

AMP in horizontal cells. When applied at low concentrations, VIP, but not dopamine, consistently depolarizes carp horizontal cells. This depolarization does not appear to be related to cyclic AMP accumulation in horizontal cells. Rather, the VIP seems to act directly on the membrane to increase conductance to one or more ions. Thus VIP appears to exert two distinct effects on horizontal cells: a depolarization of resting membrane potential and a promotion of the synthesis of cyclic AMP. An intriguing question is whether one receptor mediates these two effects, that is, is linked to both adenylyl cyclase and a membrane channel, or whether there are two subtypes of VIP receptors on carp horizontal cells. In either case, VIP may play a dual role in retinal function: its ability to alter membrane potential may mediate a relatively rapid transfer of information, while its ability to promote cyclic AMP accumulation could allow for the modulation of neuronal function over a longer period of time.

*Note added in proof:* In recent experiments it was found that 1  $\mu$ M VIP produced responses similar to those shown here, indicating that the 10  $\mu$ M concentration used is well above threshold.

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#### References and Notes

1. F. S. Werblin and J. E. Dowling, *J. Neurophysiol.* **32**, 339 (1969).
2. W. K. Stell and D. O. Lightfoot, *J. Comp. Neurol.* **159**, 473 (1974).
3. A. T. Ishida and G. L. Fain, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 5890 (1981).
4. E. M. Lasater and J. E. Dowling, *ibid.* **79**, 936 (1982).
5. J. W. Rowe and K. H. Ruddock, *Neurosci. Lett.* **30**, 57 (1982).
6. J. E. Dowling and B. Ehinger, *Proc. R. Soc. London Ser. B* **201**, 7 (1978); W. L. Hedden and J. E. Dowling, *ibid.*, p. 27.
7. R. Van Buskirk and J. E. Dowling, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 7825 (1981).
8. Four types of horizontal cells have been identified in the cyprinid retina; three are driven exclusively by cones and one by rods (2). The most common of the horizontal cells is the cone-driven  $H_1$  cell, which appears to use  $\gamma$ -aminobutyric acid (GABA) as its transmitter [R. E. Marc, W. K. Stell, D. Bok, D. M. K. Lam, *J. Comp. Neurol.* **282**, 221 (1978)]. After isolation, approximately 75 percent of the horizontal cells take up GABA (D. O'Brien and E. M. Lasater, unpublished observations). We infer from this that results obtained from isolated horizontal cells reflect mainly the properties of the  $H_1$  cells.
9. M. Quirk, L. L. Iversen, S. R. Bloom, *Biochem. Pharmacol.* **27**, 2209 (1978).
10. C. Borghi *et al.*, *Life Sci.* **24**, 65 (1979).
11. R. W. Kerwin, S. Pay, K. D. Bhoda, C. J. Pycoc, *J. Pharm. Pharmacol.* **32**, 561 (1980).
12. M. Schorderet, J.-Y. Sovilla, P. J. Magistretti, *Eur. J. Pharmacol.* **71**, 131 (1981).
13. M. Longshore and M. H. Makman, *ibid.* **70**, 237 (1981).
14. K. J. Watling and J. E. Dowling, *J. Neurochem.*, in press.
15. R. Van Buskirk and J. E. Dowling, *Proc. Natl. Acad. Sci. U.S.A.* **79**, 3350 (1982).
16. The concentration of VIP in the ejection drug pipette was usually 10  $\mu$ M. The dilution between drug pipette and cell was determined by applying known concentrations of KCl and comparing the observed depolarization with that found when isolated horizontal cells were bathed in various concentrations of KCl (21). From this we estimate the maximum dilution was 20 percent and thus the concentration of VIP at the cell surface was at least 8  $\mu$ M.
17. Not in every preparation did we observe responses to VIP. However, in those experiments that gave positive results, every cell tested ( $N = 3$  to 9 per culture dish) gave responses. In the negative experiments, none of the cells ( $N = 1$  to 3) responded. We think it likely that in the latter experiments VIP was not ejected from the delivery pipette owing to binding to the micropipette glass (see legend to Fig. 2).
18. K. B. Seamon, W. Padgett, J. W. Daly, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 3363 (1981).
19. K. J. Watling and M. Williams, *Eur. J. Pharmacol.* **77**, 321 (1982).
20. J. E. Dowling, E. M. Lasater, R. Van Buskirk, K. J. Watling, *Vision Res.* **23**, 421 (1983).
21. M. Tachibana, *J. Physiol. (London)* **321**, 141 (1981).
22. Supported in part by NIH grants EY-00811 (J.E.D.), EY-00824 (J.E.D.), and EY-05476 (E.M.L.) and by an award from the Retina Research Foundation, Houston. K.J.W. was supported in part by a travelling fellowship from the Medical Research Council, England, and an award from Fight-for-Sight, Inc., New York City.

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## Cerebral Cortices of East African Early Hominids

**Abstract.** An endocast of the frontal lobe of a reconstructed skull, which is approximately 2 million years old, from the Koobi Fora region of Kenya appears to represent the oldest human-like cortical sulcal pattern in the fossil record, while the endocast from another skull from the same region produces an endocast that appears apelike in its frontal lobe and similar to endocasts from earlier South African australopithecines. New analysis of paleoanatomical evidence thus indicates that at least two taxa of early hominids coexisted in East Africa.

The oldest human-like brains in the hominid fossil record were considered represented by endocranial casts from South African australopithecines (1, 2), which are between 2.5 to 3.0 million years old and on the average of  $\sim 440$  cm<sup>3</sup> (3). The sulcal pattern of the cerebral cortex of South African australopithecines was considered to be human-like largely because of a relatively caudal position of the lunate sulcus (2), which delineates the rostral border of visual cortex in anthropoid primates (4). However, when the complete sulcal patterns of seven South African natural endocasts were compared with sulcal patterns of human, gorilla, and chimpanzee brains

(5), it was concluded that South African australopithecines appeared ape-like in their entire sulcal patterns, including the position of the lunate sulcus, as suggested earlier by observations about the lunate sulcus in the Taung endocast (6).

I now report my studies of fossil hominid cranial remains from the Koobi Fora region of Kenya that are between 1 and 2 million years old (7). Endocranial surfaces of fragments from numerous individuals were studied, and whole endocasts were prepared (8) from reconstructed skulls KNM-ER 1470 and KNM-ER 1805.

Figure 1 illustrates the sulcal pattern near the orbital edge of the left frontal lobe of the endocast from KNM-ER 1470, a specimen that was found in area 131, 35 m below the KBS (Kay Behrens-meyer site) Tuff of the Koobi Fora region, and later reconstructed (9-11). A branch of the inferior frontal sulcus is parallel to the orbital edge of the frontal lobe, which is formed in part by a gyrus delimited medially by this branch. This condition is derived and represents the typical configuration found in extant humans (4, 5). The sulci identified as the horizontal and ascending branches of the Sylvian sulcus ( $R'$  and  $R$ , Fig. 1) form the anterior and posterior boundaries of Brodmann's area 45 (pars triangularis) in extant humans (4). Broca's speech area in humans is formed by part of area 45 and area 44 directly caudal to it in left hemispheres (12). The frontal lobe of KNM-ER 1470 lacks a fronto-orbital sulcus that characterizes all extant ape brains (4) as well as australopithecines

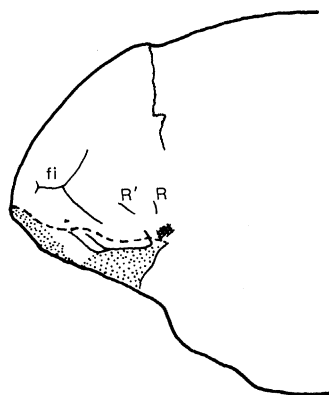


Fig. 1. Endocast of left frontal lobe of KNM-ER 1470, attributed to *Homo* and dated at less than 2 million years. Dots are reconstructed portion of frontal lobe, and hatching represents damaged area. Abbreviations: *fi*, inferior frontal sulcus;  $R'$ , horizontal branch of Sylvian sulcus;  $R$ , ascending branch of Sylvian sulcus.

from South Africa (5) (Fig. 2). Although the area between R' and R is narrower in KNM-ER 1470 than that in the human brain illustrated in Fig. 2, there is much variation in this feature and configurations similar to that of KNM-ER 1470 appear in extant humans (4). Thus, the sulcal pattern appears completely human-like in the crucial caudal portion of the orbitofrontal cortex in the left hemisphere. Since KNM-ER 1470 is older than 1.8 million years (7), it represents the oldest human-like sulcal pattern to date in the hominid fossil record.

Some of the details of the sulcal pattern of the caudal portion of the orbitofrontal region of the frontal lobe are also reproduced in the endocast of another reconstructed East African specimen, KNM-ER 1805 (11, 13), from just below the Okote Tuff of the Koobi Fora region (Fig. 3). A pongid-like fronto-orbital sulcus incises the orbitofrontal border in both right and left hemispheres. The basal view of KNM-ER 1805 reveals a long course of the fronto-orbital sulcus on the ventral surface of the right hemisphere, a feature that is diagnostic of an apelike sulcal pattern [figure 2 in (4)]. The frontal lobe of KNM-ER 1805 is clearly pongid-like and similar to frontal lobes of earlier dated South African australopithecines (5).

The cranial capacity of KNM-ER 1470 has been estimated variously to be 752 cm<sup>3</sup> (14) and 770 to 775 cm<sup>3</sup> (9), and the specimen has been included in the genus *Homo* largely on the basis of brain size (15). The human-like sulcal pattern of the frontal lobe of KNM-ER 1470 supports attribution of this specimen to *Homo*. In humans, the lateral portion of the frontal lobe has become more convoluted and the fronto-orbital sulcus has been pushed caudally to become the anterior limiting sulcus of the insula (4). Thus, the fronto-orbital sulcus is buried and does not appear on endocasts from human skulls. The human condition is derived and increased convolution of the frontal lobe is correlated with development of Broca's speech area in left hemispheres of human brains. If Fig. 1 illustrated an endocast of an extant human skull rather than that from KNM-ER 1470, one would conclude that the external gross morphology near and partially in Broca's area appeared normal and that the human in question had probably been capable of speech, as suggested by Tobias (16).

The taxonomic status of KNM-ER 1805, whose estimated cranial capacity is 582 cm<sup>3</sup> (9, 14), is uncertain and workers have questioned whether its affinities are with *Homo* or *Australopithecus* (15). The evidence presented above shows

that KNM-ER 1805 should not be attributed to *Homo*. In keeping with this, Fig. 4 shows that the shape of the endocast from KNM-ER 1805 (basal view) is similar to that from an African pongid, whereas the endocast of KNM-ER 1470 is shaped like that of a modern human. As noted by Radinsky (6), shape differences may be the result of a packaging phenomenon that reflect size differences.

The KNM-ER 1805 skull was found between tuffs dated at 1.26 and 1.8 million years of age (7). Since the sulcal pattern of this specimen is similar to those from South African australopithecines who lived 2.5 to 3.0 million years ago, it appears that pongid-like sulcal patterns had a long history in the hominid fossil record. Evidence from KNM-ER 1470 suggests that a second derived human-like sulcal pattern appears more

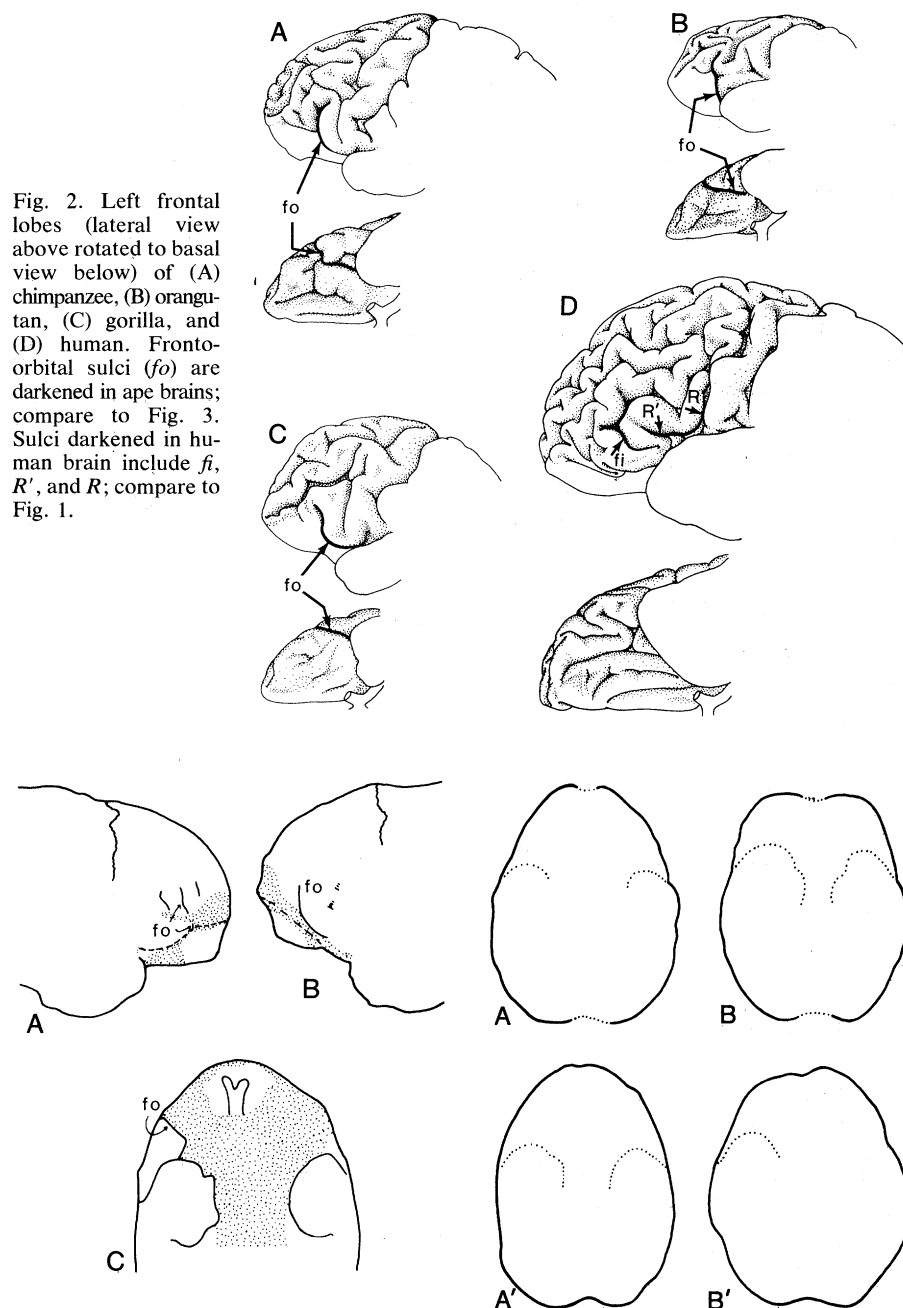


Fig. 3 (left). (A) Right, (B) left, and (C) basal views of an endocast of the frontal lobe from hominid KNM-ER 1805. Note that the fronto-orbital sulcus (fo) incises the lateral borders of the frontal lobes in (A) and (B) and continues in a long course on the ventral surface in the right hemisphere in (C). Dots represent reconstruction. KNM-ER 1805 appears ape-like and similar to earlier South African australopithecine endocasts in its frontal lobe. Fig. 4 (right). Outlines of basal views of brains of (A) a gorilla (4, p. 96) and (B) a human (4, p. 256); compared with basal views of endocasts from (A') KNM-ER 1805 and (B') KNM-ER 1470, in which the left temporal pole is missing. Note that KNM-ER 1470 appears more human-like in its shape, especially in the squareness of the frontal lobes.

recently in the fossil record and, although the modern pattern initially overlaps in time with the primitive sulcal pattern, it alone is found in extant human populations (4, 17). The evidence shows that at least two taxa of early hominids coexisted in East Africa (18).

Whether endocasts from any of the East African specimens (for example, from Ethiopia) that are older than KNM-ER 1470 will show a human-like sulcal pattern is not yet known (19). Further elucidation of the allometric relation between brain size and sulcal pattern (20) should contribute to our understanding of the timing of human origination from pongid-like stock as well as enumeration of the qualitative (nonallometric) changes in external brain morphology that accompanied this event.

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#### References and Notes

1. R. A. Dart, *Nature (London)* **115**, 195 (1925); *Nat. Hist.* **26**, 315 (1926); G. W. H. Schepers, *Transvaal Mus. Mem.* **2**, 155 (1946).
2. R. L. Holloway, "The role of human social behavior in the evolution of the human brain" (James Arthur Lecture for 1973, American Museum of Natural History, New York, 1975).
3. —, *Nature (London)* **227**, 199 (1970).
4. See C. J. Connolly [External Morphology of the *Primate Brain* (Thomas, Springfield, Ill., 1950), pp. 325–330] for a discussion of frontal lobes.
5. D. Falk, *Am. J. Phys. Anthropol.* **53**, 525 (1980).
6. The subject of South African australopithecine endocasts and their ape-like or human-like sulcal patterns is controversial [D. Falk (5); R. L. Holloway, *Am. J. Phys. Anthropol.* **56**, 43 (1981); D. Falk, *ibid.* **60**, 479 (1983). L. B. Radinsky ["The fossil record of primate brain evolution" (James Arthur Lecture, American Museum of Natural History, New York, 1979)] noted that a caudal position of the lunate sulcus was possible in the Taung endocast but not necessarily probable.
7. T. E. Cerling, F. H. Brown, B. W. Cerling, G. 118 (1979).
8. Whole endocasts in the collection of the Kenya National Museum were used to determine general brain shape. The sulcal patterns illustrated in this report were determined from partial endocasts prepared by either S. Kasinga or by D.F.
9. R. E. Leakey, M. G. Leakey, A. K. Behrensmeyer, in *The Fossil Hominids and an Introduction to Their Context, 1968–1974*, M. G. Leakey and R. E. Leakey, Eds. (Clarendon, Oxford, 1978), pp. 86–182.
10. R. E. Leakey, *Nature (London)* **242**, 170 (1973); *ibid.*, p. 447; M. H. Day, R. E. Leakey, A. C. Walker, B. A. Wood, *Am. J. Phys. Anthropol.* **42**, 461 (1974); B. A. Wood, in *Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Paleocology and Evolution*, Y. Copen, F. C. Howell, G. L. Isaac, R. E. Leakey, Eds. (Univ. of Chicago Press, Chicago, 1976), pp. 490–506.
11. R. E. Leakey, *Nature (London)* **248**, 653 (1974).
12. E. C. Crosby, T. Humphrey, E. Lauer, *Correlative Anatomy of the Nervous System* (Macmillan, New York, 1962).
13. M. H. Day, R. E. Leakey, A. C. Walker, B. A. Wood, *Am. J. Phys. Anthropol.* **45**, 369 (1976).
14. R. L. Holloway, in *Early Hominids in Africa*, C. Jolly, Ed. (St. Martin's Press, New York, 1978), pp. 379–401.
15. B. A. Wood, in *Recent Advances in Primatology*, D. J. Chivers and K. A. Joysey, Eds. (Academic Press, London, 1978), pp. 351–372.
16. P. V. Tobias [*Philos. Trans. R. Soc. London Ser. B* **292**, 43 (1981)] suggests that the "strong

development of the posterior part of the inferior frontal convolution (Broca's area)" in KNM-ER 1470 and the development of the inferior parietal lobule in OH 24 together imply that articulate speech was present in *H. habilis*. Tobias also views speech as a "predominant component" of humanization [see also P. V. Tobias, *Anthropologie (Paris)* **18**, 115 (1980)].

17. Although whole endocasts of KNM-ER 3733 and KNM-ER 3883 (attributed to *H. erectus*) in the collection at the Kenya National Museum are too rough to permit the naming of specific sulci, the horizontal direction of furrows in the frontal lobes (4) and the general shape of these lobes give these endocasts a modern appearance (that is, similar to endocasts from extant humans).
18. R. E. Leakey and A. C. Walker, *Nature (London)* **261**, 572 (1976).
19. Since hominid endocasts rarely show obvious lunate sulci, the answer to this question will probably be provided by frontal lobe regions of endocasts.
20. It is well known that bigger primate (mammal) brains are characterized by more sulci than are smaller brains [L. B. Radinsky, in *The Primate Brain*, *Advances in Primatology*, C. R. Noback

and W. Montagna, Eds. (Appleton-Century-Crofts, New York, 1970), vol. 1, pp. 209–224; —, in *The Functional and Evolutionary Biology of Primates*, R. Tuttle, Ed. (Aldine, Chicago, 1972), pp. 175–184]. Since the endocast from KNM-ER 1470 is larger than that from KNM-ER 1805, it has been suggested that differences in their frontal lobe sulcal patterns might be related to allometry [H. J. Jerison, *Primate Brain Evolution: Methods and Concepts*, E. Armstrong and D. Falk, Eds. (Plenum, New York, 1982), pp. 77–84]. In any event the modern sulcal pattern seen in the region of Broca's area in KNM-ER 1470 does have a functional and behavioral correlate, at least in extant humans—speech.

21. I thank the government of Kenya for permission to conduct research, R. Leakey for access to specimens, and the staff of the Kenya National Museum for hospitality. I am grateful to L. Jacobs, E. Mbua, N. Boaz, A. Galaburda, R. Thorington, and W. Welker for assistance and to S. Kasinga for help with casting. This work was supported by grant BNS 8203764 from the National Science Foundation.

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## Hand Preference Across Time Is Related to Intelligence in Young Girls, Not Boys

**Abstract.** Consistency of hand preference was examined in a longitudinal study of children between 18 and 42 months of age. Results showed a sex-specific relationship between hand consistency and intellectual development. Across a variety of intellectual abilities at all ages, females with consistency of handedness were precocious compared to females without such consistency. This relationship did not hold for males.

Handedness is related to the anatomical and physiological asymmetry of the brain (1). The relation between handedness and intellectual abilities in children and adults has been extensively studied for the past several decades and the findings have not led to definitive conclusions (2). Past studies have typically compared right-handers to left-handers (and occasionally mixed-handers) with handedness determined on a single occasion by preference across a variety of tasks, many of which have recently been found to be of low reliability (3). When sex was included as a factor, analyses were conducted between the sexes with no within-sex comparisons. Because of recent theory and empirical findings suggesting sex differences in neurological organization (4), we examined the relation of consistency of hand preference across time to intellectual development within sexes and found that such consistency was related to precocious development in females but not in males.

The present data were based on a longitudinal study of early development. Beginning at 12 months of age, 130 normal middle-class children were tested every 6 months until 42 months of age (5). Attrition was minimal throughout the investigation, with 91 percent (118) returning by the last assessment. At each assessment the children were given a battery of tests which included a major

standardized intelligence scale. For the infant and preschool assessments the Bayley Mental Scale and the McCarthy Scales of Children's Abilities were used, respectively. Items on these scales (beginning at approximately 18 months on the Bayley) include children's performance on drawing tasks. When scoring these items, we recorded the hand the child used to draw on each of the trials administered. The hand the child used most often on these items at each age was designated as the preferred hand (in virtually all cases the same hand was used across trials at a given age). Thus, we had available a measure of hand preference across the five assessments (18 to 42 months). Drawing hand has been found to be one of the most reliable measures of hand preference (3, 6).

Consistency in hand preference was defined by the criterion of using the same hand across the five assessment periods. Those children displaying any change in preference were designated as nonconsistent. Data analyses were based on 89 children (48 males and 41 females) who qualified for one of the two groups. Those not included provided insufficient data to permit group assignment. For males, 24 were consistent and 24 were nonconsistent; for females, 23 were consistent and 18 were nonconsistent. A binomial test indicated that the proportion of children consistent across the five