). But neoteny, as Gould would acknowledge, is not in itself a sufficient explanation for large brains. Neither, I would think, is the radiator theory, albeit accompanied by some adaptationist speculations.

NOTE
*Present address: Robert A. Barton, Department of Psychology, University of York, England.

The role of a behavior in evolution

Geoffrey P. Bingham
Department of Psychology, Indiana University, Bloomington, IN 47405
Electronic mail: gbingham@iubacs.bitnet

Plotkin (1988) argued that the effect of behaviors on the course of evolution has been ignored largely in preference for a consideration of the effect of evolutionary changes on resulting forms of behavior. If this has indeed been the trend, Falk (and the literature to which she refers) demonstrates how the balance might be redressed, allowing us to ply the cycle of changes in alternately anatomical/physiological and behavioral forms. An underlying challenge in understanding this cycle is one faced both in the study of human evolution and in the study of human behavior. The challenge is in understanding how a complex physical dynamic can become organized *functionally*, that is, organized to perform particular tasks. Meeting this challenge requires that we reveal the constraints imposed by tasks on physical organization. Ultimately, functional levels of organization comprise higher-order constraints on physical dynamics.

Falk intends to account for an observed evolutionary change in *Homo* neuroanatomy, namely, increasing relative brain size. To do so, she investigates one of the ways a new behavioral regime in evolutionary development – bipedal locomotion – constrained the system dynamic: changing the prevailing orientation of the organism in the gravitational field. In pursuing the repercussions, Falk's discussion ranges over diverse influences on hemodynamics, including muscular contraction, respiratory activity, perfusion pressures, vessel compliance, and of course, gravity. This discussion well illustrates the true challenge in understanding human behavior, the overwhelming complexity of its organization (Bingham 1988).

The complexity of the dynamics of the human and precursor species lies not only in the large number of system components, but, more important, in the interactive character of the components. In the context of locomotor tasks, the relevant subsystems, each of which is itself complex, include the musculotendon system, the link-segment system, the circulatory system, the respiratory system, and the nervous system (Bingham 1988), as well as, ultimately, the nutritional system (Carrier 1984). In locomotion, all of these subsystems interact; this means, by definition, that the system dynamics are nonlinear. Nonlinearity in turn means that the behavior of the system cannot be predicted from a knowledge of the behavior of the components studied in isolation. This is literally "the whole is more than the sum of the parts" problem advertised by Gestalt psychologists. Our current understanding of human physiology in the performance of particular tasks (e.g. locomotion) is vulnerable to the extent that the contributions of various subsystems are left out of consideration.

When the radiator theory is considered together with contributions in the literature cited by Falk (especially Carrier [1984] and work by Taylor, Schmidt-Nielsen, Heglund, Cavagna, Bramble and others cited therein), one finds a story just beginning to emerge that allows some glimmer of hope for completeness. Carrier (1984) and Falk share an overarching focus on temperature management. With the adoption of bipedal locomotion, a variety of new behavioral opportunities emerged. Among them was persistence hunting, given a number of concurrent adaptations for the management of energy and temperature flows. Carrier's analysis included

1. muscle metabolism and power-generating characteristics as constraints on gait (including stride length and frequency),
2. the mechanics (including the scaling of body mass) and energetic costs of alternative modes of locomotion,
3. hairlessness and sweating versus panting as alternative modes of temperature management in the face of heat generated by muscle metabolism,
4. respiratory mechanics and required attunements to muscle metabolism versus temperature management,
5. neural control of energy generating and temperature management components, and finally,
6. nutritional requirements for taking advantage of the persistence hunting niche.

As one of Carrier's commentators noted, however, he did not consider circulatory system constraints and interactions.

Falk's radiator theory is complementary in its focus on circulatory system modulation of brain metabolism. Falk noted an interaction between respiratory mechanics and venous circulation in the neck, but she failed to elaborate on it. The development of the vertebral plexus of veins as an alternative to the jugular vein as a means of draining blood from cerebral areas could be further motivated via this interaction. Falk noted that jugular flow is constrained during periods of expiration. This interaction would interfere with the efficient removal of excess heat from the head and neck region, especially if coupled with the most common means of dumping heat from the body, namely, panting. Carrier's (1984) account of the energetic underpinnings of persistence hunting required the decoupling of thermoregulation from respiration so that respiration might be tuned to needs of muscle metabolism. In Carrier's account, this was accomplished by using hairlessness and sweating instead of panting for heat dissipation from the body. In Falk's account, however, adequate dissipation of heat from the head and neck requires efficient circulation and this, in turn, means that circulatory egress from the head must be decoupled from the rhythmic pressures associated with a respiratory system attuned to muscle metabolism requirements. Thus, the same constraint contributes to the emergence of hairlessness and sweating and the radiator.

Of course, this body of work is encouraging, but far from complete. Plotkin (1988) argued for attention to the effect of behaviors on subsequent evolutionary changes in anatomy and physiology so that the relation between form and function might be brought into proper focus and so that the loop back to the effect of anatomical changes on behavior might be closed. Ironically, the side of the loop most heavily studied, according to Plotkin, is that which is most elusive in this instance. Falk's evaluation of the impact of the neuroanatomical change in relative brain size on subsequent behavior is not very illuminating. After noting the ill-defined nature of "intelligence," the apparent decoupling between variations in brain size and intelligence in modern man, and the importance of brain organization and reorganization apart from the issue of size, Falk confusingly and rather disappointingly opts for the brain size/intelligence story. One must sympathize with Falk to the extent that this expresses an intuition that the significant neuroanatomical change must have behavioral impact. I must also find fault, however, with the effort to convey the impression that we have any substantial inkling as to what that impact might be. There are a few extremely crude indicators of specific structural changes that may have accompanied size changes (Holloway 1983). However, we have no idea whether the size changes reflected structural changes in the numbers of neurons or glia or processes (axons and dendrites) or circulatory vessels or extracellular spacing (Armstrong 1982), where the importance of flows in the enzyme bath filling the interspaces should be underscored. Any vague ideas that we might have about structural changes are completely undermined by our predominant lack of understanding of the relation between brain and behavioral organization.

Falk appropriately refers to the radiator as removing a constraint on relative brain size. However, she also refers to the radiator as "a prime mover theory" after having criticized prime mover theories more generally. The prime mover label implies that the theory accounts for factors constraining in favor of increasing size once the limiting factor had been removed. However, the behavioral/functional impact of brain size is precisely the issue that must be addressed by such an account and just this is missing. So, Falk's radiator does not provide a full explanation for the increase in relative brain size. We now perhaps understand how it became possible, but not why it might have been advantageous.

The evolving *functional* organization of the brain remains to be discovered. How? The route has essentially been marked by Falk, Carrier, Holloway, and others. Falk (in a personal communication cited by Richards, 1989) has remarked that the adoption of a new behavioral regime such as bipedal locomotion opens new vistas on behavioral opportunities which should result in adaptive proliferation of behaviors on direct analogy to the rapid adaptive radiation of life forms following access to geographically constrained niches. Carrier's analysis of persistence hunting amounts to an investigation of such behavioral extension. I understand the frequent references to mosaic evolution as referring to the complexly interleaved collection of structures and behaviors involved in evolutionary development. Holloway (1983, p. 223) refers to "mosaics within the overall mosaic which involved the brain." These authors all note that the development of bipedalism was not an all-or-none affair. Bipedalism in the early protohuman forms was not the accomplished bipedalism of modern man. Bipedalism includes a complex collection of behaviors appearing in the context of a number of tasks. The continued exploration of these interrelated forms of behavior and their implications for anatomical and physiological organization in modern humans and as extrapolated to circumstances in evolutionary history is a promising route to unpacking successively the structures we hope to understand.

Exercise as prime mover and a cool brain

Walter M. Bortz 2d
Palo Alto Medical Foundation, Palo Alto, CA 94301

Most of the body serves movement purposes. This truth applies throughout the animal kingdom. Furthermore, during exercise blood is shunted from the digestive, excretory, and reproductive systems to the working skeleton. Only the brain is spared this diversion. Thereby the hierarchy of survival devices is asserted. In evolutionary terms, the complexity of the central nervous system parallels movement capacity.

Krantz (1968), Fialkowski (1978) and others have developed the thesis that persistence hunting was a life strategy developed as an adaptation to savannah existence and that the ecologic niche provided by the heat endurance of early man was unique. The condition of "capture myopathy," a result of hyperthermia, renders prey animals helpless (Bortz 1985). This fact was exploited by our early ancestors, who were not armed with lethal anatomic weapons, or explosive running speed. Endurance in the heat was the differential advantage.

Development of hairlessness and extraordinary sweating capacity subserved this strategy. Falk, in the radiator hypothesis, extends this reasoning by demonstrating how the brain was effectively cooled during heat burdens. Clearly the brain cannot be allowed to bake in the midday sun. Convulsions are a common result of high body temperatures.

Little is known about the physiology of the cerebral veins. It has generally been assumed that brain circulation relied only on systemic pressures and that the veins acted merely as a passive lake. But, as pointed out by Kety, elaborate homeostatic mechanisms tend the metabolic needs and protect the internal environment of the brain (Kety 1960). The veins of the brain contain smooth muscle fibers in their walls and are served by autonomic nervous fibers. In addition, the presence of monoamine oxidase at the site of the cerebral micro blood vessels represents a further mechanism allowing adaptive response (Kalaria & Harik 1987). It is estimated that 60 to 70% of the cerebral blood volume is contained within the venous network – so any small hemodynamic change could provoke marked alterations in cerebral blood flow (Nielsen & Owman 1967).

Cerebral blood flow is very sensitive to changes in carbon dioxide and oxygen levels in the blood. Similarly, several neurotransmitters which are increased during exercise have been shown to affect cerebral blood flow (Kety 1960).

A number of older studies failed to find any increase in brain blood flow as a result of physical exercise (Kleinerman & Sancette 1955; Scheinberg et al. 1954) but studies by Raichle and others using positron emitting tomography clearly show increased flow and metabolic activity in those areas of the brain subserving motor functions during exercise (Raichle 1987).

Diamond and others have demonstrated how the enrichment of the environment results in actual increases in the size of the cerebral cortex which are found microscopically to be caused by richer dendritic branching (Diamond 1967). Dustman et al. (1984) and Bashore et al. (1988) have shown how a relatively short exercise period results in increased cognitive ability. These workers propose an increased oxygen delivery mechanism as the ultimate cause of this improvement. I favor the neurotransmitters and calcium as more logical mediators. The provision of an adequate brain cooling radiator mechanism as demonstrated here by Falk represents a facilitating and enabling device.

In any case, the link between exercise load with its necessary heat modulating compensatory mechanisms and brain structure and function is not untestable as a hypothesis. Epigenic influences on brain workings are being rapidly elaborated, each revelation being more expansive and adaptive than previously guessed. If such rapid phenotypic reactivity is evident, its

impact on the evolution of the human brain becomes less obscure.

The brain drain as a means of cooling hot heads

C. L. Brace

Museum of Anthropology, University of Michigan, Ann Arbor, MI 48109
Electronic mail: *bracekzlj@umichum.bitnet*

Falk has presented a convincing case that the achievement of bipedalism was the reason for the emergence of the role of the vertebral plexus in the outflow of venous blood from the brain, and that the occipital/marginal (O/M) sinus system and the cranial emissary vein routes are equally effective means of channelling blood via the vertebral plexus back to the general circulation. She has also produced a plausible argument for why the cranial emissary vein route was the one selected in the hominid lineage associated with diurnal hunting and where cerebral expansion became evident through time.

That these constitute a radiator for the brain and that this represents a constraint on brain size and diurnal activity levels in the heat of the tropical midday sun is a credible and thought-provoking argument. Although the supraorbital pathway for arterial-venous exchange does not connect with the vertebral venous plexus and is therefore unrelated to the circulatory changes associated with bipedalism, it, too, is obviously an important part of the brain radiator phenomenon, especially in light of the concentration of sweat glands found in the overlying skin. Although Falk does not mention it, this suggests the explanation for the elimination of hair from the forehead of the hominid line, in which there is evidence for both cerebral expansion and the development of persistence hunting.

If Falk has made a good case for the reality and importance of the cerebral radiator, she has not done so in regard to its role as a "prime mover" for the expansion of the brain in the prehistoric hominid line. To consider the matter in a standard Darwinian scenario, the development of an effective cooling system for the brain would have had to follow rather then precede the pressures for the expansion of that organ. Cerebral expansion as something adaptively advantageous would then constitute the selective force that led to the development of the cerebral radiator. The "prime mover" in the expansion of the brain would have to have been the survival value of having that larger brain in the first place. Only then would selection lead to the development of an adequate radiator. It was the radiator and not the brain that was the byproduct of thermoregulatory forces.

Now we are back to basic considerations and the matter of what it was that led to the differentiation of hominid from pongid. A generation ago, Washburn did indeed help us focus our attention on the feedback between bipedalism, freed forelimbs, tool use, hunting and brain enlargement (Washburn 1960). In doing so, however, he simply paraphrased the points made by Darwin in *The Descent of Man* (1871). Darwin's expression of that feedback situation was a model of clarity: "The free use of the arms and hands, partly the cause and partly the results of man's erect position, appears to have led in an indirect manner to other modifications of structure" (1871, vol. I, p. 138). Darwin explicitly noted the effects of freeing the arms and hands from locomotor duties (1871, vol. I, p. 136) and suggested the circumstances leading to brain growth that this situation represented. Darwin also noted that the beneficiary of that set of circumstances consequently "has invented and is able to use various weapons, tools, traps, etc., with which he defends himself, kills or catches prey, and otherwise obtains food" (1871, vol. I, p. 132).

Darwin's appraisal was an exercise in deductive logic based on the givens of modern human morphology and behavior, and it is a model of both insight and caution. Fossil evidence for the earliest hominids began to accumulate a full half century after Darwin published his assessment, and, by the time Washburn produced his paraphrase ninety years after Darwin's first version, there was a modest tangible basis on which to test his deductions.

If there was a flaw in the way those deductions were tested, it was in the expectation that all of the aspects in Darwin's feedback model occurred simultaneously (and see Brace & Montagu 1965, p. 217ff. as an exemplar of this mistake). It was not just the 3.6 million-year-old footprints at Laetoli (Leakey 1979, p. 450; Leakey & Hay 1979), but, more directly, the unequivocal skeletal evidence for bipedal posture previously found at Hadar – the famous Lucy skeleton (AL-288) – which showed that bipedalism preceded the major indications of hominid brain enlargement by nearly two million years (Johanson et al. 1978, Johanson & White 1979). Even so, the evidence suggests that when allometric considerations are taken into account the gracile Australopithecine lineage, at least, displayed a somewhat larger brain relative to body size than is true for modern anthropoid apes (Holloway 1981b; Martin 1983, p. 44).

The other reasons why Washburn's view lost favor derive from the realization that the manufacture of stone tools and their use in the butchering of hunted or scavenged animals do not appear in the archaeological record until a good million years after the earliest known hominid bipeds (Leakey 1984, p. 212; Pilbeam 1980, p. 281; Toth 1987).

None of this adds up, however, to an adequate reason for abandoning Darwin's insights. All that is needed is some adjustment and, indeed, as the evidence has become available during the last twenty-five years or so, those adjustments have been made (see Brace 1979, p. 52–67; 1988, p. 80–91). First, there is no need to equate the beginning of the manufacture and use of tools with the first appearance of stone tools in the archaeological record. As Darwin specifically appreciated, the reduction of canine tooth projection and the continued survival of a slow and inefficient biped could only have occurred given the compensating presence of some sort of hand-held tool/weapon. And there is no necessity that this be made of a nonperishable material such as stone; furthermore, there is no necessary tie between stone use and hunting behavior. Washburn observed that, with the aid of a digging stick a baboon could effectively double its food supply. To that, I added the corollary that a digging stick redirected could serve as a far more effective means of defense for a slow terrestrial biped than the use of enlarged canine teeth (Brace 1979, p. 62; 1988, p. 85). Even in the absence of tangible artifacts, an assessment of the morphology of the earliest hominids leads to the Darwinian deduction that tools of some sort of perishable substance must have been a key to survival.

Hunting, and the events that led up to it, did not become a characteristic hominid activity until quite a bit later, perhaps preceded by an increasing focus on scavenging (Shipman 1986). The association of very early stone tools with the dismembering of large mammal skeletons occurs just shy of two million years ago (Gleadow 1980; Isaac 1976; 1978; McDougall et al. 1980). Archaeological and taphonomic evidence suggests that the transition from opportunistic scavenging to a recognizable hunting and gathering form of subsistence strategy occurred between two and one million years ago (Shipman 1983). This, of course, was precisely the time when hominid brain size underwent a full doubling and there was an increase in the mastoid emissary foramina, as Falk has demonstrated. It is hard to resist the idea that this was related in some fashion to the adoption of systematic diurnal hunting as an important subsistence strategy.

Finally, Falk is almost certainly justified in offering her speculation that "bigger brains were better brains." Darwin clearly understood this, although he erroneously assumed that differences in brain size between living human populations

were proportional to intelligence (Darwin 1871, vol. I, p. 140) and not to differences in bodily bulk (Brace et al. in press). When different species are compared, brain size "differs more among distantly related species, for any given body weight, than among closely related species" (Pagel & Harvey 1989, p. 1589). Certainly the relative increase in brain size that occurred as the hominid line adopted a hunting and gathering subsistence strategy implied "greater intellectual capabilities" (Brace 1988, pp. 94, 117).

Although, in Noel Coward's flippant words, only "mad dogs and Englishmen go out in the midday sun," the niche of the diurnal hunter, exploited by the evolving hominid line from the end of the Early and on through the Middle Pleistocene, presented a series of selective forces that shaped our common heritage. If the venous radiator is not the prime mover for hominid cerebral expansion, it is an important accompaniment. Falk, in bringing attention to this, bids fair to be remembered for having given an entirely new connotation to the phrase, "the brain drain."

Brain cooling via emissary veins: Fact or fancy?

George L. Brengelmann
Department of Physiology and Biophysics, University of Washington, Seattle, WA 98195
Electronic mail: *brengelm@walocke.bitnet*

The emissary veins are small and few.[1] Under some conditions, they may conduct relatively cool blood into dural venous sinuses. That does not mean that their proportion of total sinus flow is sufficient to affect intrasinus temperatures and, consequently, brain-to-sinus heat transfer. I disagree with Falk that brain cooling via emissary veins has been demonstrated[2] and do not see in their physical arrangement a design for heat exchange.

Falk is impressed that, like her car, her brain has a radiator. But our "radiator" is our entire skin surface. We are fortunate that our brains need not depend on only the exposed surface of the head for heat loss to the environment. Of the body parts, the near-spherical sections of the head are near-minimal in surface : volume ratio.

Inside the skull our concern is not with radiation, but convection – transfer of heat via a moving fluid, most effective where the ratio of heat exchanger surface area to heat transfer fluid volume is maximal. Convective heat transfer in the cooling system of Falk's car takes place not in the large collection vessels (radiator hoses, i.e., venous sinuses) but in the regions where the most surface is exposed to the least fluid volume.

Convection is so effective in well-perfused organs that core tissue temperatures are nearly uniform and only slightly above arterial temperature. As blood makes its way through a deep tissue via progressively smaller arterial branches, the relative amount of surface per unit volume of vessel increases enormously. According to theoretical studies and direct measurements by Lemons et al. (1987), blood comes into thermal equilibrium with the surrounding tissue when it reaches arterial vessels of less than 0.1 mm diameter. Large vessels, even the size of 1 mm emissary veins have relatively little surface and do not thermally equilibrate with surrounding tissues[3].

Veins from outer layers of the brain drain into superficial sinuses. These sinuses are large conduits, with low surface : volume ratios. They are well protected from gravity[4] and suited for bulk transfer, not heat transfer. Emissary and diploic veins drain into these sinuses. Their contribution to the total flow in the sinuses must be tiny. How are they to contribute to brain cooling, even of the outermost cortex? They do not plunge into the brain to rearborize as tiny vessels that can equilibrate

thermally with surrounding tissue. Whatever cooling effect they have on venous blood will have to wait until the next pass to benefit any organ.

In short, my interpretation of the vascular architecture: Once blood from the brain reaches the collecting sinuses just beneath the skull, its heat transfer days are over until it arrives somewhere again as arterial blood.

Aside from the architecture, other quantitative considerations make me doubt the significance of Falk's "radiator" mechanism. What little data we have from actual measurements do not support the speculation that blood draining from the skin of the head has an important cooling function.

How much warmer is the brain than its incoming arterial blood? A simple analysis shows that the potential heat delivered by a liter of blood can be carried away by that liter, 1°C warmer[5]. Even actively metabolizing organs do not extract 100% of their oxygen supply. Therefore, we can expect to find the internal organs in a thermal steady state in which the entire heat production is removed convectively, with the venous blood leaving less than 1°C warmer than arterial blood and slightly cooler than the extravascular tissues. On the basis of cerebral oxygen consumption and blood flow (60 ml/min and 750 ml/min, respectively, according to Rowell 1986), therefore, brain temperature need be only slightly more than 0.4°C above arterial blood temperature.

Temperature uniformity with the core organs and tissue temperatures less than 1°C above arterial temperature is borne out in actual measurements, a few from man. Graf (1959) placed thermocouple probes in patients' livers during liver biopsy. Temperatures at sites separated by 5–7 cm were within hundredths of a degree. In the same paper is a figure showing hepatic venous temperature and deep arterial temperature obtained with intravascular catheters. The difference was close to the 0.2°C that we would predict from liver blood flow and metabolism (Brengelmann 1989). In adult craniotomy patients, Whitby and Dunkin (1971) found cerebral temperature 4 cm below the surface to be 0.25°C above lower esophageal temperature (where temperature closely approximates that within arteries). Shiraki et al. (1988) recently reported data from a single young patient continuously monitored from thermocouples on a drainage catheter placed during brain surgery. Deep within the brain, temperature maintained a nearly fixed offset of 0.6°C relative to esophageal. From animals: Hayward and Baker's paper (1968) includes numerous figures showing various intracerebral temperatures to be separated only by tenths of a °C, with a fixed offset in the range of tenths of a °C relative to arterial temperature. In hyperthermic pigs, Dickson et al. (1979) found brain, kidney, and liver all to be equal within tenths of a °C.

According to these considerations and measurements, the brain is safe from thermal damage as long as its arterial supply is undiminished and arterial temperature is something like 1°C below dangerous levels[6]. Its high and fixed perfusion rate is sufficient to remove its heat production with insignificant intracerebral gradients and tissue-arterial temperature differences[7]. Its all-important thermal protection comes from the efficacy of cooling mechanisms spread over the entire body surface, not just the scalp and face. The spectacular thermal adaptations of humans are their cutaneous vasomotor and sudomotor effectors, unexcelled in the animal kingdom. High skin blood flow coupled with cooling via evaporation of large volumes of secreted sweat represent our "radiator" capability.

That's the way I see it, but then I come from a long line of people with full heads of hair who exercise a lot. Maybe I cooked my cortex.

NOTES
1. Boyd's article (1930) on the dimensions of the foramina describes the "largest of the emissary foramina," the condyloid, as being between 1 to 2 mm in diameter. The parietal, mastoid, and Vesalius foramina

were about 1 mm in diameter. Often, diameters were smaller or emissary foramina were absent.

2. Opportunities seldom arise to make the measurements in humans that would be necessary to answer these questions. I know of none that support Falk's position. Hayward and Baker (1968) did observe slight cooling in the subarachnoid space in rhesus monkeys when the scalp was cooled. But, data from such small animals have to be interpreted in the light of the fact that their heads have far more surface per unit volume of brain than humans, and that their skulls are thinner.

3. Venous drainage of the brain has the unusual feature that tiny cerebral veins do not trace the same course as their arterial counterparts, but exit via the surface. This must further expedite convective removal of heat in the outer layers since warm venous blood leaves rather than retransiting, preventing countercurrent recapture of heat. This is supported by the pattern of cooler thermal contours Hayward and Baker (1968) observed in outer layers of rhesus brains.

4. I do not understand Falk's concern with the gravity problem for the brain. The brain veins are uniquely well protected against the influence of gravity. On the surface of the head (or your hand if you hold it up in the air), veins collapse because they are above the level of atmospheric pressure in the venous circulation and would therefore have subatmospheric luminal pressures if a continuous column of blood existed down to heart level. With pressure inside less than outside, these flaccid and unrestrained vessels collapse. But within the brain, specifically in the sinuses, venous drainage is unaffected by gravity because the rigid skull prevents collapse of the veins. Intravascular pressures are subatmospheric just like a syphon, but that has no effect on flow as long as the skull is not penetrated.

5. Metabolic heat is released at the rate of roughly 5 kilocalories (Kcal) per liter of oxygen consumed. In man, arterial oxygen content is nearly 200 ml per liter of blood. If all the oxygen supplied by a liter of blood (200 ml) were to be extracted and used in metabolism, approximately 1 Kcal of heat would be the byproduct of that metabolism in a steady aerobic state. Since the specific heat capacity of blood is near that of water, the effect of taking up all the heat that can be liberated via utilization of all the oxygen in a liter of blood would be a temperature increase of approximately 1°C. The actual arterio-venous increment will approximately equal in degrees centigrade the fraction of oxygen extracted (Brengelmann 1989).

6. Given adequate resupply via drinking, rates approaching 2 liters per hour (1200 kcal of cooling) can be maintained for long periods of severe exercise such as marathon races. In a dry environment, even a warm one, this cooling potential is more than adequate to allow thermoregulation with arterial temperature less than 39°C. In a well-perfused organ like the brain, the small increment in tissue temperature above arterial temperature necessary for complete convective removal of heat leaves a wide safety margin relative to the point of onset of thermal damage.

7. When humidity or clothing interferes with evaporation during severe exercise, we need to worry about the organs whose perfusion is reduced. Renal and splanchnic blood flow are severely reduced in reflex compensation for the enormous requirement of skeletal muscle for blood flow to support muscle metabolism and for cutaneous blood supply adequate for thermoregulation. As renal and splanchnic oxygen extraction approaches 100%, their tissues rise in temperature relative to arterial blood. Brain flow is undiminished under these conditions. Therefore, the other core organs will reach dangerous temperatures first. The symposium on the Marathon, edited by Milvy (1977), is a useful compilation of articles on the response of humans to this severe stress. It includes reports of renal and hepatic damage, presumably thermal, that highlight the thermal problem for organs whose blood flow is reduced during exercise.

Selective brain cooling: A multidisciplinary concept

Heiner Brinnel

Department of Pathophysiology & Department of Medicine, Hôpital-Maternité, B.P. 0116, F-69593 L'Arbresle Cedex, France
Electronic mail: *brinnel@frsun12.bitnet*

The "radiator theory" adds another milestone to the concept of selective brain cooling in humans, a concept introduced by Cabanac and Caputa in 1978 (Caputa et al. 1978). The central

nervous tissue is one of the most heat susceptible tissues in mammals, as recently confirmed by studies in the field of hyperthermic oncology (see review in Sminia et al., in press) and one may legitimately speculate that the danger of hyperthermia is higher in the bigger and more complex brain of *Homo*.

Falk's theory is mainly based on anthropological studies of emissary foramina of the dorsal part of the head, i.e., the mastoid and parietal venous routes, which represent, from a physiological and functional standpoint, a cooling system covering the whole surface of the intracranium. The anterior part of this cooling system was the first to be explored in hyperthermic humans, and is formed by (1) the angular ophthalmic veins draining the face (Caputa et al. 1978) and (2) the spheno-pterygoid veins draining the nasal mucosa (Hirata et al. 1978). The anterior venous pathways lead to the cavernous sinus, whereas the dorsal emissary pathways lead to the posterior dural sinuses.

In living humans, the angular ophthalmic, mastoid, and parietal veins are accessible to ultrasonic Doppler recordings, and the direction of blood flow within these veins depends on the thermal state of the subject. Venous blood from the skin enters the intracranium during hyperthermia, whereas during normo- or hypothermia, no such inward blood flow occurs (Caputa et al. 1978; Cabanac & Brinnel 1985). The causal relationship between this pattern of blood flow and the effective cooling of the brain has been demonstrated: (1) Head cooling decreases tympanically indexed intracranial temperature (Tty) only during hyperthermia, i.e., when emissary venous blood flows towards the brain (Brinnel et al. 1986; Brinnel et al. 1987). During hypothermia, when emissary venous blood leaves the brain, Tty is not affected by head cooling (Brinnel, Cabanac & Caputa 1989). (2) Temporary compression of both angular ophthalmic veins under hyperthermic conditions (thereby inhibiting inflow of cool blood via these veins) decreases the thermal gradient between trunk and intracranium during the time of compression (Nagasaka et al. 1989). This gradient, reflecting brain cooling efficiency, returns to normal when the compression is released (ibid). It should be noted that when Tty is measured with a new technique (Brinnel & Cabanac 1989), that is, on the lower anterior quadrant of the tympanic membrane, no passive contamination from cool skin occurs and Tty can be considered a reliable intracranial temperature. As stressed by Falk, the few emissary venous pathways accessible for analysis or exploration by anthropologists or physiologists stand for a wide system of microscopic diploic veins distributed all over the calvaria: The amount of blood appearing on the inner side of the dura after gentle massage of the skull in a fresh cadaver is highly impressive (see in Cabanac & Brinnel 1985).

Falk's theory and her underlying work on the evolution of O/M sinuses and emissary veins in *Homo* may provide an answer to the most controversial question in the field of human brain temperature regulation: Is selective brain cooling possible when the carotid rete is lacking, as it is in the human? If a powerful heat sink is necessary for the human brain, then why did such a device as "wonderful" as the rete mirabilis disappear? The answer is that after selection for bipedalism, the increased efficacy of brain cooling mechanisms as a consequence of upright posture may have been an alternative way to achieve a sufficient heat sink for the brain without the development of the carotid rete, a quite voluminous structure within a limited space.

Posture per se may indeed be an important factor in the mechanisms of vascular brain cooling in humans. In adults, intracranial pressure (ICP) is negative in upright (sitting) position (Iwabuchi et al. 1986), allowing emissary venous blood to flow inwards according to the pressure gradient between extra-cranial and intracranial veins. In the supine position, intracranial pressure is positive (ibid). In the latter case, the extra/intracranial pressure gradient is lower, and therefore human vascular brain cooling may be less efficient. In children, ICP is

higher than in adults and remains positive even in the upright position (ibid). It is not clear whether this is due to a delay in the development of emissary venous pathways during growth. With respect to brain cooling efficiency, increased ICP in children may partly explain their particular sensitivity to high temperature and the greater risk of febrile convulsions.

In the field of clinical medicine, selective brain cooling has recently been shown to be impaired during rosacea, a common facial and basically vascular dermatosis. When such patients are submitted to passive hyperthermia, the typical inward-bound blood flow pattern in ophthalmic emissary veins is not found, and Tty remains higher than trunk temperature even when external head cooling is performed (Brinnel, Friedel, Caputa, Cabanac & Grosshans 1989). It is not known whether in such patients the enlarged O/M sinus system is predominant, as it was in robust australopithecines and still remains in 6% of modern people. Generally speaking, it seems worthwhile to check the hypothesis according to which anatomical variations in the venous drainage of the intracranium in living humans, as outlined by Falk, could be correlated in clinical medicine with an increased frequency in vascular disorders of the head. Rosacea may not be the only disease involving impaired brain cooling. Similar anomalies have been observed in cases without any dermatosis (Nagasaka et al. 1989). Several other diseases, including migraine, involve both perturbations in facial vasomotricity and disorders in intracranial venous circulation. In the case of classic or common migraine, preliminary observations made in our laboratory suggest that on the side on which the headache usually occurs the vascular mechanisms of selective brain cooling are permanently impaired and forehead skin blood flow is very low, whereas no such abnormalities are found on the contralateral healthy side.

Falk's "radiator theory" and her underlying work on venous drainage of the intracranium has the great merit of connecting very different fields of research such as anthropology and physiology, and may provide new insights on the pathophysiological mechanisms of diseases involving intracranial venous circulation.

Beardedness, baldness, and northern climate

Michel Cabanac
Departement de physiologie, Université Laval, Québec G1K 7P4, Canada
Electronic mail: *physiol@lavalum1.bitnet*

The radiator theory is on the borderline of Popperian science because it is difficult to imagine an experimental method to falsify it. Yet a large part of the excitement of science lies in the process of unifying series of separate observations into a common paradigm. This process is comparable to the elation of *eureka!* Falk, with the radiator theory, gives us an occasion to experience this joy.

Let's speculate further on two minor corollaries of the radiator theory: sea mammals, and human races. It can be hypothesized that a process analogous to that of human encephalization took place in those mammals that selected the aquatic environment when they started to live in water. This environment is 25 times more heat-conductive than air at the same temperature. Heat loss therefore poses no problem to aquatic mammals. According to the radiator theory, it should come to no surprise that the brain mass of some dolphins exceeds that of humans with the

same body mass. [See Glezer et al.: "Implications of the 'initial brain' concept for brain evolution in Cetacea" *BBS* 11(1) 1988.]

Falk mentions our hypothesis about baldness (Cabanac et al. 1984): Baldness, a racial trait, is advantageous from a thermoregulatory point of view, for it facilitates cephalic heat loss. Yet this advantage should mainly concern the dwellers of cold climates muffled up to their necks in heavy clothing, rather than naked inhabitants of warm climates who can lose heat from their whole bodies. When the body is well insulated, the head is the main venue for heat loss. The advantage of selective brain cooling, then, is to protect the brain from hyperthermia due to intense thermogenesis of muscular work and, at the same time, to store heat in the rest of the body. When hominids left the warm countries of their origins and started to invade colder continents they had to limit their heat loss by covering their naked bodies with clothes. In so doing they hid their anatomic sexual signals. The beard may have then been positively selected as a sexual signal of mature men, easily recognizable by distant observers. Because the beard also limited heat loss from the head, however, baldness may have developed in parallel fashion, thus increasing the heat loss capacity of the head.

The size of the nose and external ears is also a racial trait that might be related to the selective cooling of the brain. The venous blood of both organs is drained to the endocalvaria via emissary veins: from the conchae through the ethmoid bone for the nose, from the pinna via the mastoid emissary vein for the ear. One may speculate that both organs are radiators whose size has been positively selected, especially among people living in cold climates because of their thick insulative clothes. The external ear, in the first place, is probably not necessary for good hearing since birds hear well without it. Allen's rule states that mammals of warm climates have their heat-radiating surfaces increased by an enlargement of their ears and extremities (Allen & Schmidt 1951); it is conceivable that this rule also worked in *Homo* and that the necessity of brain cooling has contributed to the dispersion of races on top of the cactus of Falk's Figure 6.

On the possible evolution of brain cooling system in *Homo:* Sweating versus panting

M. Caputa
Department of Animal Physiology, N. Copernicus University, Institute of Biology, 87-100 Toruń, Poland

Falk's "radiator" hypothesis for brain evolution in *Homo* lineage is at first glance very well constructed. It ties together hydrostatic consequences of bipedalism with the release of a thermal constraint on brain size. There is one weak spot in this construction, however. To cool the brain selectively, the parietal and mastoid emissary veins collect cool blood from the skin to send it *into the cranial cavity* (Cabanac & Brinnel 1985). This is quite opposite to the hydrostatic needs the vertical posture imposes, that is, draining cranial blood primarily to vertebral plexes of veins via parietal and mastoid emissary veins. Hence bipedalism would not facilitate brain cooling but would make it more difficult.

From this point of view, combined hydrostatic and thermolytic benefits of evolutionary changes in cranial vascular system are rather unlikely. Nevertheless, the "radiator" hypothesis of hominid brain evolution appears to be noteworthy. Concerning the release of a thermal constraint on brain size, I wonder why hominids did not rely on panting and carotid rete to cool their brains as artiodactyls and some carnivores do? It is obvious that the angular change in chest position as a result of vertical posture, would increase the energetic cost of panting. (Ribs must be lifted instead of oscillating freely during each respiratory cycle.) In addition, panting seems to impose a constraint on behavioral responses. Hence brain cooling with-

out panting mediation could also be a factor releasing a thermal constraint on brain size, since nonpanting bipedal primates must have obtained more freedom for their behavior than panting quadrupedal animals. Nasal heat loss without panting, however, was no longer sufficient and another means of selective brain cooling developed in primates. It requires copious sweating from the face, scalp, and neck. Cool venous blood from the head skin is then collected not only by the cavernous sinus but also by other dural sinuses via both emissary and diploic veins. We can imagine the human brain, under hyperthermic conditions, as being profusely perfused with the cool venous blood.

The two subsequent evolutionary adaptations of the brain cooling system in *Homo* lineage might concern deep body temperatures, which became relatively low and brain-trunk temperature differences, which reached rather high value in humans (Narebski 1985). Low body temperature may be advantageous because it augments the safety margin between normal and maximum tolerable body temperature (Narebski 1985). According to Schmidt-Nielsen (1983), however, the safety margin remains uniformly at about 6°C, irrespective of the level of normal body temperature in different groups of warm-blooded vertebrates. On the other hand, the big difference between normal brain and trunk temperature should be advantageous because in mild hyperthermia brain temperature is likely to remain constant with little effort from the system for selective brain cooling. Along this line, the lowered body temperature could be an adaptation for attaining the high brain-trunk temperature difference.

In summary, the evolution of the brain cooling system in hominids must have resulted in multiple changes leading to the dramatic increase in brain size in the genus *Homo*.

Venous drainage of the brain

M. Christopher Dean

Department of Anatomy and Developmental Biology, University College London, London, WC1E 6BT, United Kingdom

Several aspects of Falk's target article warrent comment: I am not personally convinced that an increased frequency of the enlarged occipital-marginal intracranial venous sinus system is as typical of "robust" australopithecines and *Australopithecus afarensis* as has been suggested here and elsewhere. Enlarged occipital-marginal venous sinuses are certainly not present in Omo L388-y6 (Holloway 1981a), now generally accepted to be a juvenile "robust" australopithecine and in some specimens these sinuses are clearly only enlarged unilaterally (SK 859, SK 1585, and KNM ER 407, see Kimbel 1984). Moreover, the sigmoid sinuses in the "black skull" KNM WT 17000, seem, in my opinion, to be easily as large as they are in larger brained "gracile" australopithecines such as Sts 5. I cannot imagine where more blood could have come from to enlarge the occipital sinuses in KNM WT 17000, especially in such a small-brained hominid. I suggest in fact that they were most likely absent in this important early *Paranthropus* specimen, which is presumed to be ancestral to later specimens of *p. boisei*.

I believe the suggestion that blood in an enlarged occipital-marginal sinus system drains preferentially into the vertebral venous plexus rather than into the internal jugular veins is incorrect. Both the transverse sinus-sigmoid sinus system and the occipital-marginal sinus systems deliver blood to the jugular bulb. Indeed, in any case the vertebral venous plexus has a major communication with the jugular bulb, as does the marginal sinus that courses in the dura at the level of the foramen magnum (see Matsushima *et al.* [1983], Figures 4 and 6). As all of these venous channels communicate extracranially at the jugular bulb, no "exclusive" drainage route to the thorax can be predicted from the pattern of sinuses in the cranial cavity. These facts alone are sufficient to refute the physiological advantages ascribed to different groups of early hominids hypothesized on the basis of bony grooves observed in their posterior cranial fossae. I would argue further that in any case, physiological advantages are not likely to be unilateral in specimens with only one enlarged occipital marginal sinus.

Further support for my view comes from the following: The vertebral venous sinus system consists of extraspinal and intraspinal portions (Breschet 1819) but only the extraspinal portion is a major drainage route from the brain in man (Zouaoui & Hidden 1989). The extraspinal portion must anastamose with veins that drain into the external jugular vein. Shenkin *et al.* (1948) have in fact demonstrated that up to 22% of the blood in the external jugular veins is derived from blood travelling to the brain in the internal carotid artery. Blood within the extraspinal portion of the vertebral venous plexus may then easily pass into the external jugular veins, as may blood leaving the cranium via emissary veins.

The vertebral venous plexus acts as a reservoir for venous blood returning from the head during *transient* shifts in intrathoracic pressure that occur, for example, while lifting heavy objects or while straining. Blood passes into it primarily from the jugular bulb (Matsushima *et al.* 1983), the posterior condylar emissary veins (Braun & Tournarde 1977; Zouaoui & Hidden 1989) the basilar plexus anteriorly and sometimes even the inferior petrosal vein via the hypoglossal canal (Shiu *et al.* 1968). The system has a limited capacity and blood from it must eventually return to the thorax and heart via the azygos system of veins. That the internal jugular veins in primates are more important than the vertebral venous plexus and azygos system for returning blood to the heart is evidenced by the fact that the combined diameter of both internal jugular veins always far exceeds that of the azygos vein.

I believe that increased numbers of diploic or emissary foramina in hominids probably relate to a greater mass of vault bone with an increased arterial blood supply from the meningeal vessels, which then requires an increased venous drainage system. I do share the view, however, that heat regulation of the brain is vitally important and that some contribution to brain cooling in modern humans occurs through countercurrent heat exchange along the internal jugular and internal carotid arteries as well as in the cavernous sinus and through cooler venous blood running close to the surface of the brain in the venous sinuses (Cabanac 1986). Unfortunately, nakedness and the ability to sweat profusely, which I believe were likely to have been the most important adaptations to temperature regulation among early hominids, are not preserved in the fossil record.

Heat stress as a factor in the preadaptive approach to the origin of the human brain

Konrad R. Fialkowski*

Iglaseegasse 68, 1190 Vienna, Austria

Falk has proposed the following scenario for the evolution of the brain that eventually led to *Homo sapiens:*

> bipedalism → development of a radiator → opportunity for brain expansion (→ means "results in").

The lack of a radiator resulted in the lack of brain expansion according to Falk's research findings. Both results, in my opinion, constitute a sound achievement.

The possibility of brain expansion, however, is not equivalent to the brain expansion itself. Using Falk's example: Having a big radiator does not necessarily mean that we must connect it to a big engine. It could cool a small engine as well. To transfer the

opportunity for brain expansion into expansion itself requires that a selective pressure for a bigger brain be in operation; this pressure is alluded to in section 6, but only in the context of "speculation that is separate from the radiator theory." This is insufficient. Either radiator theory is not the theory of brain expansion (and presents only a valuable contribution to the brain expansion theory) or the source of selective pressure – the "need" to build a big engine for the big radiator – must be identified.

A mechanism for the selective pressure cannot be derived from the radiator theory. Falk accordingly invokes a mechanism external to her theory (section 6). The selective mechanism, however, must result not only in increased brain volume (for which radiator theory provides a reasonable background) but, most important, in a unique and more parallel reorganization of the human brain in comparison to apes. Falk agrees: "This concept of 'neurological reorganization,' developed most notably by Holloway (1975), is extremely important for thinking about hominid brain evolution." Any theory of brain expansion must explain this brain reorganization toward parallelism. Falk invokes only a traditional "selection for intelligence" ("intelligence in its multifaceted sense . . . would have been adaptive for early hominids").

This approach was perhaps best summarized by Eckhardt (1987, p. 207): "Expansion in brain size, which probably also involved some structural reorganization (Jerison 1983), was in all likelihood a response shaped by many influences and one which produced many benefits broadly related to enhanced cognitive powers." It is interesting to note, however, how the "selection for intelligence" approach justifies a more parallel structure for the human brain. The line of reasoning is as follows:

1. The human thinks.
2. The human brain is more parallel.
3. Thus, when humans began to think the brain began to become more parallel.

There is no other reason why the structure of the human brain should become more parallel, except this: that it is. Having this opportunity I would like to present how reliability adaptation, cited by Falk in section 4.1.3 as "Fialkowski's heat stress hypothesis" deals with the same problem. The steps in the reasoning are as follows:

1. Heat stress damages neurons and impairs the functions of the brain as a whole.
2. For survival of prehumans, only the functions of the brain as a whole were important.
3. Does there exist any way of reorganizing the structure of the brain that would maintain the functions of the brain as a whole in spite of the destruction of a number of neurons?
4. The answer to the question is affirmative. John von Neumann (1963) demonstrated ("Probabilistic logic and the synthesis of reliable organisms from unreliable components," 1963) that, generally, such a structure can exist but it must be (a) more parallel, and must (b) contain more elements than the initial structure (whose functions would be impaired more for the same number of damaged elements).
5. Following von Neumann's principle, if such "reliability adaptation" to heat stress took place, then the structure of the adapted brain must be more parallel, and must contain more elements in comparison to an unadapted brain.
6. Both features deduced from von Neumann's theory, specific for such adaptation, can be found in the human brain. Either it is a coincidence (but for two features, both present, it is not too probable) or such adaptation to heat stress indeed took place (which is more probable).

Thus, reliability adaptation justifies both an increase in brain volume and its parallelism *without invoking any selective pressure for thinking*. Human thinking came later (Fialkowski 1978; 1986) as a new feature of the changed brain structure. In contrast to the traditional approach, according to which the human brain emerged as a result of *adaptation* to intellectual requirements of

hominids' environment, the heat stress approach postulates the emergence of a bigger and more parallel brain as a result of adaptation, increasing its reliability under heat stress, which, by coincidence, was appropriate (*preadapted*) for abstract thinking. This has far-reaching consequences (Fialkowski 1987; in press).

In invoking a selection mechanism, Falk had two choices: the traditional (adaptive) approach or the preadaptative approach. Each fulfills her requirements for a selection mechanism. She chose the traditional one: "I suggest that intelligence *was* adaptive for hominids." It was indeed adaptive, for prehumans as well as for wolves and chimpanzees, but it provides insufficient justification especially for the onset beginning of the brain growth. Besides that, another problem, however, remains that concerns *Homo sapiens* exclusively: Why do human brain capabilities far exceed those required for hunting?

Any adaptation fulfills the selective requirements that cause the adaptation and usually just those requirements. Sometimes, however, by chance, it may at the same time fulfill a quite different set of selective requirements in the same environment. Then adaptation to the initial set constitutes a preadaptation to the latter set (Mayr 1970, p. 356).

Was this not the case with the human brain? Only if this brain was both adapted to heat stress and preadapted to abstract thinking could the mental capabilities of the human brain be out of all proportion to the limited selective pressure for more intelligence that apparently operated in the hominid environment. Otherwise, convincing reasons must be presented to explain why this pressure was to that extent qualitatively different from the pressures operating on all other known species. Advocating the traditional approach, this fact is usually overlooked.

The preadaptative approach results in quite different timing for the scenario of human origin. For example, based on this approach, the time of emergence of speech can be determined (Fialkowski 1988, p. 323–24). It is worth noting that the assessment of the time of speech origin is in reasonable agreement with the paleoanthropological evidence presented by Laitman and Reidenberg (1988, p. 107). The same could be said about Falk's results. They are readily compatible with the preadaptative approach.

NOTE
*Konrad R. Fialkowski is a former member of the Committee for Evolutionary and Theoretical Biology of the Polish Academy of Sciences, Warsaw, Poland.

Master Mechanic, may I? Evolutionary permission versus evolutionary pressure

Barbara L. Finlay
Department of Psychology, Cornell University, Ithaca, NY 14853
Electronic mail: *j9py@cornella.bitnet*

The singularity of human evolution has allowed ingenious but unconstrained speculation and theory-building. Even in this context, Falk has made a novel contribution. Though metabolic constraints have long been considered as central sources of allometric stability in brain-body relationships across vertebrates, the principal concern about metabolism has always been constraints on the acquisition of energy for building and maintaining brains, and not the dissipation of energy from the brain. The range of detail, from giraffes to male pattern baldness, is impressive as well as entertaining.

Nevertheless, when available theories appear to account for human evolution and the particular features of big-brainedness and intelligence many times over, the goal must be the elimination of some theories and the integration of the remainder. I will

deal only briefly with the testing of this theory, discussing the issue of theory integration at greater length, particularly contrasting theories of evolutionary pressure with evolutionary permission (and evolutionary constraint).

Establish necessity. Falk has done a reasonable job of demonstrating the possibility that different radiating capabilities of facial and brain circulation in bipedal anthropoids could have permitted the change in brain size. The search for the damning fact, however, must be undertaken in greater earnest. Is it in fact brain temperature and not the temperature or performance of some other organ system that limits activity in hot environments? If the opportunity for facial cooling is prevented, to what extent is the capacity to do work or cranial temperature compromised? Is the degree of compromise such as to affect only conditions of high energy expenditure, or would it have the degree of generality explicitly required? Is the bipedal posture required for the radiator to operate? If so, how do bicyclists do it? In any other vertebrate radiation, is there a link between the efficiency of brain cooling and brain size?

It is not difficult to set up explicit tests of the need for brain cooling; it is somewhat more difficult to show these requirements actually did operate in the natal savannas.

Permission versus pressure. The many scenarios that have been proposed to account for the rapid change in hominid brain size usually contain separable components of permissive conditions for the evolution of large brain size and intelligence, and direct pressure for that evolution. Proponents of pressure scenarios usually assert that the permissive conditions are general and easily met, but that the selective advantage conferred by a particular capacity like tool use is so clear that it could drive evolutionary change. Some arguments mix permission and pressure, for example, a change in primate social structure producing available midwifery and long-term parental care might create the bootstrapping conditions necessary for the further evolution of larger brains, more elaborate and extended social interaction, and longer-term, didactic parental care (for example, Trevathen 1987). Falk's argument is that the evolutionary bottleneck is in fact the literal neck, or the cooling properties of the circulation therein. Opening a bottleneck, however, does not drive a change, and a secondary argument for an evolutionary pressure is required. Falk chooses general intelligence, as separately exhibited in social intelligence, language, planning for the future, and so on.

This is a reasonable argument, for as Falk points out, the value of the varied uses of intelligence to primates have been discussed and demonstrated repeatedly. One might quibble that metabolic permission plus the selective advantage of general intelligence requires genius giraffes (or at least superior mentation in any other animal with a suitable brain cooling system), but we will leave this aside. There are other allometric and embryological data that can contribute to this argument. Hofman (1989) has pointed out that though the size of the neocortex is what apparently distinguishes the human brain, in fact, the human neocortex is allometrically "expected" for its overall brain size. Across vertebrate radiations, the extent of neocortex is related exponentially to overall brain size. So if a larger brain size occurs, it follows that a greater proportion of cortex must make up that brain.

The pattern of neurogenesis of the brain described for a number of vertebrates could account for this regular relationship. The neocortex and cerebellum contain the last neurons to be "born" in vertebrate brain development; that is, neurons undergo their final division last in these two structures. Viewed from the beginning of neurogenesis forward, this means that the stem cells producing the cortex and cerebellum are being generated for a longer time than all other structures, and linear extension of gestational time or the time for neurogenesis could produce an exponential increase in the precursor pool for the neocortex. Regularities in the temporal pattern of neurogenesis in vertebrates seem a likely source for the regularities

in brain organizational changes seen under conditions of heterochronic changes in developmental length. That is, longer gestation regularly produces a bigger brain composed of proportionately more cortex and cerebellum because the precursor pool of the cortex and cerebellum can double and redouble during a longer gestation.

What is the significance of neurogenesis for Falk's argument? The specific case is that for selection to produce an improvement in some particular capacity, say language, the only embryological route might be the production of a bigger brain overall. Traits such as social intelligence, fretting about the future, and doing science might be secondary pleiotropic effects of this developmental constraint. A metabolic alteration gives permission for the evolution of a particular skill. An embryological constraint allows the expression of this skill only though the blunderbuss of a generally enlarged cortex.

I would suggest that the only way out of the morass of competing particular, multiply-specified scenarios for the evolution of human intelligence is to get a better understanding of the structural ways brain can change, within the context of metabolism as now extended by Falk. The language of developmental and metabolic permission and constraint can and must become much more systematic.

Tyger! Tyger! burning bright. William Blake wrote of the mystery of the creator of the tiger. Not the least of of Falk's contribution is to add an extra layer of allusion to this poem, which I quote in closing:

> What the hammer? what the chain?
> In what furnace was thy brain?
> What the anvil? what dread grasp
> Dare its deadly terrors clasp?

The causes of brain enlargement in human evolution

Robert Foley
Department of Biological Anthropology, University of Cambridge, Cambridge CB2 3DZ, United Kingdom
Electronic mail: *raf10@phx.cam.ac.uk*

Falk's argument that large brain size in *Homo* is related to thermoregulatory factors introduces yet another strand to the debate concerning human encephalization. That debate has intensified in recent years, mainly through approaches that placed large human brains into the context of brain size and life history among animals generally (Eisenberg 1981; Jerison 1973; Martin 1981).

It is widely accepted that mammalian brain size is closely related to body size, although there is some disagreement about the exact allometric coefficient of this relationship (Jerison 1973; Martin 1981). Beyond this, the comparative approach has linked large relative brain size to a variety of life history, ecological and social parameters (Table 1). To this must now be added what can broadly be termed thermoregulatory (and, by inference, either environmental, or more likely, activity pattern) factors.

In the study of human evolution it is unusual for the principal problem to lie in the plethora of possible explanations for encephalization, as it does here. Empirically, it may be difficult to assess the relative importance of these explanations, for, as can be seen from Table 1, there is evidence that many of these parameters changed in an expected direction as brain size increased during the course of human evolution. The issue becomes, as much as anything, methodological.

Table 1 (Foley). *Parameters that have been shown to be significantly correlated with relative brain size in primates and other mammals. Significance in hominid evolution refers to changes relative to the African apes and supporting palaeobiological or archaeological evidence.*

Parameter Source	Source	Significance in hominid evolution
Life History Parameters		
Gestation Length	Harvey et al. 1986	Probably relative unchanged
Lifespan	"	Considerably extended in modern humans
Neonate Weight	"	Modern humans are relatively altricial, with smaller neonate weight.
Weaning Age	"	Greatly reduced in most modern people, especially in food producing societies (Lee, in press)
Age of First Reproduction	"	Marginally later than African apes; males more variable
Interbirth Interval	"	Similar to gorilla, shorter than chimp (Lee, in press)
Ecological Parameters		
Home Range Area	Clutton-Brock & Harvey 1980	Greatly enlarged (Foley 1984; 1987)
Dietary Quality	Clutton-Brock & Harvey 1980	Higher quality (Hill 1982; Foley 1987)
Maternal Metabolic Rate	Martin 1981	Unknown
Social Parameters		
Group Size	Dunbar (in press)	Larger in modern humans, probably larger in most hominids
"Social Complexity"	Humphrey 1976	Enhanced
Grooming Rate	Dunbar (in press)	?
Communication	Cheney et al. 1986	Language, symbolism, etc.

Historically, explanations for encephalization (or the pattern of hominid evolution in general) have been in terms of either "prime movers" or multifactorial and cybernetic factors. The former are intellectually satisfying in that they are directly causal, linking a number of parameters in a strongly hierarchical manner. Over the years, a number of such prime movers have been proposed, including hunting (e.g., Washburn & Lancaster 1968), tool-use (Darwin 1871), and reproductive rate (Lovejoy 1981). Their disadvantage is that they may be considered simplistic and too deterministic. In particular, it is often difficult to establish any true starting point given the preexistence in time and priority in effect of many biological and ecological factors.

Systems models have the advantage of being more complex and therefore closer to biological reality. Such explanations link any number of parameters as a set of mutually interacting

variables with much greater scope for reciprocal cause and effect. For example, while greater levels of meat eating may enhance nutritional status and therefore promote improved neural growth rates, better brains may in turn improve hunting efficiency – i.e., the causality may go both ways, and become part of a repetitive feedback loop. While incorporating more complexity, however, these models often lapse into merely stating that everything is related to everything else, and therefore lose their explanatory value.

An alternative approach, as indicated by Falk, is to distinguish different types of factor; she, for example, recognized "constraints" versus "selective pressures." This categorization may be expanded to include: conditions, causes, consequences, and constraints. Conditions would represent the environmental, ecological, or social context in which an organism is living, or more particularly, the competitive context of evolution. The "causes" refer to the actual selective pressures operating to favor particular characteristics of the individual organism, especially those that promote reproductive success. Constraints, as Falk points out, consist of the mechanical context in which these selective pressures must operate (phylogenetic, ontogenetic, energetic, etc.), and consequences refers to the changed circumstances of any of the other three factors as a result of an evolutionary change. Each of these factors should be differentiated and incorporated in any evolutionary explanation, including that of hominid encephalization.

The radiator theory is characterized by Falk as the relaxation of a constraint. The condition for that relaxation is bipedalism, and the conditions for bipedalism are in turn taken to be savanna environments. Encephalization becomes a consequence of these changes, and hence a byproduct of other evolutionary changes. The problem that arises, however, is whether the other correlates of large brain size (Table 1) are also mere side effects, or whether there are further factors involved that may influence what are considered to be the selective pressures operating on hominid evolution.

As Falk indicates, occupying open, seasonal habitats in Africa represented a new set of problems for hominids (Foley 1984; 1987). Particularly important is the increased patchiness of resource distribution, through time (seasonality) and space. Greater foraging time, longer day ranges, and larger home ranges are expected adaptations to these patchier resource bases (Foley 1987). These are also factors that lead to greater encephalization among primates generally (Clutton-Brock & Harvey 1980). Although Falk notes the thermal and thermoregulatory consequences of longer ranging, with brain size increasing as a consequence, an equally good case can be made that new foraging behavior placed direct selective pressures on brain size, which in turn led to the need for better thermoregulation of the brain. Alternatively, such foraging behavior may have promoted larger group sizes, and hence social pressures for encephalization (Dunbar, in press). Either way, these models would place considerable emphasis on actual selective pressures for intelligence, not just the relaxation of a constraint. More efficient neural thermoregulation would have been positively selected for by increasing encephalization.

This in turn takes us back to the four explanatory factors "C's" – conditions, causes, constraints, and consequences, and the recognition that they are not really independent. In particular, a constraint is only a constraint if it is not overcome by selection, and hence where selective pressures are greatest – for example, in the *Homo* line as opposed to the robust lineage – what is a constraint may be overcome if there is strong selection favoring large brains.

To return to Falk's automechanical analogy, if you need a bigger engine, you design a bigger radiator; not knowing anything about the history of the internal combustion engine, I would hazard a guess that engines have dragged up the size of cooling radiators, not vice versa. The same was probably true of human brain size. Henry Ford would no doubt have said (see

Humphrey 1976): "Never build a bigger radiator than necessary."

Aristotle redivivus? Multiple causes and effects in hominid brain evolution

O.-J. Grüsser
Department of Physiology, Freie Universität, Arnimallee 22, 1000 Berlin 33, Germany
Electronic mail: *gruesser@zedat.fu-berlin.dsp.de*

Historical notes. More than 40 years ago, as a lad in high school, I learned from our excellent biology teacher, Hermann Linder (1948), that Aristotle recognized man as having the highest relative brain weight in all animals, but that he did not correlate this observation with the intellectual development of the human species. He indeed believed that the main function of the brain is to serve as a radiator, cooling the blood of the body:

> For of all the parts of the body there is none so cold as the brain; . . . nature has contrived the brain as a counterpoise to the region of the heart with its contained heat, and has given it to animals to moderate the latter, combining in it the properties of earth and water. For this reason, it is that every sanguineous animal has a brain. . . . The brain, then, tempers the heat and seething of the heart. In order, however, that it may have itself a moderate amount of heat, branches run from both blood-vessels, that is to say from the great vessel and from what is called the aorta, and end in the membrane which surrounds the brain. . . . When the nutriment steams upwards through the blood-vessels, its refuse portion is chilled by the influence of this region [i.e. the brain] and forms fluxes of phlegm and serum. . . .

> Of all animals, man has the largest brain in proportion to his size; and it is larger in men than in women. This is because the region of the heart and of the lung is hotter and richer in blood. This again explains why man, alone of animals, stands erect. For the heat, overcoming any opposite inclination, makes growth take its own line of direction, which is from the centre of the body upwards (Parts of animals translation, Barnes 1964, p. 1015f).

Since those high school days, I have assumed that Aristotle supported the hypothesis that the heart and the blood are the instruments of sensation and intelligence (Parts of animals, p. 647) and the brain only serves as a cooling radiator just because he wanted to tease his teacher Plato, who claimed that the brain was the seat of the immortal, divine part of the tripartite soul. In Plato's model, the two mortal components, the animal and the vegetative soul, are seated in the spinal cord or the liver respectively (Timaios, 73 B-E). Falk's radiator theory finally brings peace to the contradictory views of the intellectual heroes of Greek antiquity and puts the hypothesis of Aristotle as a *conditio sine qua non* of Plato's view on brain function.

Brain and body temperature. As the textbooks of physiology and biochemistry (e.g. Stryer 1981, Schmidt & Thews 1989) tell us, the daily metabolic rate of the human brain comes from the oxidative metabolism of about 120g glucose corresponding to 420 Kcal. The blood supply of the brain is in the range of 750 ml/minute, independent of whether man is at rest, working at a heavy physical task or solving complex mathematical equations. Only the *regional cortical blood flow* seems to change under the different load conditions, while the overall cerebral blood flow is kept constant by the sum of myogenic and metabolic auto-regulative mechanisms. From the two numbers mentioned, one can easily estimate the maximum *arterio-venous temperature difference*, assuming that only the blood flow through the brain removes the heat produced by metabolic mechanisms. One ends with a figure of 420 Kcal/2700 1 = 0.156° C. This value is well within the limits of daily fluctuations of body temperature.

Overall energy consumption, i.e., heat production, varies in adult man between an average of 1800 Kcal per day at rest and 6000 Kcal or more at maximum physical activity. Assuming a physically trained 70 kg male working at maximum strength for one hour during the "ecological niche of mid-day hunting" under hot and arid climatic conditions, his brain would produce about 17.5 Kcal per hour, which are dispersed in 45 liters of blood, while his muscular activity produces about 400 Kcal per hour, spread through about 750 liters of blood. This causes an arterio-venous temperature increase of 0.533° C in the blood flowing through the muscle. The question is therefore not how to cool the brain under these conditions, but how to reduce the blood temperature elevated due to muscular work as quickly and as effectively as possible and prevent "overheated" blood from reaching the brain. The increase in body temperature produced by strenuous muscle work is about 23 times that produced by the brain. To disperse this heat into the surroundings by means of radiation, convection and evaporation *Homo* has developed several effective adaptive mechanisms in contrast to the nonhuman primates: nakedness, increased numbers of sweat glands at the body surface, adaptive sweating behavior (e.g. reduction of sweat salt content after adjusting to arid climate), preplanned water intake and salt balance. In addition to these mechanisms, some racial specializations have evolved, like skin pigmentation and short curly hair, which build a well-ventilated layer of moist air over the head during walking, thus protecting the skull against direct radiation from the sun. Since the surface of the head and neck is only 9 percent of the body surface, its contribution to balancing body temperature is modest. The trunk, and in particular the extremities, play a much greater role (Witzleb in Schmidt & Thews 1989). Body temperature equilibrium is seriously affected, for example, after bilateral amputation of the legs or large burn scars. Brain temperature increases when body temperature regulation by means of mechanisms *outside* the head-neck region becomes insufficient. Baldness, in my opinion, is also not an adaptation to hot climates, as bald people prefer to wear hats even in moderate sunshine.

The cerebral venous system. The venous outflow of blood in man differs indeed from that in quadrupeds. Clinical investigations on cerebral blood flow confirm that the blood supply between jugular veins and the vertebralis plexus alters with body position. What one has to keep in mind, however, is that this change does not shift the main blood stream from the direct intrathoracic inflow via the Venae subclaviae to the intraspinal part of the vertebrate venous plexus. As every textbook of human anatomy teaches, there are effective direct connections between the vertebrate plexus and the *Vena subclavia*, i.e., this section of venous blood flow is also under the control of respiratory change in intrathoracic pressure. Nevertheless, venous outflow through the intraspinal part of the vertebrate plexus is increased in erect man. Due to continuous gravitational forces, this part of venous outflow from the brain would guarantee a more constant flow. This does not contribute essentially to regulation of brain temperature, however, as seen in astronauts living in the weightless state for weeks or months and showing no evidence of disturbed brain function due to circulatory or temperature problems, despite the fact that their daily work load corresponds to about 3000 Kcal. They do show a marked swelling of the face, however, and, even more important, a considerable amount of extracellular fluid is redistributed through the body, leading to an increase in extracellular fluid volume in the intrathoracic space (K. Kirsch, personal communication 1989, cf. also Thornton & Ord 1977; Blomqvist et al. 1980). I agree with Falk that the changes in venous blood outflow from the brain associated with upright posture occurred automatically when hominids began to walk in an erect position. This change, however, is caused only in part by gravitational forces. The change in shape of the cervical vertebrate column from a curved s-shape to a straighter structure is also a factor (Vidal et al. 1986), decreasing the functional resistance in the intraspinal part of the vertebrate venous plexus, which is indeed also present in quadruped primates. Increased venous outflow
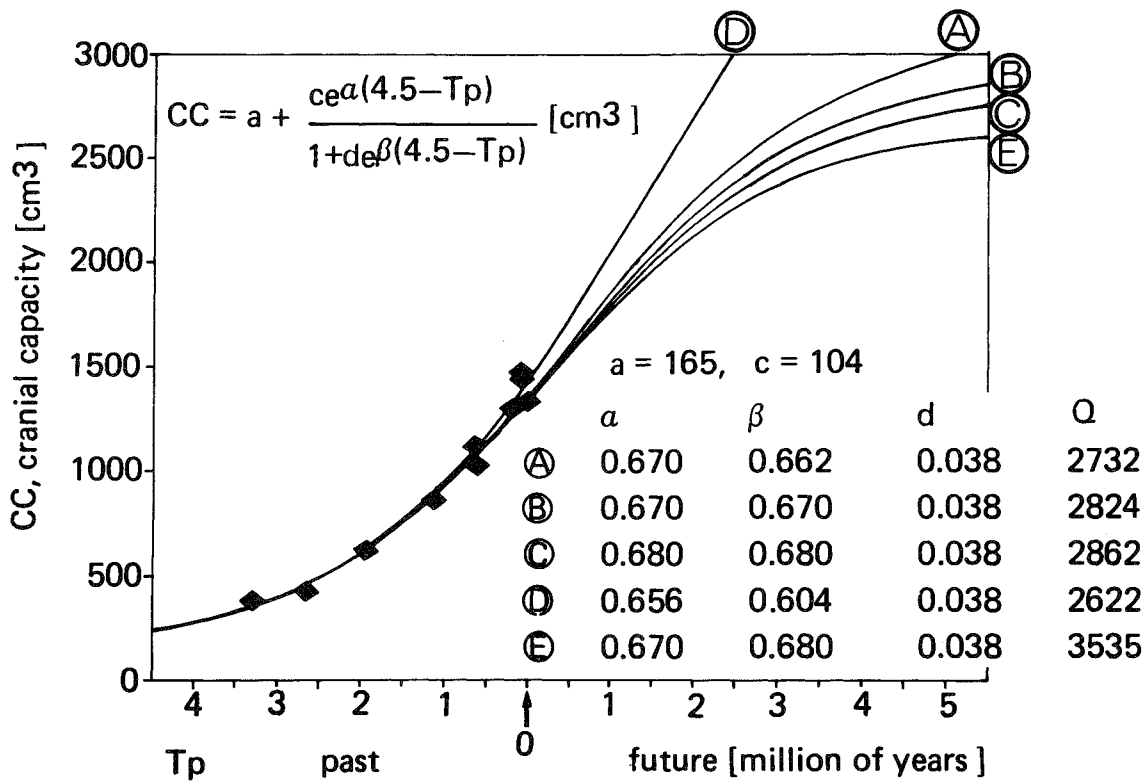
Figure 1.   (Grüsser). Phylogenetic brain growth function (cranial capacity, CC) as a function of time T_p, (eq. 1). Curve A fits data best, whereby CC values for present-day man (1345 cm³) were weighted by a factor 7. The individual data points are mean CC-values taken from the literature (Grüsser & Weiss 1985).

is a byproduct of erect position and was used *after* brain size had increased.

Multiple causes and effects in hominid brain evolution. In rejecting Falk's radiator hypothesis, I wish to draw attention to some recent quantitative studies on phylogenetic growth of the hominid brain (Grüsser 1982; Grüsser & Weiss 1985; Grüsser et al. 1985). From the relevant literature, estimates on dating (T_p), average brain weight or endocranial volume (CC) and body height of different hominids and present-day man were collected. In addition, a list of individual data on CC and T_p in 92 specimens ranging from *Australopithecus afarensis* to *Homo sapiens sapiens*, provided by Dr. K. Jacobs, at that time at the Department of Anthropology, University of Texas, Austin, was used for model computations. From the averaged data (Figure 1) a phylogenetic brain growth function was derived:

$$CC = a + ce^{\alpha(4.5-T_p)}/\{1 + de^{\beta(4.5-T_p)}\} \; [\text{cm}^3] \qquad (1)$$

whereby a, c, d, α and β are constants and T_p is measured in millions of years. The exponential function in the numerator lumps together all "progressive" components of the increase in hominid brain size, while the term in the denominator represents all inhibiting factors in phylogenetic brain development. This equation is also very applicable to individual data from *Homo habilis* to *Homo sapiens sapiens* (Figure 2, for detail see Grüsser & Weiss 1985). It turned out that optimum fitting functions were obtained when α approximated β.

Because of the scatter in the paleoanthropological data caused by the uncertainty of dating, errors in estimating cranial capacity as well as the variability of CC, it is difficult to recognize nonmonotonicities in hominid brain evolution superimposed on equation (1). There was presumably an initial "kick" in hominid brain evolution, caused by rather effective genetic mutations occurring at the transition period between *Australopithecus afarensis* and *Homo habilis*, but other mutations or "chaotic"

changes in brain growth conditions might have occurred later.

To analyse the data further, we tried to apply some statistical analysis, treating the data of Figure 2 as a random sample scattering around a monotonically increasing function. From the individual values plotted in Figure 2, "pairs of neighbours" of first to seventh order were formed. From these pairs "local differential quotients" (LDQ) were computed according to the following rule:

$$LDQ = (CC_n - CC_{n-j})/(T_{p(n-j)} - T_{pn}) \; [\text{cm}^3/\text{myr}] \qquad (2)$$

whereby *j* is the order of the respective neighbor, *n* the position of a specimen in the chronologically ordered list of data. The algebraic means of these "local" differential quotients were computed for time periods of 0.25 millions of years and plotted as a function of T_p (Figure 3). This transformation represents an estimate of phylogenetic growth velocity in the hominid brain (mm³/year), which can be compared with the derivative of equation (1)(= β, figure 3 dashed curve):

$$d(CC)/d(T_p) = -c\alpha e^{\alpha(4.5-T_p)}/\{1 + d\alpha e^{\alpha(4.5-T_p)}\}$$
$$[\text{mm}^3/1000 \text{ years}] \qquad (3)$$

With some reservations, one can conclude from Figures 1–3:

(a) The empirical data do not support the idea of Gould and Eldridge (1977) that in hominid brain evolution short periods of increase in hominid brain size alternated with longer periods of "punctuated equilibria," because hominid brain growth velocity during the last 2.5 million years was greater than null.

(b) There exists a not very robust statistical tendency toward acceleration in hominid brain growth in early *Homo habilis* and during the transition period between *Homo erectus* and *Homo praesapiens*.

(c) The data support the theory that human brain growth will continue into the future. From the data presented, this prediction is a more likely derivation than its contrary.
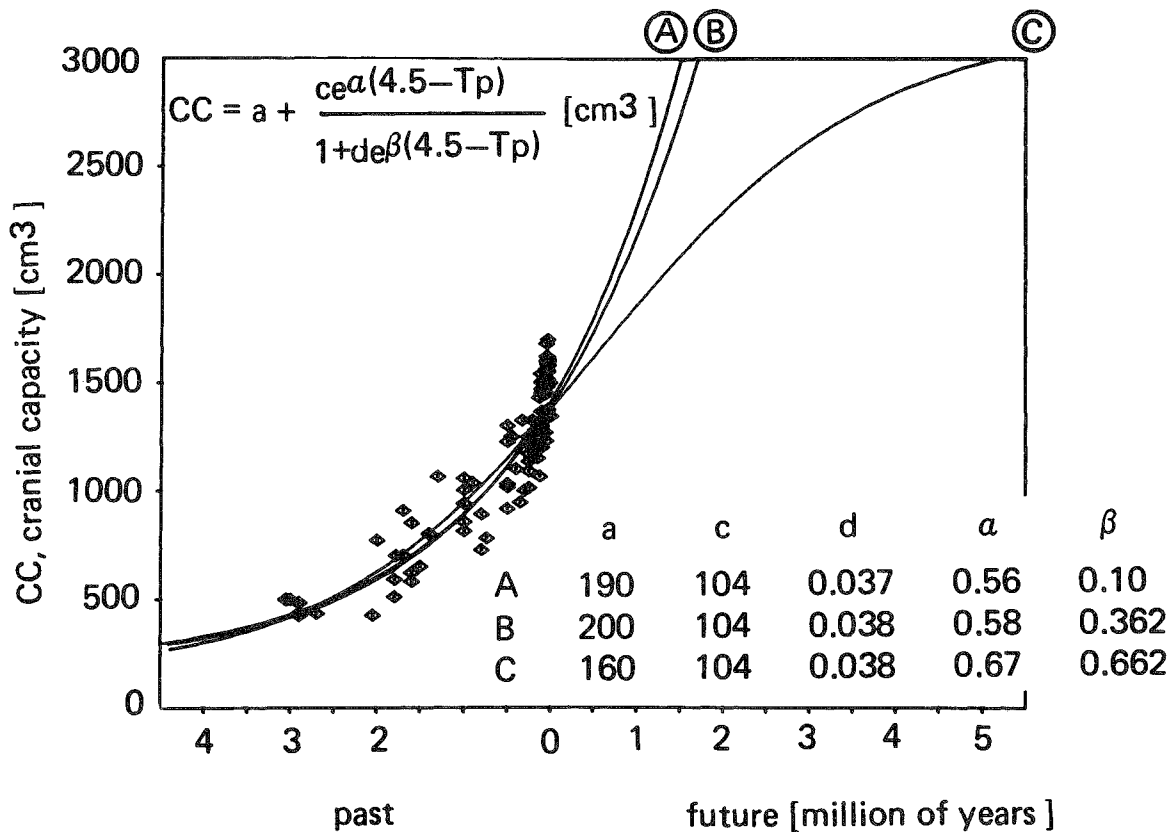
Figure 2. (Grüsser). Phylogenetic growth function of cranial capacity CC (ordinate). Data from individual specimens. Curve C corresponds to curve A of Figure 1 (Grüsser & Weiss 1985).

When predicting further phylogenetic brain growth relatively far into the future, the question arises whether the circulatory system could supply enough blood to the enlarged brain. I believe that a blood supply of up to 1250 ml/minute
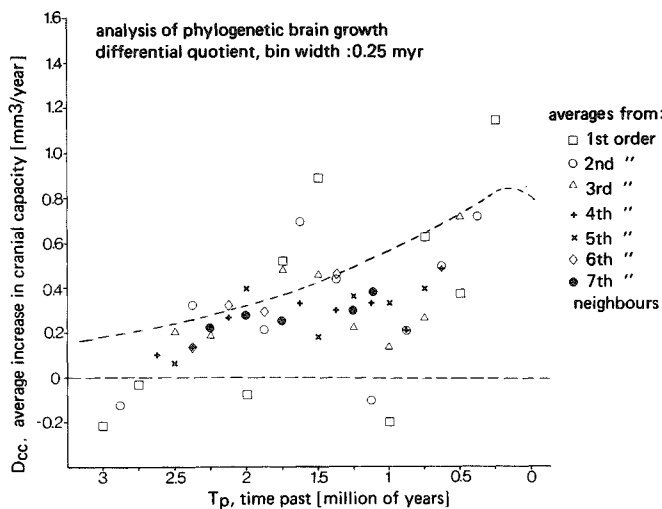

Figure 3. (Grüsser). Out of individual values of the data base "local differential quotients" were computed (explanation see text, equation 2) from neighbors of 1st to 7th order and the averages of these values obtained in bins of 0.25 million years were plotted as a function of T_p (abscissa). The dashed curve is the first derivative of equation (1) as expressed in equation (3). Dimension on ordinate mm³/yr. Note that maximum of the phylogenetic brain growth velocity is reached during the last bin.

could be provided to the human brain by the circulatory apparatus without great difficulty or fear of overheating of cerebral tissue. This argument is based on observations in human dwarfs with normal skull and brain size but a small body and a correspondingly shifted relative increase in brain blood supply. Their mental and physical capacity indicates that in an average-sized man the human neck muscle system and the blood circulation system would indeed be able to support a head with considerably increased relative CC-values.

In searching for the causes of a phylogenetic increase in the hominid brain and positive selection mechanisms, I think one has to analyze a whole network of contributing factors. In addition to some essential genetic mutations which may have occurred during the transition period between *Australopithecus afarensis* and *Homo habilis* and perhaps also between *Homo erectus* and *Homo sapiens sapiens*, one can find a multitude of causes acting as selection factors and interrelated to each other in feedback mechanisms; the following come to mind: Nakedness facilitated increased motor activity in arid climates, leading to a larger area of action for early *Homo* with a corresponding increase in probability of survival. Perception of extrapersonal space was enhanced when body posture became erect, as compared with quadruped locomotion, thereby increasing chances of survival in the open savannah. The hands became free to improve tool making and in particular tool application during locomotion. This led to a differentiation in social organization due to tool implementation in group hunting and dividing up the catch. The long-range planning necessary prior to hunting, tool manufacture, and the fabrication of water bottles (from skins) all increased the hunting efficacy of the socially organized group. Water taken on the hunt automatically extended the action radius of *Homo*. Furthermore, tools bettered their chances against the enemy. All these factors raised survival probability, as did improvement in long-term planning and

topographic memory. The gradual increase in intelligence, correlated with brain size, changed the strategies of partner selection, presumably improving mating chances for both men and women, and led to better care of offspring on the part of the more intelligent mothers. I am also of the opinion that the quality of stone tool production ("protoesthetics") was a selective factor, especially for females, in the choice of a mate. Together with a self-rewarding mechanism for successful tool production, this could explain the enormous over-production of stone tools found at some sites.

Finally, it should be mentioned that brain growth and neocortical differentiation with the development of "new" cytoarchitectonic cortical areas during hominid evolution was accompanied – at least during the last half million years – by the development of neocortical brain regions, utilized for quite different tasks, depending on the respective state of human society. For example, reading and writing have been in existence for not longer than 6,000 years (Földes-Papp 1975). An analysis of some "abstract" drawings in cave paintings of *Homo sapiens sapiens* or engravings on bones as rudimentary precursors of writing indicates that this cultural activity of man goes back at most 30,000 years. One can exclude the possibility that a cortical region specialized for reading and writing had developed during such an extremely short period. Nevertheless, we know that the symptom of *alexia* with or without *agraphia* appears when a right-handed patient suffers from a left parietotemporal lesion. Competence in reading and writing evidently requires a certain cortical area, which either developed as nonutilized "surplus-structures" during phylogenesis of the hominid brain (not very probable) or was and is used in illiterate societies for other tasks. We think that visual *pars-pro-toto* functions (e.g. recognizing fire when you only see smoke) or reading animal tracks, undoubtedly an important faculty for the hunting *Homo*, are subserved in the analphabet by those parieto-temporal areas used in literate man for reading and writing (Grüsser 1988).

One can easily argue that all the factors mentioned above not only contribute to phylogenetic brain growth but also interact with each other, especially in mate selection and protection of offspring. They thus serve as a complex Darwinian mechanism for phylogenetic increase in hominid brain size and support the genetically programmed "internal trend" of this development considerably.

Upright posture and cranial hemodynamics in humans and other "tall" animals

Alan R. Hargens and J.-Uwe Meyer
Space Physiology Laboratory (239-17), NASA-Ames Research Center, Moffett Field, CA 94035
Electronic mail: *ahargens@nasamail.nasa.gov.*

Falk presents an interesting but rather speculative "radiator" theory for brain evolution in humans. Much of her theory revolves around the argument that cranial blood flow is aided by adaptations of the anatomy and physiology of veins that drain the head. Normal blood perfusion to the brain, however, depends more on input pressures of arteries and arterioles that feed intracranial capillary vessels rather than venous drainage. By way of an extreme example, a primary adaptation to upright, tall posture in the giraffe is elevated arterial blood pressure at the heart level. This natural hypertension maintains normal blood pressure and blood flow at the level of the head (Van Citters et al. 1968; Hargens et al. 1987). Other mechanisms that control local blood flow and capillary perfusion include hormonal, metabolic, and myogenic regulations of smooth muscles within the arterial wall (Guyton 1986).

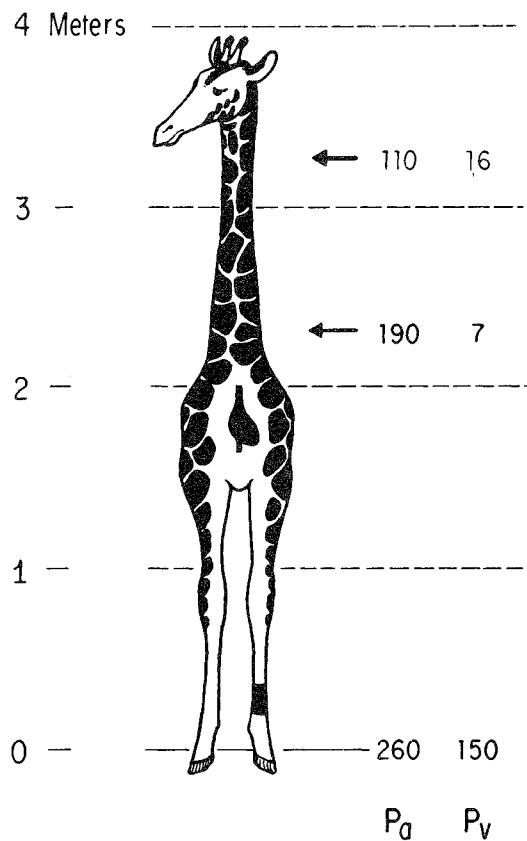Contrary to Falk's statement in section 3, para. 3, gravita-

Figure 1. (Hargens). Mean arterial P_a and venous P_v pressures in the giraffe at hydrostatic levels between the head and feet during upright, standing posture. All pressures are in units of mmHg. Modified from Hargens, Millard, Pettersson, & Johansen 1987. (Reprinted by permission from *Nature* 329: 59–60. Copyright © 1987 Macmillan Magazines Ltd.)

tional pressure effects are more pronounced in the arterial rather than the venous system. As evidenced by directly measured blood pressures in the giraffe (Figure 1), arterial pressures match to a large extent the difference in hydrostatic height between the heart and a specific artery, whereas venous pressures do not (Hargens et al. 1987). In fact, the blood pressure gradient down the jugular vein is about one-tenth and in the opposite direction of that expected for a column of blood from the top of the neck to its base. This nonhydrostatic pressure gradient down the giraffe's jugular vein along with the aforementioned myocardial hypertension suggest that blood cascades from the head down the neck and that no siphon-like mechanism aids cerebral bloodflow (see also Seymour & Johansen 1987).

Falk indicates that blood preferentially shifts from the jugular drainage to the vertebral plexus because the latter has a greater number of vessels with smaller diameters. Unfortunately, for this mechanism to operate, the number of small drainage vessels must be extremely great, because blood flow Q is directly proportional to the fourth power of the vessel's radius r according to Poiseuille's law:

$$Q = \frac{\pi \Delta P r^4}{8 \eta l}$$

where ΔP is pressure gradient along the vessel, η is blood viscosity, and l is blood vessel length (Guyton 1986). Thus, vessel radius is by far the most important factor regulating local blood flow. Hence, the logic of Falk's argument is not very convincing with respect to the importance of numbers of veins versus vein size.

Falk's radiator hypothesis

Ralph L. Holloway

Department of Anthropology, Columbia University, New York, NY 10027

Given that the human brain represents about 2% of body weight and consumes approximately 20% of our metabolic resources at any given moment, there would be a certain appeal to an hypothesis which recognized this and tied it into a synthesis with hominid mosaic evolution. Unfortunately, what is offered here is a large mass of indigestible speculation, and some rather remarkable transformations of fancy into reified "facts" of which Falk seems to be convinced. Examples: "Selection for the radiator of *all* emissary veins . . . appears to have released a thermal constraint that limited brain size in other hominids and pongids . . ." (Figure 5 legend). Or: "The Hadar and robust australopithecine and the gracile australopithecine through *Homo* lineage have different systems for draining blood from the cranium. In the former, an enlarged O/M sinus *has been selected for and fixed* whereas emissary foramina of robust australopithecines *occur in frequencies approximating . . . those of apes . . . high frequencies of emissary foramina are selected for over time.* (emphasis added; Figure 4, legend).

There is not a shred of empirical evidence that natural selection has worked on these venous drainage patterns. One cannot test whether or not the *apparent* high frequency of the O/M drainage system in robust australopithecines was a polymorphism, one end of which could have become fixed in the O/M direction purely through *random genetic drift*. No empirical evidence exists that brain size is limited by a thermal constraint (beyond metabolism), either within, between, or among species! Increase in brain size among hominids, including between early and late "robust" forms, or between *Homo habilis* and *Homo erectus*, could be attributed to increase in body size, as there is some reasonable evidence for brain-body size correlations that are statistically significant, even within species (see Holloway 1980). Falk's scenario ignores this possible avenue.

How many times is it necessary to reiterate to physical anthropologists that a correlational analysis is not a causal analysis? Thus, there is no solid empirical evidence for any of the following:

1. a selective advantage to either drainage system in hominids, apes, living human, or even monkeys;

2. that any significant relationship exists between brain size and adaptive behavioral repertoires (read "intelligence," or "information processing," two terms often used to cover our ignorance) either within or between species of primates whatever Van Valen's (1974) musings and Falk's conjectures;

3. a causal or biologically meaningful relationship between either form of the drainage pattern and bipedal locomotion; that is, there is no evidence to indicate that some subset of bipedal locomotor variability correlates with any subset of variability in venous drainage pattern;

4. a clear separation of the ecological habitats or locomotor and behavioral adaptations between early and late robust australopithecine hominids and even earlier gracile ones, and those constituting early *Homo* (speculations abound, but evidence is simply not there);

5. that cooling of the brain during hyperthermia (caused by any behavioral patterns including bipedalism) *inadvertently*

removed a constraint that previously prevented brain enlargement;

6. that a constraint of *any kind* was against previous hominoid or earlier hominid brain enlargement;

7. an understanding of the nature of the exact interrelationships between those features of "mosaic evolution" mentioned by Falk, such as bipedalism, brain enlargement, brainbody allometry, reorganization, selection for venous drainage patterns, freeing of the hands, reduction of cortical areas devoted to toes being co-opted for the hands, language, etc. These are unknown, probably unknowable, and are presently nontestable;

8. the idea that bipedalism arose to reduce surface area receiving solar heat loads first suggested by Fialkowski is interesting. How can one ever demonstrate, however, a connection between standing upright to reduce body surface area from the fossil record? At best, Falk's speculations agree with Fialkowski's speculations.

At this level of speculation, I could easily assert that as the Pliocene progressed and aridity increased, the distances between shade trees increased and hominids developed bipedalism so that they could stand in the shade during midday more easily, thus reducing the risk of hyperthermia, inadvertently leaving the hands free to make sombreros.

But the problems with Falk's presentation here are more than simply reifying relationships that are undemonstrated. There are some serious problems with the data themselves. For example, is the Omo 338 specimen regarded as a part of the robust sample? Taung? There is no consensus on these or other specimens. Where is there any evidence for O/M drainage in any of the recently discovered early robust hominids, for example, WT 17000? The disposition of the sigmoid sinus is not support for an O/M drainage pattern missing in the originals. Given the sorry state of most fossils in the mastoid and parietal regions of the basal and dorsal cranial regions, how can one be certain one is correctly scoring emissary veins or O/M drainage patterns? In general, the older the hominid specimens geologically, the more damaged they are. Are parietal emissary veins related to brain cooling or to some other physiological function? What do differences between 25, 50, and 75% mean when the sample size for different hominid groups is less than five in many cases? Where, incidentally, is there any evidence (in light of the above) for "continued elaboration of the radiator" suggested by Falk's Figure 5? In that same paragraph (p. 15) Falk cites herself (Falk 1980a) as the source for the fact that *Homo* has three times as much brain weight as would be expected for a primate of its body size. Surely she must be aware that Passingham (1973; 1975a) showed this much earlier. This was common knowledge in the '70s (e.g., Radinsky 1978), once allometry came into vogue, and was probably appreciated in the 1960s by Jerison and Stephan, among others.

In short, whatever the proposed virtues of a "mechanistic theory," I think the radiator theory has too many leaks to be taken seriously.

Welcome light on a hot topic

Harry J. Jerison

Department of Psychiatry and Biobehavioral Sciences, UCLA Medical School, Los Angeles, CA 90024
Electronic mail: *JERISON@DTUMPI51.BITNET*

This delightful, original, and superbly documented contribution was so much fun to read and so convincing that it is almost above criticism. The basic ideas are completely acceptable, and it now seems obvious (having read Falk) that the hominid brain did not become enlarged until there had been earlier evolution

of a good radiator. Falk's evidence is convincing. Her paper will be a classic in paleoanthropology.

It may be a classic, but it would be insulting not to criticize, so I offer these criticisms in a constructive spirit. The crucial issue for me remains the selection pressures that may explain evolutionary changes in the brain, and Falk's concluding remarks, "beyond the radiator theory," should be read carefully. I would emphasize even more than Falk that intelligence in the evolutionary sense must be "multifaceted." "Multidimensional" may be an even better word to suggest that there must be many varieties of intelligence that are reflected by the many places in the evolutionary tree in which encephalization has appeared. For example, rats and stoats (ermines) are similar in body size and must have similarly effective radiators, but the stoat has about twice as much brain for its body size (Kruska 1988). The explanation for its encephalization must lie in the adaptations (which must require more brain tissue for their control) of this small carnivore as compared with the rat. My inclination, like Falk's, is to call such adaptations intelligent (Jerison 1985), but except for the dimension of information-processing capacity, they are likely to be quite different from those involved in human intelligence.

I wish to comment on two more points, although not crucial to Falk's analysis, points she mentions that are important for comparative and evolutionary neurobiology. Early in her paper, Falk quotes Holloway to the effect that one cc of brain in humans is not equivalent to one cc of brain in chimps. This is sort of an obvious idea, but it is wrong in a fundamental way. It may sound right, because species-typical behaviors must be controlled by species-typical systems in brains, and these must be different in different species. But it has been extraordinarily difficult to pinpoint such differences. In fact, modern neurobiology is based on the assumption that small pieces of tissue from homologous brain structures of different species, including the human species, are basically similar, both structurally and functionally (White 1989). "Small pieces," incidentally, are of the order of cubic millimeters rather than centimeters, for a proper metaphor that reflects the order of magnitude of biological neural networks that can be analyzed at this time. A correct statement would then be that a cubic millimeter of homologous brain tissue from a chimpanzee and a human (and presumably an australopithecine) are, to an unusual extent, equivalent, and one could extend this to rats and cats and rhesus monkeys, to reflect functional thinking in neurobiology. The surprise is that the statement, which appears to be true for the rest of the neocortex, fails in the visual system. Primary visual cortex is "equivalent" in all mammals with the exception of the "higher" primates (monkeys, apes, and people). Primary visual cortex is also equivalent within the "higher" primates, including monkeys and people (Rockel et al. 1980).

The crucial issue in differentiating species concerns brain homologies. At the cellular level, most of us would consider the various specialized nerve cells, such as pyramidal or stellate cells, as homologous, various nuclear structures such as mammilary bodies or basal ganglia as homologous, and primary auditory or primary visual neocortex as homologous. (I am treating the problem of homologies in the nervous system a bit cavalierly. Brains are phyletically diverse enough to support cladistic analysis from brain trains, for example, as in Johnson et al. 1982.) This is why the difference between higher primates and other mammals was so surprising, because it can be interpreted as showing that at least some features in the primary visual systems are not homologous among all mammals. The reorganization of the brain that has accompanied the evolution of different species has been with respect to the homologous systems. We may thus recognize that the "higher" primate primary visual system probably evolved when the ancestral "higher" primate first appeared, during the Oligocene epoch, some 30 million years ago, or earlier.

The unique feature in the organization of the human brain is the presence of very large language areas (and homologous structures in the "nonlanguage" hemisphere), but even for the language area, the identification of species differences is surprisingly difficult. It is apparently true that there is an unusual, perhaps unique, pattern of dendritic arborization in Broca's area (Scheibel et al. 1985), but on the whole one cannot recognize tissue from language areas as different from those of other nonvisual sensory regions of the human or other mammalian neocortex, except for differences related to absolute (not relative) brain size. The differences in pattern are between hemispheres within the human brain, of course. A Broca's area has not been identified in chimpanzees; if it were, the first hypothesis would be that it would be differentiable from its homologue in the other hemisphere by the same kind of difference in the pattern of arborization as that in the human brain.

The second point has to do with the puzzle of within- and between-species differences and the brain-intelligence connection in people. I have no idea why within-species effects are decoupled from between-species effects, but the decoupling occurs for anatomical as well as physiological and behavioral dimensions. There is an almost perfect correlation between cortical surface and brain volume between species (log data; r = 0.995). The correlation is much lower and may fall to zero within species. I discuss this in Jerison (1982b), and the issue is reviewed from an evolutionary perspective by Lande (1979). The decoupling, which Falk mentions, is worth special study, but until it is understood we must continue to recognize that encephalization is a between-species (or between-genera) higher order evolutionary phenomenon, and within-species effects are still poorly understood.

I would like to indicate, finally, that I come down with the language advocates in prime-mover theories mainly because of the uniqueness of the human brain with respect to the language areas. Language is the Rolls Royce of brain adaptations, run by a massive brain system. And I accept Falk's view that it could evolve only because a radiator was in place to cool the engine.

The radiator hypothesis: A theory in "vein"

William H. Kimbel
Institute of Human Origins, 2453 Ridge Rd., Berkeley, CA 94709

Central to the value of Falk's hypothesis are the paleontological data. The sole evidence for the basal portion of the "gracile australopithecine" lineage is one specimen from Laetoli (ca. 3.5 Myr). This specimen, L.H. 21, was shown to have the transverse-sigmoid (T/S) drainage pattern (Kimbel 1984), on which basis Falk separates the *entire* Laetoli *A. afarensis* sample from that of Hadar, which has the occipital/marginal (O/M) system. Since Falk contends that the O/M pattern is "fixed" in "basal robusts," this is a very convenient taxonomic operation; the pattern is "fixed" so long as every departure from it is excluded. Variation in cranial venous drainage patterns among and within extant ape and human populations, also documented throughout the hominid fossil record (Kimbel 1984; Falk 1986), militates against separating the Laetoli and Hadar specimens at the species level on the basis of this character alone. (Falk appeals to Tuttle for support, but Tuttle's [1988 p. 399] most recent review concludes that "critics of the single-species hypothesis [that *A. afarensis* constitutes one species] have not assembled adequate

compelling evidence against it.") Falk's confused approach to hominid systematics is illustrated by her treatment of the Taung skull, the type-specimen of *A. africanus* ("gracile australopithecines"). Here, Tobias & Falk (1988) have found evidence of an enlarged O/M system in a species previously considered to show fixation of the T/S drainage system. The analogous taxonomic conclusion, however – that the Taung specimen is a "robust australopithecine" (as the type specimen, it will *always* be *A. africanus*) – is avoided.

Although not apparent in the present article, Falk's arguments regarding the appearance and significance of the network of emissary veins is based on a single feature (the mastoid foramen) in a sample of only 14 "scorable" crania spanning the nearly 2.0 Myr leading to *H. erectus* (Falk 1986). Falk combines what virtually all workers consider to be distinct species, *A. robustus* and *A. boisei*, into a single "robust australopithecine" category – obscuring the fact that 50% of the small *A. robustus* sample (4) has this feature, whereas 40% of Falk's comparably small "gracile" group (5) shows it. This is the reverse of Falk's expectation, and in view of the limited samples representing *A. afarensis* (1) and *H. habilis* (0!), I can find no trend whatever in the pre-*H. erectus* record of emissary foramina. Falk adopts the ad hoc position that South and East African "robusts" constitute "races" of one species (see also Falk 1988), a handy, but epistemologically problematic, taxonomic retreat in which a few paleoanthropologists find refuge from the primary data of phylogeny.

Falk attributes a major role to the O/M system and emissary veins in channeling venous blood to the vertebral plexus based on the experiments of Epstein et al. (1970) and Dilenge & Perey (1973) on rhesus macaques (*Macaca mulatta*). Although these workers demonstrated that much of the intracranial venous blood exited through the vertebral system when animals were in the upright position, rhesus macaques lack an occipital sinus (Weinstein & Hedges 1962) and Epstein and co-workers (1970, p. 336) "saw little evidence" of the role of emissary veins in cerebral venous drainage in their subjects! Venous blood may reach the vertebral system in the absence of flow within these structures, via the sigmoid sinus, which links the vertebral and internal jugular systems with the superior petrosal, petrosquamous, and transverse sinuses (Padget 1957). This suggests that enlarged O/M sinuses, or an elaborate network of emissary veins, are *not* a necessary condition for the drainage of a significant proportion of venous blood through the vertebral system.

Falk's belief that there was a selective advantage to the T/S system in the "gracile"-*Homo* lineage depends entirely on the assumption that this primitive retention was secondarily complemented by an elaborate network of emissary veins that evolved *only* in this lineage *simultaneously* to assist in draining venous blood to the vertebral system with the adoption of habitual upright posture *and* provide a cooling mechanism for the brain in hominids subjected to hyperthermia in the "hot African savanna mosaic." Since bipedalism presumably evolved only once in the ancestry of hominids, what is the differential selective advantage of alternative venous drainage routes (O/M vs. T/S with emissary assistance) if, as Falk suggests, most of the blood is channeled preferentially to the vertebral system in all upright hominids irrespective of drainage route? Indeed, in reference to the enlarged O/M system in the Taung specimen, Tobias & Falk (1988, p. 312) conclude that "we may be dealing with a genetic polymorphism that expresses itself with widely varying frequencies among populations of ancient and modern hominids." This bears more than a superficial resemblance to my own conclusion (Kimbel 1984).

Furthermore, while selective brain cooling in humans seems to be a reasonable expectation under conditions of induced hyperthermia, the principal means of brain thermoregulation in such circumstances is through heat exchange in the cavernous sinus between warm carotid blood and venous blood cooled by evaporation from the moist nasal mucosa and facial sweating (e.g., Baker 1982; Cabanac & Caputa 1979; Dean 1988). As this same pattern of venous flow to the cavernous sinus is common to many mammals (with and without a carotid rete), including higher primates, does Falk doubt that it was also present in all early hominids? Falk severely misinterprets Cabanac & Brinnel (1985) by suggesting that the presence or number of visible emissary veins is a reflection of the size and significance of the entire emissary network, whereas these authors merely used these vessels (which in any case communicate with outflowing blood in the dural sinuses) to determine the direction of blood flow under different thermal conditions. This error would presumably lead Falk to conclude that the lack of osteological indications of emissary veins in a species means that said species also lacks the entire emissary network! This does not lend confidence to the logical extension of Falk's theory that "robust" early hominids possessed a brain cooling mechanism less effective than that which cooled the small brains of their "gracile" cousins. The brain cooling role of the emissary veins draining the posterior part of the head is, and remains, conjectural.

Finally, Falk plunges into pure speculation, propping up a shallow hypothesis with a cartoon-like adaptationist narrative. Citing Blumenschine (1987) in support of the fantastic statement that "postural changes allowed early hominids to open a noonday scavenging niche" does not do justice to the careful work this author and others have done to elucidate clues to early hominid scavenging activities. What evidence is there to support the attribution of a scavenging niche of *any* kind to *any* hominid prior to the appearance of *H. habilis* at ca. 2.0 Myr, at least 2 Myr subsequent to the advent of hominid bipedalism? What is the evidence to suggest that *if* early hominid foraging produced the degree of overheating observed under laboratory conditions of induced hyperthermia then such a fate was reserved for members of one lineage only ("evidence" of emissary veins notwithstanding)? Falk presents Shipman & Harris' (1988) inferences regarding the preferred closed/wet habitat of East African "robust australopithecines" as uncontested findings, ignoring Vrba's (1988, p. 420; see also White 1988) critique, which concludes that the distribution of *A. boisei* across East African habitats "does not depart significantly from random." Vrba further concludes that the "gracile" species *A. africanus* occupied wetter, more wood-covered, mesic habitats than did the later South African "robust" species *A. robustus*, the reverse of Falk's claim based on an uncritical acceptance of Robinson's adoption of Brain's (1958) misinterpretation of the South African hominid-bearing cave breccias (see Grine 1981). Nor is there any evidence from the earlier part of the hominid-bearing record to sustain the proposed sharp ecological divergence between Falk's "basal robust" and "basal gracile" species (Andrews 1989; Bonnefille et al. 1987). Put simply, Falk has erected a fictitious Pliocene world within which to accommodate a hypothesis based more on conviction than on a sound data base and the logic of scientific method.

Relating brains, blood, and bipedalism

Grover S. Krantz
Anthropology Department, Washington State University, Pullman, WA 99164-4910

Falk's target article is an attempt to answer "the perplexing question of why bipedalism preceded the dramatic increase in brain size in *Homo* by at least 1.5 million years." The clear assumption is that these two traits ought to have evolved together. Given that birds and kangaroos are also bipeds, and so were half of the dinosaurs, I fail to see any necessary connection between bipedalism and brain size.

That intelligence is related to brain size is clear in Falk's view

– and in mine, as well. That all animals would select for increased brains if they could seems equally obvious. But whether the brain's cooling system has been a major constraint is less clear. The nutritional requirements of rapidly building a functioning brain in each individual are a major problem; supplying that organ throughout life is an unparalleled metabolic drain. Cooling the brain seems almost trivial by comparison.

Falk's paper presents an interesting and valuable compilation of information on hominid cranial circulation, but the relevance of all aspects to each other is sometimes unclear. The following are some of the problems I noticed.

Clearly an endocranial cooling system is needed with enlarged brains, but it seems unwarranted to imply that its absence will *prevent* that enlargement. One could view the emissary vein system in *Homo* as a cooling device that developed rather easily *along with* brain expansion, as needed. Treating it as a precondition is almost like saying horses had to evolve tall molar crowns *before* they could adapt to grasslands. I also fail to see any reason why the cooling system described (or a similar one) could not have evolved in the robust Australopithecine lineage – if they had any need for it. After all, the gracile lineage evolved this system from a precondition of its absence.

It was interesting to learn how giraffes handle blood flow from their lower parts (though it has no relevance to the problem at hand). That "muscle pumps and antigravity suits may come into play for humans as well" was a puzzling statement. It is well known that humans have "muscle pumps" in their leg veins. It is equally obvious that we do not have a good "antigravity suit" of tight skin and fascia in our legs.

Modern anatomical data cited by Falk do *not* demonstrate, as she claims, that the occipital/marginal (O/M) sinus is designed to drain directly into the vertebral plexus. What is shown is that it can drain there *or* into the jugular. Thus we do not know for sure which way the O/M sinus drained in the Hadar and Robust Australopithecines.

Falk rightly points out the high density of sweat glands on the human forehead but she fails to note their scarcity on the rest of the scalp. Cranial hair neutralizes the evaporative cooling effect of the little moisture that occurs there. The emissary veins of the parietal and mastiod foramina can hardly be part of the "radiator."

The most disturbing part of the entire paper stems from the clearly stated contrast between the two functions of our emissary vein system. We are told that during upright stance these veins pass blood *out of* the braincase and send it on to the vertebral plexus. We are also told that during hyperthermia these veins pass cooled blood *into* the braincase. Thus, blood flows in either direction, depending on the circumstances. The problem here is that while foraging in midday and under maximum heat stress, the body is also normally erect. Which way does the blood flow – *in* for its supposed cooling effect, or *out* from hydrostatic necessity? You can't have it both ways at the same time.

Despite the negative tone of the foregoing paragraphs, I do see some important work here. Venous blood return from the high-perched head, and cooling of the brain contained within it, remain as anatomical problems that were handled by our ancestors. How the two are or are not related may require more study. Falk's paper provides much data and opens an area of investigation that has been barely touched upon until now. If Falk has not hit the nail on the head, at least she has not smashed her thumb in the attempt.

Have cooler heads prevailed?

John Limber
Department of Psychology, University of New Hampshire, Durham, NH 03824

Like the ancients, Falk speculates that human intellect springs, albeit indirectly, from the circulatory system. As I understand it, the idea is that developments in the cranial system of veins in gracile hominids, somehow triggered by the circulatory dynamics of bipedalism, resulted in a highly efficient brain "radiator" that was an important necessary but not sufficient condition for subsequent rapid growth in *Homo* brain size. Other hominids, lacking these developments and unable to take the heat of competition, were doomed.

Falk weaves an intriguing web of speculation around a variety of facts and plausible assumptions. I resist being even more enthusiastic about the theory because I do not fully understand it, perhaps in part because of my own ignorance of the primate cranial circulatory system. I will try to organize my remarks around, first, a number of questions and problems that I have with the "radiator theory," and second, a few obvious suggestions that may be more or less useful in furthering that theory.

I have no doubt about the fundamental importance of emissary veins in cooling the brain. What I do not quite follow is the logic of the argument relating differences between "robust" and "gracile" blood drainage systems to the – presumably – differential evolution of these emissary veins. Granting for the moment a fundamental difference here in response to bipedalism, I do not yet understand how the causally effective "cooling" emissary veins evolved in *Homo because* of either the lack of the enlarged occipital/marginal (O/M) sinus or the presence of the transverse-sigmoid (T-S) sinus. In terms of the author's figures, I want to understand better why the diagram in Figure 2A – but not that of 2B – leads to the emissary foramina in Figure 3. Falk rejects Kimbel's (1984) suggestion that both systems are "functionally equivalent," yet I am unsure as to what "function" is at issue. Kimbel simply seems to be concerned about venous drainage and does not see any adaptive advantage in one over the other. In contrast Falk – if I am reading between the lines correctly – is concerned about the *pre*adaptive value of the T-S system as a "radiator." This seems to be the core of the "radiator theory" – one functionally equivalent drainage variant (T-S) inadvertently equips the individuals so equipped to benefit rather than suffer should they happen to develop a relatively large brain. This is the only conclusion that makes any sense to me; yet why doesn't Falk address this directly?

In the same vein, I am also puzzled about the evident variability in O/M and T-S structures. Are the 5% to 25% of humans with the large O/M configuration *"Homo hotheads"* and consequently less intelligent? Is it possible to explain a universal trait like language or the large human brain itself on a less than universal foundation? Even more ominous for my reconstruction of the "radiator theory" core is Kimbel's (1984) report that only 2 of 105 chimpanzees do not have T-S drainage.

Other related questions concern the development of these drainage systems. Is it possible that there is a developmental explanation of the structures? Several investigators (Browning 1953; Woodhall 1939) suggest that human neonates and infants have large O/M systems. One obvious similarity between these humans and Falk's "robust" hominid is cranium size. Could it be that the continued growth in *Homo sapiens* in itself tends to lead into the dominant T-S system? Of course, this could suggest that the "gracile" drainage system is a *result* of a larger cranium, not its cause. While the chimpanzee data above are not consistent with this simple idea, the factors involved in the developmental variability in human ontogeny may shed light on the between-species variability Falk is concerned with.

Similarly, can I be assured that the differences in emissary

foramina tallied in the somewhat obscure Figure 4 actually result from more or less direct genetic differences rather simply being *effects* of being bipedal? For example, would any large primate continuously maintained in an active upright position gradually develop larger and more pronounced, "pumped up" emissary veins, leading to more effective cooling and more readily observed foramina – and ultimately in the "radiator theory" – strengthening its mind?

All of the above issues aside, several direct empirical ways seem available to evaluate the "radiator theory." Does my brain heat up more as I am doing a given amount of work while in a prone rather than a vertical position? Physical models of varying venous drainage systems can be constructed – with and without hair and at varying angles to vertical – and their differential cooling properties directly quantified. With such data in hand, perhaps we could really understand something about brain evolution and the "radiator theory."

Boiling over in the great rift valley

Arnold B. Scheibel

Departments of Anatomy and Cell Biology, Psychiatry and the Brain Research Institute, UCLA Medical Center, Los Angeles, CA 90024

Falk has done us all a service in proposing her radiator theory in an effort to account for the amazing recent growth of the human brain. Most of the usual explanations are by now well known, including as they do (and as Falk summarizes them) social hunting, warfare, language, tool production, enhanced sexual and social bonding, and a number of others. Each probably played a part so all undoubtedly have some degree of validity. Bipedalism almost certainly set the stage but, as the author points out, that stage was set at least a million and a half years earlier. I think she is right in the broadest possible sense in suggesting that "intelligence was adaptive for hominids . . . and that bigger brains were better brains." Within this context, the radiator theory generates a good deal of appeal, especially when it is seen, again as Falk suggests, as a necessary prerequisite for the enormous brain growth that accompanied it.

For me, the principal problem is a quantitative rather than a qualitative one. Is the emissary vein system sufficiently regular in its appearance, and sufficiently robust in its dimensions to carry the volume of blood necessary to provide a significant temperature difference? This is not a trivial problem nor, I suspect, is the solution trivial either. Anatomical variability, especially that of vessel systems, and veins very much more than arteries, constitutes one of the givens of anatomical studies. A bit of reading of (unfortunately long-forgotten) texts and discussion with several colleagues confirms my own recollection of great diversity in paths, and in the number of the emissary vessels, and those loops, retes, and plexuses that lurk in foramina of the skull. If the magic key to enhanced brain growth of the past two million years indeed lies in this arrangement, would there not have been more convincing selection for this structural motif? One thinks of other examples of radiator systems developing in living forms from similar climatic settings. The elephant provides a dramatic case in point, with its enormous fan-like ears – structures sufficiently large and invariant to have developed secondary functions as signalling devices. The broad range of winged insects may provide another example. Many entomologists feel that wing-like extensions developed initially as cooling devices and were only later adapted as devices to permit flight.

I would like to see Falk collaborate with a group who can help her put her thesis to the test. Why not attempt blood flow measurements of individuals in various states of physical and intellectual activity or temperature loading? Noninvasive methods for studying blood flow are already in use. Resolution may

be the problem, but techniques for superposing of positron emission topography (PET) and magnetic resonance imaging (MRI) data are becoming available. These may allow certain conclusions to be drawn about the degree of blood flow shunting through the skull table under various states of activity, the degree of "distensability" available to such conduits, and the functional similarity or dissimilarity in these systems from one individual to the next. The last point may also be of more than passing interest in view of the frequently quoted information regarding Dean Swift's 2,000 cc brain vis-à-vis the 1,000 cc brain of Anatole France.

Clearly the Falk Hypothesis is audacious and, at first sight, even counterintuitive. All the more reason to try to put it to the test. Of one thing we may be sure. Right or wrong, it is not likely to be forgotten!

Overheated brains: Radiation of radiators?

Brigitte Senut

Laboratoire d'Anthropologie du Muséum national d'Histoire naturelle, UA. 49 au CNRS, Institut de Paléontologie du Muséum, Paris, France

My first reaction to Falk's target article is that the "radiator theory" is probably not going to cool down the debate on human origins and evolution, but heat the furnace of hominid phylogeny.

The differences in the venous drainage patterns in fossil hominids have been known since 1967, when Tobias pointed out the peculiar system present in *Zinjanthropus boisei* from Olduvai. Since then, the field of palaeoneurology has developed through new discoveries of skulls which have led to the extensive anatomical work of Falk. The new theory proposed here raises several diverse points and has the merit of trying to draw them together. However, several points of imprecision make it difficult for readers to follow Falk's path.

One major criticism is that nowhere in the target article can we find a complete list of the extant genera and fossil specimens, including their taxonomic attribution. This becomes critical in view of the hot debate about taxonomy in fossil hominids. For example, Falk considers KNM ER 1813 a "gracile *Australopithecus*" (e.g., *Australopithecus africanus*) in Figure 1 and supposedly in the rest of the article. What would have happened to the calculated percentages if it had been treated as *Homo habilis* (as is usually done by palaeoanthropologists)? Throughout the text, the African apes are considered as a single group, but does that group include *Pan troglodytes, Pan paniscus, Gorilla gorilla gorilla* and *Gorilla gorilla beringei?* Do we have an idea of the variation, if any, in the venous drainage among these?

Another main point is that the bipedalism of early hominids is treated without defining it: It is now widely accepted that early men were partly bipedal and partly climbers. Most primates do not have a single mode of locomotion; the same animal can move in very different ways (Fleagle 1980). In these cases, would the venous drainage system change with each type of movement or would it adopt an intermediate mode of circulation?

Another detail in Falk's paper seems difficult to accept: It is not because you do not walk bipedally that your hindlimbs are not weight-bearers; and if you are not a terrestrial biped, but a tree-dweller, you must be a grasper (see sect. 2, para. 5). But in climbing, the feet are also weight-bearers and not necessarily graspers! The pattern exhibited by early men does not exist today and is probably a composite one: They were neither chimpanzees nor modern men.

According to Falk, only the erect biped with his head up would show the transverse-sigmoid (T-S) pattern. What would become of the "supine" modern babies? Should we place them in another genus? What do we know about the ontogeny of

veinous drainage in man and apes? If Kimbel (1984) is right, human babies exhibit a pattern close to that of the adult, but they don't walk upright. How can we explain that? This point would deserve clarification. What would be the pattern in adult gibbons? One point not mentioned at all by Falk is the evolution of the shape of the brain. The main and obvious difference between man and nonhuman primates is the location of the *foramen magnum* as well as the occipital swing, which probably explains why the heads and necks of chimpanzees are not completely upright even during climbing. I have the feeling that we are dealing with correlated movements rather than cause/effect relationships.

I agree completely with Falk when she speaks of the "cliché of the freed hands" (understood for manipulative action). Bipedalism, in my view, never freed hands *sensu stricto*. All animals that manipulate (including man, probably), do so in a seated posture (cf. most nonhuman primates). I am surprised to see again this old image of the "large-brained *Homo*" as the manipulative animal. Since 1969, we know about the small quartz flake artifacts in the Shungura Formation in Ethiopia (see Chavaillon 1976; Coppens 1980); there is no reason why these couldn't have been manufactured by Australopithecines. Moreover, Susman (1988) has recently clearly demonstrated that *Paranthropus robustus* had the anatomical skill to make precision movements. I would be extremely prudent in speculating about the evolution of intelligence in *Homo* as long as it cannot be defined clearly: Is cultural evidence necessary and sufficient for demonstrating intelligence? We probably have to rethink completely our established perception of the early hominids.

With respect to phylogeny, there is a problem with defining a primitive and a derived feature. As long as we don't know the state of a feature, we cannot seriously propose a phylogeny. How is the derived or primitive aspect of the veinous drainage pattern estimated? Would the T-S pattern or O/M (occipital/marginal) pattern be the primitive one? If the O/M pattern were ancestral, we could not use that very feature to link robust Australopithecines with *Australopithecus afarensis*, as it would be just a primitive retained feature. It would be interesting to know what the pattern was in *Proconsul africanus* and in other apes and monkeys (including Platyrrhines). One interesting datum is the variability observed in *Australopithecus afarensis* by Johanson, White, and Coppens in 1978. Either this is a true variability of the *afarensis* group and the split into two different lineages is incorrect, or *Australopithecus afarensis* is not a valid species and we would have two taxa at Hadar (as already suggested by several authors, including myself and other French colleagues).

The last question raised in the paper concerns the privileged adaptation of gracile Australopithecines to the savannah and of robust Australopithecines to more humid environments. Most of the hyperrobust Australopithecines (*Australopithecus boisei*) however, lived in the same environments as *Homo habilis*, who supposedly inhabited opened milieux. Moreover, at Hadar, *Australopithecus afarensis* (a gracile species) was living in a gallery forest environment that was not really dry and open! We must not forget that early hominids could walk and move; they needed water to survive. This water was present in rivers, close to which there was (like today) a patch of gallery forest where shade was available, even in the dry season. Early man did not have to live under a hot sun all day long. Modern populations living in the desert under hot situations build their own shade. Vis-à-vis the dayhunting adaptation hypothesis related to the cooling system of the brain, this would mean that males and females evolved different types of venous drainages. Do we have any evidence of that? Finally, how can Wheeler's hypothesis explain the presence of very dark skinned people and animals with fur in the thickest forests of the world?

This new theory will no doubt raise a lot of questions, but this is one of the goals of scientific research: to provoke discussion and debate. What remains clear is the anatomical description;

the interpretation is another story. Falk's attempt to relate several phenomena is quite interesting, but I wonder whether the causal-effects she singles out are not simply correlated but isolated phenomena. In any case, scientists' brains will certainly heat up for some time to come in attempting to resolve most of the questions raised here.

The cost of a large brain

B. Holly Smith

Museum of Anthropology, University of Michigan, Ann Arbor, MI 48109

Brain volume doubled over the two million years of evolution of the genus *Homo*, increasing in a series of steps from 700 to 1400 cc (see Falk, sect. 2, para 6. The net rate of this change was about 0.1 darwin (one darwin represents change in a linear dimension by a factor of e per million years – a unit developed for evolutionary studies by Haldane [1949]). This is slow compared to other known rates of size change in Pleistocene mammals (see Gingerich 1983). Falk's work adds to our understanding of why hominid brain evolution might have been so slow by explaining an important physiologic constraint on the evolution of large brains.

The list of constraints on brain size evolution is becoming remarkably long. It has been suggested that a larger brain operates under tightened physiologic constraints: The larger the brain the lower the threshold for damage through increased maternal blood pressure (a danger to the fetal brain), oxygen deprivation, and temperature increase (Falk, sect. 4.1; Hofman 1983; Mettler 1955). Along the same lines, it is plausible (although difficult to demonstrate) that a lowered tolerance to variations in physiologic conditions also results in increased levels of psychoses (Mettler 1955). Bipeds face particular difficulties in giving birth to large-brained offspring, and apparently, hominids sacrificed some locomotory efficiency when pelvic width increased to accommodate larger-brained newborns (Lovejoy 1975). The brain is a metabolically expensive organ; it consumes some 20% of the energy of a resting human compared to a 9% cost to a chimpanzee or a 2% cost to an average marsupial (Hofman 1983). Since metabolic rate increases by a negative allometric coefficient of 0.75 with body weight (Kleiber's Law, Kleiber 1932) larger animals gain a "break" in the cost of maintaining each gram of tissue. Thus, it is conceivable that part of the documented increase in body size in the genus *Homo* was necessary to afford a large relative brain size. It also appears that brain size is tightly linked with virtually all parameters of life history (Harvey & Clutton-Brock 1985; Martin 1983; Sacher 1959; 1978; Smith 1989), and may be the "pacemaker" of vertebrate growth and aging (Sacher & Staffeldt 1974, p. 603). Large brains are found in animals with relatively long gestation, long juvenile periods, delayed reproduction, and long life – in other words, animals committed to the so-called "*K*-strategy" of reproduction (see Martin 1983). An enlarged brain probably requires such a life history in order to realize its potential – larger brains would be of little use to short-lived mammals.

The costs of a large brain seem enormous – (1) increased energy requirements for a given body size, (2) perhaps increased size (with its ecological ramifications), and (3) a furthered commitment to the strategy of few offspring with ever increasing parental investment in gestation and in postnatal feeding, protection, and training. Add (4) increased sensitivity to maternal blood pressure, perhaps also to aspects of brain chemistry, (5) required alteration of circulatory pathways to oxygenate and cool the enlarged brain, and (6) the difficulty of parturition in a large-brained biped. Falk also points out that the initial increase in hominid brain size took place in a demanding context: Hominids evolved in the tropics as a high-endurance

food collector and predator that could operate through the heat of the day when other animals could not.

How could such an organism afford the costs of enlarging relative brain size? For natural selection to bring about enlarged brains, the benefit must exceed the cost. The magnitude of the costs taken together emphasizes that *a life taking advantage of this brain must have been immensely profitable.* In this light it seems nearly absurd to argue, as some do, that evolutionary increase in brain size does not signify increased "intelligence," a word I would use to characterize the sum of a host of individual abilities such as memory, learning, flexibility in behavior, language, innovation/creativity, problem solving, and even including such disparate qualities as hand-eye coordination and ability to function in a social "landscape." It is also difficult to imagine that a system under such extreme physiologic constraints would evolve especially rapidly, and these constraints could have been responsible for the modest rate of increase in hominid brain size observed through the Pleistocene.

In conclusion, it is often noted that *Homo* has not posted an increase in brain size in the last 80,000 to 100,000 years. This is sometimes ascribed to a lack of benefit to any further increase, but, as Falk's article might suggest, this could just as well be due to a network of physiologic constraints that have not been (or cannot be) overcome. It is probably still best to be as smart as possible.

The influence of thermoregulatory selection pressures on hominid evolution

P. E. Wheeler

School of Natural Sciences, Liverpool Polytechnic, Liverpool, England L3 3AF

Almost all attempts to account for the evolution of some of the more unusual aspects of human thermoregulation have inevitably been somewhat speculative, since the relevant physiological systems are not preserved in the fossil record of extinct forms. What is particularly interesting about the target article by Falk is that it actually presents direct evidence about the evolutionary history of a recently described brain cooling mechanism. This thermoregulatory effector system is unusual in that its likely occurrence can be determined from an examination of the hard tissues of the cranium.

The theory that bipedalism and a functionally naked skin initially evolved because the hominoid primates ancestral to the hominids lacked a selective brain cooling system (Wheeler 1984; 1985; 1988) is not inconsistent with the discovery of such a mechanism in modern humans. The first hominids would have lacked the extensive evaporative nasal surfaces and carotid rete used by many other savannah mammals to protect their brains from hyperthermia (Wheeler 1984) and the detailed studies of the cranial circulation presented here by Falk show that that the alternative system using the emissary veins (Cabanac 1986) could have only evolved after bipedalism was already well established. Consequently, the thermoregulatory benefits of bipedalism, which greatly reduces radiant energy gain and facilitates convective and evaporative heat loss by raising the body surfaces into more favourable airflows and temperatures, will still have been particularly important to a mammal dependent on whole-body cooling to avoid damaging elevations of brain temperature.

It appears that a coherent picture may be emerging that unites the major distinctive features of hominids, together with the thermoregulatory selection pressures likely to have been acting on these primates. First, the evolution of bipedalism and a functionally naked skin would have increased core temperature stability in a thermally stressing environment. Excessive elevations of deep brain temperature could then be pre-

vented by regulating the temperature of its arterial blood supply. Subsequently, a reorganisation of the cranial circulation to cope with the hydrostatic problems posed by bipedalism may have permitted the evolution of a localised cooling system affording additional protection to the delicate superficial layers of the cerebral cortex.

If these thermoregulatory adaptations were acquired by hominids living in hot savannah mosaic habitats they need not necessarily be associated with, or indicative of, behaviours involving vigorous exercise, persistence hunting or otherwise (sections 4.1 & 5.1). Even in the absence of strenuous muscular activity, bipedalism and selective brain cooling will have conferred two distinct thermoregulatory benefits in open equatorial conditions. First, the resulting increased tolerance of environmentally induced thermal stress would have allowed hominids to remain in the open for longer, and at higher temperatures. This greater independence from shade-seeking would have been particularly advantageous to animals with the likely feeding ecology of the early hominids, exploiting resources characterised by dispersed or patchy distributions (Foley 1987; Lovejoy 1981). Consequently, since they would probably have spent most of their time searching for or moving between scattered food sources, their potential feeding rates will have been higher the less their movements were restricted by the need to seek shade during the hottest period of the day. Second, both adaptations would also have reduced the necessary drinking water intake of these animals, a factor of major importance in relatively arid habitats. Bipedalism achieves this by lowering the experienced environmental heat load requiring dissipation by the evaporation of water from the body surfaces. Localised brain cooling in later hominids will have increased their ability to tolerate modest elevations in core temperature. This may have enabled them to store some of the energy gained from their surroundings until conditions permitted its loss by nonevaporative means, a strategy used by many mammals with more elaborate brain cooling systems inhabiting hot arid environments (Mitchell et al. 1987).

It cannot be stressed strongly enough that none of these thermoregulatory adaptations will actually have caused the increase in brain size and complexity which occurred during the evolution of the genus *Homo*. As has been suggested previously (Wheeler 1984), improved brain temperature stability will simply have removed a physiological constraint on such advances, which will then only have taken place if they were favoured by other selection pressures. Perhaps the best analogy in this case is not a car radiator but a modern supercomputer. Information processing devices, both neuronal and semiconductor, generate significant quantities of heat and are vulnerable to damage by excessive rises in temperature. This problem of heat dissipation limits circuit density, presenting a major obstacle to electronic engineers in their endeavours to design ever more powerful machines. To overcome this constraint and achieve the enormous computing potential of the latest Cray 2 supercomputer, capable of more than one billion operations per second, required the "thermoregulatory advance" of immersing its tightly packed circuits in a bath of liquid fluorocarbon maintained at about 20°C. As in the case of the evolution of the human brain, the development of such an elaborate cooling system does not inevitably lead to higher performance machines, but it does make them possible.

A minor point concerns Falk's note (sect. 5.1.1) that male baldness could be a thermoregulatory adaptation. Extreme caution is required when suggesting this or any other adaptive explanation for such a highly variable characteristic, particularly since it is only usually acquired in modern humans at an age which may have been beyond the normal reproductive lifespans of individuals in earlier hominid populations.

Causes and consequences in the evolution of hominid brain size

A. Whiten
Scottish Primate Research Group, Psychological Laboratory, University of St. Andrews, St. Andrews, Fife, KY16 9JU, Scotland
Electronic mail: *pssaw@sava.st-and.ac.uk*

It seems straightforward to consider the study of human evolution as having two simple steps: First, describe the changes which have taken place; and second, explain why they took place. Falk offers an important *descriptive* conclusion, demonstrating a striking difference between two major groupings: 100% of robust and Hadar specimens with enlarged occipital/marginal sinus systems, compared with only a quarter of other hominids – including gracile australopithecines – with the same condition. This observation is important both in determining the genealogical status of *A. afarensis* and in supporting the reconstruction of niche differentiation for robust and gracile australopithecines.

Moving on to data on the emissary foramina, the picture becomes less clear, as does the simple dichotomy of description versus explanation. In using terms like "prime mover," Falk appears to be offering a causal explanation for evolutionary changes in brain size, in which upright posture begat the radiator, and the radiator (in concert with other factors) then begat the big brain. Nowhere in the article is this stated so baldly, and it would be helpful if Falk would confirm in her Response whether this is indeed the core of the theory. The alternative, of a mere coevolution of radiator and brain, would be a relatively mundane, if plausible, scenario consistent with the *Homo* data in her Figure 5.

The evidence available to distinguish these two causal possibilities is essentially descriptive; to support the radiator theory rather than the coevolutionary alternative, it needs to be shown that the evolutionary changes occured in a particular sequence; that is, that the radiator exhibited significant elaboration before the brain showed the clear expansion it did with the emergence of *Homo*. And this hinges totally on the data available for the gracile specimens: Was the radiator really more elaborated in them than in ancestral forms? Through her Figure 4 Falk suggests that this is the case for mastoid foramina, relying on the African pongid data as representative of the ancestral condition. I have two worries about this. First, although Fig. 4 gives no sample sizes, Table 2 in Falk (1986a) shows that the 40% frequency of these foramina corresponds to just two out of five gracile specimens – not significantly different from the 16% and 30% expected from the chimpanzee and gorilla specimens respectively. Second, it is possible that any lesser occurrence of mastoid foramina is a recent change in the chimpanzee and gorilla. One might doubt this alternative if their condition were shared with other apes, but in fact Boyd's (1930) analysis included 14 orangutans, of which 11 had mastoid foramina – a proportion comparable to the human case! Given such variation, how much confidence can we have in the critical claim that such features showed evolutionary elaboration prior to *Homo*? In addition, it must not be forgotten that the data are presented as percentage of subjects exhibiting the foramina. If the radiator was so important, how did 60% of graciles cope? The same question can be asked of the 40% of *H. erectus* exhibiting neither type of foramina, despite a very large brain, and with several million years of bipedality behind them.

What of the prior causal step Falk puts forward – that evolution of the radiator was the result of bipedalism? The behaviour of present day primates may help sharpen up just what should be claimed here. Falk notes that for monkeys an upright posture is not the norm. But although the knuckle-walking habit of chimpanzees and gorillas likewise does not involve an upright posture, apes *are* truncally erect when moving in the suspensory fashion that is one of the features of

the *hominoidea*, and, more important, they feed in this posture (Fleagle 1988). Direct quantification of whether an erect trunk is the norm for apes appears not to be available (Fleagle 1988), but we can make some inferences from activity budgets. Taking chimpanzees as an example, Wrangham (1977, Table iv) reported only about 14% travelling and 6% lying down, whereas feeding accounted for 55%, resting 17% and grooming 6% of the time. This suggests that the head is in an upright position on an upright trunk for much the greater part of the day, and the position of the foramen magnum is correspondingly shifted anteriorly compared to the situation in a regular quadruped (Le Gros Clark 1970). There seems little reason to expect that all this would not apply to ancestral hominids. Although this is not bipedality, it is after all *posture* that Falk emphasises as creating the functional context for a change in the blood flow system. Given that the head of a sitting gorilla might also be higher from the ground than that of a standing Hadar individual, we are thus led by comparative analysis to question whether the critical cause of changed blood flow is proposed to be an evolutionary change in norms for *posture, locomotion*, or *head height*, or some combination of these.

These specific concerns aside, Falk's approach highlights what appears to be a relatively recent tendency to take seriously the role of evolutionary changes in certain characters that remove constraints and thus "merely" *permit* the evolution of further changes, as opposed to *positively selecting* for them. As Falk notes, additional positive pressures will be necessary for change to take place, but the point is that these pressures could have been present in a species' environment all along, only becoming operative once a constraint is removed. It is of interest that one of the major recent examples of such a "constraints" explanation is also directed at brain size, although Falk does not mention it. Originating in the observation that brain size scales to the ¾ power of body size, it has been suggested that brain size is constrained by metabolic rate and therefore by diet (Armstrong 1983; cf. Elgar & Harvey 1987; Martin 1981; McNab & Eisenberg 1989; Pagel & Harvey 1988). Milton (1988) has extended this argument to the evolution of hominid diet quality and brain size. Understanding constraints and the implications of their removal may have an important part to play in conjunction with explanations invoking positive selection. For example, "Machiavellian expertise" explanations of brain evolution are powerful in that they predict a spiralling pressure as clever individuals relentlessly select for yet more cleverness in their companions: the puzzle becomes why such escalation should ever stop, and why hominids should spiral higher than other apes (Whiten & Byrne 1988). Perhaps constraints theories will help supply the answers. [See also Whiten & Byrne: "Tactical deception in primates" *BBS* 11(2) 1988.]

The problem of variation

Adrienne Zihlman
Department of Anthropology, University of California, Santa Cruz, CA 95064
Electronic mail: *alz@ucscd.bitnet*

Upright posture and habitual bipedal locomotion have long been recognized as a hallmark of the hominid adaptation. The evolution of such a distinct structural and behavioral locomotor pattern during the course of early human evolution presumably affected other body systems along the way. Without soft tissues, the task of reconstructing the interconnections between locomotion and other systems is difficult. But Falk's radiator theory goes a long way toward bringing together physiology, brain structure and function, and locomotion; it offers an explanation for observed endocast anatomy in fossil hominids and for an initiating factor to account for rapid brain evolution during the

past two million years. Brains are no longer disembodied but now are part of a whole animal in theory as in life.

A strength of the "the radiator theory" is that it integrates a wealth of information: detailed human physiology; comparative physiology and morphology of mammals and nonhuman primates; and the anatomy of the fossils themselves.

Another strength – and to my mind the most significant – is that Falk's theory is functional; it suggests how patterns of cranial blood flow are adaptive and how one pattern may have contributed to the survival and future of the hominid lineage. Presumably, the hominids adopted a way of life in an environment where activity patterns, including locomotion, required new solutions for brain (and I would add, body) cooling.

In discussing function and adaptation, Falk's target article is less convincing when it draws systematic conclusions and argues for niche separation of the two groups of early hominids. Grant that a particular trait, such as a pattern of cranial blood flow, has adaptive value for a particular genus or species. And grant that this trait has an evolutionary history and future. Questions remain: Is this same feature reliable as a taxonomic marker? Can it be a basis for constructing a phylogenetic cactus? Falk implies that it can. Although I am inclined to agree with Falk's cactus, based on a variety of other evidence, I doubt that single morphological traits (or even several of them) can be used to produce a phylogeny. Adaptation and evolutionary history are so intricately bound that it is very difficult to separate them for taxonomic purposes.

Aside from the problem of separating adaptation from ancestry, the problem of variation – the fact of the natural world – is not easily dealt with in phylogenetic schemes. A case in point is the placement of AL 288 ("Lucy") from Hadar, Ethiopia. In Falk's scheme this specimen, because it is part of the Hadar group, must be placed on the robust lineage. The diagnostic cranial anatomy is not preserved in this specimen, but in its innominate and limb morphology AL 288 is nearly identical to Sterkfontein specimens, which are considered gracile australopiths. In phylogenetic schemes, all specimens rarely fit neatly because the everpresent enemy, variation, is there to plague investigators.

Fossils also do not lend themselves to detailed conclusions about niche separation based on diet, locomotion or habitat. Falk's discussion of the robust and gracile australopiths as vegetarians and omnivores, respectively, is refuted by the reality of the lives of free-ranging primates. A characteristic of primates is that although their diet is predominantly vegetarian, almost all of them eat a range of foods that include insects and animal protein, gums, fruit and leaves – they are by definition, omnivores. The distinction between vegetarian robust australopiths and omnivorous gracile australopiths, though appealing, remains dubious because living primates don't divide up their world that finely.

More specifically, our closest living relatives, the chimpanzees, are described by Francois Bourliere as "clever opportunists, eclectic in their tastes and displaying a strong tendency to omnivory . . . able to take advantage of a variety of habitats and situations" (1985, p. 20). Were early hominids, as fairly recently transformed African apes, any less opportunistic or adaptable?

Recent field research has challenged our stereotype of the large-bodied African ape, the gorilla, as a strict vegetarian and inept climber. Tutin and Fernandez (1985) in Gabon indicate that gorillas eat fruit regularly (remains of fruit in 97% of fecal samples); they overlap extensively in diet with the sympatric fruit-eating chimpanzees. Other recent studies on gorillas in the Central African Republic further challenge our assumptions about their dietary and locomotor abilities. Carroll (in press) observed that not only is fruit an important dietary item, but that the gorillas eat termites, a food also associated with chimpanzees.

If we cannot characterize gorillas as ground-dwelling vege-

tarians, and if there is a great deal of overlap with chimpanzees, is a fine dietary distinction likely for robust versus gracile australopiths? More to the point, can we draw more specific conclusions from fragmentary fossils than we have been able to draw, prior to detailed field research, about living apes from complete skeletons, soft tissue and living animals? The need for studies of free-ranging primates to assist interpretation of the fossil record is apparent.

Falk's hypothesis is useful because it synthesizes data, considers locomotion, formulates an adaptive framework, and highlights issues for further research and discussion. Too often debates about human evolution rely heavily on opinion, focus too narrowly on constructing phylogenies, and ignore relevant information on function. Here Falk has presented a plausible theory that accounts for a great deal of information; such theories are not only fun to debate; they help move scientific research forward.

Author's Response

Evolution of a venous "radiator" for cooling the cortex: "Prime releaser" of brain evolution in *Homo*

Dean Falk

Department of Anthropology, State University of New York, Albany, NY 12222
Electronic mail: *df356@albny1vx.bitnet*

Seven years ago, Conroy and I (Falk & Conroy 1983) suggested that robust australopithecines may have evolved from *Australopithecus afarensis* rather than *A. africanus* as was generally accepted at that time. (We seconded Todd Olson [1981] in this opinion.) Our reasons for this suggestion were related to the physiology of bipedalism (vis-à-vis altered hydrostatic pressures across columns of blood under changed orientations) and the fact that enlarged O/M sinus systems appeared *fixed* in both the Hadar specimens and robust australopithecines. We wrote:

> We do not believe the frequency distribution of this trait in the robust lineage can be accounted for by random sampling bias. For example, if we assume that the robust australopithecine sample is drawn from a population with a frequency of this trait equivalent to that of modern populations (10%), then the theoretical binomial probability of randomly selecting six skulls all having this trait is 0.000001. If the frequency of the trait approached the highest limits known for some local *Homo sapiens* populations (25%, W. Kimbel, personal communication), then the probability of recovering six such skulls is still only 0.00024, that is, virtually inconceivable. (Falk & Conroy 1983, p. 779)

Without discussing the physiological evidence regarding posture and blood flow, Kimbel (1984) suggested that the venous sinus patterns of robust and other early hominids were adaptively equivalent and therefore without systematic implications. The old trees (i.e., gracile australopithecines giving rise to robust australopithecines) were allowed to stand.

In 1986, *additional* evidence on cranial blood flow in

early hominids (i.e., emissary foramina) was published and the suggestion that robust australopithecines were descended from the Hadar early hominids was reaffirmed (Falk 1986a). Subsequently, the "black skull" (WT 17000) was found (Walker et al. 1986). This specimen represented a robust australopithecine dated to 2.5 million years ago. Many workers now agree that WT 17000 was a likely descendant of the Hadar early hominids (Grine 1988). Although this "surprising" fossil was in keeping with the systematic conclusions determined from the evidence regarding cranial blood flow, there was very little discussion about the vascular evidence at the 1987 International Workshop on the Evolutionary History of Robust Australopithecines, held at the State University of New York at Stony Brook. The important O/M sinuses (which are fixed in 7 out of 7 scorable robust australopithecines and 6 out of 6 scorable Hadar specimens) are mentioned only rarely in the papers (other than mine) that came out of the conference (Grine 1988).

In short, the "field" had "written off" a functional interpretation of a dramatic enlarged feature that characterized only certain groups of early hominids, and had done so *without discussion* of the relevant physiological, physical (hydrostatic), comparative, and morphological evidence. Why would investigators do this? Hominid paleontologists are known for being a contentious lot (the reader won't have to look too hard to see evidence of this in a few of the commentaries). Many do not part easily from their published ideas or their "family trees." I cannot help thinking that the blood flow evidence would have been widely discussed if it had supported rather than refuted the "mainstream" systematic interpretations of the Hadar early hominids' and robust australopithecines' roles in hominid evolution.

However, the cranial blood flow evidence *is* dramatic and it *is* important. It deserves a hearing. I submitted the "radiator" paper to *BBS*, with the hope that it would be assessed by a wide range of experts spanning from physiologists to neuroscientists to hominid paleontologists. I have not been disappointed. Most of the commentaries are thoughtful, insightful, and constructive. The commentaries cover six broad areas (see Table 1), and I will address each in turn.

1. Clarification of the "radiator" theory

1.1. Evolution of the radiator: One step or two? Several commentators seek clarification about the number of stages involved in the radiator theory. "Was the radiator an adaptation for running about at mid-day on the savannah (only mad dogs, Englishmen, and gracile australopithecines . . .)? Or was it the mechanism by which larger brains came to be cooled as they evolved?" asks **Barton.** The answer, of course, is both. As put so baldly (to use his own term) by **Whiten,** I do indeed believe that "upright posture begat the radiator, and the radiator (in concert with other factors) then begat the big brain." (Or perhaps it would be better to state that the radiator *permitted* begetting of the big brain, as per **Finlay** and **Whiten.**) All this begetting, however, does not rule out subsequent coevolution of radiator and brain, once a radiator had begun to develop. As noted by **Krantz,** one can easily view the emissary and associated venous system as devel-

Table 1. *Headings in author's response and commentators specifically addressed*

1. Clarification of the "radiator" theory
   (Barton, Bingham, Brace, Fialkowski, Finlay, Foley, Krantz, Wheeler, Whiten)
2. Other constraints
   (Abitbol, Barton, Bingham, Finlay, Foley, Grüsser, Krantz, Smith, Whiten)
3. Vascular anatomy and physiology
   (Bortz, Brace, Brengelmann, Brinnel, Cabanac, Caputa, Dean, Finlay, Grüsser, Holloway, Kimbel, Krantz, Limber, Scheibel, Senut, Wheeler)
4. Hominid fossil record
   (Bortz, Brace, Dean, Grüsser, Holloway, Kimbel, Senut, Whiten, Zihlman)
5. Brain size
   (Abitbol, Barton, Bingham, Brace, Fialkowski, Finlay, Grüsser, Holloway, Krantz, Scheibel, Senut, Smith)
6. Suggestions for future research
   (Bingham, Bortz, Brinnel, Cabanac, Grüsser, Hargens, Limber, Scheibel, Senut)
7. Conclusion
   (Zihlman)

oping along with brain expansion. In fact, this is exactly what is suggested by Figure 5. Brain size would not have "taken off" in the first place, however, without a mechanism for coping with increased thermolytic needs. The fact that the radiator was modifiable over time (as good systems often are) does not contradict the theory.

Wheeler comments that a coherent picture may be emerging regarding thermoregulation during hominid evolution. He also sees two stages. The first involves selection for bipedalism, naked skin, and sweat glands in savannah living hominids. In addition to such whole-body cooling that regulated the temperature of arterial blood supplying the brain, Wheeler believes that, subsequently, a second stage localized cooling system (i.e., the radiator) evolved and that it provided additional protection to the cerebral cortex. Although I think that the vascular response to hydrostatic pressures started during the first stage and that this is when the radiator *began* to develop (in conjunction with bipedalism and whole-body cooling), I basically agree with Wheeler's theory.

1.2. Is the radiator a prime mover, or isn't it? Quite a few commentators were confused by my calling the radiator a prime mover of brain evolution, on the one hand, yet invoking selection for "general intelligence" as causally related to the increase in brain size across species of *Homo,* on the other. **Foley** correctly notes that prime mover theories may be overly deterministic and simplistic. **Bingham** points out that, after having criticized prime mover theories generally, I go on to refer to the radiator theory as a prime mover theory. **Fialkowski** and **Whiten** both question whether the radiator directly caused expansion of the brain, while **Brace** and **Barton** come right out and say that the radiator was *not* a prime mover of brain enlargement.

Well, was it or wasn't it? Despite my earlier definition of a prime mover as "one behavior or reflex, such as

warfare or thermoregulation, (that) was primarily responsible for human brain evolution" (Falk 1980a), I'm afraid I have to capitulate on this one. According to Fialkowski's commentary, thermoregulation was a prime mover of brain enlargement. However, according to the radiator theory (and stated in section 6 of the target article), the radiator acted as a releaser rather than a "mover" in the classical sense. As Brace lucidly put it, "it was the radiator and not the brain that was the byproduct of thermoregulatory forces." Foley also summarizes the situation well with his observation that car engines have dragged up the size of radiators and not vice versa. Thus it would have been more appropriate to call the radiator a "prime releaser," and leave the prime mover label for the primary selective pressure(s) that acted on the brain once it acquired a radiator and *could* get bigger.

2. Other constraint theories

Barton and Bingham both note that constraints on brain size other than temperature regulation have been given short shrift in the target article. Although a thorough discussion of the various constraints that have been proposed for brain size was beyond the focus of the target article, a number of commentators provide welcome discussion of this issue. Abitbol lists no fewer than eight constraints on encephalization and Foley's Table 1 provides correlates, if not constraints, of relative brain size. Smith enumerates various constraints on brain size and provides a thoughtful cost/benefit analysis vis-à-vis these constraints (see section 4). According to Smith, "for natural selection to bring about enlarged brains, the benefit must exceed the cost" – nice!

What are the constraints on brain size? Metabolic/nutritional requirements of the brain (see Armstrong 1983) is the constraint most cited by commentators (Abitbol, Barton, Krantz, Smith, Whiten). Thermal constraints are mentioned by Abitbol, Barton, Grüsser and Smith. Abitbol, Finlay, and Smith discuss developmental/embryological constraints, and the size of the mother's pelvis is also named as a limiting factor (Abitbol, Smith). As Abitbol points out, the two most cited constraints (brain metabolism and brain temperature regulation) are both subserved by cerebral blood flow (CBF). No contradiction here.

Are constraint theories such as the radiator theory useful? Whiten thinks they may help provide answers. Foley goes further and suggests that the "constraints" versus "selective pressures" (or Finlay's "permission versus pressure") dichotomy could be expanded to include "4 Cs": conditions, causes, consequences, and constraints. This is a good idea.

3. Vascular anatomy and physiology

3.1. Do emissary veins cool the brain? Several commentators question the role of emissary veins in cooling the brain under conditions of hyperthermia (Brengelmann, Caputa, Holloway, Kimbel, Krantz and Scheibel). As stated clearly in section 4.1.2 of the target article, I have *not* argued that mastoid and parietal emissary veins are by themselves capable of cooling the brain. Rather, I accept these veins as representatives of a wider network of veins.

Cabanac (1986; 1987) and his colleagues have unequivocally demonstrated that, under conditions of hyperthermia, cool surface blood in mastoid, parietal, and ophthalmic emissary veins flows *into* the braincase. Because these three emissary veins occupy dispersed positions within a wider network of emissary and diploic veins, these physiologists reasonably concluded that the *entire network* of veins delivers blood to the intracranial surface under conditions of hyperthermia.

Kimbel incorrectly states: "Falk severely misinterprets Cabanac and Brinnel (1985) by suggesting that the presence or number of visible emissary veins is a reflection of the size and significance of the entire emissary network, whereas these authors merely used these vessels . . . . to determine the direction of blood flow under different thermal conditions." Fortunately, Brinnel speaks to this exact point in his commentary:

> As stressed by Falk, the few emissary venous pathways accessible for analysis or exploration by anthropologists or physiologists stand for a wide system of microscopic diploic veins distributed all over the calvaria: The amount of blood appearing on the inner side of the dura after gentle massage of the skull in a fresh cadaver is highly impressive (see in Cabanac & Brinnel 1985).

Indeed, anyone who doubts the existence of a wide network of veins that communicate between the external and internal surfaces of the calvaria should observe Figure 5 in Cabanac and Brinnel (1985). This exercise will also dispel the notion that all emissary and diploic veins drain directly into the dural sinuses (Brengelmann, Kimbel).

Finally, Kimbel states that the *principal means* of brain thermoregulation *in hyperthermic humans* is heat exchange in the cavernous sinus between warm carotid blood and venous blood cooled by evaporation from the moist nasal mucosa and facial sweating. Although the anatomical pattern of venous drainage from the nose appears to be similar in most mammals including humans (Baker 1982), the *principal means* of brain thermoregulation differs greatly between animals with and without retes. Countercurrent heat-exchange in the cavernous sinus is important for animals that have retes, but it does *not* play a large role in brain cooling in primates (including humans), in whom "the internal carotid arteries pass through the cavernous sinus with a minimum of heat lost to the pool of venous blood there" (Baker 1979, p. 131). In fact, Brinnel suggests that the most controversial issue in the field of human brain temperature regulation is whether selective brain cooling is possible when the carotid rete is lacking, as is the case for humans. The radiator theory suggests that it is.

3.2. Whole-body cooling. According to Baker (1982), because the brain is warmer than its incoming arterial blood, the temperature of the cerebral arterial blood is the single factor that is most likely to produce significant changes in brain temperature. Several commentators picked up on the theme of whole-body cooling. Their concern, well stated by Grüsser, is not how to cool the brain under conditions of intense exercise, but rather how to reduce elevated blood temperature due to muscle work and prevent "overheated" blood from reaching the brain. Grüsser (see also Bortz, Caputa, and Dean) lists

several mechanisms that have evolved or become modified in *Homo* to release heat into the surroundings by radiation, convection, and/or evaporation: nakedness, sweat glands and adaptive sweating, water intake, salt balance, skin pigmentation, and morphology of head hair. **Brengelmann** concurs, stating that our entire skin surface acts as a radiator.

So far, so good. It is *not* logical, however, to use such reasoning to deny that emissary and diploic veins have a significant role in brain cooling under conditions of hyperthermia. Nor is it logical to so argue, as **Brengelmann** has, on the basis of clinical studies such as that by Shiraki et al. (1988). The one patient in this study had surgery to relieve intracranial pressure. Experimental procedures were done in parallel with heavy radiation therapy, a procedure that often contributes to increased intracranial pressure (ICP). Neither ICP nor the position of the patient were reported. If ICP was high, one would not expect cool blood from the skin to flow towards higher pressure within the cranium. If the patient was supine (also not reported), vascular cooling of the brain would probably be less efficient than if the patient were upright (see **Brinnel**'s commentary).

Despite exposure of the patient to an electric blanket, esophageal temperatures reported by Shiraki *et al.* remained lower than 37.4°C (1988, Figure 3), that is, not high enough to usually be considered hyperthermic. Nor is evidence provided that the patient's thermolytic responses were indicative of a hyperthermic state. For example, forehead skin temperature is shown not to be influenced by body heating in Figure 3 (even before face fanning began), although this should be a good indicator of hyperthermia. In sum, evidence is lacking that the patient was hyperthermic – a necessary condition for testing the hypothesis that emissary and other veins bring cool surface blood into the cranium under conditions of hyperthermia. Finally, in reference to their Figure 3, Shiraki et al. state that brain, ventricular, and esophageal temperatures "followed an upward trend" during fanning of the face (1988, p. 483). Yet Figure 3 clearly demonstrates that fanning of the patient's face *prevented* a rise in these temperatures, and that such a rise took place only after face fanning stopped. If anything, these data support the assertion that face fanning lowers brain temperature. In addition, this assertion is no less true because fanning of the face plus extremities also lowers brain temperature.

Contrary to the thrust of his commentary, **Brengelmann**'s Note 3 is consistent with the proposed mechanism for selective brain cooling. In short, Brengelmann's arguments are not appropriate for hyperthermic subjects. This does not mean that clinical or physiological studies can never shed light on the question of selective brain cooling (see section 4.1.1 of the target article). For example, secretion was shown to be inhibited on the trunk but not on the head during dehydration in male subjects (Caputa & Cabanac 1988), and this finding is concordant with the idea that head sweating is particularly important for thermoregulation. (Dehydration and hyperthermia are complementary and often go together.)

Wheeler stands out for his ability to envision both whole-body mechanisms for regulating temperature of arterial blood *and* the evolution of the radiator for cooling the brain further under conditions of hyperthermia. Fi-

nally, I cannot resist asking those commentators who exercise a lot, have full heads of hair (or not, see next section), and reject the existence of a radiator: when you "work out," just what do you think all that head sweating is about?

3.2.1. Baldness.
Baldness facilitates heat loss from the cranium. However, rather than being an adaptation to savannah habitats, this feature may have arisen during the subsequent evolution of *Homo* in colder habitats (**Cabanac**). Cabanac sees baldness as an adaptation for increasing the amount of heat that could be lost from the head when whole-body cooling became inhibited in colder habitats because extensive clothing was worn. In particular, Cabanac suggests that baldness arose in males to counterbalance lost skin surface due to beards. Cabanac's scenario fits with **Brace**'s idea that baldness was a thermoregulatory device that developed with both cerebral expansion and persistence hunting; it also fits with **Grüsser**'s observation that bald people prefer to wear hats in sunshine and baldness therefore does not seem to be an adaptation to hot climates. **Wheeler** is skeptical about male baldness as a thermoregulatory adaptation, noting that modern males usually become bald at ages that are beyond the probable reproductive lifespans of early hominids. On the other hand, numerous advertisements in the media suggest that it is not uncommon for (at least) American males to begin balding as relatively young adults (and ones who apparently fail to appreciate the thermoregulatory benefits of their evolved condition).

3.3. O/M versus T-S sinus systems.
Three paleoanthropologists and one psychologist seek clarification about the functions of the enlarged occipital/marginal sinus system (O/M) and the system consisting of the transverse/sigmoid sinuses *plus* the network of emissary and other veins (T-S), and their relationship to each other. **Senut** raises the question of polarity, that is, which system is primitive and which derived? To answer this, one must look at *whole* systems. The T-S system includes a derived wide network of veins that evolved during hominid evolution, and the O/M system is also specialized compared to the African pongid condition. The two systems therefore represent different derived solutions to hydrostatic pressures associated with bipedalism.

Limber asks how a basic T-S pattern that lacked an associated elaboration of veins (i.e., the African pongid condition) could lead to the evolution of emissary foramina? As discussed in section 3 of the target article, hydrostatic pressures associated with bipedalism necessitated a change in cranial blood flow patterns. With the enlarged O/M system, blood can flow straight down into the vertebral plexus – quick and easy, but without cooling benefits. On the other hand, with a wide network of emissary and other veins, blood can still flow to the vertebral plexus *and* that network has the added benefit that it can act as a radiator for the brain when needed, that is, under conditions of hyperthermia. Both systems were "able" to evolve from the African pongid condition because there were sufficient frequencies of their respective components represented in ancestral vascular systems (see Figure 5 of the target article).

With respect to the genetic basis for venous sinus patterns, **Kimbel** states:

> in reference to the enlarged O/M system in the Taung specimen, Tobias & Falk (1988, p. 312) conclude that "we may be dealing with a genetic polymorphism that expresses itself with widely varying frequencies among populations of ancient and modern hominids." This bears more than a superficial resemblance to my own conclusion (Kimbel 1984).

But Kimbel's conclusion bears a resemblance to Tobias's (1967; 1968), as summarized in the very article to which Kimbel refers (Tobias & Falk 1988, p. 310): "Tobias saw it in the light of a probably genetic polymorphism, having a high incidence in robust and hyperrobust australopithecines and a low incidence in *A. africanus* and most populations of past and present members of *Homo*." Tobias and I did refer to Kimbel's (1984) work on venous sinuses, noting that Kimbel regards the two drainage patterns as adaptively equivalent and neutral character states. Being genetically polymorphic is one thing, being without adaptive/functional value is another. I have no problem with the hypothesis that vascular systems may be genetically polymorphic *and* have selective value. In fact, current population genetic theory suggests that selection may either drive a system to fixation or maintain a polymorphism within a population (Hartl & Clark 1989, pp. 198–99).

Dean does not believe that an enlarged O/M sinus drains preferentially into the vertebral plexus of veins rather than into the jugular vein. As documented in section 3.1.1 of the target article, Browning (1953) found that 9 out of 100 human cadavers had appreciable O/M sinus systems. The O/M system drained to the vertebral plexus in 7 of these 9 cadavers. This report, and a wider anatomical literature, clearly contradicts Dean's beliefs. In the majority of humans with an enlarged O/M system, that system drains blood to the vertebral plexus instead of, or in addition to, the internal jugular vein. The fact that "all of these venous channels communicate" in no way obviates this conclusion. In fact, the connections of venous channels and the dynamic nature of cranial blood flow, depending on posture and respiration, was discussed at length in section 3.

According to **Kimbel**, "Falk attributes a major role to the O/M system and emissary veins in channeling venous blood to the vertebral plexus based on the experiments of Epstein et al. (1970) and Dilenge & Perey (1973) on rhesus macaques." This is not so. My reasons for attributing a specific role to the O/M system in hominids are stated clearly in the preceding paragraph and in section 3.1.1 of the target article. My discussion of rhesus monkey experiments (section 3) dealt with posture and cranial blood flow (hydrostatic pressures) in animals. To wit: If rhesus monkeys are held completely vertically, hydrostatic pressures cause blood to flow to their vertebral plexes. This says *nothing* about the O/M system or emissary veins in hominids.

Kimbel also asks "what is the differential selective advantage of alternative venous drainage routes (O/M vs. T/S with emissary assistance) if, as Falk suggests, most of the blood is channeled preferentially to the vertebral system in all upright hominids irrespective of drainage route?" The answer to this is that the two systems func-

tion differently vis-à-vis regulation of brain temperature, as elaborated in section 4.1.2 of the target article.

3.4. Posture/embryology. Several commentators accept the hypothesis that cranial venous blood flow changed in conjunction with selection for bipedalism (**Brace, Brinnel, Grüsser**). Only **Holloway** claims there is *no* evidence to suggest that subsets of bipedal locomotor variability correlate with variability in venous drainage patterns. His assertion is questionable because of numerous investigations pertaining to posture and blood flow in humans, monkeys, giraffes, and snakes (see Brinnel, Grüsser, and section 3 of the target article).

A few authors seem troubled by the multiple connections and dynamic nature of the cranial venous sinus system in humans. They shouldn't be. Yes, as **Scheibel** notes, there is a great diversity of paths and number of veins. Yes, as **Krantz** observes, cranial blood in early bipeds presumably could have been delivered to both the vertebral plexus and the jugular veins. **Caputa** is also right in noting that blood in emissary and associated veins can flow into the skull to cool its contents or flow out of the skull at other times. In fact, it is the diversity of venous connections that facilitates the dynamic response of blood flow to changed hydrostatic (postural) pressures. As documented in the target article, cranial blood flow *is* dynamic in humans, that is, it changes routes with altered postures and with altered thermal conditions. Along these lines, **Finlay** asks whether bipedal posture is required for the radiator to operate. **Brinnel's** commentary suggests that the radiator may indeed be more efficient in an upright posture.

Finlay, Limber and **Senut** question the significance of embryological development for the radiator theory. A *small* O/M system is typically present in adult humans (Padget 1956; 1957). During embryological development, the marginal sinus develops rostrally from the posterior venous plexus, while an occipital sinus extends caudally from the tentorial venous plexus (Butler 1957; 1967). As the cerebrum expands caudally, the transverse sinus also moves in that direction and the occipital and marginal sinuses join to complete the O/M system during late fetal development (Padget 1956; 1957). A number of authors have commented on the relatively large size of the O/M system in human fetuses and neonates (Browning 1953; Woodhall 1936; Gius & Grier 1950), and others have illustrated this system as somewhat larger in the infant than in the adult (Crelin 1969; Padget 1956). However, more work needs to be done regarding allometry and functional significance because this morphology occurs in neonates before the secondary cervical curve forms and the head is held upright by the infant.

4. Hominid fossil record

Senut notes that a complete list of fossil specimens and their taxonomic attributions has not been provided in the target article. Extensive raw data for individual specimens are provided elsewhere (Falk 1986a). With the exception of the frequency of enlarged O/M sinuses for gracile australopithecines, the frequencies shown in Figures 4 and 5 of the target article came directly from Tables

1 and 2 of Falk 1986a. Data regarding the O/M sinus in STS 5 (Tobias & Falk 1988) have since been added to the 1986 information for gracile australopithecines, causing the frequency for that feature to be reduced from 25% to 20%. All of the data included in Figures 4 & 5 have been collected (or confirmed) by myself, except for the data for O/M sinuses on Hadar early hominids (to which I have not had access). In this response, I will answer questions raised about specific fossils.

4.1. Specific fossils.

4.1.1. Laetoli hominid 21 (L.H.-21). This specimen is not included in Figures 4 and 5 of the target article, because I have not had the opportunity to score it myself. As cited in section 5 of the target article, however, **Kimbel** (1984, Table 2) scored this fragmentary specimen as lacking an enlarged O/M sinus. In Figure 6 of the target article, I have placed footprints representing Laetoli early hominids on the basal australopithecine stem of my phylogenetic cactus instead of with the Hadar early hominids. Kimbel states in his commentary that I separate "the Laetoli and Hadar specimens at the species level on the basis of this character (O/M) alone." I stated in section 5 of the target article, however, that "other evidence . . . separates the Laetoli from the Hadar specimens."

As detailed in Falk 1988, Hadar fossils appear to be significantly different from those at Laetoli in their dentitions (Blumenberg & Lloyd 1983), and presumed foot morphology (Tuttle 1985; 1987). The fossils are also from different locations (Ethiopia vs. Tanzania) and they are apparently from different times (approximately 3.2 Myr vs. 3.5 Myr). **Kimbel** (1984) scored no Hadar specimens as lacking enlarged O/M sinuses, 5 as having this system, and one (AL 162–28) as probably having it ("t"?). The enlarged O/M sinus system therefore appears to be fixed in scorable Hadar early hominids. In short, evidence spanning from head to toe separates the Hadar and Laetoli specimens, that is, lack of an enlarged O/M sinus in L.H.-21 is just frosting on the cake.

4.1.2. The Taung specimen. My treatment of the Taung skull is "confused," according to **Kimbel.** Kimbel (1984) scored Taung as lacking an enlarged O/M sinus. However, Taung's endocast clearly reproduces a right O/M sinus (Falk 1986a), as recently described and illustrated by Tobias and myself (Tobias & Falk 1988). In his commentary, Kimbel states: "Tobias & Falk (1988) have found evidence of an enlarged O/M system in a species previously considered to show fixation of the T/S drainage system. The analogous taxonomic conclusion however – that the Taung specimen is a "robust australopithecine" (as the type specimen, it will *always* be *A. africanus*) is avoided." An alternative conclusion that could be drawn from the rescoring of Taung is that the *assumption* that T/S is fixed in gracile australopithecines (Kimbel 1984) was incorrect in the first place. Indeed, if Taung's conspecifics (i.e. gracile australopithecines) were correctly assigned to *A. africanus* (see below), this is the case, since Taung *has* an enlarged O/M sinus system.

I do not mean to duck the issue of whether Taung might not really be a robust australopithecine. This is an interesting and important question. Taung was the first australopithecine found in 1924, and it was not until 1936

that another fossil australopithecine was found. At the time Taung was discovered, it was not known that there were *two* types of australopithecines. Taung was a "baby," and the fact that Taung is the type specimen for *A. africanus* does *not* guarantee that the adult specimens subsequently discovered and attributed to its species were correctly assigned. The first adult specimen found after Taung happened to be a gracile australopithecine from Sterkfontein (TM 1511). Had it been a robust australopithecine, I believe Taung would today be the type specimen for robust instead of gracile australopithecines. In light of this history, it is interesting that in addition to being the only "gracile" australopithecine with an enlarged O/M sinus system, Taung also shares an intrapalatal extension of the maxillary sinus with robust (but not other gracile) australopithecines (Conroy & Vannier 1987). If more traits are found that sort Taung with robust instead of gracile australopithecines, it may indeed be time to reassess the systematic affinities of the type specimen for *A. africanus*, as Tobias (1973) first suggested!

4.1.3. Omo L388y-6. The partial cranium of a juvenile australopithecine from Ethiopia is mentioned by both **Dean** and **Holloway.** Rak and Howell (1978) consider the specimen to be a robust australopithecine, whereas Holloway (1981; 1988) said it was probably a gracile australopithecine in 1981, and that it was perhaps a robust australopithecine in 1988. Although Rak, Howell, and Holloway agree that an enlarged O/M sinus was missing, an illustration of the specimen (Rak & Howell, Figure 4, 1978) suggests to me that both the transverse sinuses and an enlarged O/M sinus system may, in fact, have been present. I have not yet had the opportunity to view the original fossil, and it is not included in the target article.

4.1.4. WT 17000. That an enlarged O/M sinus system existed in this robust australopithecine is doubted by both **Dean** and **Holloway.** Walker et al. (1986) note that the small sigmoid sinuses appear to receive no contribution from transverse ones and therefore suggest that an enlarged O/M sinus system may have been present. Holloway (1988) could find no evidence for an enlarged O/M system on WT 17000, which is not surprising, since "the region of the occipital which would show the grooves for the occipital and marginal sinuses is missing" (Walker *et al.* 1986). I viewed an endocast from WT 17000 in 1987 and found its occipital region too eroded to score.

4.1.5. A.L. 288-1a. This specimen represents an occipital fragment from "Lucy" that has been included in the target article as one of six Hadar early hominids that Kimbel (1984) scored as having enlarged O/M sinus systems. **Senut** and **Zihlman** both raise questions about the amount of variation in the Hadar fossils. Could the Hadar material contain remains of two rather than one species of early hominid (Senut & Tardieu 1985; Zihlman 1985)? Zihlman notes that the limb morphology and innominate of AL 288 look similar to gracile australopithecine material from Sterkfontein. She also states that the diagnostic cranial anatomy (for scoring O/M sinuses) is not preserved in Lucy. Going back to an earlier description and photograph of this specimen (Johanson et al. 1982), it appears that Zihlman may be right on this point.

4.1.6. KNM-ER 1813. Many authors consider this specimen to represent *Homo habilis*, as Senut correctly notes. However, for reasons related to the morphology of the frontal lobe of the brain (Falk 1983), I consider both ER 1805 and ER 1813 to represent gracile australopithecines. See section 4.3 below for further discussion of these specimens.

4.2. Is an enlarged O/M sinus system *fixed* in robust australopithecines? There is concern on Dean's part about the fact that marginal sinuses of robust australopithecines are often enlarged on the right side. As discussed elsewhere (Falk & Conroy 1983), however, this morphology is entirely consistent with right-sided dominance of the superior sagittal sinuses in extant human and nonhuman primates. Simply put, it appears that dominance in cerebral venous drainage has been shifted from the transverse-sigmoid to the O/M system in robust australopithecines.

Dean and Holloway both suggest that the frequency of an enlarged O/M sinus system might not be as high for robust australopithecines as indicated in the target article. The seven robust australopithecine specimens that I have scored for O/M sinuses are SK 54, SK 859, SK 1585, KNM-ER 304, KNM-ER 407, KNM-ER 732, and OH 5. All seven of these specimens have enlarged O/M sinus systems. No one has questioned the accuracy of my scoring of this feature on any of these specimens. In addition, no commentator has suggested that any of these specimens are not robust australopithecines.

Above, I have listed, specimen-by-specimen, why certain other fossils could not be included in this sample. Seven out of 7 *scorable* robust australopithecines have enlarged O/M sinus systems. This strongly suggests that this feature was fixed within South and East African populations of robust australopithecines. This suggestion can only be weakened by discovery of an unequivocally identified robust australopithecine occiput that contains the appropriate region for scoring O/M sinuses, is in excellent (uneroded) condition, and clearly shows that no enlarged O/M sinus was present. That discovery has yet to be made.

4.3. Are apparent trends based on "taxonomic tricks"? According to Kimbel, my arguments regarding "the network of emissary veins is based on a single feature (the mastoid foramen) in a sample of only 14 'scorable' crania spanning the nearly 2.0 Myr leading to *H. erectus* (Falk 1986)." This is not correct. Although it is not apparent from his wording, Kimbel's comment refers only to the samples of robust (8) and gracile (5) australopithecines that could be scored for mastoid foramina (his number should have been 13, not 14). I also scored mastoid foramina for 88 African pongids, 5 *H. erectus* specimens, 6 archaic *H. sapiens*, 8 Neanderthals, 11 *H. sapiens* that lived over 10,000 years ago, and 51 extant *H. sapiens* (Falk 1986a). My published tables on emissary foramina also include comparable data on *parietal foramina* and O/M sinuses (see Falk 1986a for frequencies). *All* of this information was incorporated into my graphs and discussions about emissary veins.

Kimbel claims that it was a "taxonomic trick" to include South African and East African robust australopithecines in one sample, and that this obscures the fact that 50% of

the earlier South African robust specimens (2 out of 4) have mastoid foramina while only 40% (2 out of 5) of the "gracile" group have it. I see nothing wrong with treating all robust australopithecines together, but if Kimbel wants to separate early hominids from later hominids within a group, let's do it for the gracile specimens too. Out goes ER 1805 and ER 1813 from my gracile australopithecine sample (see section 4.1.6. above). The proper figure to compare to Kimbel's 50% for early robusts is therefore 67% (2 out of 3) for early graciles. Nothing's changed, the incidence of mastoid foramina is still higher in gracile than in robust australopithecines (i.e., 67% versus 50%).

4.3.1. Sample sizes. Sample sizes of scorable specimens across the hominid fossil record *are* small (Holloway, Kimbel, Whiten). That, alas, is a "hazard of the trade." Nevertheless, when one uses comparative data on *several features* that have been collected from African pongids, fossil hominids across the record, and extant hominids, clear trends do appear. If one were to reject the challenge of doing research in the hominid fossil record because of small sample sizes, several commentators would find themselves seeking new careers, and so would I.

4.4. Niche separation of robust and gracile australopithecines. Questions are raised by Holloway, Kimbel, Senut and Zihlman regarding the proposed separation of habitats for gracile and robust australopithecines. Zihlman's commentary highlights information that contradicts stereotypes about gorilla diets and emphasizes that more studies of free-ranging primates are needed to assist interpretation of the hominid fossil record. Zihlman's observations and suggestion seem valid.

As noted in the target article, Robinson (1963) placed gracile australopithecines in a completely different niche from robust australopithecines. Kimbel criticizes my acceptance of Robinson's ideas, and cites Vrba (1988) as support for this criticism. But does Vrba's work really refute Robinson's theory? As Vrba (1988) emphasizes, any discussion of habitat differences between gracile and robust early hominids must be grounded in the fact that approximately 2.5 million years ago, a major global cooling event occurred that initiated subsequent climatic and biotic changes in both East and South Africa. The lack of reliable dates for the South African material, and the possibility that robust localities are more recent than the gracile localities (that Vrba analyzed) make it difficult to ascertain whether apparent habitat differences for South African hominids are truly comparable, or whether they are due to the sampling of different times/climates. Thus, Vrba's hypothesis that South African gracile australopithecines lived in more wooded, wet environments than did South African robust australopithecines "remains tentative, and the problem of hominid-associated environmental change in South Africa is badly in need of additional approaches" (Vrba 1988, p. 415).

We are on firmer ground in East Africa, however. Vrba suggests that the likely habitats of East African robust australopithecines sample only one biome – "across higher-to-lower wood cover and more-or-less well-watered areas" (1988, p. 420) or, put another way, "the vegetational margins of major water bodies" (1988, p. 422). On the other hand, Vrba thinks that *Homo habilis* was a

biome generalist spanning from open grasslands to water-marginal woodlands. As long as the East African robust australopithecines were eating their veggies in predominantly wood covered habitats (i.e., were not running around under the hot savannah sun), I see no inconsistency between Vrba's work and the radiator theory.

But is there evidence that robust and gracile australopithecines really occupied distinct ecological niches, as Robinson suggested? Kay and Grine (1988) address this question by using experimental evidence gleaned from hominid teeth in conjunction with dietary information from extant primates (see **Zihlman**'s commentary). They conclude that South African robust australopithecines appear to have eaten hard food items, whereas gracile australopithecines seem to have subsisted on softer foods including leaves and fleshy fruits. More to the point (see Vrba 1988 for summary), robust australopithecines in both South and East Africa are currently regarded as strict vegetarians (although the two forms may have differed somewhat in their diets). (As discussed below, early *Homo* were apparently more eclectic in their tastes.) As in Robinson's day, there is currently good reason to suppose that the two forms of australopithecines occupied different niches.

4.4.1. Of foraging, scavenging and hunting. Referring to the target article, **Kimbel** states: "Citing Blumenschine (1987) in support of the fantastic statement that "postural changes allowed early hominids to open a noon-day scavenging niche" . . . does not do justice to the careful work this author and others have done to elucidate clues to early hominid scavenging activities. What evidence is there to support the attribution of a scavenging niche of *any* kind to *any* hominid prior to the appearance of *H. habilis?*" I do not think that my citation of Blumenschine (1987) is an injustice to his work. He has clearly shown that Plio/Pleistocene hominids had sufficient, specified scavenging opportunities as well as the means to exploit them. In Blumenschine's own words (1987, p. 383), he has reconstructed a "possible hominid scavenging niche." Furthermore, as per **Brace**'s commentary, there is no need to equate the *beginning* of scavenging with the first appearance of stone tools, any more than there is a need to equate the latter with the earliest production of perishable tools. Foraging activities were also attributed to early hominids in the target article and, as **Wheeler** emphasizes, thermoregulatory adaptations would have been advantageous for hominids travelling between dispersed resources in a patchy environment.

Brace cites archaeological and taphonomic evidence as indicating a transition from opportunistic scavenging to recognizable hunting and gathering between two and one million years ago. Because this time period was also characterized by an increase in brain size and frequencies of emissary foramina, Brace suggests that a relationship exists between these features and adoption of systematic diurnal hunting. **Bortz** also believes that the radiator network of veins facilitated hunting. Specifically, he comments that exercise causes increased blood flow and metabolic activity in motor areas of the brain. Thus, a brain cooling radiator would have been an enabling or facilitating device for exercise in general, and hunting in particular. Finally, **Grüsser** also mentions hunting in early hominids in conjunction with long-range planning

and social organization. Although these ideas are interesting, a disadvantage of hunting as a prime mover of brain evolution is that it suggests that selection for increased brain size acted differentially on males (Falk 1980a).

5. Brain size

The suggestion that hominid brain size may have increased as a result of selection for multifaceted intelligence receives mixed responses. The remarks of five commentators range from cautious to negative. **Barton** thinks the concept of selection for general intelligence is woolly and imprecise, and **Bingham** finds the idea confusing and disappointing. **Senut** also notes that intelligence has not been clearly defined and suggests, not unreasonably, that one should be prudent in assessing the evolution of intelligence in *Homo*. **Holloway** simply states that there is no evidence of a significant relationship between brain size and intelligence, either within or between species. Finally, **Fialkowski** believes that large brains were initially selected to resist heat stress, and that "abstract thinking" came later.

Seven other commentators were more enthusiastic. **Finlay** is receptive to the concept of selection for general intelligence, and **Jerison** takes it a step further by suggesting that an appropriate word to describe intelligence would be "multidimensional." **Brace, Grüsser, Krantz,** and **Scheibel** all agree that the increase in brain size that occurred during hominid evolution was related to selection for intelligence. In addition, **Smith**'s elegant analysis of the costs and benefits of increased brain size provides some of the best support for this concept. It is interesting that both **Abitbol** and **Grüsser** suggest that human brains might get even larger in the future. This possibility must be tempered by consideration of "costs," however, such as the difficulties bipeds have in giving birth to large-brained offspring (see Smith's commentary).

Brace and **Jerison** raise the important point that the relationship between brain size and intelligence *across* species is decoupled from their relationship *within* species. As Brace notes, differences in brain size between living human populations appear to be proportional to body size rather than intelligence. **Jerison** comments that within-species effects are poorly understood, and emphasizes the importance of continuing to recognize that encephalization is a higher order (i.e., between species or genera) evolutionary phenomenon. **Scheibel** reminds us that Dean Swift's brain was approximately 2000 cm³, whereas the volume for Anatole France was about 1000 cm³.

5.1. Structural changes in the brain. There are few indications of the specific structural changes that accompanied the increase in brain size during hominid evolution, as **Bingham** correctly observes. **Jerison,** more than any other commentator, addresses the question of structural changes in hominid brains. **Holloway** was quoted in the target article to the effect that one cc of chimp brain does not equal one cc of human brain. Jerison states, however, that it is extremely difficult to pinpoint structural differences in tiny portions of homologous brain tissue from different species. He concludes that cubic millimeters of homologous brain tissue from chimpanzees, humans, and

(presumably) australopithecines would appear equivalent in all areas *except* primary visual cortex (which is unique among mammals and similar in higher primates including humans). This information provides an important basis for exploring the evolution of brain structure.

Jerison goes further and identifies a unique feature in the organization of the human brain, namely, a large language area. He discusses the difficulty of distinguishing tissue from Broca's speech area (which occurs in the left frontal lobe of humans) from other nonvisual cortical tissue, but points out that differences *do* exist in the pattern of dendritic arborization of this region between the left and right (homologous) sides. Jerison further suggests that right/left differences in dendritic arborization could be sought in regions of chimpanzee brains that are proposed as homologues of Broca's area in humans. This is an excellent suggestion.

Along somewhat similar lines, **Grüsser** discusses the neurological bases for tasks such as reading and writing that occurred very recently in human evolution. He is right that competence in these tasks requires certain cortical areas. Grüsser's suggestion that these cortical areas existed and were used for other interpretive tasks in preliterate societies is intriguing, and makes me all the more sympathetic to **Jerison**'s case for language (in its broad sense) as the "Rolls Royce of brain adaptation."

6. Suggestions for future research

Several commentators have proposed experimental or clinical procedures for further investigating the relationships between blood flow patterns, posture, and the regulation of brain temperature in humans. **Limber** (see also **Bortz**) suggests that physical models of venous drainage systems could be constructed and tested to yield quantitative information about their respective cooling properties. **Scheibel** would like to see noninvasive scanning techniques (e.g., PET scans) used to quantify variations in blood flow patterns relative to thermal conditions and physical activity. Finally, **Brinnel** raises the interesting possibility of using the resources of clinical medicine to investigate the possible correlation of venous drainage patterns (e.g., enlarged O/M sinuses) with vascular disorders.

Although there have been some recent investigations of vascular evolution in primates (e.g., Diamond 1988), comparative studies of the venous system(s), posture, and regulation of brain temperature would be welcome in a number of nonhuman primates including gibbons, chimpanzees, and gorillas (**Senut**) and orangutans (**Whiten**). **Cabanac** has also opened interesting questions about these variables in sea mammals.

I am happy that **Hargens'** & **Meyer's** illustration of arterial and venous blood pressures in the giraffe is reproduced with their commentary. Contrary to the impression one might get from their commentary, however, the nonhydrostatic pressure gradient down the giraffe's jugular vein was discussed in section 3 of the target article. The fact that the jugular vein of an upright giraffe collapses does *not* obviate the fact that gravitational pressures are generally more pronounced in venous than in arterial systems. Poiseuille's law aside, I suspect the giraffe has a whopping vertebral plexus of

veins and believe it would be worthwhile to explore this possibility through anatomical dissection.

The time is ripe for someone to do a comparative study of neck anatomy and head carriage vis-à-vis cranial vascular systems in humans and nonhuman primates. Results of this study could then be applied to several interesting problems: The evolution of head carriage in hominids (cervical vertebral column [**Grüsser**], position of the foramen magnum [**Senut**], etc.) could be investigated and compared to the evolution of postcranial aspects of bipedalism. The interaction between the respiratory mechanics associated with the shift to bipedalism and other anatomical/physiological variables (e.g., neck anatomy, venous circulation) is a related area that is worthy of investigation (**Bingham**). The proposed comparative study of human and nonhuman primates would also apply to important questions **Whiten** raises about the interaction of truncal erectness, locomotion, head height, and cranial blood flow in African apes. In short, the *top of the neck* is a particularly important (and available) focus for future research.

7. Conclusion

Although I share concern about using single morphological traits to produce phylogenies (**Zihlman**), the cactus is a hardy plant. Mine's got feet (Laetoli versus Hadar) and teeth (gracile versus robust australopithecines) and even brains (ER 1805 versus *Homo*). The "radiator" theory is built on data that span living apes, the hominid fossil record, and extant people. These data include cranial capacities, frequencies of mastoid and parietal foramina, and frequencies of enlarged O/M sinuses. To interpret these data, information has been incorporated from the medical, physiological, physical, and zoological sciences. A synthetic and *functional* interpretation has emerged that appears to account for the data. Simply put, the "radiator" theory "hangs together" and the notion that enlarged O/M sinuses were without adaptive significance in early hominids does not.

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Letters "a" and "r" appearing before authors' initials refer to target article and response respectively.

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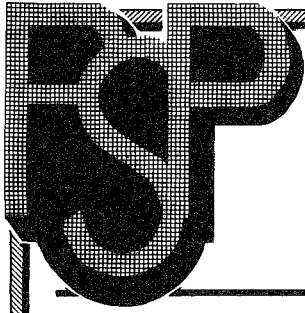
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"Configural Association Theory: The Role of the Hippocampal Formation in Learning, Memory, and Amnesia" by R. J. Sutherland and J. W. Rudy

"Cortico-Hippocampal Interplay: Self-Organizing Phase-Locked Loops for Indexing Memory" by Robert Miller

"Maternal Modulation of Infant Glucocorticoid Stress Responses: Role of Age and Maternal Deprivation" by Mark E. Stanton and Seymour Levine

"Habituation of Plasma Catecholamine Responses to Chronic Intermittent Restraint Stress" by Maria Konarska, Robert E. Stewart, and Richard McCarty

A recent issue included a set of papers based on presentations at a Society for Neuroscience workshop, "Hippocampal Cellular Activity and Spatial Cognitive Processing," organized by Phillip J. Best.

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