Table 1. Effects of satiation on mean time spent in the stimulus-on condition (S^D) and mean number of oscillations. Maximum possible time in S^D was 90 minutes.

Subject No.	Time in S^D (min)		No. of oscillations	
	Hungry	Satiated	Hungry	Satiated
1	67.91	42.98	21.7	2.0
2	65.92	41.84	36.0	3.7
4	18.83	10.95	19.3	1.7
5	17.47	8.13	29.7	3.0
6	59.36	16.64	70.0	2.3
Group mean				
	45.90	24.11	35.3	2.5

tensities (for example, 0.4 to 0.5 ma) subjects generally spent between 25 and 75 percent of the session in S^D. These group results were representative of shock-intensity effects for all the individual subjects.

After several shock intensities had been tested, an "intermediate" shock value (either 0.4 or 0.5 ma) was selected for each subject—one which, on the basis of the earlier results, was considered likely to produce a fairly good balance between the positive and negative tendencies in the situation. The values in the "hungry" column at the left of Table 1 show that at the selected shock intensities individual subjects averaged from 20 to 75 percent of the session in S^D, with a group mean of approximately 50 percent. During the remainder of the experiment, shock intensity was kept constant at intermediate values.

To study the effects of variations in the hunger drive we satiated the subjects with condensed milk a few minutes before the start of three experimental sessions, according to a procedure described in (*2*). The three satiation sessions were compared with sessions under the usual "hungry" conditions—that is, the three experimental days that immediately preceded days on which satiation tests occurred.

Table 1 shows that food satiation reduced (i) the mean amount of time spent by each subject in S^D and (ii) the number of oscillations between S^D and TO. An analysis of variance revealed that the "time in S^D" differences were significant beyond the .02 level, whereas the differences in "number of oscillations" were significant beyond the .001 level. By decreasing the power of the appetitive factors in the situation, satiation apparently brought about an increase in the net effect exerted by the aversive factors (*4*).

Our current work with the new technique is focused on the study of variations in the relative frequency of reward and punishment with shock intensity and hunger drive held constant. Figure 1 illustrates for a single subject some typical results that occurred as a result of changes in these frequencies. When only food was possible during S^D (lower curve) the subject spent most of the session in S^D and rarely oscillated between S^D and TO. On the other hand, when both food and shock (0.4 ma) occurred relatively frequently (upper curve), the subject spent about half the time in each condition and displayed pronounced oscillation from one condition to the other. It might be added that when no food but only shocks were possible in S^D, the subject invariably terminated S^D at the beginning of the session and rarely turned it back on. Although differing among themselves in absolute rate of oscillation and in variability of performance, the other subjects exhibited qualitatively similar effects. Oscillations were most frequent at intermediate relative frequencies of reward and punishment (*5*).

The principal difference between this procedure and some earlier methods of studying conflict lies in the provision that subjects can initiate as well as terminate the conflict situation. This provision makes the procedure similar in some important respects to procedures used in several recent studies (*6*), in which subjects could control the onset as well as the offset of a particular set of experimental conditions. Unlike the present experiment, however, those studies did not explicitly program any punishment during the "on" condition. Even so, subjects in those experiments still produced onsets and offsets—a result which suggests that certain events which seemingly involve only positive reinforcement may also have aversive properties. Therefore, findings from studies which permit subjects to control both the presentation and the termination of a given stimulus condition may eventually necessitate a revision of the traditional criteria used to distinguish conflict behavior from other types of behavior.

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1. See, for example, E. R. Guthrie, *The Psychology of Human Conflicts* (Harper, New York, 1938); N. E. Miller, in *Personality and Behavior Disorders*, J. McV. Hunt, Ed. (Ronald, New York, 1944), vol. 1, p. 431; P. L. Broadhurst, in *Handbook of Abnormal Psychology*, H. Eysenck, Ed. (Basic Books, New York, 1961), p. 726.
2. E. Hearst, *J. Comp. Physiol. Psychol.* **56**, 1027 (1963).
3. In the study cited in (*2*) subjects could only terminate S^D; following a termination, S^D came on again after a fixed time interval (5 minutes) no matter what the subject did.
4. A prior experiment (*2*) seems to eliminate as an explanation the possibility that a food-associated stimulus may itself become strongly aversive for satiated subjects, as well as the possibility that the results are primarily due to a reduction in general activity following satiation.
5. Subjects have generally displayed relatively infrequent oscillation between S^D and TO when no shocks were possible. For example, rat No. 6 averaged fewer than ten oscillations per session when neither food nor shock was possible in S^D; this result can be compared with the records for this subject shown in Fig. 1. Such findings suggest that subjects were not pressing the lever because mere stimulus change was reinforcing or because the stimulus accompanying S^D or TO was inherently aversive. N. E. Miller, however, has proposed that conflict may have a marked potentiating effect on pressing for mere stimulus change, an explanation that cannot be ruled out at the present time.
6. A. G. Hundt and D. Premack, *Science* **142**, 1087 (1963); N. H. Azrin, *ibid.* **133**, 382 (1961); J. B. Appel, *J. Exptl. Anal. Behav.* **6**, 423 (1963).

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Hominid Bipedalism: Independent Evidence for the Food-Carrying Theory

Abstract. *Habitual food carrying has been suggested as a possible major factor in making bipedal locomotion biologically advantageous so that it was selected for in early hominid evolution. This speculation, supported by slight observations of captive macaques, has now acquired greater plausibility from four recent independent reports of wild and semi-feral bipedal, food-carrying apes and monkeys from the Congo, Tanganyika, Japan, and a Puerto Rican monkey colony. The most striking evidence of the relationship between food-transport and bipedal walking comes from a troop of Japanese monkeys where the locomotor habit emerged as part of a chain of new behaviors initiated with a changed food supply.*

In 1961 I suggested that hominid bipedalism might have arisen initially in connection with carrying of food from one place to another, perhaps when a primate living in the open country began to depend on scavenged meat from carnivore kills for its food (*1*). A pilot study of a juvenile stumptailed macaque confirmed my suspicion that when presented with a large and not immediately consumable food burden, such as a large grapefruit, the normally quadrupedal monkey would shift to a bipedal gait in order to remove himself and his food to a safer place. Observation of this behavior, readily elicited in a single young macaque, could hardly suffice as evidence for the factors involved in the momentous transformation of our own ancestors into habitual bipeds. However, since the publication of my paper in 1961, several pieces of entirely independent evidence have been reported from widely separated places, by observers whose judgments about what they saw can hardly have been influenced by my hypothesis, if indeed they were aware of it. The subjects of these observations were wild chimpanzees in the former Belgian Congo reported by Kortlandt (*2*), wild chimpanzees in Tanganyika studied by Goodall and Van Lawick (*3*), rhesus macaques living on Cayo Santiago, off Puerto Rico, under essentially feral conditions (*4*), and Japanese macaques on a small island in Japan, investigated by Kawai (*5, 6*). In each case, the animals, all of which are normally quadrupedal, were observed and in three instances photographed walking or running bipedally while carrying food. The maximum distance over which bipedal locomotion while carrying food was observed is 30 meters.

Occasional bipedalism has been noted in chimpanzees, gorillas, orangs, various monkeys, and even prosimians, but in these instances the posture was not attributable to food carrying. The gibbon is well known for bipedal locomotion (with the arms held high) when on the ground. Except for the gibbon, whose terrestrial bipedalism is normal, and whose extremely long arms would make quadrupedal walking on the ground even more awkward than bipedalism, nonhuman primates seem to use bipedal locomotion under most circumstances as a rather inefficient playful or (in the case of the gorilla) threatening behavior. Captive primates can of course be trained to bipedal walking and standing for several minutes at a time. Under wild conditions the only situation in which bipedal locomotion might under proper environmental conditions develop into a highly useful habit would seem to be in conjunction with food carrying.

In the speculation about factors involved in natural pressures toward more frequent bipedalism among the ancestors of man, it has been suggested that weapons or tools were the first objects regularly transported, forcing the carrier to assume an upright gait (*7*). As far as I know, no one has observed wild or quasi-feral primates carrying objects usable either as tools or weapons while in a bipedal posture. Goodall (see *8*) saw wild chimpanzees carrying twigs (to be used in extracting termites from their nests) up to distances of 800 meters, but they did not walk upright in such cases. I should not like to insist that wild nonhuman primates will never be seen walking upright, carrying sticks or stones as tools or weapons; the evidence so far is simply negative. The four field observations of bipedalism described here were all connected with food carrying.

Kortlandt photographed a chimpanzee in its natural Congo forest habitat, walking bipedally and carrying several pawpaws. He comments (*2*, p. 134), "Apparently they walked bipedally in order to have their hands free—for example, to carry or eat fruit." Further, he notes that under natural conditions, when the animals were not running on all fours to avoid danger, bipedal locomotion accounted for 10 percent to 15 percent of all observed ground locomotion.

In the article by Goodall and Van Lawick there is a photograph (*3*, p. 293) of a chimpanzee walking bipedally out of a tent, its hands laden with bananas; it is stated that chimpanzees were seen "loading their arms with choice wild fruits, then walking erect for several yards [meters] to a spot of shade before sitting down to eat."

In a color motion picture taken of rhesus macaques at the experimental island colony on Cayo Santiago, off Puerto Rico, there are several sequences dealing with the feeding behavior which occurs when factory-manufactured hard "chow" biscuits are thrown onto the ground for the monkeys in a small forest clearing. The monkeys, which have been awaiting their food, rush violently toward the scattered biscuits, with the most successful animals loading large amounts into their arms and against their chests. Thus encumbered with many small biscuits, they rise to the bipedal position and run off in various directions, presumably to places where they can consume the food in relative privacy. The change from normal quadrupedal gait to effective bipedal running is abrupt and striking, as shown in this film (*9*).

The most instructive report of all, though it is unfortunately not accompanied by photographs, is that of Kawai (*5*) on the semiwild Japanese macaques of Koshima, a coastal island in Miyazaki Prefecture, southern Japan. The monkeys on Koshima have been under observation since 1952, when "provisioning," the deliberate feeding of the animals to bring them out of the heavy forest into open areas where they could be more easily observed, was started. The food provided was sweet potatoes. In 1953 a 1½-year-old female monkey "invented" the washing of the tubers (apparently they were usually rather dirty, just as they had been dug from the fields), and by 1962 this habit had spread as a cultural trait to most of the rest of the troop, except for the infants and a few very conservative old members. Having become used to washing the sweet potatoes in fresh-water streams, the animals began to frequent the island beach, washing the tubers in seawater, starting around 1959. By 1962, 71 percent of the troop were walking in the sea, swimming, and even collecting mollusks and other seafoods. Meanwhile, wheat (in the grain) was added to the provisions supplied by the observers, scattered on the beach sand. Until 1960 the monkeys tediously picked each grain up separately, but then one or more monkeys made another invention, that of scooping up handfuls of sand and wheat, which they then carried down to the water to sluice away the sand from the grains. This technique the observers describe as "the placer-mining selection method"; it had been adopted by 14 out of the 58 members of the troop at the last report. I now quote Kawai in full (*5*, p. 15, para. 4):

> "It is worthy of note that recently the monkeys on Koshima Island, more often than among any other troop of monkeys, maintain an erect posture or bipedalism for many minutes. They assume an erect posture when they try to catch food from a person in their own hands and when they collect food in the sea. Sweet-potato washing and placer-mining selection em-

ployed in picking up wheat *both require that the monkeys carry the sweet-potato and the sand to the beach in their two hands so that they have to walk on their feet* [my italics]. It is often observed that they can cover a distance of from 20 to 30 meters in from 5 to 6 minutes."

Although I am puzzled by the extremely slow movement implied by a time of 5 or 6 minutes to travel 20 or 30 meters, the rest of Kawai's account presents no problems. It could be objected that the improved bipedalism in this group of Japanese macaques resulted from imitative learning of the bipedal behavior of their human observers during the last decade. On the other hand, other groups of Japanese monkeys have been under close human observation for equal periods without becoming notably bipedal; the environmental stimulus to bipedal locomotion seems to be unmistakably linked to food carrying. Miyadi (*10*, p. 785) in a review of studies of Japanese monkeys shows a photograph of a macaque standing upright in the sea, holding a food-tray; he does not state the locality, nor does he explain how tray-carrying behavior came to be used for food washing in this instance.

The hypothesis I advanced in 1961 was perhaps too much intertwined with the idea that meat carrying alone could have provided a sufficient stimulus to habitual bipedalism in a prehominid primate. We now have evidence that food washing in the sea, or even the handling of large amounts of wild fruit, can elicit bipedal locomotion under appropriate conditions. Hardy's hypothesis (*11*) of an "aquatic past" for man was doubtless extreme, but some of his notions seem less improbable in the light of Kawai's remarkable report. In many parts of Southeast Asia, macaques have taken up a beachcombing existence; I am not aware of any reports of bipedal locomotion to an unusual degree among these littoral primates, but perhaps previous observers did not pay sufficient attention to the matter. If beach-dwelling macaques should prove to have postural and locomotor habits significantly different from their hinterland kin, along with their obviously distinctive dietary pattern, this would be evidence of considerable importance.

One of the few nonprimate mammals known to use extrasomatic objects as tools (aside from materials assembled for nest or dam building) is the sea otter, who does so in order to crack open mollusk shells. For a very long time, man has preempted the best littoral environments for food gathering in those parts of the world also inhabited by the pongids; there do not appear to be any reports of chimpanzee beachcombers, for example. If the littoral environment were as favorable to the emergence of bipedalism, and other human-like behaviors, as it seems to have been for the Koshima macaques, perhaps this may help to explain the stone hurling and apparently other confusingly human attributes of the hairy creatures encountered around 480 B.C. on the West African coast by the Carthaginian explorer Hanno, from whose account we derive the word *gorilla* for an animal which is more likely to have been the chimpanzee (*12*).

I am not suggesting that mankind stems from malacophagous macaques or chimpanzee beachcombers, nor that our bipedalism was acquired in Lamarckian fashion. For natural selection to operate on the skeleton and musculature, a sustained change of habit, presumably in a new environment, must have preceded the onset of significant changes in gene frequencies. If there are ecological situations in which bipedal locomotion enhances the survival of breeding populations of primates, and in which individuals differ genetically with respect to phenotypically different bone and muscle features which are relevant to bipedal locomotion, evolutionary changes in the direction of more efficient bipedalism should occur. In the case of the hominids, we know that such changes have indeed taken place. The reports of occasional bipedalism among wild or semiwild apes and monkeys, and of the Koshima macaques in particular, indicate the kinds of conditions which, if sufficiently prolonged, might have served to get the forelimbs of our ancestors off the ground for good.

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3. J. Goodall and H. Van Lawick, *Natl. Geograph. Mag.* **123**, No. 3, 272 (1963).
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7. S. L. Washburn, in *The Evolution of Man's Capacity for Culture*, J. N. Spuhler, Ed. (Wayne State Univ. Press, Detroit, 1959); in *Classification and Human Evolution*, S. L. Washburn, Ed. (Aldine, Chicago, 1963).
8. In a paper by J. R. Napier [*Discovery* (Mar. 1963), p. 12], there is a photograph by J. Goodall which shows a chimpanzee preparing a twig prior to using it as a termite-extracting implement.
9. J. A. Gavan (Health Center, Univ. of Florida, Gainesville) can provide the information on the location of this film.
10. D. Miyadi, *Science* **143**, 783, 785 (1964).
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Behavioral-Neurochemical Correlation in Reactive and Nonreactive Strains of Rats

Abstract. *Male and female rats of the Maudsley reactive and Maudsley nonreactive strains were tested in the open-field to obtain ambulation and defecation scores. They were later killed, and their brains were dissected into five portions and analyzed for serotonin. Males defecated more and ambulated less than females, and nonreactive males ambulated more and defecated less than reactive males. These behavioral differences were significant* ($p < .05$). *A statistically significant difference was found for the amounts of serotonin in specific regions of the brain between males and females (males higher) and between reactive and nonreactive males (reactive higher). Significant negative correlations between serotonin values in specific regions of brain and ambulation scores were found in these animals viewed as a group or even within a given strain and sex.*

It has been shown by Maas (*1*) that two inbred strains of mice which differ emotionally as measured by a modification of Hall's open-field test (*2*) have significantly different concentrations of serotonin (5-HT) in a dissected portion of brain consisting of diencephalon, mesencephalon, and pons. The more emotional strain, BALBc/J, has higher concentrations than the less emotional strain, C57BL/10J, the values being 1.37 ± 0.046 and 1.07 ± 0.037 μg/g ($p < .01$), respectively. In this report we present data on the 5-HT content of various areas of the brain in a different species, the rat. The animals were also tested for open-field behavior and the scores obtained were examined for cor-