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Brain Endocast Asymmetry in Pongids and Hominids: Some Preliminary Findings on the Paleontology of Cerebral Dominance

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ABSTRACT Observations on petalial asymmetry for 190 hominoid endocasts are reported, and their statistical differences assessed. While all taxa of hominoids show asymmetries to various degrees, the *patterns* or combinations of petalial asymmetries are very different, with fossil hominids and modern *Homo sapiens* showing an identical pattern of left-occipital, right-frontal petalias, which contrasts with those found normally in pongids. Of the pongids, *Gorilla* shows the greater degree of asymmetry in left-occipital petalias. Only modern *Homo* and hominids (*Australopithecus, Homo erectus,* Neandertals) show a distinct left-occipital, right-frontal petalial pattern. Analysis by χ^2 statistics shows the differences to be highly significant. Due to small sample size and incompleteness of endocasts, small-brained hominids, i.e., *Australopithecus*, are problematical. To the degree that gross petalial patterns are correlated with cognitive task specialization, we speculate that human cognitive patterns evolved early in hominid evolution and were related to selection pressures operating on both symbolic and spatiovisual integration, and that these faculties are corroborated in the archaeological record.

The last decade has witnessed a considerable resurgence of interest in anatomical and functional asymmetries of the cerebral hemispheres.[1] In general, the empirical support for anatomical asymmetry appears well-documented and extensive; (Geschwind and Levitsky, 1968; Galaburda et al., 1978; Hochberg and LeMay, 1975; Kimura, 1973; LeMay, 1976; LeMay and Culebras, 1972; LeMay and Geschwind, 1975; Nottebohm, 1977; Wada et al., 1975; Witelson and Pallie, 1973; Yeni-Komshian and Benson, 1976). The functional asymmetries suggested are somewhat more speculative, but provocative nevertheless (e.g., McGlone 1980; Herron 1979). In general, a picture has emerged that indicates that in most human individuals, language functions are more strongly represented in the left cerebral hemisphere, and the right hemisphere more involved with nonverbal, visuospatial tasks. This general concensus is naturally oversimplified, but remains the dominant and empirically-supported position at the present time. Sex differences in the degree of symmetrical organization for these two basic functions remains a controversial area, but as McGlone's (1980) very exhaustive and judicious review indicates, the evidence favors the viewpoint that male brains are organized more asymmetrically than those of females. Whether or not this present viewpoint is demonstrable, remains for the future. In any event gross morphological examination of both adult and infant (including foetal) cerebral hemispheres does show a highly significant statistical *correlation* between handedness and asymmetries. We stress the word *correlation*, demurring from any advocacy of causation at this time.

The numerous publications of LeMay and her colleagues (see literature cited and above)

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[1] We are aware that evidence is also emerging for asymmetry patterns in noncortical brain regions for a variety of animals, including *Homo sapiens.* Since this article is not meant to represent a total review of lateralization and asymmetry problems and is directed toward the paleoneurological evidence in human evolution, we are omitting the noncortical evidence from our article. The volume edited by Diamond and Blizard (1977) Evolution and Lateralization of the Brain, should be consulted for other examples.

on petalial patterns in hominoid endocasts and living human subjects have provided a welcome and long-sought-for connection between paleoneurological research on fossil brain endocasts and the continually growing empirical record of modern anatomical and functional asymmetry of the cerebral hemispheres in primates.

It is not our intent to review all of these studies in this article, but rather to present some preliminary results of our studies on the largest collection of hominoid endocasts presently existing, which is composed of 135 pongid and 41 fossil hominid brain endocasts. We do this in the hope that our comparative and evolutionary frameworks will be a useful base for furthering our understanding of brain asymmetries and their functional significance, and to offer a set of hypotheses for further testing.

We further wish to demonstrate that even the early hominids (i.e., australopithecines) show decidely human rather than pongid patterns of hemispheric asymmetry, although larger samples will be necessary to prove the tentative conclusion we draw here. We interpret this finding to mean that a human pattern of cerebral organization did occur early in hominid evolution (ca. 3×10^6 million years), and that natural selection operated to enhance specialized facilities for behavioral repertoires, minimally consisting of spatiovisual competence, symbol-processing (i.e., primitive social communication based on symbol systems), and skills in processing visuospatial information that were important to early hominid lifeways. We admit that these conclusions are speculative, but fully compatible with the brain-endocast data, the comparative brain evidence, and the growing complexity of associated archaeological contexts, particularly from East African hominid sites (Isaac, 1976; Isaac et al., 1976; Leakey, 1971).

MATERIALS AND METHODS

During the last decade a large number of undistorted pongid endocasts have been made using a rubber latex method as described elsewhere (Holloway 1978, 1980b, 1981a). Table 1 provides a breakdown of this sample by species.

In addition, the senior author (R.H.) has been preparing endocasts of most of the available hominid crania, and while individual endocasts have been described in the literature (Holloway 1972, 1975, 1980a, 1981a,b,e), the total available sample has not been brought together for statistical analysis in the past. The sample of hominid endocasts now numbers 41. It is an unfortunate fact that many of the hominid endocasts are incomplete, or in some cases so seriously distorted or fragmentary as to preclude observations of asymmetries. We have noted these facts in Table 1.[2]

In assessing asymmetries, we examined the total sample of hominoid endocasts for the presence or absence of petalias (see Table 1 and 2) in (1) frontal and occipital regions; and (2) asymmetries in lateral extent of frontal and posterior width from the mid-sagittal plane. Our observations were scored in ordinal-level measurements (i.e., greater, lesser, equal, yes, no, neither, slight, or pronounced). Table 2 indicates the variables studied. These observations were then coded numerically, punched onto data cards, and analyzed using χ^2 statistics, as provided in the "Crosstabs" subprogram of SPSS (Statistical Package for the Social Sciences, Nie et al., 1975).

As Table 1 indicates, we broke our total sample of 190 endocasts into 9 groups. The pongid sample and modern *Homo sapiens* were broken down according to taxonomic principles. *Homo erectus* was retained as a "label" for hominids in Africa, Europe and Asia, which have medium-sized brains, and we use the term "Homo erectus" as a grade, appreciating that controversy exists with regard to actual genetic relationship. Similarly, large-brained fossil hominids are referred to as Neandertals, and include both the Rhodesian and Swanscombe endocasts.

"Small-brained early hominids" is our term for those hominids that minimally include the species *A. africanus* and *A. robustus.* OH12 and 13, and KNM-ER 1805 and 1813 may or may not be *Australopithecus*, but are, in any event, small-brained, and roughly contemporaneous. It should be stressed that of this sample of 13, only 3 endocasts are complete: KNM-ER 1805 and 1813, and OH5. All other pongid and moderm *Homo sapiens* are complete.

Before discussing the results, some comments regarding certain endocasts are neces-

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[2] Table 1 includes *only* those endocasts for which one of us (R.H.) believed a secure judgment of asymmetries could be made. All pongid endocasts (N = 139), and those of modern *Homo sapiens* (N = 14) were complete and undistorted. *Homo erectus* IV was not regarded a secure judgment, and thus rejected, although one of us (R.H.) believes there is a slight left-occipital petalia, both in the posterior and lateral sense. KNM-ER 1470 is a distorted cranium, and so is the endocast, in which the left temporal lobe is anteriorally displaced. In our opinion, this distortion does not seriously affect the occipital poles, or prefrontal widths. The endocast of STS5 from Sterkfontein, South Africa, was not regarded as a reliable specimen for judging petalial patterns.

TABLE 1. The pongid and hominid sample

Group	Number	Completeness
Gorilla gorilla	40	total
Pan paniscus	41	total
Pan troglodytes	34	total
Pongo pygmaeus	20	total
Modern *Homo sapiens*	14	total
Hominids	41	(variable)
Small-brained early hominids	SK1585, SK859, MLD1, OH12, OMO 338y, STS19, OH13, STS60, KNM-ER1805, 1813, OH5 (N = 11)	posterior or anterior only "total"
Homo erectus	OH9, I, II, VI, VII, VIII (Indonesia) KNM-ER3733, 3883, Choukoutien III L, E, L, de Sale, Solo I, IV, V, VI, IX, X, XI (N = 20)	(variable)
Neandertal	Spy I and II, la Quina, Gib. I, Gib. II, La Chapelle-aux-Saints, La ferrassie, Djebel Ihroud I, Rhodesian, Swanscombe, Neandertal cap. (N = 10)	(variable)

Composition of the total hominoid sample of endocasts used in this study. Only the pongids and modern *Homo sapiens* have totally complete and undistorted endocasts. "Variable" means that while some portions were missing, either the frontal or occipital portions were complete enough for scoring. KNM-ER 1805 and 1813 are "total," lacking only small portions of their bases. OH5 is also regarded as "total."

TABLE 2. Asymmetries observed

Region	Observation
1. Which occipital petalia most posteriorally projecting	left, right, neither (var. 1)
2. Occipital width	left, right, neither (equal), (var. 2)
3. Both left occipital petalia *and* occipital width in combination	yes, no (var. 3)
4. Frontal petalia	left, right, neither (var. 4)
5. Combination of left occipital and right frontal petalia	yes, no (var. 5)

List of total variables observed for the purpose of this preliminary article.

sary. The endocast of OH5, a robust australopithecine from Tanzania, was included in the sample, even given the poor alignment of the occipital portion of the crania, and the difficulty in determining whether or not petalial formations existed. That there is a right frontal petalia, in terms of the more anteriorially projecting frontal pole, seems certain; the lateral extent of the right prefrontal portion that is undamaged appears wider than on the left side. While we judge the lateral width of the occipital region to be greater on the left side, the reconstruction of the cranium makes a fully confident judgment very difficult. The left occipital pole is judged to be slightly more posterior. For these reasons, OH5 is included in this sample, but with some trepidation and caution, given the original condition of the cranium.

The gracile australopithecine endocast of STS60, from Sterkfontein, South Africa, is without the occipital region on both sides. In the frontal region, while both sides are lacking complete orbital margins, there *is* a clear suggestion of a right-frontal petalia, in the lateral extent of the prefrontal region. However, the right side is less complete than the left, which is unfortunately damaged in the Broca "cap" region, making comparisons very difficult. STS60 is also included in the sample, but only with regard to its frontal portion. In other cases, such as SK1585, the frontal regions are missing, but the occipital lobes can be scored.

Finally, some further methodological observations are in order. Other authors (e.g., LeMay, 1976; LeMay et al., in press) have used "scan" pictures, or photographs of the dorsal surfaces of endocasts. We have relied on gross visual examination of both the dorsal and inferior surfaces by rotating the endocasts through the axis of the midsagittal plane. We regard this as a necessary step, since it is possible to see a more projecting occipital petalia in a dorsal view on one side, but a reversal when viewed from the inferior surface. While this occurs very infrequently, we believe both views should be carefully checked before assigning a value to one side in terms of posterior petalial extent. This anomaly seems to be related to an occasional downward projection of

TABLE 3. Variation 1: Occipital pole most posterior

Group	Left	Right	Neither	Total
Gorilla gorilla	28	3	9	40
Pan troglodytes	12	9	13	34
Pan paniscus	20	10	11	41
Pongo pygmaeus	5	4	11	20
Homo sapiens	12	1	1	14
Early hominids	6	1	0	7
Homo erectus	15	2	2	19
Neandertals	8	1	0	9

This table shows the distribution among groups of occipital petalia. Note the high number of cases for all pongids in the "neither" column, and the high number of cases for "left" in *Gorilla* and *Pan paniscus.*

TABLE 4. Variation 2: Occipital width greatest

Group	Left	Right	Neither	Total
Gorilla gorilla	7	2	31	40
Pan troglodytes	0	3	31	34
Pan paniscus	1	4	36	41
Pongo pygmaeus	1	0	19	20
Homo sapiens	11	0	2	13
Early hominids	6	1	1	8
Homo erectus	17	1	1	19
Neandertals	8	2	0	10

This table shows the distribution of occipital width. Notice the large number of cases of "neither" for all pongids.

the occipital pole, which if not correctly viewed, can mask its petalial characteristic.[3]

In doing the statistical comparisons, we have relied upon the "Crosstabs" routine of SPSS, since the χ^2 tests are robust, and a number of ancillary tests are provided, such as the phi (ϕ) statistic, Cramer's V for larger tables, uncertainty coefficient, t and b, and Somer's D. In fact, however, the χ^2 tests were sufficient for the questions we were asking.

THE HYPOTHESES

We wished to test the following hypotheses in asymmetries of this large sample: (1) extant pongids show significant intergroup differences in their petalial patterns; (2) different hominid groups show significant differences in their petalial patterns; (3) there are significant differences between fossil hominids and modern *Homo sapiens* in petalial patterns; (4) there are signifiant differences between pongids and modern *Homo sapiens* in petalial patterns; (5) there are significant differences between *early* hominids and pongids in petalial patterns.

It is necessary to emphasize that the results to follow are preliminary in two senses: (1) the data collected to date are ordinal rather than interval in nature; (2) our chi-square tests have been done using noncollapsed taxa. By this we mean that the pongids are kept in their specific taxa and not combined as a group, nor are the hominids. (In fact, collapsing the taxa makes very little real difference in the final results regarding the levels of statistical significance (or lack) between taxa. As will be seen in the Tables 3–7, the patterns are different between pongids and hominids, and to a minor extent, among pongids. We intend to expand upon these results in a later publication.)

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[3] This fact has been noted for the endocast of the Indonesian *Homo erectus*, (PITH I) in Holloway (1981c). LeMay (1976:361) discusses fossil hominid endocast petalias as reported in the literature, and we strongly recommend her article as an excellent review of these problems. PITH I, however, is particularly confusing, and the left-occipital petalia is more projecting when the endocast is rotated through its sagittal plane. McGregor (1925) concluded the opposite, but the longitudinal sinus becomes a very visible and thick right transverse sinus, which deflects the smaller right occipital pole lateral and superiorally. The right-prefrontal width is somewhat larger on PITH I. The Rhodesian endocast reported in Pycraft et al. (1928) is said to be lacking any strong asymmetries of the occipital poles, and a similar conclusion was pronounced by LeMay (1976:361) on the basis of Anthony's (1913) discussion of the La Quina endocast. In fact, the Rhodesian endocast *does* show a slight left occipital petalia in posterior projection, but the damage to the cranium in the right occipital-parietal-temporal portion rules out any secure evaluation of lateral occipital width comparisons. The frontal lobe of Rhodesian *Homo* is another matter, however, as its right frontal pole is *clearly more* anteriorally projecting, and the prefrontal width is clearly greater on the right rather than left side. The left parietal width, from the sagittal sinus appears fuller to this observer (R.H.) than on the right side. Consequently, this specimen is taken to show a left-occipital, right-frontal petalial pattern, albeit a weak one. The La Quina endocast shows a weak left-occipital and right-prefrontal pattern, although one must be cautious of this appraisal given the endocast's lack of detail.

TABLE 5. Variation 3: Both left occipital petalia and greater width

Group	Yes	No	Total
Gorilla gorilla	7	33	40
Pan troglodytes	0	34	34
Pan paniscus	1	40	41
Pongo pygmaeus	1	19	20
Homo sapiens	10	3	13
Early hominids	6	2	8
Homo erectus	16	3	19
Neandertals	7	3	10

Distribution of cases with both left-posterior and lateral-occipital petalias. Notice the reversal of pattern between pongid and hominid groups.

TABLE 6. Variation 4: Right-frontal, lateral

Group	Left	Right	Neither	Total
Gorilla gorilla	2	17	21	40
Pan troglodytes	5	8	21	34
Pan paniscus	4	22	15	41
Pongo pygmaeus	1	6	13	20
Homo sapiens	0	14	0	14
Early hominids	0	4	0	4
Homo erectus	1	12	0	13
Neandertals	2	8	0	10

Distribution of right-frontal petalia in width. Notice that while pongids show this more often on the right side than left, most pongid cases score "neither," a pattern reversed from all hominoid groups.

TABLE 7. Variation 5: Left occipital–right frontal combination

Group	Yes	No	Total
Gorilla gorilla	13	27	40
Pan troglodytes	4	30	34
Pan paniscus	14	27	41
Pongo pygmaeus	3	17	20
Homo sapiens	11	3	14
Early hominids	2	1	3*
Homo erectus	11	1	12
Neandertals	7	2	9

*Note: Includes KNM-ER 1805, 1813, and OH5.
Distribution of "classical" left-occipital, right-frontal petalias. Again, the pattern is clearly reversed between pongid and hominid groups.

RESULTS

Hypothesis 1: Within–Pongid sample

Tables 3–8 show that there are petalial differences between pongid taxa. *Gorilla* shows a clear preponderance of left-occipital petalias, both A-P and lateral, compared to *Pan p., Pan t.,* and *Pongo*.[4] These differences are reflected in the significance figures for columns 1, 2, and 3 in Table 8. Right frontal lateral petalial patterns do not show significant differences when *Gorilla* is included in the sample. (See Table 4, and Column 4 in Table 8). When *Gorilla* is excluded from the sample, (see row 2, Table 8), occipital pole, parietal width, and right frontal petalial patterns are not significantly different. However, when left-occipital (A-P) and right-frontal (lateral) petalias are examined combined with *Gorilla* excluded, the differences are significant, and Table VII shows that this effect is dependent on *Pan p.*, which has the highest score of cases (N=14) showing both effects. Note, however, from Tables 4–7, there are a large number of cases in the columns for "neither," and "no."

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[4] Table 2 indicates that we also studied the distribution of occipital petalia in graded terms i.e., prominent, slight, or neither. *Gorilla* was significantly different than either chimpanzee species or orangutan, in that out of 40 cases, 24 showed a prominent left occipital petalia, whereas in the other species, the distribution was much more even between right and left sides, and the number of cases in the "left-prominent" category were always less than in the "left-slight" category. The resulting X^2 was 46.5, with 15 d.f., with a significance of 0.0000.

TABLE 8. Chi-square statistics

Group comparisons	Var. 1 Occipital pole (anterior position)			Var. 2 Occipital width			Var. 3 Both occipital length & width			Var. 4 Right frontal lateral petalia			Var. 5 Combination of left occipital right frontal		
	χ^2	d.f.	sig.	χ^2	d.f.	sig.	χ^2	d.f.	sig.	χ^2	d.f.	sig.	χ^2	d.f.	sig.
Pongids only	16.8	6	0.0100	13.4	6	0.0364	11.2	3	0.0105	10.3	6	0.1103	7.2	3	0.0648
Pongids, gorilla excluded	5.3	4	0.2602	3.5	4	0.4777	1.6	2	0.4569	9.2	4	0.0562	6.2	2	0.0462
Pongids and *Homo sapiens*	24.2	8	0.0021	70.1	8	0.0000	58.5	4	0.0000	29.2	8	0.0003	23.6	4	0.0001
Hominids and *Homo sapiens*	1.9	6	0.9244	5.4	6	0.4873	0.8	3	0.8373	3.8	3	0.2844	1.4	3	0.6991
Hominids only	1.8	4	0.7670	2.8	4	0.5930	0.85	2	0.6539	1.4	2	0.4834	1.4	2	0.4966
Pongids and Hominids (modern *Homo sapiens* excluded)	31.7	8	0.0001	108.4	8	0.0000	90.8	4	0.0000	35.8	8	0.0000	36.8	4	0.0000
	(See Table 3)			(See Table 4)			(See Table 5)			(See Table 6)			(See Table 7)		

Chi-square analyses on each of variables in Tables 2–7 for different groups. χ^2, chi-square; d.f., degrees of freedom; sig. significance level. Notice the change in χ^2 and significance figures between row 1 and row 2, when *Gorilla* is removed.

Thus there are significant differences between pongid taxa for petalial patterns, although the overall pattern is not human.

Hypothesis 2: Within-Hominid sample

No significant differences in petalial patterns are evident from the statistics in Table 8. However, as Tables 3–7 show, the small sample sizes and incompleteness of specimens are serious obstacles, particularly when the small-brained group is considered. Note that in Table 7, this group is reduced to three. Nevertheless, Tables 3–7 do suggest that there is a clear-cut reversal of pattern of petalial distribution between hominids and pongids, and that hominid groups display the same pattern among themselves.

Hypothesis 3: Hominids and modern Homo sapiens

No significant differences are apparent in any of the petalial patterns. That is, hominids (small-brained hominids, *H. erectus*, and Neandertals) show the same petalial configuration as modern *Homo sapiens*.

Hypothesis 4: Pongids and modern Homo sapiens

All petalial patterns are significantly different, even with *Gorilla* included, a taxon showing a high degree of left occipital (A-P) petalias.

Hypothesis 5: Pongids and hominids, modern Homo sapiens *excluded*

All petalial patterns are significantly different with high χ^2 values.

Thus, the data collected thus far *do* support three major conclusions: (1) there are petalial differences between pongid taxa, but they do not, as a group, show the same petalial configuration as *Homo*; (2) the hominids show the same petalial configuration and pattern combination as modern *Homo sapiens*; (3) the hominids are distinctly different in petalial distribution and pattern from pongids.

DISCUSSION

We are aware that the fragmentary and incomplete nature of many of the fossil hominid endocasts requires considerable caution in interpreting the results found thus far. It would be wonderful if the sample sizes were larger, and the endocasts totally complete and never distorted. Nevertheless, we believe that the sample of 41 endocasts used in this study have been very carefully appraised and represent the best sample to be found anywhere. All statistical exercises on incomplete data have their limitations, but on the basis of this sample, the *combination* of petalial patterns does not appear significantly different from that known for modern *Homo sapiens*. We cannot rule out the possibility that the petalial patterns are more exaggerated in a quantitative (size) sense for modern *Homo sapiens* than in earlier hominids, and one would expect, purely on a logical basis, some evolutionary continuity in brain evolution between ourselves and hominids existing some three million years ago.

The petalial patterns we have studied are quite distinct between pongids and ourselves; this suggests that while true asymmetries of a cortical nature may exist in the extant pongids their patterns and underlying evolutionary history have not been as strongly selected for as ours, and such selection pressures for whatever concomitant behavioral attributes are correlative have been operating since the time of the australopithecines. We cannot explain the greater degree of asymmetry in the gorilla endocasts, particularly for the left side, observations that have also been published on the crania sometime ago (e.g., Groves and Humphrey 1973).

Morphological asymmetries in primate brains are becoming more commonly described in the literature. Falk (1978) has indicated asymmetries in Old World monkeys in the anterior orbital margin of the frontal lobe (with the right significantly longer than the left), the rectus sulcus, and the Sylvian fissure. LeMay et al. (in press) have presented evidence suggesting petalial asymmetries in the pongids, both in A-P and lateral extent, although many of the cases are scored as "equal," a pattern which our studies support. Yeni-Komshian and Benson (1976) reported different patterns in temporal lobe asymmetry between humans, chimps, and macaques.

Behavioral or functional asymmetries, however, appear very rarely in the primate literature. Dewson (1976) provides evidence of auditory task specialization in macaque left temporal lobe (see also Peterson et al., 1978), but demonstrable and empirically-founded differences in 'handedness," for example, still elude us (see below). Aside from Schaller's (1963:77) observations of right-handed breast-beating in mountain gorilla, the literature does not support any strong degree of handedness in the Anthropoidea as a whole, although side preferences can be trained in the laboratory[5] (Hamilton, 1977; Warren and Nonneman, 1976; Warren, 1953, Beck and Barton, 1972; Deuel, 1975; Gautrin and Ettlinger, 1970; Lehman, 1978, 1980). There does not appear to be any evidence from pongids that visual-spatial tasks are differentially impaired through right or left cerebal lesions, a form of experimentation that we sincerely hope will not be conducted in the future. Pongids do not talk and humans do. Putting aside the controversial aspects as to whether or not pongids can be trained to manipulate symbols and generate grammars, they do not appear to do so in *natural* settings.

We believe that all of the above indicates a discontinuity, at least functionally, between what human and pongid brains do, although further testing may someday shed light on naturally-occurring functional (behavioral) asymmetries in higher primates other than *Homo*. Our results suggest that our brains are *more* asymmetrically organized than pongids,[6] and that the *pattern* is relatively invariant, and has been for perhaps as much as 3×10^6 years, although our present sample for *Australopithecus* cannot really support such a conclusion. The *Homo erectus* materials, however, do support such a stance, and perhaps we should expect to find antecedent evidence for such a *Homo* pattern in earlier populations of the transition between *Australopithecus* and *Homo*.

It should be emphasized that our hominid sample, in showing a similar petalial pattern to modern *Homo sapiens*, e.g., left-occipital, right-frontal, is a correlative suggestion that most hominids were possibly right-handed; it is not a proof. The data reviewed earlier in the introduction of this paper, and LeMay's (in press) observations make it clear that there is no *obligatory association* between handedness

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[5] Post et al. (1980:182) suggest a possible right-handed feeding pattern in *Papio cynocephalus* in the Amboseli National Park. Although the total proportion was 0.514 for the *group as a whole* (right-handed), the authors suggest that on further statistical analyses their data ". . . are consistent with the hypothesis that baboons exhibit nonrandom preferences in hand use, i.e., manual asymmetry, during feeding behavior." The authors point out that their p of 0.514 differed significantly from the expected value of 0.500, given the heterogeneity around the mean estimate.

[6] We mean this in two senses: (1) the petalial configurations are stronger or more pronounced in hominids (particularly modern *Homo*); (2) our initial X^2 runs using sexed pongid endocasts did not indicate any signifiant differences in asymmetries related to sex. Much of the literature (as McGlone's 1980 review indicates) suggests that male brains are more asymmetrically organized than those of females. Given the difficulties of assigning a correct sex designation to all of fossil hominid crania and thus endocasts, we are not able to test the hypothesis that this difference occurs in our hominid sample.

and cerebral lateralization,[7] since there are known cases of right-handed people with right-occiptal, left-frontal petalias, and some left-handed people with the "classical" right-handed petalial pattern. The association between right-handedness and a left-ocipital, right-frontal petalial pattern is statistically high, and we mean *correlative* in that sense. While we do not believe that such petalial pattern effects, either in pongids, or in our own family, can be explained purely by allometry or size scaling, it perhaps deserves a closer look than we have given it. The absence of such effects in the relatively large pongid, *Pongo*, would seem to vitiate such a claim.

We believe these studies impinge on a number of important issues regarding human evolution. First of all, this evidence suggests that brain evolution was an important early component in hominid evolution, despite the obviously smaller brain sizes. In short, the evidence does suggest important reorganizational change in brain structure and function during Australopithecine times, a position that one of us has long maintained (Holloway, 1966, 1972, 1975, 1976a,b, 1978, 1981d,e.). It suggests that we should critically refocus upon the concept of mosaic evolution usually invoked to claim just the opposite (McHenry, 1974, 1975; White, 1980), and restrict its use to a broad, generic conceptual framework, rather than as a more variously conceived organ-by-organ timetable of evolutionary change. The petalial patterns we have found herein are thus the *third* aspect of evidence for early brain reorganization in hominid evolution. The first was the more human-like gyral and sulcal configuration of the lunate sulcus on the Taung endocast (Holloway, 1975, 1981d, but also cf, Falk, 1980a, b), suggesting a decrease in lateral extent of primary visual striate cortex (area 17).[8] The second aspect is the matter of a higher relative brain size and E.Q. in early hominids than in pongids (Holloway, 1976b; Holloway and Post, in press).

Second, these studies provide some suggestions, regarding gestural (e.g., Hewes, 1973, 1976; Falk, 1980c) versus cognitive origins of language behavior. The presence of human petalial patterns in early hominid endocasts cannot prove the existence of language by symbol systems in any given hominid including the Neandertals. Such evidence is not merely supportive, however, particularly when viewed in the associated archaeological context, (i.e., stone-tool making). Unfortunately, we do not know enough about which taxon made the earliest stone tools to standardized patterns, nor do we really know about the cognitive properties of such actions, although one of us (R.H.) has discussed the question in considerable detail before (Holloway, 1969, 1981e).

Finally, there are four aspects of the hominid fossil record that encourage us to offer some guarded speculations regarding selection pressures for cerebral asymmetries. All four spring from one major fact: that social cooperative behavior in hominid evolution was a primary and significant adaptation that permitted prolonged infant dependency periods, altricial brain and behavioral relationships, and an interdependency between brain enlargement, learning, and social nourishment. These four aspects are: (1) stone-tool making to standardized patterns; (2) utilization of relatively permanent home bases; (3) throwing abilities, where both force and accuracy were combined; (4) richer social communicative skills, where sharing of experience, both social and material, was intensive and extensive.

We regard these four aspects as all requiring more elaborate cognitive functioning of (a) symbolic or other code-parsing, and (b) spatiovisual integration. Increased competence in both modalities is commensurate with both the faunal and archaeological associations, insofar as larger and more varied faunal lists are associated with the evolving *Homo* lineage, and tool kits increase both in terms of variety of implements and their sophistication. Appreciation of objects moving concurrently in time and space hardly needs elaboration as an adaptive behavioral mode, but we are thinking of it in at least three ways: (a) the ability to compute trajectories in time and space *with force and accuracy* (object throwing, speroids, spears bolos, etc.); (b) to navigate back and forth from home bases or other relatively permanent shelter areas to hunting/collecting sites; (c) to transmit relatively detailed information about positions in space, time and distance, of other animal/plant communities, or other resources, such as water, stone material, etc. We believe that the symbolic coding of these activities required hemispheric specialization and integration, and ultimately this is how we view the evidence of petalial asymmetries in our brains and those of earlier hominids: as but one pheno-

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[7] We find the phrase "... obligatory association between handedness and cerebral lateralization..." useful and concise, and wish to thank Dr. Joan Witkin for providing it.

[8] The quantification argument for this fact has been partly provided in Holloway (1976b), and more extensively in Holloway (1979).

typic "widow" on the evolution of complex cognitive functioning.

There are many questions we have chosen not to discuss in this article, such as possible sex-related differences in cognitive functioning, the functional reasons behind cerebral asymmetries in the first place (e.g., Levy, 1969, 1976), or different models of the genetics of handedness and lateralization, particularly in a sociobiological context, where sexual dimorphisms in hunting and gathering tasks and abilities may well have been under natural selection pressures. We can only speculate about these issues, but we do believe that the endocast evidence will show promise in the future toward providing testable hypotheses.[9] These will also be dependent upon having more endocast data, and a clarification of just what male-female differences do exist in human cognitive functioning. We suspect, but clearly cannot prove, that natural selection did operate on differential task competence between male and female hominids early in our evolutionary ancestry, with males being more asymetrically organized than females in their cerebral cortices, and that hunting and collecting behavior have some neuroanatomical basis, as do skills in social communication. Hopefully, paleoneurology as well as related nuerobiological inquiry may someday provide us with a clearer data base for such questions.

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[9] M.C. de La Coste-Lareymondie has recently discovered that the corpus callosum in modern *Homo sapiens* is sexually-dimorphic, being relatively larger in females in the posterior or splenic section. This observation, *if* corroborated within a larger sample, is concordant with the clinical picture of less asymmetry in female brains, and would have important evolutionary implications. See Lacoste-Uitamsing, and Holloway (in press).

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