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LB1's virtual endocast, microcephaly, and hominin brain evolution

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ABSTRACT

Earlier observations of the virtual endocast of LB1, the type specimen for *Homo floresiensis*, are reviewed, extended, and interpreted. Seven derived features of LB1's cerebral cortex are detailed: a caudally-positioned occipital lobe, lack of a rostrally-located lunate sulcus, a caudally-expanded temporal lobe, advanced morphology of the lateral prefrontal cortex, shape of the rostral prefrontal cortex, enlarged gyri in the frontopolar region, and an expanded orbitofrontal cortex. These features indicate that LB1's brain was globally reorganized despite its ape-sized cranial capacity (417 cm^3). Neurological reorganization may thus form the basis for the cognitive abilities attributed to *H. floresiensis*. Because of its tiny cranial capacity, some workers think that LB1 represents a *Homo sapiens* individual that was afflicted with microcephaly, or some other pathology, rather than a new species of hominin. We respond to concerns about our earlier study of microcephalics compared with normal individuals, and reaffirm that LB1 did not suffer from this pathology. The intense controversy about LB1 reflects an older continuing dispute about the relative evolutionary importance of brain size versus neurological reorganization. LB1 may help resolve this debate and illuminate constraints that governed hominin brain evolution.

Introduction

Since the 2004 announcement of the new hominin species, *Homo floresiensis* (Brown et al., 2004; Morwood et al., 2004), controversy has surrounded the interpretation of its type specimen, LB1 (Argue et al., 2006). Here we review our earlier studies pertaining to this controversy and provide background for new material that is presented below. Using ratios constructed from gross measurements that capture overall shape of endocasts, our initial study (Falk et al., 2005a) revealed that LB1's virtual endocast has an unusual suite of characteristics, the combination of which sets it apart from all other known hominins. It resembles endocasts of *Homo erectus* in its relative height, the disparity between its maximum and frontal breadths, the relative widths of its caudal and ventral surfaces, and its long, low lateral profile (Falk et al., 2005a). The relative length of LB1's orbital surface (and certain segments thereof) sorts it with *Homo sapiens* (Falk et al., 2005a). LB1's small cranial capacity and brain size/body size ratio (relative brain size), on the other hand, sort it with apes and australopithecines (Falk et al., 2005a).

Our interpretation of LB1's endocast differs from those of workers who believe that LB1 represents a modern human who was afflicted with primary or secondary microcephaly rather than a new hominin species (Hall et al., 2004; Henneberg and Thorne, 2004; Weber et al., 2005; Jacob et al., 2006; Martin et al., 2006a,b; Richards, 2006; Martin, 2007; Rauch et al., 2008). Scientists agree, however, that microcephaly is not a simple or easily defined pathology. Primary microcephaly (also called 'true microcephaly,' 'primary autosomal recessive microcephaly,' or 'microcephaly vera,') is a genetically and clinically heterogeneous condition that, to date, has been associated with at least seven autosomal recessive loci and five associated genes, as well as various maladies that would once have been precluded from this diagnosis (Falk et al., 2007a). Affected individuals are frequently from consanguineous unions, and have been reported from many parts of the world.

To address the hypothesis that LB1 was a microcephalic *H. sapiens* rather than a member of a new species, we conducted an earlier comparative study of virtual endocast shape in 10 normal humans and nine extremely varied (heterogeneous) microcephalics who included individuals with different demographics and types of microcephaly, and had appropriately-sized braincase volumes (Falk et al., 2007a). The purpose of studying such a heterogeneous sample was to identify features that might be generally

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representative of microcephalics. Eight gross measurements that are traditionally used to capture brain shape were obtained electronically from the virtual endocasts, and used to generate ratios to characterize their shapes (see Falk et al., 2007a for landmarks and other details). Discriminant and canonical analyses were employed to study shape differences between the two groups and backward stepwise discriminant analysis was used to identify the most powerful discriminators. Two ratios that quantify cerebellar protrusion and relative frontal breadth, and capture shape features that are widely reported for microcephalics in the clinical literature (Hofman, 1984; Peiffer et al., 1999; Mochida and Walsh, 2001; Trimborn et al., 2004; Gilbert et al., 2005), mathematically sorted our samples of normal and microcephalic virtual endocasts. A classification function that incorporated these ratios was then used to classify LB1, a dwarf, and one microcephalic that allegedly resembles LB1 (Martin et al., 2006b) as either a normal or a microcephalic human (Falk et al., 2007a). LB1's relative frontal breadth and (lack of) cerebellar protrusion sorted it with normal rather than microcephalic *H. sapiens* (Falk et al., 2007a), which is consistent with our earlier findings (Falk et al., 2005a,b). On the other hand, the dwarf and microcephalic that was alleged to resemble LB1 were classified as microcephalics. The cranial capacity of the dwarf (752 cm^3) was somewhat larger than those of the microcephalics we studied and we believe it suffered from secondary microcephaly (Falk et al., 2007a).

Despite statistical results that were highly significant (even with our small sample sizes) and that supported the conclusion that LB1 was not a microcephalic (Falk et al., 2005b, 2006, 2007a,b), numerous workers continue to argue that LB1 was a pathological *H. sapiens* who suffered from microcephaly (Martin, 2007), Laron Syndrome (Hershkovitz et al., 2007, 2008), cretinism (Obendorf et al., 2008), or microcephalic osteodysplastic primordial dwarfism type II (MOPD II) (Hall et al., 2004; Rauch et al., 2008). An assumption that is at the heart of these various hypotheses is that LB1's ape-sized cranial capacity (417 cm^3) is too small to be from a normal hominin that lived 18,000 years ago (Martin, 2007). However, LB1's endocast reproduces a highly convoluted cerebral cortex with a unique combination of derived features, "which are consistent with capabilities for higher cognitive processing" (Falk et al., 2005a:242). Because these derived features occur in multiple areas across its surface, LB1's virtual endocast appears to represent an "epitome of neurological reorganization" (Falk et al., 2007b:42).

However, some workers have dismissed the concept of neurological reorganization as an "outlandish form of special pleading….[that] unavoidably requires the emergence of some entirely new principle in the development of the brain of the Flores hominid" (Martin, 2007:14), and one reviewer of the present paper repeatedly asserted that s/he knew of no study that correlates brain shape features with behavior. The following section provides background regarding neurological reorganization that addresses these assertions.

Historical background

Concerns about inferring cognitive abilities from the external morphology of brains or endocasts have a long tradition, partly because this endeavor was historically associated with phrenology, which was rightfully dismissed at the end of the 19th century as a pseudoscience (Gould, 1981). Further, although sulcal patterns have, traditionally, been of paleoanthropological interest (Dart, 1925, 1940, 1956; Smith, 1927), sulci usually do not correlate precisely with the borders of functionally-defined cytoarchitectonic fields (Zilles et al., 1997; Amunts et al., 1999). Despite these caveats, however, gross sulcal patterns have been associated with enlarged cortical representations (and related changes in cortical shape) that subserve functional (behavioral) specializations in mammals including carnivores (Welker and Campos, 1963) and primates (Falk, 1981, 1982), in a phenomenon that Harry Jerison has labeled the "principle of proper mass" (Jerison, 1973). For example, raccoons have greatly enlarged forepaw representations in their primary somatosensory cortices in which, remarkably, the various digit and palm pad areas are demarcated from one another by sulci, and this derived cortical morphology is attributed to the fact that raccoons use their forepaws to an unusual degree to explore their environments (Welker and Campos, 1963).

It is also well known that dramatic changes may occur in sensory and motor cortices during a human's lifetime as revealed by medical imaging studies of Braille readers and upper limb amputees, which demonstrate that the cerebral cortex can exhibit long-term adaptations, including enlargement or relocation of specific representations such as those for hands (Amunts et al., 1997). Further, gross cortical features entailing sulcal depths or patterns have been identified in people with exceptional abilities such as highly-trained musicians (Amunts et al., 1997; Schlaug, 2001; Bangert and Schlaug, 2006).

Rather than being "an outlandish form of special pleading …. [that] unavoidably requires the emergence of some entirely new principle" (Martin, 2007:14), the concept of neurological reorganization has enjoyed a long and respected tradition in paleoanthropology (Dart, 1925, 1940; Smith, 1927; Gould, 2001). Ralph Holloway, in particular, has championed the idea that endocasts may be used to detect cerebral "organizational change" that is "reflected in convolutional patterns, hemispheric asymmetries, and size-shape morphometric patterns as analyzed through multivariate statistical techniques" (Holloway, 1983b:215). Further, Holloway has expressed the view that "features of neural organization such as increased neuron size, dendritic branching and glial neural rations, and decreased neural density…. are better correlated with behavioural efficiency than cranial capacity per se" (Holloway, 1973:457). Holloway, in fact, has argued that neurological reorganization occurred during early hominin evolution with little, if any, concomitant increase in brain size (Holloway, 1983a).

Other studies that have demonstrated regularities in brain organization across placental mammals have shown that this phenomenon does not preclude species-specific adaptations in the brain (Finlay and Darlington, 1995), contrary to Martin (2007). In fact, one of the most authoritative discussions of cortical organization and evolution suggests "that the cortex is a veritable hotbed of evolutionary reorganization" (Preuss, 2001:140), and notes that "functional imaging studies in humans indicate that higher-order cognitive tasks engage multiple cortical areas dispersed across the cortical mantle, areas that are probably linked by direct corticocortical connections. The evolution of new cognitive abilities might involve the enhancement of existing links between areas, or even the establishment of links between previously unconnected areas" (Preuss, 2001:156) - or "rewiring" to put it metaphorically. Although the debate about brain size versus neurological reorganization has been polarized in the past (Falk and Gibson, 2001), it is now clear that both were important during hominin evolution, and that new information and approaches are helping to reconcile what Stephen Jay Gould called "a falsely perceived dichotomy":

> Moreover, the commingling of cellular with biometric studies, and of growths and sizes of parts and wholes with research on microarchitectural and cellular reorganization, testifies to the healing of past controversies, and to a coordinated approach using the most fruitful themes of both sides in a falsely perceived dichotomy (Gould, 2001:xvi).

Below, we review and extend our earlier observations about brain shape in microcephalics (Falk et al., 2007a), and discuss the