References and Notes

1. Recent psycholinguistic theories of sentence processing strongly imply a serial processing model, where higher-level analyses develop toward the end of the clause [see J. A. Fodor, T. G. Bever, M. F. Garrett, *The Psychology of Language* (McGraw-Hill, New York, 1974)]. The most explicit serial model is found in G. A. Miller, *IRE Trans. Inform. Theory* **IT-8**, 81 (1962).
2. Practised shadowers have a stable shadowing latency at which they reliably shadow normal prose materials. The shadowers in this experiment had extensive training in earlier experiments [see W. D. Marslen-Wilson, thesis, Massachusetts Institute of Technology (1973); *Nature* **244**, 522 (1973)].
3. For details of the latency-measurement techniques see references in (*2*). The latency measurements are accurate to ± 10 msec.
4. Normal, WR errors are as frequent at short as at long latencies. Although the majority of these errors were made by subjects shadowing at shorter latencies, this trend was not significant (t = 1.153, d.f. = 11, $P < .20$).
5. See, for example, D. R. Reddy, L. D. Erman, R. B. Neely, *IEEE-AFCRL Conference on Speech Communication and Processing* (1972), pp. 334–337; R. Kaplan, in *Natural Language Processing*, R. Rustin, Ed. (Algorithmics, New York, 1973).
6. The research reported here was part of a Ph.D. dissertation submitted to the Department of Psychology, Massachusetts Institute of Technology, May 1973. I thank Drs. M. F. Garrett, J. A. Fodor, A. W. F. Huggins, M. C. Potter, L. Rips, H.-L. Teuber, and L. K. Tyler for their advice. Support was provided by a grant to M.I.T. from the Alfred P. Sloan Foundation, and by NIMH grant HD0516802 to Drs. Fodor and Garrett. Preparation of the manuscript was supported by a grant to me from the Spencer Foundation.

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Primate Evolution: Analysis of Trends

Cartmill (*1*) has advanced challenging arguments concerning the origin and persistence of primate specializations in the visual system and in grasping coordination. These specializations are hypothesized to have been strongly influenced by ancestral tendencies to subsist in a significant degree by predation on visually located and manually captured insects and other prey in the forest canopy and undergrowth. A subsequent exchange of views between Raczkowski and Cartmill (*2*) was useful in clarifying questions stimulated by the original article, but did not succeed in eliminating misinterpretations of the claims of certain other writers. I shall first examine a conclusion related to the logic of evolutionary arguments, and then discuss misconstruals of certain views of Le Gros Clark, indicating ways in which his discussion of arboreal influences on primates has much more significant implications than were credited to it.

In setting the stage for his evolutionary arguments, Cartmill discussed aspects of the logic of explanation. He noted that scientific explanations are frequently of a type involving deductions from certain givens, including lawlike generalizations—a statement which quite properly allows for other kinds of explanation. He continued, citing Simpson (*3*) and other writers, "yet some evolutionary biologists and philosophers of science . . . have argued that evolutionary explanations do not involve any such generalizations, and hence are not subject to refutation by counterexamples" (*1*, p. 436).

It is not necessary here to consider problems associated with "covering law" views of explanation (*4*), although these are important to a fuller analysis of the arguments advanced. It is true that writers referred to by Cartmill emphasize the frequency with which evolutionary explanations are of a different kind. However, the empirical use of counterexamples does not have to be tied to explanations of a covering law variety. "Counterexample" can stand for other things than its common designata in formal logic, and a useful meaning in the present context is, briefly, "observation inconsistent with hypothesis." In reconstructing trends in a certain lineage, a hypothetical explanation based on incomplete fossil remnants may well be subject to refutation by counterexample. Simpson's recent book (*3*) conveys to me no suggestion that he considers evolutionary explanations of necessity immune to such refutation, contrary to Cartmill's claims.

In the interest of brevity, I shall consider mainly the views of Le Gros Clark in the following arguments, but aspects of the conclusions concerning the vitality of these views apply also to certain overlapping claims made by earlier and subsequent writers. Cartmill has chosen to articulate much of his discussion around "the arboreal theory" (*1, 5*)—a term that can be useful for identifying a close-knit set of arguments, but which is not helpful in the role of referring to partially contradictory groups of propositions by several writers who have dealt with a wide variety of arboreal influences. Nevertheless, Cartmill effectively showed that certain earlier arguments about expected consequences of arboreal life are erroneous. From such specific demonstrations, he jumped to the more general kind of statement that the comparative evidence "does not support the idea that the selection pressures of arboreal life favor the replacement of tree shrew-like morphology by primate-like morphology" (*1*, p. 438). Elsewhere he concludes, "evidently, the close-set eyes and grasping extremities typical of extant primates are adaptations to some activity other than simply running about in the trees; arboreal life per se cannot be expected to transform a primitive tree shrew-like primate into a lemur. Le Gros Clark's version of the arboreal theory is not adequate" (*1*, p. 439).

In the face of such a conclusion it is genuinely important to look at examples of what Le Gros Clark actually said, and to determine whether he based his inferences on the condition of "simply running about in the trees" or, as stated elsewhere, on "selection pressures imposed by arboreal locomotion per se" (*1*, p. 442). In the context of influences associated with arboreal life (*6*), he emphasized "the replacement of the grasping functions of the teeth by the use of the forelimb for prehension rather than simply for support and progression" (p. 126), and "the enhancement of the use of the hands as tactile organs" (p. 204). In the same context, he built on certain ideas of G. E. Smith (*7*) and Smith's predecessors, relating these ideas to more recent findings, to provide concepts that help systematize knowledge and suggest hypotheses about primate evolution. He noted the importance of the conjunction of visual and tactual developments in providing "opportunities for exploring objects of the immediate environment, and for comprehending their significance" (*6*, p. 266), and gave important place to the idea that the associated differentiation of the cerebral cortex eventually increased in quite general ways the potentials for adapting to environmental change. Obviously his treatment of such concepts will have to be made more specific, as new knowledge permits, and inevitably a number of his views will require modification, as new research results are attained. Yet certain of his emphases have stood the test of developing knowledge remarkably well, and have provided a model for gaining insight into primate evolution by exploring, where feasible, the more fine grained aspects of neural, behavioral, and fossil evidence, and by seeking in somewhat simpler behavioral and cerebral advances the sources of more complex later adaptations (*8, 9*).

The immediately preceding claims about Le Gros Clark's syntheses can be made more plausible by indicating, at least in rough sketch, how his ideas on the evolution of substrates for primate intellect complement the views of other writers, and illuminate the consideration of primate visual learning (*10*). He emphasized (*9*) that the particular conjunctions of visual, tactile, and manipulative advances favored by the arboreal existence of primates have two kinds of implications. First, in the development of the individual, the joint effect of information from these sources fosters the ability to understand and react adaptively to the environment, a view having points in common with the contributions of Hebb (*11*) and Piaget (*12*). Second, during evolution, these advances interacted in contributing to more general intellectual capacities. It is consistent with the first implication that young macaques gave test performances suggesting impaired form discrimination learning after early deprivation of pattern vision, and were retarded in achieving visual-motor coordinations following a rearing period when they could not see their limbs (*13, 14*). In a case of more complex behavior, the ability of chimpanzees to solve visual-manipulative problems was found to depend on previous experience (*15*). It is consistent with the second implication that prosimian species, which show generally less capability for fine manipulation and, in many cases at least, less apparent potential for diurnal vision than species of Anthropoidea, have shown less capacity for learned adaptation to objects and for visual discrimination learning (*16*) than have most of the latter species for which data are available (*17*).

Previous discussions of the evolution of the varied facial displays of many primates have called attention to the need for associated capacities in such matters as visual acuity and stereopsis (*18*), advances which, according to Cartmill's views and other theoretical statements, received major impetus early in primate history. Definitive data on the amount and kinds of information actually communicated in primate exchanges are generally lacking. Of course, many expressive behaviors, even in the pongids, are stereotyped and not likely to transmit much information used by conspecifics. Yet it is known that some nonhuman primate visual signal patterns, as well as patterns involving other modalities, have a wide variety of gradations, are differently organized by different individuals in similar circumstances, convey messages of some complexity, and are responded to in different ways depending on the context in which they are emitted (*19*). As primates came to depend more on learning in managing social interactions and other behavior, the different learning experiences of the members of any social group should have produced greater relative variability within groups in terms of certain reaction tendencies. It can therefore be argued that the dual needs to discriminate an increasing variety of messages in the output of an individual, and to learn to respond in some degree on the basis of the conditional probabilities of different responses of others, given their unique reaction tendencies, involved increasing information processing loads (*20*).

Selection for cerebral advances, which must have accompanied these processing demands, must also have been related to primate trends toward increased duration of childhood dependency. For longer childhood can be expected to produce adults better prepared for social living. It provides time to gain the extensive variety of experience needed (*21*) in complex types of discrimination learning, and to sample the diversity of common and rare behaviors expressed in a large group. Among the more intriguing results of environmental restriction research is the indication that organisms with more versatile brains need greater amounts of early experience in order subsequently to achieve species potentials in adaptive learned response (*11, 13, 22*). This further suggests that there must have been close association between selection for greater intellectual capacity and for longer childhood. Analysis in these terms reinforces earlier theoretical studies (*22, 23*) that have sought to link the lengthening of primate prematurity to the benefits of more complex social learning, and reflects views of Le Gros Clark about the evolution of the brain.

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References and Notes

1. M. Cartmill, *Science* **184**, 436 (1974).

→ D. Raczkowski, *ibid.* **187**, 455 (1975); M. Cartmill, *ibid*, p. 456.

3. G. G. Simpson, *This View of Life* (Harcourt, Brace & World, New York, 1964).
4. See, for example, P. K. Feyerabend, in *Minnesota Studies in the Philosophy of Science*, H. Feigl and G. Maxwell, Eds. (Univ. of Minnesota Press, Minneapolis, 1962), vol. 3, pp. 28–97; M. Hesse, *The Structure of Scientific Inference* (Univ. of California Press, Berkeley, 1974).
5. M. Cartmill, in *The Functional and Evolutionary Biology of Primates*, R. Tuttle, Ed. (Aldine-Atherton, Chicago, 1972), pp. 97–122.
6. W. E. Le Gros Clark, *The Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, 1959).
7. See, for example, G. E. Smith, *Nature (Lond.)* **125**, 820 (1930).
8. W. E. Le Gros Clark, *J. Anat.* **64**, 371 (1930); *ibid.* **79**, 123 (1945).
9. ———, *The Antecedents of Man* (Quadrangle, Chicago, 1971).
10. Several constraints must be borne in mind when examining questions about the evolution of primate intellect. These include the difficulty of devising measures that are comparable across species (complicating factors being species differences in effectors, motivational patterns, and predispositions for specialized kinds of learning that may become confounded with more general learning capacities); the uncertainty about the contributions of genetic and environmental variances to the expression of different behaviors; the frequently elusive nature of brain homologies; the great incompleteness of knowledge on neural bases of intellect; the lack at many points in primate evolution of fossil cranial remains to provide guiding hints about cerebral potential; the limited knowledge about the brain furnished by fossil craniums when they are available; and the fact that existing species do not represent evolutionary sequences.
11. D. O. Hebb, *The Organization of Behavior* (Wiley, New York, 1949). Hebb has offered extensive arguments, in a context of neurological development, for the importance of early learning in making possible the subsequent appearance of higher-order perceptual and intellectual processes.
12. J. Piaget, *The Origins of Intelligence in Children* (Norton, New York, 1963) (original French edition, 1936). Piaget has emphasized the importance in the psychological development of the human infant of learning based on biological mechanisms present at birth, which comes to produce, and enlist as a base for further advance, coordinations of vision, prehension, and other sensorimotor adjustments.
13. A. H. Riesen, in *Comparative Psychology*, D. A. Dewsbury and D. A. Rethlingshafer, Eds. (McGraw-Hill, New York, 1973), pp. 395–428.
14. R. Held and J. A. Bauer, Jr., *Science* **155**, 718 (1967).

→ H. G. Birch, *J. Comp. Psychol.* **38**, 367 (1945).

→ A. Jolly, *Anim. Behav.* **12**, 560 (1964); *ibid.*, p. 571.

17. It seems a safe assumption that very early primate ancestors of modern Anthropoidea were, at best, not superior in general intellectual capacities to the average of the modern prosimians that have been tested.
18. R. J. Andrew, in *Evolutionary and Genetic Biology of Primates*, J. Buettner-Janusch, Ed. (Academic Press, New York, 1964), vol. 2, pp. 227–309; J. A. R. A. M. van Hooff, in *Primate Ethology*, D. Morris, Ed. (Aldine, Chicago, 1967), pp. 7–68.

→ W. A. Mason and J. H. Hollis, *Anim. Behav.* **10**, 211 (1962); P. Marler, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), pp. 544–584; R. A. Gardner and B. T. Gardner, *Science* **165**, 664 (1969); E. W. Menzel, Jr., in *Behavior of Nonhuman Primates*, A. M. Schrier and F. Stollnitz, Eds. (Academic Press, New York, 1974), vol. 5, pp. 83–153.

20. It cannot be claimed that primates with the more advanced brains inevitably rely on learning as a mediator of differential response to complex visual patterns, for young rhesus monkeys reared in isolation were found to develop fear reactions when exposed to pictures of monkeys engaging in threat behavior [G. P. Sackett, *Science* **154**, 1470 (1966)]. Nevertheless, there is evidence that in this species early experience influences the efficiency of sending and receiving information by facial response, and facilitates the later performance of complex social interaction, as when each member of a triad reacts to each of the others in a single social episc → [R. E. Miller, W. F. Caul. I. A. Mirsky, *J. Pers. Soc. Psychol.* **7**, 231 (19 → C. O. Anderson and W. A. Mason, *J. Comp. Physiol. Psychol.* **87**, 681 (1974)]. For discussions of other primate adaptations, such as behavioral traditions, learning about the environment, and response to competition, postulated to have interacted significantly with advances in learning capacity, see R. J. Andrew, *Science* **137**, 585 (1962); S. L. Washburn and D. A. Hamburg, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), pp. 607–622; A. B. Shaklee and R. B. Shaklee, *Am. Anthropol.*, in press.
21. D. M. Rumbaugh, in *Primate Behavior*, L. A. Rosenblum, Ed. (Academic Press, New York, 1970), vol. 1, pp. 1–70.
22. A. Jolly, *The Evolution of Primate Behavior* (Macmillan, New York, 1972).
23. G. A. Bartholomew and J. B. Birdsell, *Am. Anthropol.* **55**, 481 (19 → K. R. L. Hall and M. J. Goswell, *Primates* **5**, 59 (1964); E. L. Simons, *Primate Evolution* (Macmillan, New York, 1972).

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Obviously, an explanation of a set of evolutionary trends in a lineage can be challenged in many ways—say, by pointing out that the supposed lineage is not a lineage, or that the supposed trends do not characterize it (*1*). If Shaklee wishes to call all these counterexamples, and to invent another term for the use which I specified (*2*), I have no objections. The cited paper by Feyerabend (*3*) begins by conceding that "covering law" theories of explanation adequately represent the relation between empirical generalizations and empirical instances; Feyerabend is concerned with denying that a similar model applies to cases where one formal theory is being replaced by a more inclusive one (as in the replacement of Galilean mechanics by Newtonian mechanics). This is irrelevant to the points questioned by Shaklee. I continue to feel that a proposed explanation can be rejected if the *explanans* is deducible from the *explanandum*, so that "Some arboreal species develop grasping extremities (and this is one of those)" is not an adequate explanation of the fact expressed by "This arboreal species has developed grasping extremities" (*4*). If a proposed explanation applies to lineages for which it is known not to hold, it has no explanatory force for those instances where it does hold; otherwise, the conjunction of any two contemporaneous events would form a satisfactory explanation of one of them (for example, "The explanation of the heath hen's extinction was the commercial success of talking motion pictures"). In fact, we usually lack satisfactory explanations for extinctions and many other kinds of evolutionary phenomena, and we ought to recognize this; we cannot solve puzzles unless we admit to being puzzled.

I am not sure what Shaklee is claiming about Le Gros Clark. True, Le Gros Clark felt that the hands increased in tactile sensitivity and manipulative importance during primate evolution, but this is a description of a trend, not an explanation. If I read Le Gros Clark correctly, he believed that this trend was explained in its initial stages by the demands of acrobatic arboreal locomotion: "compared with claws . . . [enlarged, soft pads at the ends of the fingers] provide a much more efficient grasping mechanism for animals which find it necessary to indulge in arboreal acrobatics, for by their greater pliability they can be adapted with much more precision to surfaces of varying size and texture. They also come to be richly supplied by sensory nerves and thus to form tactile organs with a high degree of sensitivity" (*5*).

If Le Gros Clark is not claiming that arboreal locomotion selects for enlargement of pads and reduction of claws (with consequent progressive transfer of tactile and manipulative functions from the face to the hands), then he is offering no selective explanation at all, but only a description of what happened. Contrary to what Shaklee suggests, I have great respect for the work and accomplishments of Le Gros Clark; I am persuaded, not only that he was offering a general explanation of several primate evolutionary trends, but that this explanation was sufficiently concrete and vulnerable to be subject to refutation. This is an important accomplishment, and betokens uncommon mental clarity and courage.

Similar things could be said about the work of F. W. Jones and G. E. Smith. I am not sure that as much could be said for some of the additions and reformulations offered by Shaklee. Some of what Shaklee says seems to me to conceal a rather teleological approach to evolutionary phenomena. Grasping hands are of great importance as manipulatory organs in many higher primates, but grasping specializations of the foot appear to have preceded those of the hand, and (as Shaklee himself points out) most prosimian species use their grasping hands very seldom for manipulating objects. It follows that everything Shaklee says about the interaction of the hand and eye in manipulation is applicable at best to certain lineages of anthropoids, and is irrelevant to the question of why Eocene primates developed grasping extremities and most arboreal rodents and carnivores did not—unless one regards prosimian adaptations as a lot of desperate half-measures that had to be adopted along evolution's predestined march toward the Anthropoidea. Although some of Shaklee's remarks about social behavior, visual communication, and lengthened infant dependency may well be helpful in understanding some aspects of anthropoid evolution, they too are beside the point in attempting to explain why tarsiers and lemurs have come to differ from tree shrews, squirrels, and *Plesiadapis*, which is the question at issue here.

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References and Notes

1. M. Cartmill, in *The Functional and Evolutionary Biology of Primates*, R. Tuttle, Ed. (Aldine-Atherton, Chicago, 1972), pp. 97–122.
2. ——, *Science* **184**, 436 (1974).
3. P. K. Feyerabend, in *Minnesota Studies in the Philosophy of Science*, H. Feigl and G. Maxwell, Eds. (Univ. of Minnesota Press, Minneapolis, 1962), vol. 3, pp. 28–97.
4. Statistical laws of the form "70 percent of all lineages adapting to life in the trees develop grasping extremities" are not applicable here, because the number of instances covered is finite and we cannot generate new instances to test the generalization. Such a "law" would just be a summary of observations, and could not provide an explanation for the observations it summarized. Even if grounded in something beyond these observations, such a law could only explain the frequency distribution of grasping extremities, not their occurrence in particular lineages. The point is made more forcibly by M. Brodbeck, in Feigl and Maxwell (*3*, pp. 247–248).
5. W. E. Le Gros Clark, *The Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, ed. 3, 1971), p. 173.

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