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CHAPTER 12

Hominin paleoneurology: Where are we now?

Dean Falk*

School for Advanced Research, Santa Fe, NM, USA
Department of Anthropology, Florida State University, Tallahassee, FL, USA

Abstract: Hominin paleoneurology is the subfield of paleoanthropology that investigates brain evolution in human ancestors. For over a century, paleoneurologists have focused on analyses of cranial capacities (as surrogates for brain size) and endocranial casts (endocasts), which are prepared from the interiors of fossilized braincases and reproduce details of external brain morphology. This review discusses recent improvements in our understanding of hominin brain evolution in terms of brain size, sulcal patterns, and cortical shape features. To the extent possible, the evolution of neurological reorganization is assessed in light of findings from paleoneurology. In order to make inferences about cognitive evolution, paleoneurologists interpret their data within a framework that incorporates behavioral information from comparative primatological studies and findings from comparative neuroanatomical and medical imaging investigations. Advances in our knowledge about the evolution of the prefrontal cortex (Brodmann's area 10) provide an example of a productive synthesis of comparative neuroanatomical and behavioral research with investigations of the fossil record of hominin endocasts.

Keywords: brain shape; brain size; endocast; lunate sulcus; neurological reorganization; paleoneurology; sulcal patterns.

Introduction

Hominin paleoneurologists study fossilized skulls and casts of their braincases (endocasts) to investigate the evolution of the brain and cognition in our ancestors. Although endocasts sometimes occur naturally, they are traditionally prepared by casting the insides of braincases with latex, or some other molding material. In recent years, however, it has become common to acquire "virtual endocasts" electronically by using 3D imaging techniques, such as computed tomography (Falk, 2004). Virtual endocasts are easier to reconstruct, manipulate, and measure than traditionally prepared ones.

*Corresponding author.
Tel.: +1-850-644-7016; Fax: +1-850-645-3200
E-mail: dfalk@fsu.edu

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Endocasts reproduce a good deal of information about the brain, including its general shape, and details of some of its associated blood vessels, cranial nerves, and cranial sutures. With luck, endocasts also reproduce information about the convolutions of the brain that were imprinted on the inner walls of the braincase during life. The convolutions, or folds of gray matter on the brain's surface, consist of bulges (gyri) and the grooves (sulci) that separate them. Sulcal patterns have been a focus of hominin paleoneurology for over a century, although the amount of information about them that is reproduced on hominin endocasts is usually quite limited, as described below. Partly because of this, and partly for historical reasons (Falk, 2009b), hominin paleoneurology is a highly contentious field (Falk, 2011).

Brain size, which is a less controversial topic than hominin sulcal patterns, is also an important parameter for assessing hominin brain evolution. A longstanding debate continues about the relative importance of the evolution of brain size versus that of the internal reorganization of the brain's connections, components, and neurochemistry (neurological reorganization). Below, I describe current findings about hominin brain evolution that paleoneurologists have gleaned from comparisons of the skulls and endocasts of apes and hominins. The evolution of brain size is discussed first, followed by speculation about the mode and tempo of neurological reorganization as indicated by sulcal patterns in two parts of the brain and certain details of brain shape.

Brain size

Brain size is estimated by measuring the cranial capacities of fossil skulls or, alternatively, the volumes of their endocasts (in cubic centimeters, cm^3). Ideally, cranial capacities should be decreased by a corrective factor to compensate for the volume of fluids and meninges that occupy the braincase along with the brain. It is quite common, however, for cranial capacities to be used without correction as proxies for brain size. By analyzing cranial capacities and estimates of body size (often based on postcranial remains), earlier researchers hypothesized that both the absolute mass of the brain and its size relative to body mass (relative brain size, RBS) increased independently during the evolution of the major clades of primates, as well as during the evolution of other mammals (Jerison, 1973; Radinsky, 1979).

More recent quantitative analyses have verified that selective pressures for enlarged brains began early in primate evolution but have also revealed that brain size decreased independently in some branches of old world monkeys, new world monkeys, and strepsirhines (Montgomery et al., 2010). (As an aside, Montgomery et al. (2010) analyzed brain and body size in the tiny type specimen for *Homo floresiensis* (LB1) and concluded that the data fit within the broader context of primate phylogeny (Falk et al., 2009).) Larger-bodied primate species tend to have smaller measures of RBS than smaller-bodied ones, although there are exceptions such as extremely large-brained *Homo*. Partly for this reason, numerous analytical techniques and indices that "subtract" allometric scaling associated with body size from brain size (e.g., encephalization quotient, EQ; index of progression, IP) have been developed to quantify the extent of encephalization in mammals, including nonhuman and human primates (see Falk, 2007a for review).

Recent studies suggest that brain mass is more indicative of advanced cognitive abilities in primates than measures that control for body size, such as IP and EQ. Thus, "the functional integration of different brain regions is so strong that the brain as a whole is a relevant unit for cognitive performance" (Deaner et al., 2007:121; Herculano-Houzel, 2009, Chapter 15). The emerging preference for data based on brain mass is not surprising in light of problems inherent in constructing and using indices that control for body size. These problems include difficulties in identifying appropriate reference groups for baseline data, challenges in selecting exponents for

regression equations, and results that (because of artifacts that are inherent in the methodology) tend to overestimate indices for smaller-bodied species and underestimate them for larger-bodied ones (see Falk, 2007a for details).

Another emerging trend is a preference for absolute over RBS as the best indicator of advanced cognition. For example, "Only in terms of absolute mass and the rate of change in absolute mass has the increase in brain size been exceptional along the terminal branch leading to humans. Once scaling effects with body mass have been accounted for the rate of increase in relative brain mass remains high but is not exceptional" (Montgomery et al., 2010:11). Researchers studying neurogenesis have reached a similar conclusion: "The most likely brain alteration resulting from selection for any behavioral ability may be a coordinated enlargement of the entire nonolfactory brain" (Finlay and Darlington, 1995:1578).

Human brains are large

Human cranial capacities (and brains) are, by far, the largest of all the primates. As shown in Fig. 1, when extreme outliers are excluded, human cranial capacities vary from around 1100 to 1700 cm^3, and they are completely separated from those of the great apes. (One researcher who included outliers reported cranial capacities for normal humans that ranged from 790 to 2350 cm^3 (Dart, 1956)!). A figure of 1350–1400 cm^3 commonly appears in the literature as an estimate for the mean cranial capacity in living people. This is about three times the size of the mean estimate of 450 cm^3 for australopithecines (Falk et al., 2000). Various workers have also shown that the volumes of the brains (and, separately, neocortices) of living people are, on average, three times the size predicted for nonhuman primates that are scaled to the same body size as humans (Passingham, 1973, 1975; Stephan et al., 1970). This frequently cited observation is consistent with the following conclusion based on comparative behavioral and neuroanatomical data: "The most practical measure for distinguishing intelligence and predicting the presence of humanlike mental skills in hominid fossils is absolute brain size" (Gibson, 2001:92). So whether or not one examines absolute brain size or RBS,

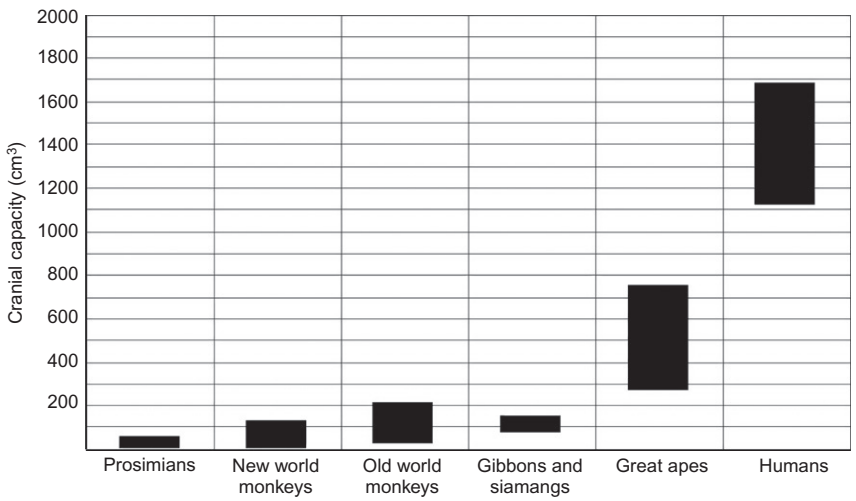

Fig. 1. Cranial capacities as approximations of the ranges of brain sizes in extant primates. Reproduced from Falk (2007a) with permission.

it appears that the mass of the brain increased approximately threefold in the lineage leading from *Australopithecus* to extant *Homo*. Further, the old adage that absolute brain size suddenly "took off" in *Homo* around 2 million years ago needs revision in light of relatively new discoveries of fossil hominins, which suggest that brain size began to increase considerably earlier in the *Australopithecus* ancestors of *Homo* (Falk, 2004, 2007a).

Conclusion regarding brain size

From the above brief discussion, it is understandable that numerous researchers advocate brain size as the most important parameter that changed during hominin brain evolution. However, brains evolved not only in size but also in their neurological organization. Other researchers, therefore, favor neurological reorganization as the most important aspect of hominin brain evolution. As Stephen Jay Gould observed a decade ago, the debate about the relative importance of brain size versus neurological reorganization is based on a false dichotomy (Gould, 2001). Both are important. Studying neurological reorganization is trickier than assessing brain size evolution because most of the changes related to internal wiring, relative sizes of different parts of the brain, and neurochemistry are not revealed in braincases or on endocasts. Nonetheless, investigators are able to obtain hints about neurological reorganization from the sulcal patterns and shape features that, with luck, are reproduced on hominin endocasts.

Neocortical reorganization of sulcal patterns

Human cerebral cortices have a greater number of sulci than those of apes, which is associated with several factors including allometric scaling of the cortical surface relative to brain volume (Jerison, 1973, 1975), an increase in the number of cortical areas that developed during primate brain evolution (Kaas, 2000; Kaas and Preuss, 2008) and constraints related to the evolution of cortical wiring (Hofman, 2001, Chapter 18). The additional sulci in humans are mostly unnamed (Connolly, 1950). Although ape and human brains share most of their named sulci and fissures, the configuration of sulci that appear on the external cortical surface in two regions of the brain is derived in humans compared to apes (and monkeys): (1) the caudal lateral border of the orbitofrontal cortex (Fig. 2) and (2) the rostral border of primary visual cortex (V1 or BA 17). Because cortical reorganization in these parts of the human brain is associated with changed sulcal patterns, the relevant sulci have been investigated on ape and hominin endocasts with an eye toward gaining insight into the pattern and timing of cortical reorganization during hominin evolution, as well as its relationship to brain enlargement. However, the discussion of sulcal patterns on hominin endocasts has been, and continues to be, highly controversial (Holloway, 2008), partly for historical reasons (Falk, 2011).

Sulcal pattern difference 1

As detailed by Connolly (1950), the lateral border of the caudal part of the frontal lobe of all genera of great apes is consistently incised by a fronto-orbital sulcus (*fo*) that courses caudally on the orbital surface toward the temporal pole (see diagram for *Pan* in Fig. 2). This is never the case for human brains. Instead, human brains typically manifest a sulcal pattern in which two rami of the Sylvian fissure (*R'*, *R*) delimit the rostral and caudal boundaries of the *pars triangularis* (BA 45) (which, in the left hemisphere, is part of Broca's speech area consisting of BA 45 and BA 44, see diagram for *Homo* in Fig. 2). Although sulci often fail to delimit cytoarchitectonic regions reliably (Amunts et al., 2007; but see Fischl et al., 2008), these two branches of the Sylvian fissure

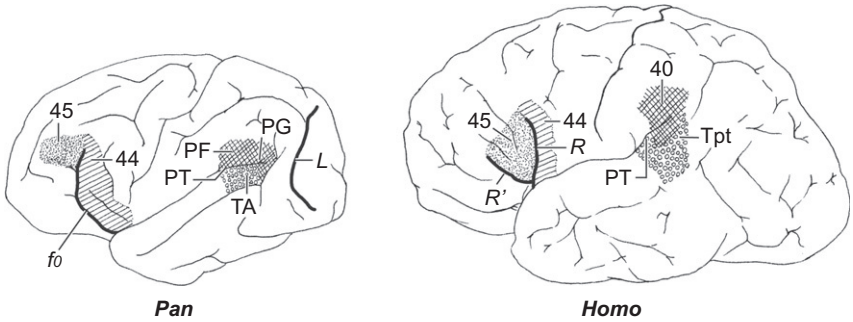

Fig. 2. The classic language areas in left hemispheres of humans and their proposed homologs in chimpanzees. In humans, Brodmann's area (BA) 44 and BA 45 constitute Broca's speech area, while PT (planum temporale), Tpt (temporoparietal), and BA 40 are part of Wernicke's receptive area for language. Proposed homologs of human BA 40 and Tpt with chimp areas PF/PG (inferior parietal lobule) and TA (part of temporal lobe), respectively, are based on cytoarchitectonic and functional similarities and are tentative. The sulci associated with Broca's speech area in the left hemisphere of humans form a distinctive pattern (as do the sulci in the same position on the right) that differs from the sulcal pattern in the frontal lobes of monkeys and apes. The fronto-orbital (*fo*) and lunate (*L*) sulci of the chimpanzee brain and the two sulci delimiting the *pars triangularis* (*R'*, *R*, anterior horizontal and anterior ascending rami, respectively, of the Sylvian fissure) in the human frontal lobe are thickened for illustrative purposes. See Falk (2007b) for details. Figure modified after Falk (2007a) and Schenker et al. (2008); © Dean Falk, reproduced with permission.

bear a predictable relationship to the free surfaces of BA 45 and BA 44 in human brains (Amunts et al., 1999). This indicates that they are potentially good landmarks when studying hominin endocasts (which reproduce only the surface of the cortex): Thus, "there are regions, i.e., the free surfaces of the triangular and opercular parts, in which the probability is very high of localizing areas 45 and 44, respectively" (Amunts et al., 1999:339).

Connolly hypothesized that *fo* does not appear on the lateral surface of human brains because it was displaced caudally by the opercularization of the frontal lobe as brain size increased during hominin brain evolution (Connolly, 1950:330). According to Connolly, *fo* became buried within the brains of humans, where it became part of the anterior limiting sulcus of the insula. The distinction between the sulcal patterns in this part of the frontal lobes of apes and humans is consistent and has paleoneurological significance because of the association of the human pattern with neurological reorganization related to language (Falk, 1983; Tobias 1987). Significantly, an apelike *fo* is present on the ape-sized natural endocast of Taung (the type specimen for *Australopithecus africanus*) (Dart, 1929; Falk, 1980, 2009b).

Figure 2 has an important implication for paleoneurology. In human brains, the rostral part of Broca's speech area (area 45) and the area that borders it ventrally (area 47, not labeled in Fig. 2) together form a slight bulge, which has been called "Broca's cap." Some workers equate this with a bulge that appears in the same general region on ape brains. Cytoarchitectonic evidence, however, reveals that these bulges are not equivalent. In chimpanzees, the bulge is formed by area 44 and sometimes part of area 45 (Sherwood et al., 2003) instead of areas 45 and 47, and of course, apes do not have speech (Falk, 2007b). One should therefore be cautious about inferring that a bulge in this general location on an ape brain or on a small early hominin endocast is equivalent to Broca's cap of humans. What is needed to interpret an early hominin endocast in this region is information about the precise sulcal pattern. Does the endocast have an apelike *fo*? If not, does it reproduce two sulci that suggest

the presence of a *pars triangularis*? One cannot always determine the answer to these questions from hominin endocasts, but they should be asked.

Sulcal pattern difference 2

The second sulcal pattern that is relevant for hominin paleoneurology concerns the lateral representation of the primary visual cortex (V1), which is relatively smaller and located noticeably more caudally in humans than the homologous area in monkeys and apes (Connolly, 1950). In nonhuman anthropoids, the rostral border of V1 is approximated by a large crescent-shaped sulcus (*L* in *Pan*, Fig. 2) formerly called the *Affenspalte* (ape sulcus). At the beginning of the twentieth century, Grafton Elliot Smith hypothesized that V1 of humans was bordered by a homologous sulcus, the name of which he changed to "lunate sulcus" (*L*) in keeping with its recognition in humans (Smith, 1903, 1904a,b). Long ago, Smith hypothesized that, as hominin brains enlarged and evolved, the lateral representation of V1 and its bordering *L* were displaced caudally by expansion of the adjacent parieto–occipito-temporal association cortices.

Smith's protégé, Raymond Dart, picked up on his hypothesis in 1925 when he identified and illustrated what he thought was a caudally displaced *L* on the ape-sized endocast of Taung (Fig. 3). Based solely on this identification, Dart concluded that Taung's brain was neurologically advanced toward a human condition because it had relatively expanded nearby association cortices that displace *L* caudally (Dart, 1925). Unfortunately, Dart had incorrectly identified the lambdoid suture of the skull (which had been reproduced on the endocast) as *L*—an identification that Dart's colleagues, including Smith, were skeptical about (Falk, 2009b). Unpublished materials in the Raymond Dart collection of the archives of the University of Witwatersrand reveal that Dart identified 14 additional sulci on the Taung endocast in addition to the two that he identified in his 1925 publication, and that he

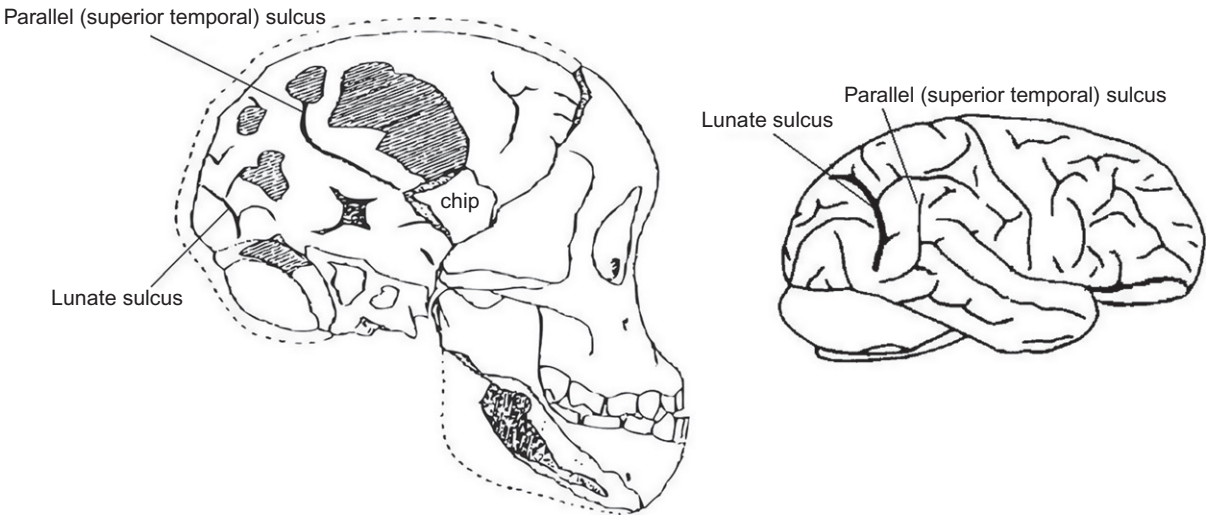

Fig. 3. Dart's (1925) illustration of the right side of the Taung natural endocast, facial fragment, and jaw compared to the right side of a chimpanzee brain. The feature Dart identified as the lunate sulcus is actually the lambdoid suture. Notice that the lunate sulcus on the chimpanzee brain (thickened for illustrative purposes) is more rostally located than the suture that Dart misidentified as the lunate sulcus on Taung. Reproduced from Falk (2011) with permission.

knew he had a lunate sulcus problem (Falk, 2009b). In a previously unpublished illustration (reproduced in Falk, 2009b), Dart illustrated the lambdoid suture on the Taung endocast for the first (and perhaps only) time and hypothesized that a portion of Taung's *L* coursed directly underneath it (Falk, 2009b). Although most of his contemporaries did not accept Dart's identification of *L*, his incorrect interpretation of that feature on the Taung endocast has been used in recent years to bolster the hypothesis that caudal regions of the hominin brain became reorganized prior to reorganization of other areas (mosaic brain evolution) and before evolutionary brain expansion in hominins (Barton and Harvey, 2000; Holloway, 2001; Holloway and Kimbel, 1986). We now know from his unpublished manuscript that Dart, on the other hand, favored a global rather than mosaic view of neurological reorganization (Falk, 2009b).

Current findings regarding the lunate sulcus

Through the years, lunate sulci of humans have been described as shorter, more variable in their configurations, and appearing less frequently than in the other anthropoids (Connolly, 1950; Ono et al., 1990). A recent study provides welcome, if unsurprising, quantitative support for the observation that humans have relatively reduced primary visual cortex compared to other anthropoids and that the volume of V1 in apes is predictable from the position of *L* (de Sousa et al., 2010; see also Fischl et al., 2008). The authors concluded that "the position of the lunate sulcus on fossil endocasts may provide information about brain organization" (de Sousa et al., 2010). However, another study that used high resolution MRI to assess the presence/absence of *L* in 110 adult humans revealed that the rare occurrences of sulci in, or near, the occipital lobes that superficially resemble those of ape lunate sulci were discontinuous beneath the surface and did not approximate the rostral border of V1 (Allen et al., 2006). In other words, there is little, if any, evidence in support of the view that contemporary humans have lunate sulci. It, thus, appears that *L* was lost at some undetermined time during hominin brain evolution. If so, a *lack* of lunate sulci on the brains of hominins, although difficult to verify because this sulcus does not reproduce well on hominoid, including human, endocasts (Le Gros Clark et al., 1936; Connolly, 1950), is the derived condition associated with cortical reorganization.

The only australopithecine endocast that is currently hypothesized to reproduce an "unmistakenly posterior placement" of *L* is that from Stw 505 (*A. africanus*) from Sterkfontein (Holloway et al., 2004). Because of this one endocast, the authors conclude that neurological reorganization occurred in caudal parts of early hominin brains prior to reorganization in other parts of the brain, and prior to brain enlargement. For various reasons, I am unconvinced that the feature identified as *L* on the Stw 505 endocast is that sulcus. If *L* was lost during human brain evolution, as seems likely from Allen et al. (2006), the hypothesis of a derived caudally located *L* in ape-sized australopithecine brains requires that this sulcus was an ancestral retention that was displaced caudally from an apelike location in conjunction with a (derived) differential expansion of association cortices just rostral to it, but with no overall increase in brain size. Another requirement is that, after being displaced caudally in small-brained hominins, *L* was subsequently lost in conjunction with the increase in overall brain size in *Homo*. To me, the hypothesis that *L* was located relatively caudally in early hominins is not parsimonious and, so far, it lacks convincing paleoneurological support from endocasts.

The evolution of cortical sulci

What alternative hypothesis might explain the evolution (or devolution) of the lunate sulcus?

A broad approach to this conundrum is to ask why the cerebral cortex remains smooth in smaller-brained species, yet becomes highly convoluted in larger-brained ones (Van Essen, 1997). The evolution of mammalian, including primate, cortical folding patterns probably entailed many factors, including alterations in the durations of neurogenesis (Finlay and Darlington, 1995). As noted, it has also been associated with optimization of neurological wiring patterns (Hofman, 2001, Chapter 18; Kaas, 2000; Kaas and Preuss, 2008) and an increase in the number of cortical areas with increasing brain size (Kaas and Preuss, 2008; Preuss, 2007a,b). At an allometric level, "convolutions increase with brain size primarily because the expansion of the cortical sheet outpaces the minimal area needed to envelop the underlying cerebral volume" (Van Essen, 1997:314; see also Jerison, 1973). Van Essen's tension-based theory of the formation of convolutions and sulci during brain development takes these various factors into account (Van Essen, 1997, 2007; Van Essen and Dierker, 2007) and is helpful for elucidating how *L* might have been lost during hominin evolution.

Van Essen hypothesizes that the development of gyral and sulcal patterns during prenatal and perinatal development is mediated by mechanical tensions along the axons as cortical–cortical connections are formed (Fig. 4). Thus, as neurons

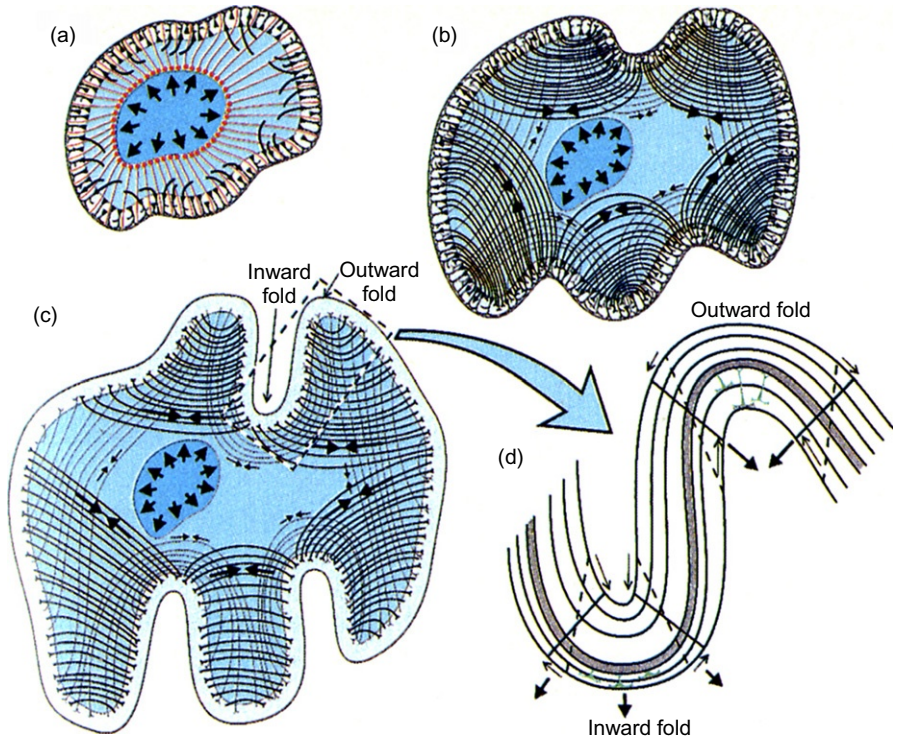

Fig. 4. In Van Essen's illustration of his tension-based theory of how convolutions develop, tightly interconnected regions of the cortical surface begin to swell and change the external shape of the cortex before the sulci that separate them are completely formed. Reproduced from Van Essen (1997) with permission.

migrate to the cortical plate and make connections there, tensions between strongly interconnected areas pull them together creating an externally protruding gyrus. Sulci, on the other hand, are inward folds that separate regions that have weak interconnections. Accordingly, "consistency in folding may reflect consistent patterns of connectivity among nearby areas" (Van Essen and Dierker, 2007: 212). Van Essen's hypothesis may also shed light on sulcal patterns that are relatively variable. "If cortical sulcal patterns are reflective of the tension of subcortical and corticocortical axonal projections (Van Essen, 1997), then it may be that the variability in the location of a cortical area relates to the degree of heterogeneity in its pattern of connectivity" (Fischl et al., 2008: 1978). An important implication of Van Essen's model is that the shape of the brain's surface changes as gyri and sulci develop and that these changes may begin to take place due to tensions from areas that are expanding (becoming strongly interconnected) (Fig. 4b) *before* sulci are fully formed (Fig. 4c). As discussed below, this possibility may have important implications for hominin paleoneurology.

Van Essen's hypothesis suggests that *L* may have been lost during hominin evolution because of changing patterns of cortical interconnections associated with the posterior and medial displacement of visual cortex. The lunate sulcus in monkeys and apes separates strongly interconnected visual areas from bordering association cortices, with which the former are relatively weakly connected (Van Essen, 1997). It seems likely that, as hominin brains increased in size and became neurologically reorganized, the strength of the interconnections between visual areas and the bordering association cortices increased in conjunction with the increase in the absolute and relative size of the latter (Falk and Gibson, 2001; de Sousa et al., 2010). The lunate sulcus may, thus, have disappeared in the ancestors of humans because the regions it formerly separated became more strongly interconnected with each other as the cortex reorganized.

Summary and conclusion regarding sulcal patterns

The options are very limited for gleaning information about the evolution of cortical folding patterns from fossil hominin endocasts. Ape and human brains consistently differ in their named sulci in only two parts of the cerebral cortex. In both cases, expanded association cortices appear to have displaced adjacent regions caudally as the cerebral cortex enlarged and reorganized during hominin brain evolution: In the frontal lobes, two new sulci (*R'*, *R*) appeared in humans that approximate the borders of the *pars triangularis* of Broca's speech area in the left hemisphere (and its homologous area in the right hemisphere) as the apelike *fo* was displaced caudally beneath the exterior surface of the brain. The second area entailed enlargement of the parieto–occipito-temporal association cortices, which displaced the primary visual cortex caudally. Unlike the first region, however, the evolution of this part of the hominin cerebral cortex entailed the loss of a major sulcus, *L*, as the primary visual cortex became more strongly interconnected with bordering association cortices (Allen et al., 2006; de Sousa et al., 2010).

Unfortunately, *L* does not reproduce well on endocasts from either apes or humans (Connolly, 1950). The fact that sulcal patterns of humans are derived both rostrally and caudally suggests that hominin brain evolution entailed global reorganization of the cerebral cortex (Dart, 1929; Falk, 2009b), contrary to the assertion of "mosaic brain evolution" in which the caudal portion of the brain is asserted to have evolved before other regions (Barton, 2001; Holloway, 2001; de Sousa et al., 2010). Ever since Dart misidentified the lambdoid suture for *L* on the Taung endocast (Dart, 1925, 1929; Falk, 2009b), assessment of the presence and location of *L* on early hominin endocasts has been muddied by paleopolitics (Falk, 2011). Although *fo* reproduces better on ape endocasts than *L*, it has received considerably less attention in the paleoneurological literature (Falk, 2009b). It would be wonderful if hominin endocasts reproduced crystal clear sulcal patterns,

but they do not. They do, however, reveal a good deal of information about shape features of the cerebral cortex that appears to be associated with cortical reorganization.

Neocortical reorganization of endocast (brain) shape

Although a good deal of attention has been given to the evolution of brain size, and some attention has been focused on the evolution of sulcal patterns, researchers are just beginning to apply imaging and geometric morphometric techniques to the study of brain shape changes during hominoid ontogeny and phylogeny (Chapter 13). Results show that brain shapes of humans and chimpanzees (as reproduced on virtual endocasts) are distinctive for each species at birth, and for each, they continue to change dynamically during infancy and childhood (Dosenbach et al., 2010; Neubauer et al., 2010; Ventrice, 2011). Human infants experience an early shape globularization of their brains that does not occur in chimpanzees before or after birth, which has been interpreted as a uniquely human trait that may be related to the evolved cortical reorganization that underpins derived human behaviors and cognitive abilities (Neubauer et al., 2010). Asymmetries in the gross brain shape of humans have also been associated with such traits, including language and handedness (see below).

Brains of anthropoid primates are functionally lateralized, which is superficially manifested in gross difference in the shapes of the two cerebral hemispheres. As is well known, cerebral lateralization is especially marked in humans, in whom the neurological substrates for language and right-handedness usually depend largely on the left hemisphere, whereas processing of more holistic endeavors such as musical activities is largely the domain of the right hemisphere (Falk, 2010; Chapter 6). In keeping with this, shape asymmetries of the whole brain, known as petalias, are more dramatic in humans than in the other higher primates (LeMay et al., 1982). Additionally, human brains are derived compared to apes and early hominins in the gross shapes of certain parts of their brains (Falk et al., 2000).

Petalias

Asymmetrical brain shape is the norm for adult humans, in whom the most frequent petalia pattern, known as the Yakovlevian torque, combines a more protuberant and wider right frontal lobe with a more protuberant and wider left occipital lobe (Fig. 5) (Galaburda et al., 1978; Chiu and Damasio, 1980; LeMay, 1984; Toga and

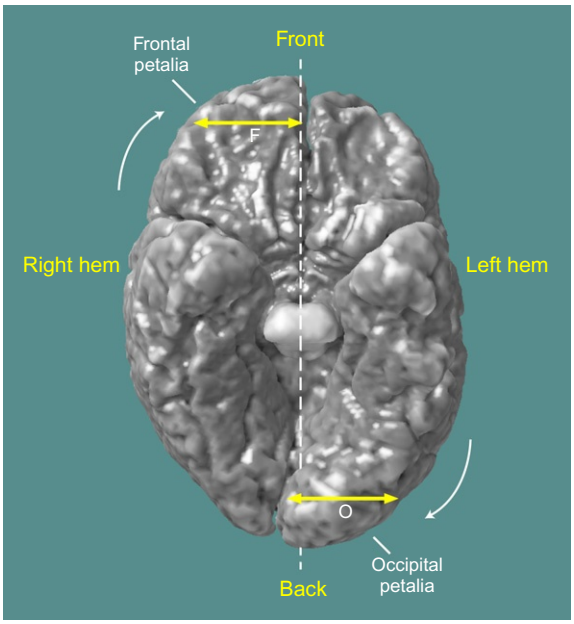

Fig. 5. The most common petalia pattern in the human brain, consisting of a right frontal and left occipital petalia. This rendering of the inferior surface of a human brain is from a magnetic resonance imaging (MRI) scan that has been exaggerated to illustrate the typical human petalia pattern and Yakovlevian torque. Reproduced from Toga and Thompson (2003), courtesy of Dr. Arthur W. Toga and Dr. Paul M. Thompson, Laboratory of Neuro Imaging at UCLA.

Thompson, 2003; Kivilevitch et al., 2010). This right frontal, left occipital petalia pattern is statistically correlated with right-handedness, whereas the reversed left frontal, right occipital petalia pattern is associated to some degree with left-handedness (LeMay, 1977; LeMay et al., 1982). The latter is especially true for left-handed women, particularly if the degree of the petalias is extreme (Bear et al., 1986). As noted, these petalia patterns exist to a lesser degree in nonhuman primates and early hominins (LeMay et al., 1982). Accordingly, the relatively extreme torques in human brains is viewed as the result of a prolonged evolutionary trend for brain lateralization (Falk, 2009a, 2010).

Ventrice (2011) has recently observed that the ontogenetic development of human petalia patterns is a dynamic process during which shape torques change directions. According to Ventrice, brain shape of infants and juveniles are typically characterized by left frontal and right occipital petalias, which is the reverse of the most common adult pattern. This surprising new finding needs confirmation, but should be kept in mind when interpreting petalia patterns from australopithecine infants or juveniles such as the Dikika infant (*Australopithecus afarensis*) and Taung juvenile (*A. africanus*). On a technical note, because of shape torques, the midline of brains meanders a bit and the common practice of mirror-imaging missing parts of hominin endocasts around an estimated midsagittal plane is bound to introduce some error in both shape and brain size estimates. One way to minimize reconstruction error is to use automated computer programs for establishing the most optimal midsagittal plane (Falk and Clarke, 2007).

Shape of the lobes

As noted, Van Essen's tension-based theory of the formation of convolutions suggests that evolutionary changes in the patterns of neurological connections influenced local shapes of the cerebral cortex, which paved the way for the formation of sulci separating less interconnected regions (as well as the reverse process in which sulci may have disappeared as previously separated areas became increasingly interconnected) (Van Essen, 1997). Findings regarding sulcal patterns and endocast shapes of two different genera of fossil hominins (*Paranthropus* and *Australopithecus*) that lived contemporaneously in Africa between approximately 2.6 and 1.9 million years ago are consistent with this hypothesis (Berger et al., 2010; Falk et al., 2000). As far as I have been able to determine from their endocasts, the brain size and sulcal patterns of both groups were similar and apelike (Falk, 2009b; Falk et al., 2000). Brain shape, however, differed markedly between the two genera. The robust australopithecines (*Paranthropus*) are thought not to have been directly ancestral to *Homo*, which is consistent with certain apelike features of their endocasts compared to those of *Australopithecus*—the genus that is believed to have given rise to *Homo* (Berger et al., 2010).

Endocasts of *Paranthropus* were primitive in their relatively pointed frontal lobes (when seen in dorsal view) compared to *Australopithecus*, which had frontal lobes that were more squared off at the rostral lateral borders (Falk et al., 2000) (Fig. 6). Consequently, the overall perimeter of *Paranthropus* endocasts has a teardrop shape compared to *Australopithecus* endocasts. The orbital surfaces of the frontal lobes of *Australopithecus* are also expanded ventrally compared to the flatter orbital surfaces of *Paranthropus*. It is noteworthy that the frontal lobes of *Australopithecus* are elongated rostrally in a region that corresponds to Brodmann's area 10 (BA 10) in both apes and humans. When viewed basally, *Australopithecus* endocasts have temporal poles that are expanded and pointed rostrolaterally compared to the relatively stubby temporal poles of *Paranthropus* and African apes (for illustrations and further details, see Falk et al., 2000).

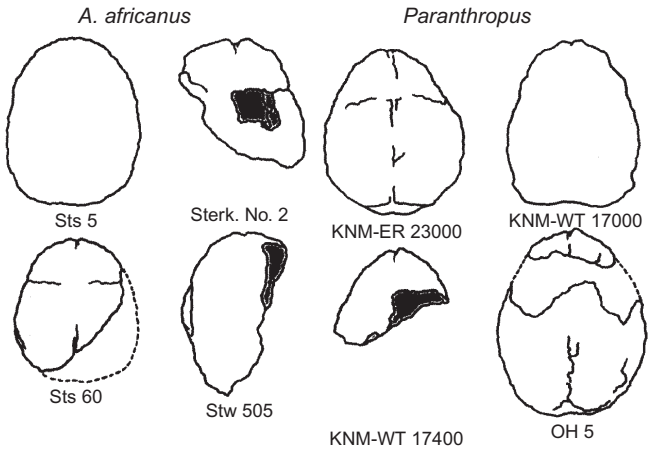

Fig. 6. Shape differences between similarly sized endocasts of *Paranthropus* and *Australopithecus africanus*, seen from dorsal view (with the frontal lobes located superiorly). Specimen numbers are next to endocasts, some of which are fragmentary. Compared to *Australopithecus*, endocasts of *Paranthropus* have more pointed frontal lobes, which give the overall perimeter of their endocasts a teardrop shape. Rather than being pointed, the frontal lobes of *Australopithecus* are broader, with sides that are more squared off laterally. Reproduced with permission from Falk et al. (2000).

Raymond Dart's observations of the Taung endocast that recently came to light also suggest that the shape of the prefrontal cortex was derived toward a human condition in *A. africanus* compared to apes (Dart, 1929; Falk, 2009b). Additionally, Dart observed that the occipital pole of *Australopithecus* projected caudally relative to the cerebellar pole, which is another feature that may be derived in *Australopithecus* compared to *Paranthropus* and apes (Falk et al., 2009). (For the sake of completion, Dart also believed that the caudal lateral portion of Taung's temporal lobe was expanded and somewhat derived toward a human condition, although I have not compared this feature in different australopithecines (Falk, 2009b).

Interestingly, *Paranthropus* endocasts reproduce an enlarged occipital/marginal venous sinus caudally, as do most, if not all, of the scorable specimens belonging to *A. afarensis* (Falk et al., 1995). This feature has been observed in Taung (Tobias and Falk, 1988) and possibly in a fragmentary occipital fragment (Stw 187a) (Lockwood and Tobias, 2002) among the available *A. africanus* specimens. Since brain sizes were very similar in the two genera of australopithecines (Falk et al., 2000), their different blood drainage patterns, as well as the derived cortical shape features of *Australopithecus*, were not the result of allometric scaling. With respect to the latter, and consistent with Van Essen's hypothesis, it is reasonable to speculate that certain neurological regions may have become more interconnected and derived toward the human condition in *Australopithecus*, thus causing the noted shape changes, although these had not become pronounced enough to cause changes in their sulcal patterns—at least to an extent that can presently be inferred from endocasts.

Conclusion regarding endocast (brain) shape

Most of the information about hominin brain evolution that paleoneurologists can reliably glean from endocasts is limited to details about brain size and the gross shape of the cerebral hemispheres (including asymmetries) and lobes of the brain. Unfortunately, although sulcal

patterns in the caudal lateral part of the frontal lobes and near the rostral lateral borders of primary visual cortex are potentially informative, they do not reproduce well on hominin endocasts and have, therefore, been subject to intense controversy (Falk, 2011). In other words, apart from gross size and shape of the brain, endocasts offer few hints about the trajectory of brain evolution in hominins.

Comparative neuroanatomical studies: Implications for hominin paleoneurology

In order to assess more fully the nature of the evolved neurological substrates that underpin human cognitive abilities, paleoneurologists must turn to findings from comparative neuroanatomy, neurochemistry, genetics, and functional imaging studies such as those discussed in this volume (Falk, 2010). Although a thorough review of the relevant literature is beyond the scope of this chapter, some studies that have particularly important implications regarding neurological features that seem to be evolutionarily advanced in humans are briefly described here. To begin, and as noted above, the most obvious derived characteristic of human brains is that they are absolutely and relatively large, averaging about three times the size for australopithecines as well as three times the size expected for nonhuman primates of similar body size (Passingham, 1973, 1975; Stephan et al., 1970). Despite their large mass, however, the "quest for uniqueness" in human brains has been frustrated because

> "the human brain has the number of neurons that is expected of a primate brain of its size; a cerebral cortex that is exactly as large as expected for a primate brain of [its size]; just as many neurons as expected in the cerebral cortex for the size of this structure; and, despite having a relatively large cerebral cortex . . ., this enlarged cortex holds just the same proportion of brain neurons in humans as do other primate cortices. . .. This final observation calls for a reappraisal of the view of brain evolution that concentrates on the expansion of cerebral cortex and its replacement with a more integrated view of coordinate evolution of cellular composition, neuroanatomical structure, and function of cerebral cortex and cerebellum"
> (Herculano-Houzel, 2009:10)

According to Herculano-Houzel (2009; Chapter 15), what is unique about the human brain is that humans have the largest absolute number of neurons among primates and probably other animals. This fits nicely with the fact that people also have the largest brains, by far, of any primate.

As the research of Herculano-Houzel (2009) and Herculano-Houzel et al. (2010) illustrates, the search for advanced brain features in humans has become less focused on gross anatomy and more concerned with cytoarchitecture, neuronal connections, and functions at the cellular level. At one point, for example, the relative size of the human frontal lobe was believed to be differentially large. However, Semendeferi and her colleagues have demonstrated that the overall size of human frontal lobes is not greater than expected for brains of their size. Instead, it now appears that alterations in internal wiring and differential enlargement occurred during hominin evolution in certain subareas of the prefrontal cortex including BA 10 (Semendeferi and Damasio, 2000; Semendeferi et al., 2001, 2002), while other areas such as Brodmann's area 13 (BA 13, part of the limbic system) decreased in relative size (Semendeferi et al., 1998). Human prefrontal cortex is especially important for higher cognitive processing in humans, in keeping with the finding that differential expansion of white matter (Schoenemann et al., 2005) and pronounced gyrification (Armstrong et al., 1993; Rilling, 2006) have also been described for this part of the brain.

Because the relative size of human BA 10 is twice that of both bonobos and chimpanzees,

Semendeferi (1994) suggested that this area of the cerebral cortex increased in relative size at some point along the line from the first hominins to the early representatives of the genus *Homo*. Recently, she and her colleagues compared the spacing organization of neurons in layer III in frontopolar (BA 10), primary motor (BA 4), primary somatosensory (BA 3), and primary visual cortex (BA 17) in ape and human brains (Semendeferi et al., 2011) (Fig. 7). Their results strongly suggest that the horizontal spacing distance (HSD) between neurons increased in BA 10 (but not the three other areas) in hominins after they split from the ancestors of chimpanzees in a manner that facilitated complex interconnectivity and information processing (Fig. 7). Interestingly, similar histological findings have also been reported for human BA 44/45 (Broca's area) (Schenker et al., 2008), which raises the fascinating possibility that the human prefrontal cortex was widely reorganized during hominin cognitive evolution (Semendeferi et al., 2011).

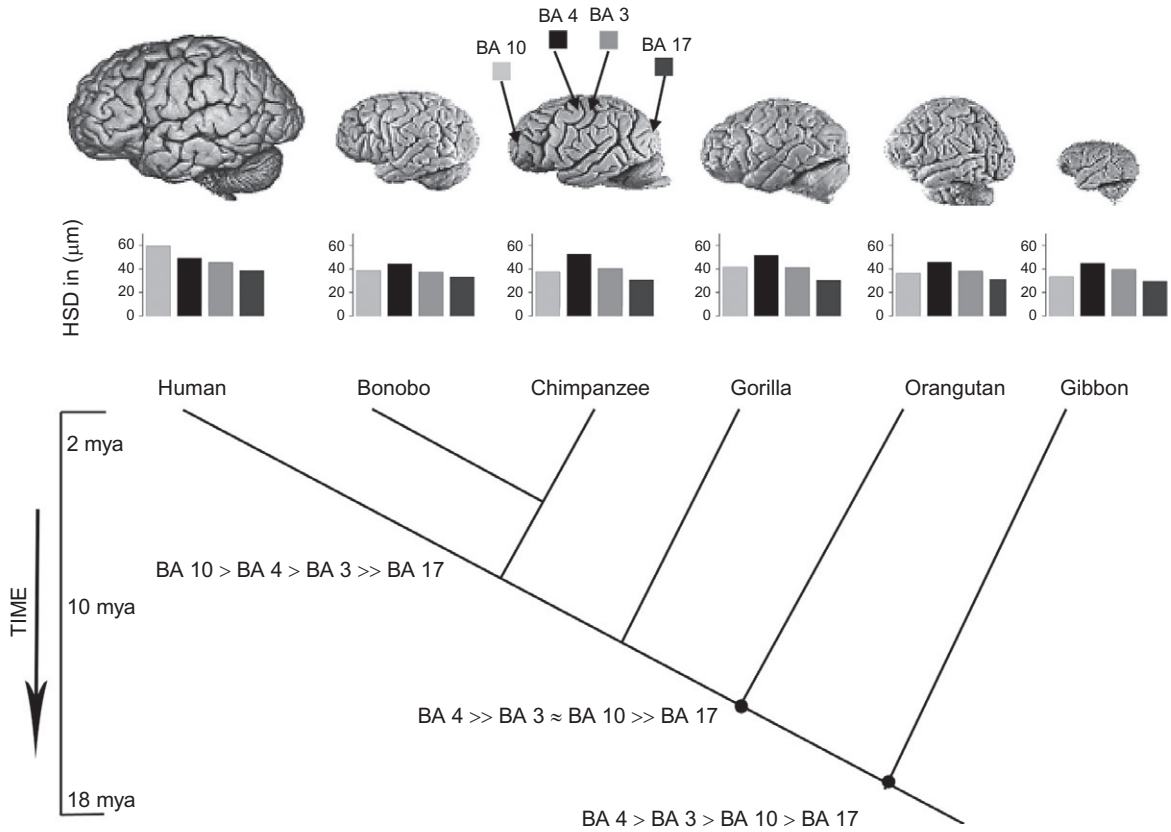

Fig. 7. Cladogram showing left lateral views of the human and ape brains and the relative degree of horizontal spacing distance (HSD) of neurons in four areas of their cerebral cortices (BA 10, BA 4, BA 3, BA 17). Symbols: >, greater HSD between neurons; >>, statistically significant greater HSD between neurons; ≈, HSD about the same. After human and chimpanzee lineages split, the HSD of BA 10 in humans became the largest (indicating more complex connectivity) compared with the three other cortical areas in the human brain and compared with BA 10 in the apes. Reproduced with permission from Semendeferi et al. (2011).

The size and organization of the human frontal pole clearly stands out from that of apes and its functions constitute one of the most fascinating puzzles in cognitive neuroscience (Burgess et al., 2005; Gilbert et al., 2006). This area has been implicated in a range of activities including "watchfulness," remembering to carry out intended activities, aspects of recollection, anticipating the future, multitasking, switching between externally versus internally oriented thoughts, and integrating limbic input to arousal, motivation, and intentions (Burgess et al., 2005; Koechlin and Hyafil, 2007; Tucker and Holmes, 2011). Thus, a key adaptive advantage of an evolved frontopolar cortex may have been "an ability to pursue long-term behavioral plans and at the same time respond to demands of the physical or social environments... the frontopolar cortex may have played an even more critical role in the gradual formation of complex behavioral and cognitive routines such as tool use in individuals and societies, that is, in human creativity rather than complex decision-making and reasoning" (Koechlin and Hyafil, 2007:598).

Concluding remarks

I have spent some time reviewing the literature on BA 10 because it is an excellent example of research that is beginning to shed light on the evolution of advanced cognitive abilities in hominins based on a synthesis of findings from paleoneurology and comparative neuroanatomy. As we have seen, the shapes of the frontal lobes that are reproduced in the frontopolar region on endocasts of *Australopithecus* and *Paranthropus* appear expanded toward a human condition in the former but not the latter. This observation is consistent with Semendeferi et al.'s (2011) hypothesis that an increase in the horizontal spacing between neurons and an associated increased complexity in connectivity occurred in BA 10 of our ancestors' brains at some point after our lineage split from that of chimpanzees. When, exactly, this change began during the approximately 7 million years of hominin evolution is unknown. However, the comparative paleoneurological evidence regarding brain size, frontal lobe shape, and sulcal patterns (including an apelike fronto-orbital sulcus in *Australopithecus*) suggests that the early stages of prefrontal cortical evolution may have been underway in the *Australopithecus* population(s) that gave rise directly to *Homo*. Indeed, Raymond Dart would have embraced this hypothesis, as shown by his 1929 unpublished monograph, which languishes in the archives of the University of Witwatersrand.

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